საქართველოს ხმელეთის მოლუსკების მრავალფეროვნება და გეოგრაფიული განაწილება

ლევან მუმლაძე

სადისერტაციო ნაშრომი წარდგენილია ილიას სახელმწიფო უნივერსიტეტის
მეცნიერებათა და ხელოვნების ფაკულტეტზე სიცოცხლის შემსწავლელ
მეცნიერებათა დოქტორის აკადემიური ხარისხის მინიჭების მოთხოვნის შესაბამისად
სიცოცხლის შემსწავლელ მეცნიერებათა
სადოქტორო პროგრამა

ხელმძღვანელი:
დავით თარხნიშვილი - ბიოლ. მეცნ. დოქტორი, პროფესორი
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ილიას სახელმწიფო უნივერსიტეტი
თბილისი 2013

განაცხადი

როგორც წარდგენილი სადისერტაციო ნაშრომის: “საქართველოს ხმელეთის მოლუსკების მრავალფეროვნება და გეოგრაფიული განაწილება” ავტორი, ვაცხადებ, რომ ნაშრომი წარმოადგენს ჩემს ორიგინალურ ნამუშევარს და არ შეიცავს სხვა ავტორების მიერ აქამდე გამოქვეყნებულ, გამოსაქვეყნებლად მიღებულ ან დასაცავად წარდგენილ მასალებს, რომლებიც ნაშრომში არ არის მოხსენიებული ან ციტირებული სათანადო წესების შესაბამისად.

ლევან მუმლაძე

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31.05.2013

წინამდებარე სადისერტაციო ნაშრომი წარმოადგენს ჩემს მიერ განხორციელებული კვლევების შედეგებს რომელიც ეძღვნება საქართველოს მალაკოფაუნის შესწავლას. ნაშრომი ეყრდნობა 7, იმპაქტ ფაქტორიან ჟურნალში გამოქვეყნებულ ან გამოსაქვეყნებლად მომზადებულ პუბლიკაციას რომლებიც ქვემოთ მითითებულა შესაბამისი რომაული ნომრებით:

I. **Mumladze L**, Tarkhnishvili D, Pokryszko BM (2008) A new species of the genus Helix from the Lesser Caucasus (SW Georgia). ***Journal of Conchology*** 39:483-485

II. Pokryszko BM, Cameron RAD, **Mumladze L**, Tarkhnishvili D (2011) Forest snail faunas from Georgian Transcaucasia: patterns of diversity in a Pleistocene refugium. ***Biological Journal of the Linean Society*** 102:239-250.

III. Tarkhnishvili D, Gavashelishvili A, **Mumladze L** (2012) Palaeoclimatic models help to understand current distribution of Caucasian forest species. ***Biological Journal of the Linean Society*** 105:231-248

IV. **Mumladze L** (2013) Shell size differences in Helix lucorum Linnaeus, 1758 (Mollusca: Gastropoda) between natural and urban environments. ***Turkish Journal of Zoology*** 37:1-6

V. **Mumladze L**, Tarkhnishvili D, Murtskhvaladze M (2013) Systematics and evolutionary history of large endemic snails from the Caucasus (Helix buchi, H.goderdziana). ***American Malacological Bulletin***31(2) 1-10

VI. **Mumladze L, Camron RAD, Pokryszko BM** (2013) Endemic Land Molluscs in Georgia (Caucasus): how well are they protected by existing reserves and National Parks? ***Journal of Molluscan Studies***(Submitted)

VII. **Mumladze L** (2014) Sympatry without co-occurrence: exploring the pattern of the distribution of two Helix species in Georgia using Ecological Niche Modeling approach. ***Journal of Molluscan Studies*** (Submitted)

აბსტრაქტი

საქართველოს ხმელეთის მალაკოფაუნა (Mollusca, Gastropoda; ლოკოკინები და ლოქორები) 250-ზე მეტისახეობის მოლუსკს ითვლის, რომელთაგან>25% საქართველოს, ხოლო, 65 % - მდე კავკასიის ენდემია. ზოგადად საქართველოს ბიომრავალფეროვნებისდაცვა და შენარჩუნება ეროვნული და საერთაშორისო პრიორიტეტია.ამისთვის აუცილებელი წინაპირობა ცოცხალი ორგანიზმების შესახებ საკმარისი ცოდნაა. საქართველოში ბინადარი მოლუსკების შესახებ ასეთი ცოდნა მწირია და მოძველებული და ისძირითადად გასული საუკუნის 80-იან წლებამდე გროვდებოდა. მას შემდეგ ამ მიმართულებით ღირებული თითქმის არაფერი გაკეთებულა.

ჩემი სადისერტაციო ნაშრომი წარმოადგენს საქართველოს ხმელეთის მოლუსკების მრავალფეროვნების, ბიოგეოგრაფიული, ეკოლოგიური და კონსერვაციული-კომპლექსური კვლევის შედეგებს. დისერტაციაში წარმოდგენილია ბიბლიოგრაფიული ნაწილი სადაც კატალოგიზებულია და გაანალიზებული 1900 წლიდან დღემდე გამოქვეყნებული ნაშრომები საქართველოს მალაკოფაუნის შესახებ.

არსებული ლიტერატურული და ასევე საკუთარი მონაცემების საფუძველზე, სადისერტაციო კვლევის ფარგლებში დაიგეგმა და შეიქმნა საქართველოს, ხმელეთის ყველა სახეობის მოლუსკის (250 და მეტი) გავრცელების რუკა და მრავალფეროვნების ცენტრების ანალზი. ასეთი ბაზის არსებობა მნიშვნელოვანია სამომავლო კვლევების დაგეგმვისა და კონსერვაციული საქმიანობისათვის.

სადისერტაციო კვლევის ფარგლებში აღწერილია ახალი სახეობა- გოდერძის ჰელიქსი (*Helix goderdziana).*ასევე, კავკასიის ენდემური მოლუსკების (ბუხის (*Helix buchii*) და გოდერძის ჰელიქსების)სისტემატიკის და ევოლუციური ისტორიის გამოკვლევის მიზნით განხორციელდამორფოლოგიური და გენეტიკური კვლევა რის შედეგადაც დადასტურდა გოდერძის ჰელიქსის ტაქსონომიური სტატუსი და დადგინდა მისი (ასევე ბუხის ლოკოკინის) სახეობად ჩამოყალიბების შესაძლო დრო და სცენარი.

სადისერტაციო კვლევის ფარგლებში, თანამედროვე და პალეო-კლიმატური მოდელების გამოყენებით განვახორციელეთპოტენციური რეფუგიუმების მოდელირება და ცხოველთა და მცენარეთა დისპერსიის გზების ანალიზები. ასევე გავაანალიზეთ მოლუსკების ფაუნის თანამედროვე განაწილება, მსგავსება სხვა რეგიონების ფაუნასთან და საქართველოს (ამ შემთხვევაში კავკასიის) რეფუგიუმის შესაძლო როლი გამყინვარების შემდგომი რეკოლონიზაციის პროცესებში. ანალიზების შედეგები აჩვენებს მრავლობითი, გამყინვარების დროინდელი რეფუგიალური არეების არსებობას საქართველოში. თუმცა აქ გადარჩენელი მალაკოფაუნის წვლილი თანამედროვე ჩრდილოეთ რეგიონების, გამყინვარების შემდგომი ფაუნის ჩამოყალიბებაში უმნიშვნელოა რაც დიდი კავკასიონის როგორც მოლუსკებისათვის მნიშვნელოვანი ბარიერის როლზე მეტყველებს.

დისერტაციის შემდეგი ნაწილი წარმოადგენს მოლუსკების ეკოლოგიურ კვლევას სადაც მოდელ ორგანიზმად შეირჩა ვაზის ლოკოკინა (*Helix lucorum*). გამოკვლეული იქნა ვაზის ლოკოკინის გავრცელების მოდელი და მექანიზმები. ასევე გამოკვლეული იქნა ნიჟარის მორფოლოგიური ცვალებადობა ანთროპოგენური და შედარებით ბუნებრივი პირობების ქვეშ. შედეგები მიუთითებს ვაზის ლოკოკინის გვიანდელ, გამყინვარების დროინდელ ექსპანსიაზე საქრთველოში, რაც ადამიანის მასიურ გავრცელებას უკავშრდება. ასევე ნაჩვენებია რომ ვაზის ლოკოკინა სინანთროპული სახეობაა საქართველოში,ანთროპოგენურ გარემოში არსებობის გარკვეული ადაპტური მექანიზმებით.

სადისერტაციო კვლევის ბოლოო ნაწილი ეხება საქართველოს მალაკოფაუნის კონსერვაციას. გამოყოფილია საქართველოს და კავკასიის ენდემური მოლუსკების მრავალფეროვნების ცენტრები საქართველოს ტერიტორიაზე და გაანალიზებულია მათი დაცულობის ხარისხი დაცული ტერიტორიების საშუალებით. ნაჩვენებია რომ დაცული ტერიტორიების დღევანდელი ქსელი ვერ უზრუნველყოფს ენდემური მალაკოფაუნის მნიშვნელოვანი ცენტრების დაცვას და სასურველია რომ დაცული

ტერიტორიების დაგეგმარებაში გამოყენებული იქნას მოლუსკების (და ასევე სხვა უხერხემლოების) შესახებ არსებული ინფორმაცია.

Abstract

Terrestrial malacofauna (snails and slugs) of Georgia includes more than 250 species, of which >25% areGeorgian and around 65% areCaucasian endemics. Conservationof Georgian malacofauna has a national and international significance, since Georgia lies within the Caucasusbiodiversity hotspot. To achieve this objective, a basic knowledge onthe composition and distribution of Georgian moluscsis needed. The relevant informationis scarce, incomplete and outdated, becausevery littleinformation was published since the early eightieth of the last century.

The present thesis isaimed to initiate a complex study of the diversity, biogeography, ecology and conservation of Georgian malacofauna and therefore, it contains some research direction (each with published or submitted papers in peer reviewed journals).

The first part of the dissertation is a bibliography which includes the analysis of papers published since 1990 up to date exploring every aspect of Georgian malacofauna. There are provided analyses of key trends in malacological researches in Georgia.

Based on own and bibliographic data I generate the distributional maps of each mollusc species inhabiting in Georgia. Based on distribution maps I revealed the richness pattern which can be used either in future research or conservation purposes.

During my PhD work, I (with my colleagues) described a new species (Helix goderdziana). To provide a comprehensive systematicpicture and reconstruct evolutionary processes of two endemic Helix species (Helix buchii and H. goderdziana), morphometric and molecular genetics studies were conducted and showed that H. goderdziana and H. buchiiare both valid but sister species. We also provide some scenarios of their evolutionary histories.

Another suit of aims was to investigate a distribution of glacial refugees and the possible postglacial dispersion mechanism of species using GIS modeling; also the composition and comparison of Georgian malacofauna with others and its role as a source in structuring postglacial faunas further north. The study supported the multiple refugee system in the

Caucasus (and Georgia). It was shown that species dispersal patterns is essential either modern distribution of species or for the reconstructing of Paleo distribution. Georgian malacofauna (and Trans Caucasian malacofauna in general) has a minor role in the structuring northern postglacial malacocenoses.

I also studied some ecological peculiarities H. lucorum as a model species. I investigate the distributional pattern of this species and its shell morphological variability. I found that H. lucorum is largely an anthropogenic species with a limited distribution to human modified landscapes and some morphological adaptations associated with the human disturbance.

The last subject of my PhD study was conservation of malacofauna of Georgia. By analyzing the Georgian and Caucasian endemic molluscs diversity and distribution, I clearly showed that the current protection status of Georgian malacofauna is insignificant and needs serious further study.

The thesis is entirely based on the papers published by the autor. Other parts of this work are a short introduction and discussion of the subjects covered by the thesis with deeper analysis of malacological literature dedicated to the study of Georgian malacofauna.

მადლობა

ჯერ კიდევ საბაკალავრო საფეხურზე სწავლის დროიდან მოყოლებული დღემდე ყურადღებისა და მხარდაჭერისათვის მადლობა მინდა გადავუხადო პროფესორ დავით თარხნიშვილს და პროფესორ ერისტო ყვავაძეს. მათ დიდი გავლენა მოახდინეს ჩემს სამეცნიერო შეხედულებების ჩამოყალიბებაზე. ასევე განსაკუთრებული პატივისცემით მინდა აღვნიშნო ბრიტანელი პროფესორი რობერტ კამერონი და პოლონელი პროფესორი ბეატა პოკრიშკო რომლებიც რეგულარულად მიწევენ კონსულტაციებს ჩემს კვლევით საქმიანობაში. ასევე მადლობა მინდა გადავუხადი ბევრ ჩემ კოლეგას ვინაც რეკომენდაციები, რჩევები და სხვა სახის დახმარება გამიწია ცალკეული კვლევითი ნაშრომების მომზადებისას (მათი სახელები და გვარები მითითებულია თითოეული ნაშრომის ბოლოს).

სადისერტაციო ნაშრომის მომზადდა ილიას სახელმწიფო უნივერსიტეტის, ეკოლოგიის ინსტიტუტის (ყოფილ ცოცხალი სამყაროს შემსწავლელ მეცნიერებათა ფაკულტეტი) ბაზაზე და ინდივიდუალური სამეცნიერო-კვლევითი გრანტული დაფინანსების საშუალებით (1.Rufford Small Grants; ID - 10442-1.(http://www.ruffordsmallgrants.org/rsg/projects/levan_mumladze); 2. რუსთაველის ეროვნული სამეცნიერო ფონდი; ID - 2 – 2 / 04);

სარჩევი

ცხრილების და გრაფიკების ჩამონათვალი

შესავალი

საქართველო (კავკასია)პლეისტოცენური რეფუგიუმია რომელიც ათასობით და ასეულ-ათასობით წლის განმავლობაში „ინახავდა“ რელიქტურ ბიომრავალფეროვნებას კლიმატის პერიოდული მერყეობის ფონზე (Van Andel & Tzedakis, 1996; Hewitt, 1999; Petit et al., 2003). თანამედროვე კავკასიის ცხოველთა და მცენარეთა სამყარო ძალზე მდიდარი და გაჯერებულია ენდემური და რელიქტური სახეობებით (Kikvidze & Ohsawa, 1999; Denk, Frotzler & Davitashvili, 2001; Milne & Abbott, 2002). ერთი მხრივ ბიომრავალფეროვნების უნიკალურობა და სიმდიდრე ხოლო მეორე მხრივ ადამიანის ზემოქმედებით წარმოქმნილი საფრთხეები დაედო საფუძვლად კავკასიისეკორეგიონის გლობალური თვალსაზრისით მნიშვნელოვან რეგიონად - “ცხელ წერტილად“ აღიარებას(დღეისათვის სულ 34 ასეთი რეგიონია გამოყოფილი)რომელთა დაცვა და შენარჩუნება თანამედროვე საზოგადოების პრიორიტეტია (Mittermeier et al., 2004; Zazanashvili et al., 2004).მიუხედავად განსაკუთრებულობისა და გლობალური მნიშვნელობისა საქართველოს ბიომრავალფეროვნება არასაკმარისადაა შესწავლილი იმისათვის რომ შეგვეძლოს მისი ეფექტური დაცვა და მდგრადი გამოყენება. ისევე როგორც მსოფლიოს სხვა ქვეყნებში, საქართველოს ბიომრავალფეროვნების შედარებით კარგად გამოკვლეული ჯგუფებია ხერხემლიანი ცხოველები, შემდეგ მცენარეები და ყველაზე ნაკლებად უხერხემლო ცხოველები. ამის მიზეზი ერთი მხრივ უხერხემლო ცხოველთა ნაკლებად ქარიზმატულობა ხოლო მეორე მხრივ სახეობათა დიდი მრავალფეროვნებაა. ამავდროულად უხერხემლო ცხოველთა ზოგიერთი ჯგუფი განსაკუთრებულად მდიდარია ენდემურობის მხრივაც და წარმოადგენენ მნიშვნელოვან კომპონენტს ბუნებრივი ეკოსისტემების ფუნქციონირებაში (Heywood, 1995).

ჩემი სადისერტაციო კვლევის ობიექტს წარმოადგენს საქართველოს ბიომრავალფეროვნების ერთი კომპონენტი - ხმელეთის მოლუსკები (ტიპი: Mollusca:

Gastropoda) რომელიც აერთიანებს ნიჟარიან (ლოკოკინები) და უნიჟარო (ლოქორები) ფორმებს.

მოლუსკები ერთერთი ყველაზე მრავალრიცხოვანი და ამავდროულად მგრძნობიარე ჯგუფია გარემოს ცვლილებების მიმართ (Lydeard et al., 2004). ამდენად, მათი კვლევა მნიშვნელოვანია ერთი მხრივ მრავალფეროვნების დაცვის და შენარჩუნების თვალსაზრისით, ხოლო მეორე მხრივ კონსერვაციული პრიორიტეტების შესარჩევად რადგან მოლუსკები ცნობილი არიან როგორც გარემოში მიმდინარე ცვლილებების ინდიკატორები და მრავალფეროვნების სუროგატი ორგანიზმები (Moritz et al., 2001). გარდა აღნიშნულისა, არაერთგზის ნაჩვენებია რომ მოლუსკები წარმოადგენენ ეფექტურ მოდელ სისტემებს ფუნდამენტური ევოლუციური და ეკოლოგიური პრობლემების კვლევის საქმეში (Davison, 2002; Glaubrecht, 2009; Hayes et al., 2009; Holland & Cowie, 2009). სამწუხაროდ,საქართველოში, მოლუსკების შესწავლაზემალზე ცოტა მეცნიერი მუშაობდა. გასული 20-30 წლის განმავლობაში საქართველოში არ არსებობდა საკმარისად ძლიერი სამეცნიერო - ტექნიკური ბაზა და ინტელექტუალური რესურსი, რაც მოიზიდავდა და უბიძგებდა სტუდენტებს მოლუსკების შესწავლისაკენ. ასეთ პირობებში შეუძლებელი იყო მოლუსკების შესახებ ახალი ინფორმაციის შეგროვება და თანამედროვე კვლევითი მიღწევების დანერგვა მოლუსკების კვლევისა და კონსერვაციის სფეროში.

ჩემი სადისერტაციო სამუშაოები გამომდინარეობდა შემდეგი კვლევითი ინტერესებიდან:

(1) საქართველოში მალაკოლოგიური კვლევების შესახებ არსებული ბიბლიოგრაფის კატალოგიზება და ანალიზი;

(2) საქართველოს ტერიტორიაზე ბინადარი მოლუსკების სახეობრივი მრავალფეროვნების ინვენტარიზაცია;

(3)მოლუსკების მრავალფეროვნების და ენდემურობის სტრუქტურული აღწერა;

(4) ისტორიულ-ბიოგეოგრაფიული და ეკოლოგიური პროცესების ანალიზი, რომელთაც განაპირობეს მოლუსკების თანამედროვე ფაუნის ფორმირება;

(5) მოლუსკების ცალკეული სახეობების სისტემატიკა-ტაქსონომიის, ფილოგეოგრაფიისდა ეკოლოგიის კვლევა;

(6) მოლუსკების ფაუნის და განსაკუთრებით ენდემური მოლუსკების კონსერვაცია.

მოლუსკების ფაუნის ფართო სპექტრითკვლევა იძლევა მნიშვნელოვან წინაპირობას იმისათვის რომ მეტი ახალგაზრდა დაინტერესდეს ამ დარგით. ცხადია, რომარცერთზემოთ ჩამოთვლილსაკითხზე (გარდა პირველისა) ერთი ან თუნდაც რამდენიმე სადისერტაციო პროექტის განმავლობაში ამომწურავი პასუხების მიღება არაა შესაძლებელი, მაგრამ კვლევების ინიცირება და პირველი შედეგების მიღება საფუძველია შემდგომი ეტაპების მისაღწევად. მოცემულ საკითხებზე,2007 წლიდან დაწყებული, ილიას უნივერსიტეტის ეკოლოგიის და ზოოლოგიის ინსტიტუტების ბაზაზე მიმდინარეობს აქტიური მუშაობა და წინამდებარე სადისერტაციო ნაშრომი წარმოადგენს სწორედ ამ სამუშაოების შედეგებს.

დისერტაციის მომდევნო თავებშიმოცემულიასადისერტაციო ნაშრომში შესული საკვლევი საკითხების ძირითადი ჯგუფების მოკლე მიმოხილვებიშესაბამისი პუბლიკაციების (რომაული ციფრებით) მითითებით. შედარებით ფართოდაა გაშუქებული საკითხები რომელთაც პუბლიკაციები ნაწილობრივ ან არ ფარავს.

კვლევის მასალა და მეთოდების მიმოხილვა

სადისერტაციო სამუშაოები ჩატარდა როგორც საკუთარი საველე სამუშაოების დროს მოპოვებული მასალის, ასევე ლიტერატურული მონაცემების და სამუზეუმო კოლექციების (ილიას უნივერსიტეტის ზოოლოგიის ინსტიტუტის კოლექცია) გამოყენებით. ლიტერატურული მონაცემების ორგანიზება კვლევის მნიშვნელოვანი ნაწილია რაც გულისხმობს პუბლიკაციებიდან, მონოგრაფიებიდან და ვებ-სივრციდან ფაქტობრივი მასალის ამოკრეფას. ასეთი ინფორმაცია გამოყნებული იქნა II, III, V-VIII პუბლიკაციებში.

გარდა არსებული ბიბლიოგრაფიული მონაცემებისა, 2006 წლიდან 2012 წლის ჩათვლით რეგულარული ექსპედიციების დროს შეგროვებული იქნა დიდი

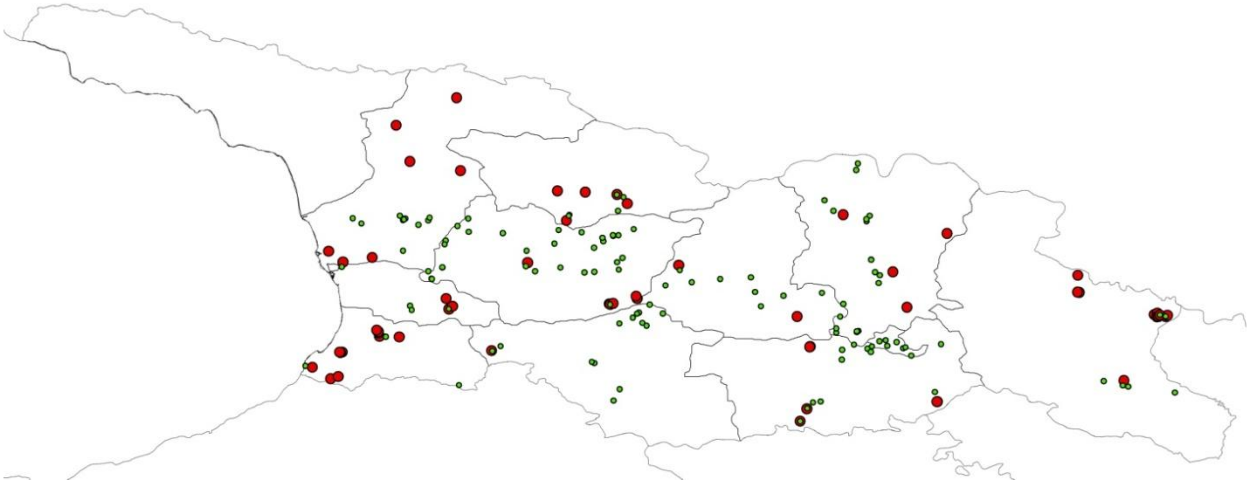
ოდენობით მალაკოლოგიური მასალა (სურ. 1) რომლის მხოლოდ ნაწილის დამუშავება მოხერხდა დღემდე.

საველე სამუშაო

კვლევითი ამოცანის მიხედვით ველზე მასალის შეგროვება სხვადასხვაგვარად ხდებოდა.

მალაკოცენოზების (ერთი გეოგრაფიულ-ლანდშაფტურ ერთეულის მოლუსკების თანასაზოგადოება) აღწერისა და შედარების მიზნით (II და VI პუბლიკაცია) დაგეგმილი მასალის შეგროვების პროტოკოლი შემდეგნაირია (მეთოდი 1): საკვლევ ტერიტორიაზე ხდება 20X20 კვ. მ. ფართობის შერჩევა (როგორც წესი 2 ან მეტი კვადრატი) შემთხვევითად ან მკვლევარის შეხედულებისამებრ (დამოკიდებულია ამოცანაზე). თითოეულ კვადრატში 1-2 საათის განმავლობაში იძებნება ცოცხალი მოლუსკები და ნიჟარები. ამ დროს მაქსიმალურად უნდა ინახოს ყველა მიკროჰაბიტატი რომ უზრუნველყოფილი იქნას სხვადასხვა ეკოლოგიის სახეობის დაფიქსირება. განსაკუთრებით მშრალ ამინდში მოლუსკებს ახასიათებთ აგრეგაციული განაწილება, ამიტომ პირდაპირი ძებნის დროს ასევე ფიქსირდება ადგილები სადაც მოლუსკები მეტად იყრიან თავს. პირდაპირი ძებნის შემდეგ ხდება ნიადაგის და ჰუმუსის ფენის აღება 5-20 ლიტრამდე მოცულობით. ნიადაგის მოცულობა დამოკიდებულია ჰაბიტატის ტიპზედა მოლუსკების რიცხოვნობაზე, თუმცა ერთი კვლევის ფარგლებში ნიადაგის სინჯის რაოდენობა სასურველია ერთი და იგივე რაოდენობის იყოს (რაც უზრუნველყოფს სხვადასხვა წერტილის სინჯების შედარების შესაძლებლობას. აღნიშნული პროტოკოლი სტანდარტულია და კარგად აპრობირებული (Pokryszko & Cameron 2005). რეგიონების მიხედვით შესაძლოა შეიცვალოს პირდაპირი ძებნის დრო და ნიადაგის სინჯის მოცულობა. შემდეგი ეტაპი ნიადაგის ლაბორატორიული დამუშავებაა. ამისათვის სწრაფად უნდა გამოშრეს ნიადაგი ჰაერის ტემპერატურაზე რაც უზრუნველყოფს ცოცხალი მოლუსკების გადარჩენას. გამომშრალი ნიადაგი კი უნდა გაიცრას 1, 3 და 5 მმ ფრაქციებად და თითოეული ფრაქციიდან მოხდეს ნიჟარების ექსტრაქცია. აღნიშნული მეთოდის

სიზუსტე (სინჯში არსებული ნჯარების სრული რაოდენობის გამოყოფა) გარკვეულწილად დამოკიდებულია მკვლევარის გამოცდიდლებაზე. ამ გზით ვერ ხერხდება უნიჟარო მოლუსკების - ლოქორების რაოდენობრივი აღრიცხვა და ამდენად მეთოდი მხოლოდ ნიჟარიანი მოლუსკებისათვის გამოიყენება. მიუხედავად ამისა ნაჩვენებია რომ მეთოდი საკმაოდ ეფექტურია (Pokryszko & Cameron, 2005) და ერთადერთია მალაკოცენოზების კვლევის დროს.



სურათი 1. რუკაზე მოცემულია მოლუსკების სინჯების მოპოვების ადგილები. წითელი რგოლებით აღნიშნულია წერტილები სადაც ჩატარდა სრული ინვენტარიზაცია (მეთოდი 1 - იხ. *საველე სამუშაო*) ხოლო მწვანე წერტილებით აღნიშნულია წერტილები სადაც შეგროვდა ერთი ან რამდენიმე მოლუსკის სახეობა (მეთოდი 2).

ხშირ შემთხვევაში (პუბლიკაციები I, IV, V, VI, VII) ზემოთ აღწერილი მეთოდის ნაცვლად მიზანმიმართულად ვეძებდი და ვაგროვებდი სამიზნე სახეობას (მეთოდი 2). ამ შემთხვევაში ცალკეული მოლუსკის სახეობის ეკოლოგიური მოთხოვნილებების და გავრცელების წინასწარ მონაცემებზე დაყრდნობით უნდა მოხდეს საძებნი ადგილების და დროის შერჩევა. ზოგიერთი საკითხზე მუშაობისას საჭირო იყო ცალკეული სახეობის რიცხოვნობის აღრიცხვა რომლის დეტალური მეთოდური აღწერა მოცემულია IV პუბლიკაციაში.

ველზე მოპოვებული მასალის ნაწილს ვაფიქსირებდი 96% სპირტხსნარში შემდგომი გენეტიკური ან ანატომიური გამოკვლევის მიზნით. ველზე ასევე ვახდენდი ზუსტი

ადგილმდებარეობის დაფიქსირებას (კოორდინატები) და ყველა სხვა შესაძლო მონაცემის ჩაწერას (როგორიცაა სიმაღლე ზღვის დონიდან, ლნადშაფტის ტიპი, დომინანტი მცენარეები და ა.შ) შემდგომი ანალიზების მიზნით. სურ. 1-ზე ნაჩვენებია ჩემს მიერ სადისერტაციო კვლევის პერიოდში განხორციელებული ექსპედიციების დროს შეგროვებული მასალების ადგილმდებარეობები.

ლაბორატორიული სამუშაოები

ლაბორატორიული სამუშაო მოიცავდა სამ განსხვავებულ მიმართულებს: 1) ველზე მოპოვებული ნიადაგის სინჯების გარჩევა და სახეობების რკვევა; 2) მოლუსკების რბილი ქსოვილის ანატომიური და ნიჟარის მორფოლოგიის აღწერა; 3) დნმ-ის სექვენირება.

ნიადაგის სინჯების გარჩევა მარტივი და ამავდროულად ძლიერ შრომატევადია. გამოყოფილი მოლუსკების გარკვევა სახეობებებამდე კი საკმაოდ რთულია და დამოკიდებულია მკვლევარის გამოცდილებაზე. იმის გათვალისწინებით რომ საქართველოს მოლუსკების სარკვევევები მოძველებულია ტაქსონომიური თვალსაზრისით, ეს პროცესი კიდევ უფრო რთუდლება. მოლუსკების რკვევისათვისგამოყენებულიიქნა შემდეგი ძირითადი ლიტერატურა ყოფილი საბჭოთა კავშირის და თურქეთის მოლუსკების შესახებ: Лихарев, 1962; Likharev & Ramelmeier, 1962; Riedel, 1966; Шилейко, 1978, 1984; Лихарев & Виктор, 1980; Wiktor, 2000; Schütt, 2005; Sysoev & Schileyko, 2009.

მოლუსკების სისტემატიკა და ასევე რკვევის პროცესი მნიშვნელოვნადაა დაკავშირებული რეპროდუქციული სისტემის ანატომიასთან. სპირტხსნარში დაფიქსირებული მასალის გაკვეთამდე მოლუსკი უნდა მოთავსდეს წყალში 1-2 საათის განმავლობაში რის შემდეგაც მისი ქსოვილი რბილდება. შემდეგ ფრთხილად ხდება ნიჟარიდან რბილი სხეულის მოცილება ისე რომ არ მოხდეს არც ერთი ნაწილის დაზიანება. ქსოვილის გაკვეთა და ორგანოების დათვალიერება შესაძლებელია სტერეო მიკროსკოპის ქვეშ.

ნიჟარის მორფომეტრიული კვლევისათვის გამოვიყენე როგორც ნიჟარის პირდაპირი განაზომები (დეტალები მოცემულია მე-IV პუბლიკაციაში) ასევე ციფრული ორ და სამგანზომილებიანი გამოსახულებების ანალიზი (V).

გენეტიკური კვლევა გულისხმობს სპირტხსნარში დაფიქსირებული მასალიდან დნმ-ის გამოყოფას და სასურველი მონაკვეთების სექვენირებას. დნმ-ის გამოყოფის, ამპლიფიკაციის და სექვენირების, ასევე სხვა მეთოდოლოგიური დეტალები გადმოცემულია მე-V პუბლიკაციაში.

ანალიტიკური მეთოდები

მიუხედავად იმისა რომ საველე სამუშაოების დროს შეგროვებული მასალისათვის ზუსტი ადგილმდებარეობა დაფიქსირებულია, ლიტერატურული მონაცემებისათვის ასეთი ანფორმაცია არ არსებობს. იმისათვის რომ შესაძლებელი ყოფილიყო ლიტერატურული ინფორმაციის გამოყენება მოლუსკების გავრცელების და მრავალფეროვნების ანალიზასთვის, გეოგრაფიული ინფორმაციული სისტემის (ArcGIS 9.3; ESRI, Redlands, CA) საშუალებით დამზადებულ 20 კმ-იან კვადრატულ ბადეზე დავიტანე ყველა სახეობის გეოგრაფიული გავრცელება (დეტალები მოცემულია VI პუბლიკაციაში). ასეთი გზით მიღებული გავრცელების რუკები გამოვიყენე შემდგომი ანალიზებისათვის (ალტერნატიული შემთხვევისათვის იხ. II პუბლიკაცია).

მონაცემთა დამუშავებისათვის გამოყენებული იქნა ანალიტიკური მეთოდების ფართო სპექტრი. კერძოდ, ერთ და მრავალგანზომილებიანი პარამეტრული და არაპარამეტრული სტატისტიკური ტესტები (დეტალები და შესაბამისი რეფერენსები მოცემულია შესაბამის შრომებში - II, III, IV, V); რეგრესიული და კორელაციური ანალიზი (II, III, IV, VI, VIII); ორდინაციული მეთოდები (II, IV, V)და სხვა გრაფიკული მეთოდები (VI); გავრცელების სტატისტიკური მოდელირება (III, VII); ფილოგენეტიკური ანალიზი (V).

თავი 1.*მალაკოლოგიური ბიბლიოგრაფია*

მიუხედავად იმისა რომ საქართველოს მოლუსკების ფაუნა მწირადაა გამოკვლეული (დასავლურ ქვეყნებთან შედარებით), არსებობს ქართველი და უცხოელი მალაკოლოგების მიერ გამოქვეყნებული საკმაოდ მოცულობითი ლიტერატურა. საქართველოს მოლუსკების კვლევებთან დაკავშირებული ლიტერატურის შესახებ არ არსებობს ერთიანი საცნობარო ბაზა. ლიტერატურა გაფანტულია სხვადასხვა ბიბლიოთეკებსა და კვლევით ინსტიტუტებში რომელთა დიდი ნაწილი იოლად მოსაპოვებელი ან ხელმისაწვდომი არაა. იმის გამო რომ არ არსებობს ბიბლიოგრაფიული საცნობარო სისტემა ძნელია შესაბამისი ლიტერატურის და შესაბამისად უკვე არსებული ინფორმაციის გამოყენება. იმისათვის რომ ხელმისაწვდომი გახდეს და გაიოლდეს ბიბლიოგრაფიული ინფორმაციის გამოყენება, მე წქმოვახდინე კატალოგიზება ყველა ტიპის ლიტერატურის რომლებიც გამოქვეყნდა 1900 წლიდან დღემდე (პუბლიკაციები, დისერტაციები, მონოგრაფიები) გამოცემული სხვადასხვა ენაზე. შეგროვებული ბიბლიოგრაფიის ბაზა გამოვიყენე მალაკოლოგიური კვლევების ინტენსივობის, მიმართულებების და სხვა სახის ბიბლიოგრაფიული ანალიზებისათვის.

საქართველოს მოლუსკების შესწავლა მეცხრამეტე საუკუნის პირველ ნახევარში დაიწყეს რუსმა და ევროპელმა მკვლევარებმა. პირველი, მეცნიერული თვალსაზრისით მნიშვნელოვანი ნაშრომი ეკუთვნის მონპერეს, რომელმაც თავისი მოგზაურობის შთაბეჭდილებები აღწერა და გამოაქვეყნა 1839 და 1840 წლებში გამოცემულ წიგნებში (Dubois De Montpereux, 1839, 1840). მან აღწერა რამდენიმე ახალი კავკასიური სახეობა, რომელთაგან აღსანიშნავია ორი დიდი ზომის, კავკასიის ენდემური მოლუსკი - *Helix buchii* და *Caucasotachea calligera*. ამ დროიდან მოყოლებული რუსი და იშვიათად ევროპელი ბუნების მკვლევარები რეგულარულად აგროვებდნენ მალაკოლოგიურ მასალას საქართველოში რის შედეგადაც ხდებოდა ახალი სახეობების აღწერა და უკვე აღწერილი სახეობების გავრცელების შესახებ დამატებითი ინფორმაციის შეგროვება. პირველი ქართველი მალაკოლოგები მეოცე

საუკუნის 40-იან წლებში გამოჩდნენ რომელთაც მნიშვნელოვანი როლი ითამაშეს საქართველოს მოლუსკების ფაუნის კვლევაში (დანართი 1; სურ. 3; ცხრილი 1).

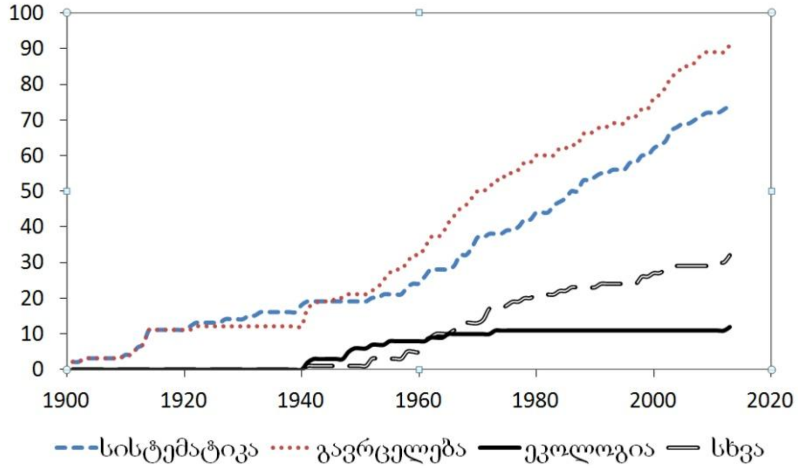
სახელი და გვარი	წლები	პუბლიკაცია
გიორგი კოკოჩაშვილი	1893 - 1981	14
გრიგოლ ჯაველიძე	1910 - 1972	13
სილიბისტრო გამცემლიძე	1908 - 1963	2
სიმონ ხოჯევანიშვილი	1915 - 1988	2
მზია ნაცვლიშვილი	1929 -	9
გურამ ლეჟავა	1930-2007	25

ცხრილი 1. ცხრილში მოცემული აინფორმაცია ქართველი მალაკოლოგების შესახებ - მოღვაწეობის წლები, მათ მიერ გამოქვეყნებული შრომების მითითებით

სადისერტაციო სამუშაოების განმავლობაში შეგროვდა და დამუშავდა ქართველების მიერ გამოქვეყნებული 65 ნაშრომი, თუმცა მათი შრომების სრული ნუსხის შედგენა ჯერ კიდევ დასასრულებელია (ცხრილი 1) რადგან სავარაუდოა რომ პუბლიკაციების ნაწილი არაკატალოგიზებული სახით ინახება სხვადასხვა დაწესებულებებში (როგორიცაა თბილისის (ივანე ჯავახიშვილის), ქუთაისის და სოხუმის უნივერსიტეტები). მასთანავე ზოგიერთი ნაშრომი არაა ხელმისაწვდომი მოქმედ ბიბლიოთეკებში (მაგალითად სიმონ ხოჯევანიშვილის 1941 წლის სადისერტაციო ნაშრომი).

მეოცე საუკუნის 40-იან წლებამდე მალაკოლოგიურ კვლევები მხოლოდ აღწერითი (ტაქსონომიური) ხასიათის იყო. 1941 წელს გამოქვეყნდა პირველი - არატაქსონომიური ტიპის შრომა სდაც არის ვაზის ლოკოკინის (*Helix lucorum* Linnaeus, 1758) ეკოლოგიური მახასიათებლების აღწერის მცდელობა (ჯაველიძე, 1941). ამ პერიოდიდან მოყოლებული, 21-ე საუკუნის დასაწყისამდე ქართველი მალაკოლოგები იშვიათად აქვეყნებდნენეკოლოგიური ან ბიოგეოგრაფიული ტიპის ნაშრომებს (სურ. 2; დანართი 1), რომელებიც ასევე დაკვირვებითი ხასიათის შრომებს წარმოადგენდნენ ცალკეული სახეობის ბიოლოოგიის ან სახეობების გავრცელებებზე (სხვაგვარად არცერთი შრომა არ ყოფილა ექსპერიმენტული ხასიათის ან შესაბამისი დროის ანალიტიკური მეთოდების გამოყენებით ჰიპოთეზაზე დამყარებული კვლევა). ამდენად ისედაც მცირე რაოდენობის კვლევებს დიდი სამეცნიერო ღირებულება არ გააჩნდათ მათი თანამედროვე დასავლურ ან რუსულ ლიტერატურასთან შედარებით. ამასთან ერთად, ნაშრომების თითქმის ნახევარი

ქართულ ენაზე სრულდებოდა, რის გამოც მიუწვდომელი იყო უცხოელი კოლეგებისთვის (სურ. 3).



სურათი 2. მრუდები აჩვენებენ საქართველოს ხმელეთის მოლუსკების კვლევებთან დაკავშირებული შრომების კუმულაციურ მონაცემებს 1900 წლიდან დღემდე მიმართულებების მიხედვით.

მეცხრამეტე - მეოცე საუკუნეების განმავლობაში საკმაოდ დიდი კონხიოლოგიური[1] მასალა დაგროვდა, რომლის დიდი ნაწილი რუსი და ევროპელი ზოოლოგების კერძო ან სამუზეუმო კოლექციებში, ხოლო შედარებით მცირე ნაწილი საქართველოს ეროვნულ მუზეუმში და ილიას უნივერსიტეტის ზოოლოგიის ინსტიტუტის კოლექციებში ინახება. 1900 წლიდან დღემდე აღწერილია საქართველოში მობინადრე 68 სახეობის მოლუსკი (მთელი მალაკოფაუნის 25%), რომელთაგან 53 სახეობის (78%) ტიპური ინდივიდები საქართველოშია მოპოვებული. სამწუხაროა, რომ საქართველოსთვის ენდემური მოლუსკების (ასევე სხვა, აქ გავრცელებული მოლუსკის)სახეობების ტიპურიინდივიდების დიდი ნაწილი (80%-ზე მეტი) რუსეთის, გერმანიის, პოლონეთის და სხვ. ქვეყნების მუზეუმებშია განთავსებული, რაც მიუხედავად დღეისათვის არსებული, გაადვილებული კომუნიკაციების გზებისა ართულებს სისტემატიკურ-ტაქსონომიური ტიპის სამუშაოების განხორციელებას.

კვლევების (და გამოქვეყნებული პუბლიკაციების) რაოდენობის ზრდის მიუხედავად 1900 წლის შემდგომ პერიოდში საქართველოში მობინადრე, ახალი სახეობების აღწერის ტემპი მკვეთრად დაეცა (105 - 1900 წლამდე და 56 – 1900 წლის შემდეგ). თუ განვიხილავთ მხოლოდ საქართველოსათვის ენდუმურ მოლუსკებს, აქ სურათი საპირისპიროს აჩვენებს. კერძოდ, 1900 წლის შემდეგ ახალის სახეობების რიცხვი 19%-

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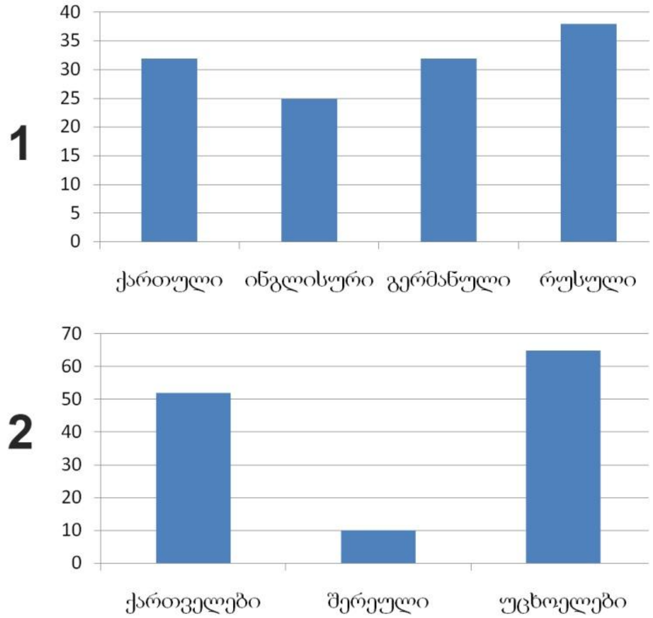
[1] კონხოლოგია ბერძნულიდან ნიჟარების კვლევას ნიშნავს. იგულისხება ნიჟარების კოლექციები.

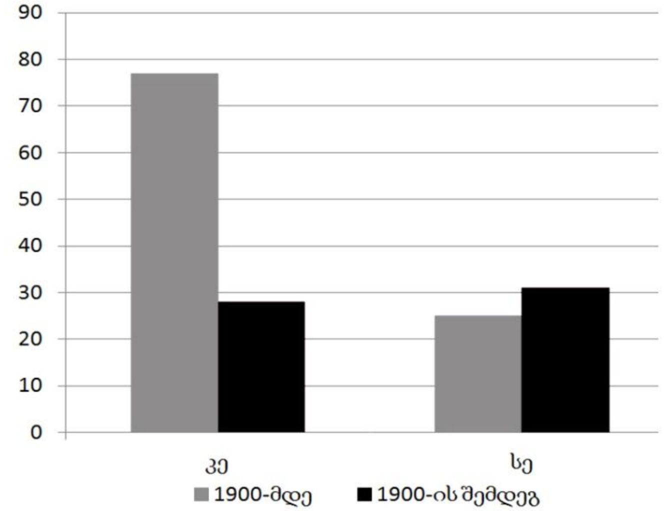
ით (25-დან 31-მდე) გაიზარდა (სურ. 4). წლების მიხედვით აღწერილი სახეობების მრუდი ნათლად აჩვენებს რომ საქართველოს მოლუსკების ფაუნის სრული ინვენტარიზაციისათვის ჯერ კიდევ ბევრი სამუშაოა გასაწევი (სურ. 6).



სურათი 3. 1 - ჰისტოგრამაზე გამოსახულია 1900 წლიდან დღემდე სხვადასხვა ენაზე გამოქვეყნებული შრომების რაოდენობა; 2 - ჰისტოგრამაზე ნაჩვენებია ქართველების, უცხოელების და ერთობლივი (შერეული) ნაშრომების რაოდენობა 1900 წლიდან დღემდე (სულ 128 ბიბლიოგრაფიული ერთეული).

პირველი მნიშვნელოვანი (როგორც ფაუნისტური ასევე ბიოგეოგრაფიული თვალსაზრისით) ნაშრომი რომელიც საქართველოში გავრცელებული ხმელეთის მოლუსკების შესახებ მეტად სრულ ინფორმაციას მოიცავს არის ლიხარევის და რამელმეიერის 1952 წლის ნაშრომი (Лихарев & Рамельмейер, 1952). აღნიშნულ შრომაში სისტემატიზებული სახით მოცემულია ყოფილი საბჭოთა კავშირის (მათ შორის კავკასიის) ხმელეთის მოლუსკების სისტემატიკის, ტაქსონომიის და გავრცელების შესახებ ინფორმაცია. ასევე ამ ნაშრომში პირველადაა მოცემული მოლუსკების მრავალფეროვნების განაწილების, ფილოგეოგრაფიის და ბიოგეოგრაფიული დარაიონების მცდელობა. ნაშრომში კავკასია როგორც დამოუკიდებელი ბიოგეოგრაფიული ერთეული ისეა გამოყოფილი, თუმცა არაფერია ნათქვამი კავკასიის შიგნით მოლუსკების მრავალფეროვნების განაწილებასა ან იქ განვითარებულ ისტორიულ-ბიოგეოგრაფიულ პროცესებზე. უკვე ამ დროისათვის კარგად იყო ცნობილი, რომ მოლუსკების ფაუნა კავკასიაში (და განსაკუთრებით საქართველოში) დიდი მრავალფეროვნებით გამოირჩეოდა. მომდევნო პერიოდში, მეოცე საუკუნის დასასრულამდე, რამდენიმე მსგავსი ტიპის

ნაშრომი გამოქვეყნდა (ძირითადად რუსი მალაკოლოგების მიერ) რომლებშიც მხოლოდ მცირეოდენი სიახლეა წარმოდგენილი ყველა ზემოთ აღნიშნულ საკითხებთან დაკავშირებით (მაგ: Шилейко, 1978, 1984; Лихарев & Виктор, 1980 - მორფოლოგიური ნიშნებზე დაყრდნობით გვთავაზობს ცვლილებებს არსებულ ფილოგენეზურ სისტემაში; ასევე მოლუსკების ბიოგეოგრაფიულ სტრუქტურაზე დამატებით არგუმენტაციას წარმოადგენენ განახლებულ ფაუნისტური მონაცემებზე დაყრდნობით) (დანართი 1).



სურათი 4. გრაფიკზე ნაჩვენებია კავკასიის (კე) და საქართველოს (სე) ენდემური მოლუსკების რიცხვი აღწერილი 1900 წლამდე და მი შემდეგ პერიოდში. კავკასიის ენდემებში არ იგულისხმება მხოლოდ საქართელოსთვის ენდემური სახეობები.

მეოცე საუკუნის ბოლო ათწლეულში, კვლევითი მეთოდების და მიდგომების რევოლუციურ ცვლილებების მიუხედავად საქართველოში აქტიური მალაკოლოგიური კვლევები არათუ გაღრმავდა არამედ სრულად შეწყდა. ამ პერიოდში და მომდევნო ათწლეულის დასაწყისში კვლავ ქვეყნდებოდა შრომები, რომლებიც კავკასიური მოლუსკების სამუზეუმო კოლექციების ანალიზის შედეგი ან არსებული ლიტერატურული მონაცემების რე-პრეზენტაციაა (დანართი 1; სურ. 2). სამწუხაროდ ეს უკანასკნელი არ მოიცავს არცერთ სიახლეს და მეტიც, მასში არაა ინტეგრირებული უახლოესი თანამედროვე ინფორმაცია და ანალიზის თანამედროვე მეთოდები.

ლიტერატურული მონაცემები მოლუსკების კვლევის შესახებ ნათლად აჩვენებს რომ საქართველოში ფუნდამენტური ეკოლოგიურ-ევოლუციური კვლევების პრაქტიკა, მოლუსკების როგორც სამოდელო ორგანიზმების გამოყენებით არ ყოფილა. ეს

ნაწილობრივ შეიძლება ჩაითვალოს მიზეზად მოლუსკების კვლევით დაინტერესებული ადამიანების სიმცირისა.

თავი 2. *საქართველოს მოლუსკების ფაუნა* (I, II, V ,VI)

მოლუსკები ფეხსახსრიანთა ტიპის შემდეგ ცხოველთა ყველაზე მრავალრიცხოვანი ჯგუფია, რომელიც 120,000-მდე აღწერილ სახეობას აერთიანებსდა გაცილებით მეტის - ჯერ კიდევ ასაღწერი სახეობის არსებობაა ნავარაუდები (van Bruggen, 1995; Stork, 1999). ზოგადად სამეცნიერო და მათ შორის მალაკოლოგიური კველევების ინტენსიფიკაციის ფონზე, ყოველწლიურად იმატებს აღწერილი სახეობების რიცხვი. ამასთანავე თანამედროვე მოლეკულური და მორფომეტრიული მეთოდების გამოყენებით ინტენსიურად მიმდინარეობს არსებული კლასიფიკაცების რევიზია, სახეობათა სინონიმიზაცია ან დაყოფა, რაც მიუთითებს რომ მოლუსკების მრავალეფეროვნების და სისტემატიკის შესახებ ჩვენი ცოდნა ძალზე არასრულია.

საქართველოს მოლუსკების მრავალფეროვნების და გავრცელების შესახებ არსებული მონაცემები გაფანტულია სხვადასხვა პუბლიკაციებში. ყველაზე სრულყოფილი და გავრცელების მხრივ დეტალური ნაშრომი 1973 წელს გამოცემული „საქართველოს ცხოვლეთა სამყარო“-ა, სადაც მოცემულია მონაცემები 220-მდე სახეობის მოლუსკის შესახებ (ლეჟავა, 1973). აღნიშნული ნაშრომი ძალზე მოძველებულია, რადგან მის შემდეგ სახეობათა რაოდენობის და მათი გარცელების შესახებ მონაცემები ზევრად გაიზარდა. ამასთანავე აღნიშნულ შრომაში გამოყენებული ტაქსონომია და სისტემატიკური სქემებისაფუძვლიანად შეიცვალა რაც ერთი მხრივ ეჭვქვეშ აყენებს მოცემული ინფორმაციის ვალიდურობას, ხოლო მეორ მხრივ თითქმის გამოუყენებელს ხდის მას არასპეციალისტებისათვის ან დამწყები მალაკოლოგებისათვის. უმრავლესობა ლოკალური ენდემური მოლუსკის სისტემატიკა კი მოძველებულია და რევიზიას საჭიროებს. ამ მიმართულებით ჩემი სადისერტაციო კვლევის ფარგლებში მიზნად დავისახე არსებულილი ტერატურული მონაცემების, ასევე ჩემი საველე სამუშაოების დროს შეგროვებული მონაცემების (სურ

1) გამოყენებით მომეხდინა საქართველოში გავრცელებული მოლუსკების მრავალფეროვნების ანალიზი.

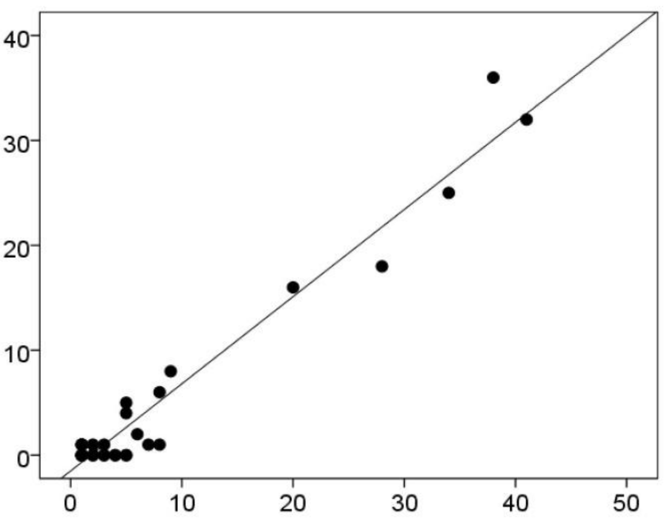
Family	GN	SpN	E%
Aciculidae	1	2	0
Agriolimacidae	3	8	13
Boettgerillidae	1	2	50
Bradybaenidae	1	1	0
Carychiidae	1	4	0
Chondrinidae	1	3	0
Clausiliidae	17	38	95
Cochlicopidae	1	5	0
Cochlostomatidae	1	1	100
Cyclophoridae	1	1	100
Daudebardiidae	4	5	80
Discidae	1	1	0
Enidae	17	28	64
Euconulidae	1	1	0
Ferussaciidae	1	2	0
Gastrocoptidae	1	1	0
Gastrodontidae	1	1	0
Helicidae	3	8	75
Hygromiidae	15	41	78
Limacidae	5	9	89
Milacidae	1	1	100
Oleacinidae	1	1	100
Orculidae	5	20	80
Parmacellidae	1	1	100
Punctidae	1	1	0
Pupillidae	2	6	33
Pyramidulidae	1	1	0
Succineidae	3	4	0
Trigonochlamydidae	5	5	100
Truncatellinidae	2	5	0
Valloniidae	2	3	0
Vertiginidae	2	7	14
Vitrinidae	3	3	33
Zonitidae	8	34	74
	114	254	

ცხრილი 2. ცხრილში წარმოდგენილია საქართველოში გავრცელებული მოლუსკების ოჯახები. GN - აღნიშნავს გვარების რაოდენობას, SpN - სახეობების რაოდენობას ხოლო E% - ენდემური სახეობების პროცენტულ მაჩვენებელს

დღევანდელი მდგომარეობით საქართველოს ტერიტორიაზე 34 ოჯახში გაერთიანებული 114 გვარის 254 სახეობის ხმელეთის მოლუსკი (ლოკოკინები და ლოქორები) ცხოვრობს (ცხრილი 2; დანართი 2). მათგან, 56 სახეობა საქართველოს, საქართველოს, ხოლო 161 სახეობა (საქართველოს ენდემების ჩათვლით) კავკასიის ენდემია. ჯამში, მოლუსკების სახეობების 63% (161) კავკასიის ენდემურია რაც ძალზე მაღალი მაჩვენებელია სხვა ჯგუფებთან შედარებით. სახეობათა 63 % (161) წარმოდგენილია 5 ყველაზე მრავალრიცხოვანი ოჯახით - *Hygromiidae, Zonitidae, Clausiliidae, Enidae* და *Orculidae* (ცხრილი 2). აღნიშნული ოჯახები ასევე გამოირჩევიან ენდემური სახეობების მაღალი პროცენტული შემცველობით. უფრო ზუსტად კი რაც უფრო მდიდარია ოჯახი სახეობებით მით უფრო მეტია ენდემური სახეობების რიცხვი ($R^2= 0.95$, $P>0,05$, (სურ. 5)) რაც მიუთითებს ზოგიერთი ოჯახის ინტენსიურ ლოკალურ რადიაციაზე.

35-დან 13 ოჯახიერთი სახეობითაა წარმოდგენილი, რომელთაგან ერთი (*Cochlostomatidae*) მონოტიპური ოჯახია (ერთი გვარით და ერთი სახეობით არის წარმოდგენლი). ეს უკანასკნელი (*Toffoletia lederi* (Boettger, 1881)) ამავდროულად კავკასიის ენდემური

და რელიქტური სახეობაა და კონსერვაციული თვალსაზრისით განსაკუთრებულ ყურადღებას საჭიროებს.

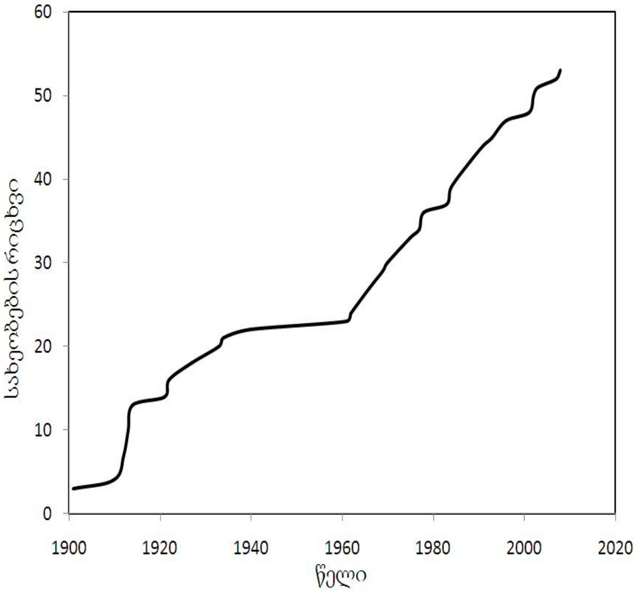


სურათი 5. ნაჩვენებია თითქმის წრფივი დამოკიდებულება ოჯახებში სახეობათა სრულ რაოდენობასა (აბსცისა) და ენდემური სახეობების (ორდინატა) რაოდენობას შორის.

უკანსკნელი 100 წლის განმავლობაში აღწერილი სახეობების რაოდენობის განაწილება აჩვენებს რომ მწირი მალაკოლოგიური კვლევების ფონზე ახალი სახეობების პოვნის ტენდენცია არ კლებულობს (სურ. 6). ამდენად, სავარაუდოა, რომ მოლუსკების სახეობების რაოდენობა მნიშვნელოვნად გაიზარდება მომავალში. მოლუსკების უმრავლესობა როგორც ნაკლებად მოძრავი ორგანიზმები ხასიათდებიან ვიწრო ეკოლოგიური მოთხოვნილებებით და ამავდროულად სწრაფი ადაპტირების უნარით (Cameron et al., 2003), რაც ხშირად სახეობათა ინტენსიური ლოკალური რადიაციის მიზეზია. მოლეკულურ გენეტიკური კვლევები აჩვენებს რომ მცირე (რამდენიმე ათეულ კმ) ტერიატორიაზე, რომელიც მიკროჰაბიტატების მრავალფეროვნებით გამოირჩევა, შესაძლოა მორფოლოგიურად ძლიერ მსგავსი და გენეტიკურად იზოლირებული სახეობების კომპლექსებით (მაგ: კრიპტული სახეობები) იყოს წარმოდგენილი (მაგ: Cowie, 1995; Douris et al., 1998; Chiba, 1999; Faher et al., 2013). ამ მიმართულებით საქართველოში (და მთლიანად კავკასიაში) ინტენსიური კვლევები არ ჩატარებულა და არ გვაქვს მონაცემები იმისთვის რომ ვიმსჯელოთარის თუ არა მოლუსკების გენეტიკური მრავალფეროვნება უფრომაღალი, ვიდრე ჩვენს მიერ წარმოდგენილი მრავალფეროვნება (რომელიც ეყრდნობა მხოლოდ მორფოლოგიურ აღწერებს), თუმცა ჩვენს მიერ 2008 და 2013 წლებში გამოქვეყნებული შრომები ნათლად აჩვენებს რომ

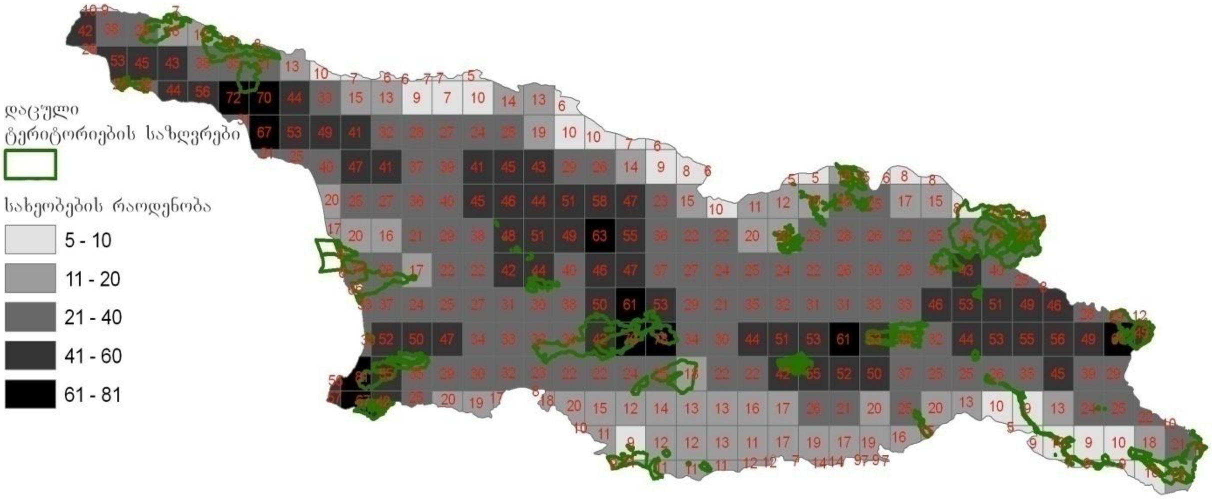
ამის ალბათობა მაღალია. კერძოდ, 2008 წელს ჩვენს მიერ აღწერილი იქნა მოლუსკის ახალი სახეობა - გოდერძის ჰელიქსი (*Helix goderdziana* Mumladze, Tarkhnishvili et Pokryszko, 2008) რომელიც ყველაზე დიდი ზომის ხმელეთის მოლუსკია პალეარქტიკის მასშტაბით (V). 2009 წელს გამოცემულ მონოგრაფიაში, სისოევი და შილეიკო ეწინააღმდეგებიან *H. goderdziana* - ს როგორც დამოუკიდებელ სახეობად განხილვას (Sysoev & Shileyko, 2009). ამ მიზნით ჩვენი სამუშაო ჯგუფის მიერ განხორციელდა კომპლექსური სისტემატიკური კვლევა მორფოლოგიური და მოლეკულურ გენეტიკური მეთოდების გამოყენებით. შედეგად ნაჩვენები იქნა რომ გოდერძის და ბუხის ლოკოკინა არიან ევოლუციური სახეობები (რეციპროკულად - ერთმანეთის მიმართ- მონოფილეტურ კლადებს ქმნიან) ღრმა გენეტიკური განსხვავებებით. ბუხის ლოკოკინის არეალი ნაწილობრივ ფარავს გოდერძის ლოკოკინას არეალს თუმცა ისინი მკვეთრად განსხვავებულ ჰაბიტატებში ცხოვრობენ. მიუხედავად ძლიერი ვიზუალური მსგავსებისა (შესაძლოა კრიპტულ სახეობაბდ მათი განხილვა) ბუხის და გოდერძის ლოკოკინა კარგი ეკოლოგიური სახეობები არიან (I,V).

დანართ 3-ში მოტანილია ცალკეული მოლუსკის (234 სახეობა) გავრცელბის რუკები 20 კმ-ის სიზუსტით. ამ რუკების ’შეკრების ’შედეგი ნაჩვენებია სურათ-7-ზე რომელიც ნათლად გამოხატავს მოლუსკების მრავალ-ფეროვნების განაწილებას საქართველოში. მოლუსკების მრავალ-ფეროვნების ძირითადი ცენტრების (41 და მეტი სახეობა 20 კვადრატულ კილომეტრში) განაწილება დიდწილად ემთხვევა ფართოფოთლოვანი ტყეების გავრცელების საზღვრებს. უფრო ზუსტად კი



სურათი 6. აღწერილი სახეობების კუმულაციური მრუდი წლების მიხედვით.

შეიძლება გამოიყოს აფხაზეთის ტყიანი მასივი, სამეგრელო-იმერეთის კირქვიანი ზონა ბორჯომის რაიონთან ერთად, ბათუმის მიმდებარე ტყიანი მასივი (კინტრიშის, მაჭახელას და აჭარისწყლის ხეობები), თრიალეთის ქედის აღმოსავლეთ ნაწილი და კახეთის კავკასიონის ტყის ზონა (სურ. 7) (მოლუსკების მრავალფეროვნების განაწილების ანალიზისათვის გამოყენებული მეთოდების დეტალებისათვის იხ. პუბლიკაცია VI).



სურათი 7. რუკაზე ნაჩვენებია ხმელეთის მოლუსკების სახეობრივი მრავალფეროვნების განაწილება 20X20 კმ-იანი კვადრატების მიხედვით. ციფრები კვადრატებში მიუთითებს სახეობების რიცხვს რაც ასევე აღნიშნულია ფერების გრადაციით. მწვანე კონტურებით ნაჩვენებია დაცული ტერიტორიების საზღვრები.

თითქმის ანალოგიურ სურათს იძლევა მხოლოდ საქართველოსთვის ან მხოლოდ კავკასიისათვის ენდემების მრავალფეროვნების განაწილება იმ განსხვავებით, რომ საქართველოს ენდემური მოლუსკებისათვის კახეთის კავკასიონი არ გამოირჩევა ენდემური სახეობების მრავალფეროვნებით (ამ და ენდემური მოლუსკების მრავალფეროვნებასთან დაკავშირებულ სხვა საკითხების შესახებ დეტალები მოცემულია VI პუბლიკაციაში). მიუხედავად იმისა, რომ ინტუიციურად მოლუსკების მრავალფეროვნების გავრცელების მოდელი ლოგიკურია, სავარაუდოა რომ სახეობების გავრცელების შესახებ ინფორმაცია დიდი ოდენობით ცდომილების შემცველი იყოს. ისევე როგორც მხოლოდ ენდემური მოლუსკების შემთხვევაში (VI) საერთო მრავალფეროვნების განაწილების კორელაციური ანალიზი აჩვენებს, რომ

უჯრების მრავალფეროვნება უარყოფითად კორელირებს ცენტრალური დასახლებული პუნქტებიდან მანძილთან. კერძოდ რაც უფრო იზრდება დაშორება ცენტრალური ქალაქებიდან მით უფრო ეცემა მრავალფეროვნება (R^2=-0.4, P<0.001). ასეთი უარყოფითი კორელაციური კავშირი მეტყველებს იმაზე რომ დასახლებული პუნქტებისგან მოშორებულ ტერიტორებზე ნაკლები მრავალფეროვნება შესაძლოა იყოს არტეფაქტი. სამომავლო, ინტენსიური საველე კვლევების შედეგად შესაძლოა სურ-7-ზე ნაჩვენები მოდელი მნიშვნელოვნად შეიცვალოს.

თავი 3. *ბიოგეოგრაფია და ფილოგეოგრაფია (II , III, V)*

ცხოველთა და მცენარეთა თანამედროვე გავრცელება, გარდა თანამედროვე გარემოს პირობებით და სახეობათა შორისი დამოკიდებულებებისა, განპირობებულია ისტორიული პროცესებით და მოვლენებით (Lomolino et al., 2006). დედამიწის ზედაპირმა და ეკოსისტემებმა დღევანდელი სახე უკანასკნელი ორი ათეული მილიონი წლის განმავლობაში მიიღეს. თუმცა ეს პერიოდი კლიმატის და გეოლოგიური პროცესების ძლიერი ცვლილებებით ხასიათდებოდა. ასეთ პირობებში მკვეთრად იცვლებოდა ცხოველთა და მცენარეთა გავრცელების სურათიც (Graham & Grimm, 1990; Jansson, 2003).

დღევანდელი დიდი კავკასიონის მთიანი სისტემა მიოცენის დასაწყისში იზოლირებულ კუნძულს წარმოდგენდა დიდ პარათეტისის ზღვაში და დაახლოებით 6-7 მილიონი წლის წინ მოხდა მისი სახემელეთო დაკავშირება მცირე აზიის და ცოტა მოგვიანებით ჩრდილოეთ ხმელეთის ნაწილებთან. მომდევნო პერიოდებში რამდენჯერმე მოხდა დიდი კავკასიონის იზოლაცია კასპიისა და შავი ზღვის შემაერთებელი არხებით. ამ დროს, მცირე კავკასიონი, ჯერ დიდი კავკასიონისგან იზოლირებული და ბალკანეთთან დაკავშირებული (12 მლნ წელი და უფრო ადრე) იყო, ხოლო მოგვიანებით (11 მლნ წლიდან) ცენტრალური აზიის მასივს შეუერთდა (Steininger & Rogl, 1984; Rogl, 1998, 1999). ამგვარად დიდი კავკასიონს და მცირე კავკასიონს განსხვავებული გეოლოგიური ისტორია აქვთ და მათი ინტენსიური

დაკავშირება პლეისტოცენში (2.5 მლნ - 11000 წელი) მოხდა. გეოლოგიური ცვლილებების თანმდევად მნიშვნელოვნად იცვლებოდა კლიმატიც. თუ ადრეული მიოცენის ეპოქა ტროპიკული კლიმატით ხასიათდებოდა, მოგვიანებით იგი თანდათან გამკაცრდა. ხოლო დაახლოებით 6 მილიონი წლის უკან მკვეთრი კლიმატური გამშრალება (მესინის კრიზისი) დაიწყო, რამაც საფუძვლიანად შეცვალა ცხოველთა და მცენარეთა გავრცელების სურათი (Azanza et al., 2000; Thompson, 2005). ამდენად შეგვიძლია თამამდ ვთქვათ რომ კავკასია თანამედროვე კლიმატურ-ლანდშაფტური სახის მიღებას მესინის კრიზისის ან მისი შემდგომი პერიოდიდან იწყებს. შემდგომი მნიშვნელოვანი კლიმატური მოვლენები უკვე გამყინვარების პერიოდებს უკავშირდება. სწორედ აქ იკვეთება კავკასიის მნიშვნელოვანი როლი, რადგან დიდი კავკასიონი უკვე ბარიერის როლს თამაშობდა ცივი კლიმატის უფრო სამხრეთით გავრცელებაში რაც დიდი კავკასიონის ქედის სამხრეთით რეფუგიუმების არსებობაში გამოიხატებოდა.

უკანასკნელი პლეისტოცენური გამყინვარების ეპოქაში (110 – 11 ათასი წელი) კავკასიის რეფუგიუმი მნიშვნელოვან როლს თამაშობდა სახეობების და ეკოსისტემების შენარჩუნებაში რომლებიც პერიოდული დათბობების დროს იწყებდნენ მიგრაციებს (Van andel & Tzedakis, 1996; მაგ: Barrington & Paris, 2007; Hewitt, 1999; Tarkhnishvili & Gokhelashvili, 1999). სახეობათა არეალების მკვეთრი შემცირება და შემდგომ გაფართოება მნიშვნელოვან გავლენას ახდენდა სხვადასხვა რეგიონის (ძირითადად რეფუგიუმების ჩრდილოეთით მდებარე ტერიტორიების) ფაუნის ფორმირებაზე და სახეობათა დივერგენციის პროცესებზე (Hewitt, 1999; Tarkhnishvili & Gokhelashvili, 1999).

დიდი რაოდენობით კვლევები მიძღვნილია გამყინვარების შემდგომი კოლონიზაციის გზებზე, ინტენსივობაზე და შედეგად მიღებული ბიოგეოგრაფიული მოდელების კვლევაზე (Sommer & Zachos, 2009; Habel et al., 2010). ამავდროულად შედარებით ნაკლებია ცნობილი რეფუგიუმების შიგნით მიმდინარე პროცესებზე და

თავად რეფუგიუმების სტრუქტურაზე. ამ მხრივ ერთერთი ყველაზე ნაკლებ შესწავლილი კავკასიაა.

სახეობათა და თანასაზოგადოებათა თანამედროვე გავრცელების ანალიზით, ასევე გენეტიკური კვლევებით შესაძლებელია წარსული მოვლენების საკმაო სიზუსტით აღდგენა და ისტორიული ბიოგეოგრაფიის და ფილოგეოგრაფიის შეკითხვებზე პასუხების მოძებნა. ჩემი სადისერტაციო კვლევის ნაწილი მიეძღვნა (1) კავკასიის და მასთან ახლომდებარე რეგიონების ანალიზს როგორც პოტენციური რეფუგიუმებისა ზოგიერთი ცხოველის და მცენარის თანამედროვე გავრცელებაში (III); (2) კავკასიის მალაკოფაუნის სტრუქტურის ანალიზს და შედარებას სხვა რეგიონების (ევროპა) მალაკოფაუნასთან რათა გაგვერკვია თუ რამდენად მნიშვნელოვანი როლი ეკავა კავკასიის რეფუგიუმს, უფრო ჩრდილოეთ რეგიონების მალაკოფაუნის ფორმირებაში (II); (3) როგორც მოდელ სახეობები, გვარი *Helix* - ის ენდემური სახეობების გენეტიკური კვლევა მათი ფოლოგეოგრაფიული ისტორიის აღდგენის მიზნით (V).

პალინოლოგიური მონაცემების მიხედვით კავკასიაში გამყინვარების დროინდელი რეფუგიუმი შავი ზღვისპირეთში (კოლხეთის დაბლობი და სამხრეთაღმოსავლეთ შავიზღვისპირეთი) იყო შემორჩენელი (van Andel & Tzedakis, 1996) თუმცა არსებობს ალტერნატიული მოსაზრებაც. კერძოდ დიდი კავკასიონის ქედის სამხრეთით რამდენიმე რეფუგიუმი არსებობდა (Velichko & Kurenkova, 1990; Tarkhnishvili et al., 2000; Tarkhnishvili et al., 2001). ერთი ან მეორე შეხედულების პირდაპირი მტკიცებისათვის საკმარისი მონაცემები არ მოიპოვება და ამდენად რთულია ზუსტი სურათის აღდგენა. კავკასიაში, გამყინვარების დროინდელი რეფუგიუმების გავრცელების შესახებ უფრო სრული წარმოდგენისათვის ჩვენს მიერ გამოყენებული იქნა GIS მეთოდებზე დაყრდნობით რელიქტური სახეობების თანამედროვე გავრცელების მოდელები, რომლებიც ექსტრაპოლირებული იქნა წარსულზე (წარსულის კლიმატური სცენარების გამოყენებით) სახეობა სპეციფიური დისპერსიის კომპონენტის ჩართვით. მიღებული შედეგები აჩვენებენ რომ კავკასიაში არსებობდა

რეფუგიუმების სისტემა, რაც თანხმობაში მოდის Velichko & Kurenkova - ს (1990) შეხედულებებთან (დეტალები მოცემულია III პუბლიკაციაში).

სადისერტაციო კვლევის ფარგლებში განვახორციელეთ ბუხის და გოდერძის ლოკოკინების (*H. buchii*, *H. Goderdziana*) ფილოგენეტიკური შესწავლა. გნეტიკურმა კვლევამ აჩვენა რომ ორივე სახეობა მონოფილეტურია ერთმანეთის მიმართ და მათი იზოლაცია სავარაუდოდ მილიონ წელს ითვლის. თუმცა, გამყინვარების დროს გოდერძის ლოკოკინა შემორჩა დასავლეთ მცირე კავკასიონზე რაც აისხება მის დღევანდელ გავრცელებაში (V პუბლიკაცია). ეს შედეგი თანხმობაში მოდის კავკასიური სალამანდას (*Mertensiella caucasica*) გავრცელებასთან. მცირე კავკასიონის დასავლეთ და ცენტრალურ ნაწილში სალამანდრას სხვადასხვა ევოლუციური ხაზია (ერთმანეთისგან რამდენიმე მილიონი წლით დაშორებული) გავრცელებული და დასავლეთ ხაზის ჩრდილო აღმოსავლეთ საზღვარი ემთხვევა გოდერძის ლოკოკინის გავრცელების საზღვარს (Tarkhnishvili et al., 2000; Tarkhnishvili et al., 2008). ამდენად ცხადია რომ დასავლეთ მცირე კავკასიონი გარკვეულ პერიოდებში იზოლირებული რეფუგიუმის სახით არსეობობდა კოლხეთის და სხვა ჩრდილო-აღმოსავლეთ კავკსიის რეფუგიუმებისაგან. ამავდროულად მოლუსკების სახეობათა დიდი ნაწილი საქართველოში და ზოგადად კავკასიაში გავრცელებულია ფრაგმენტულად თუმცა ხასიათდებიან შემოსაზღვრული არეალით კოლხეთის, აჭარის და ჩრდილო დასავლეთ თურქეთის შავიზღვის პირეთით რაც კოლხეთის დიდი, ერთიანი რეფუგიუმის არსებობაზე მიუთითებს (II პუბლიკაცია). ამდენად, ფაუნისტური და გენეტიკური კვლევები ჯერ-ჯერობით არ იძლევიან მყარ არგუმენტაციას კავკასიის გამყინვარების დროინდელი, რომელიმე ერთიანი ისტორიული სცენარის სასარგებლოდ რაც დამატებითი კვლევების საჭირებაზე მიუთითებს.

განსხვავებული სურათი გვაქვს კავკასიის რეფუგიუმიდან გამყინვარების შემდგომი კოლონიზაციის გზების კვლევის შემთხვევაში. მოლუსკების ფაუნის შედარებითი ანალიზი კავკასიის ჩრდილოეთით მდებარე რეგიონების ფაუნასთან აჩვენებს რომ კავკასიას არ ქონდა მნიშვნელოვანი როლი გამყინვარების შემდგომი

რეკოლონიზაციის პროცესებში ჩრდილოეთის მიმართულებით (II პუბლიკაცია). ეს მოვლენა შეიძლება აიხსნას იმით რომ დიდი კავკასიონის ქედი დაუძლეველ ბარიერს წარმოდგენდა მოლუსკებისთვის რომელთაც ზოგადად სუსტი დისპერსიის უნარი აქვთ (Aubry et al., 2006). ეს სცენარი არ არის უნივერსალური სხვა სახეობათა სხვა ჯგუფებისთვის. კერძოდ, ნაჩვენებია რომ ჩრდილოეთ ევრაზიის ტყის სოკოების (ბაზიდიომიცეტების) გამყინვარების შემდგომი ფლორის ჩამოყალიბებაში კავკასიამ მნიშვნელოვანი როლი ითამაშა (Ghobad-Nejhad et al., 2012).

თავი 4. *ვაზის ლოკოკინის გავრცელება და ეკოლოგია* *(IV, VII)*

ცალკეული სახეობის მოლუსკის ევოლუციურ - ეკოლოგიურ კვლევა მნიშნველოვანია კომერციული თვასაზრისით (Welch & Pollard, 1977), ფუნდამენტური ევოლუციური (მაგ: Pfenninger et al., 2007), სისტემატიკური (მაგ: Winston, 1999; Rissler & Apodaca, 2007) და კონსერვაციული (მაგ: Brown et al., 2008) საკითხების გადასაჭრელად. ამდენად ამოცანების სპექტრი ისევე როგროც პოტენციური საკვლევი ობიექტების (ამ შემთხვევაში მოლუსკების სახეობები) რიცხვი დიდია. საქართველოში მსგავსი ტიპის კვლევები პრაქტიკულად არ განხორციელებულა (გარდა 1941 წლის სადისერტაციო ნაშრომისა, სადაც არის ვაზის ლოკოკინის - *Helix lucorum* Linnaeus, 1758 (ევროპაში ცნობილია როგორც "თურქული" ან "საჭმელი" ლოკოკინა) ცხოვრების ნირის შესწავლის მცდელობა (ჯაველიძე, 1941)).

სადისერტაციო კვლევის ფარგლებში განხორციელდა ორი კვლევითი პროექტი რომლებლიც მიზანდ ისახავდა სამოდელო სახეობის მოლუსკის ევოლუციურ - ეკოლოგიურ კვლევას (IV, VII). ასეთ სამოდელო სახეობად შევარჩიე ვაზის ლოკოკინა (*H. lucorum*) რომელიც ფართოდაა გავრცელებული საქართველოში. მისი ბუნებრივი არეალი ხმელთაშუაზღვის ქვეყნები, სამხრეთ და აღმოსავლეთი შავიზღვის პირეთია. უკანასკნელი 50 წლის განმავლობაში ვაზის ლოკოკინამ დაიწყო გავრცელება აღმოსავლეთ და ჩრდოლეთ ევროპის ქვეყნებში და ინვაზიური სახეობად ითვლება (Falkner et al., 2002; Mienis & Rittner, 2010; Peltanova et al., 2012). საქართველოში და

კავკასიაში ამ სახეობის გავრცელება ყოველთვის ბუნებრივ მოვლენად განიხილებოდა, თუმცა ადამიანის საცხოვრებელთან მჭიდრო კავშირი ბადებს გარკვეულ ეჭვს მისი ინვაზიურობის შესახებ. მართლაც ვაზის ლოკოკინა ძირითადად ადამიანის მიერ სახეცვლილ ლანდსაფთებში ცხოვრობს და არ გვხვდება ხელუხლებელ ბუნებრივ ჰაბიტატებში. საქრთველოში (და ზოგადად კავკასიაში) ვაზის ლოკოკინის არსებობის შესახებ არსებობს მოსაზრება რომ იგი გვიან პლეისტოცენში ან ჰოლოცენში ადამიანის მიერ იქნა ინტროდუცირებული (Lubell, 2004). საქართველოში ვაზის ლოკოკინის გავრცელების არეალი მეოცე საუკუნის პირველ ნახევარში კოლხეთის დაბლობით და მისი მიმდებარე დასახლებული პუნქტებით, ასევე თბილისის და რუსთავის შემოგარენით შემოიფარგლებოდა (ჯაველიძე, 1940; Лихарев & Раммельмейер, 1952). მოგვიანებით საქართველოს სხვა რეგიონებშიც დაფიქსირდა ვაზის ლოკოკინის არსებობა. ნაკლებ სავარაუდოა რომ მეოცე საუკუნის პირველ ნახევარში მისი შეზღუდული არეალი გავრცელების არასაკმარისად შესწავლის შედეგი იყო, რადგან ვაზის ლოკოკინა სინანთროპული სახეობაა და ყველაზე იოლად შესამჩნევია მოლუსკებს შორის.

ვაზის ლოკოკინის შეზღუდული გავრცელება საქართველოში შესაძლოა რამდენიმე ჰიპოთეზით აიხსნას. ერთერთი ასეთი ჰიპოთეზა სახეობათშორისი ურთიერთობაა - კონკურენცია მის ახლონათესავ (იგივე გვარის) სახეობასთან - ბუხის ლოკოკინასთან (*Helix buchii*), რომელიც კავკასიის ენდემია და ძირითადად ფართოფოთლოვანი ტყეების ბინადარია. VII პუბლიკაციაში GIS - ის საშუალებით აგებულმა მოდელებმა აჩვენა რომ ვაზის ლოკოკინისა და ბუხის ლოკოკინების ნიშების პოტენციური არეები გადაიფარება (>40%) თუმცა დღემდე მათი თანაცხოვრების შემთხვევა არ დაფიქსირებულა. მხოლოდ 2 წერტილში ეს ორი სახეობა ერთამანეთს ძალიან უახლოვდება მაგრამ მათ შორის მკვეთრი წარმოსახვითი ბარიერია (VII). ვაზის ლოკოკინის ყველა დღემდე მოპოვებული ყოფნის წერტილი მეტ-ნაკლებად ადამიანის მიერ სახეცვლილია. ხშირ შემთხვევაში ასეთი ადგილები ესაზღვრება ბუხის ლოკოკინისათვის გამოუსადეგარ ბუნებრივ ჰაბიტატებს მაგრამ მის მიერ ამ

ადგილების ათვისება არ ხდება რაც მიუთითებს მისი გავრცელების სხვა მალიმიტირებელი ფაქტორების არსებობაზე (როგორიცაა მაგალითად მტაცებლები ან პარაზიტები).

ვაზის ლოკოკინა, მიუხედავად ძლიერი პირდაპირი წნეხისა, წარმატებულად მრავლდება ყველა სახის ანთროპოგენურ ლანდშაფტში. მისი უნარი გადარჩეს და წარმატებით გამრავლდეს ადამიანის სიახლოვისას შესაძლოა დაკავშირებული იყოს ზრდის და გამრავლების მექანიზმის ადაპტაციებთან (IV პუბლიკაცია).

თავი 5. *მალაკოფაუნის კონსერვაცია (VI)*

თანამედროვე ცივილიზაცია ბუნებრივი გარემოს დეგრადაციის მთავარი გამომწვევი მიზეზია (Vitousek et al., 1997a,b; Pimm & Raven, 2000). მიუხედავად საზოგადოების მზარდი მონდომებისა და დანახარჯებისა იმისათვის რომ შენარჩუნებული იქნას ბუნებრივი გარემო, მაინც ვერ ხერხდება საკმარისი ინვესტიციის განხორციელება ბუნების ეფექტური კონსერვაციისათვის (James et al., 1999; James et al., 2001). სწორედ ამის გამო ხორციელდება კვლევები კონსერვაციული პრიორიტეტების გამოყოფისათვის რაც გულისხმობს ერთის მხრივ მეტად მრავალფეროვანი და ამავდროულად მოწყვლადი რეგიონების იდენტიფიცირებას (ეკორეგიონები გლობალურ (Myers, 1988; Myers et al., 2000) და დაცული ტერიტორიები ლოკალურ (Gaston et al., 2008) მასშტაბში), ხოლო მეორე მხრივ სუროგატი სახეობების ან სახეობათა ჯგუფების შერჩევას რომელთა კონსერვაცია უზრუნველყოფს სხვა სახეობების ან ეკოსისტემების კონსერვაციას (Caro & O'Doherty, 1999).

“Conservation Intarnational” – ის მიერ საქართველო (და მთლიანად კავკასია) 1999-2000 წლიდან ოფიციალურად განიხილება როგორც ბიორავალფეროვნების ცხელი წერტილი (Zazanashvili et al., 1999; Myers et al., 2000). თავისთავად ცხელ წერტილად აღიარება არ იძლევა გარანტიას რომ ბუნების კონსერვაცია სწორი მიმართულებით განხორციელდება, თუმცაღა ასეთი სტატუსი ქმნის უკეთეს გარემოს კონსერვაციული პროექტების განხორციელებისათვის. განსაკუთრებით მნიშვნელოვანი პროექტებია

დაცული ტერიტორიების ქსელის შექმნის და განვითარებისკენ მიმართული პროექტები რადგან გასული 23 წლის განმავლობაში, ყველა განხორციელებული, ცალკეული სახეობის კონსერვაციისაკენ მიმართული პროექტი თითქმის უშედეგოა (არ არსებობს პოზიტიური შედეგის ამსახველი თუნდაც ერთი მაგალითი) ან ვერ ხერხდება შეფასება. დღეისათვის საქართველოში არ არსებობს არცერთი კონსერვაციული ღონისძიების (მათ შორის არც დაცული ტერიტორიების ქსელის) ეფექტურობის შეფასების მექანიზმი რაც ეჭვქვეშ აყენებს შემდგომი ნაბიჯების მიზანმიმართულობას (Chape et al., 2005; Hayes, 2006). უფრო მეტიც, დღემდე არსებული დაცული ტერიტორიების დიდი უმრავლესობა შექმნილია არასაკმარისად დასაბუთებული მოტვაციის საფუძველზე. მაგალითის სახით შეიძლება განვიხილოთ ყაზბეგის და თუშეთის ეროვნული პარკები, რომლებიც საქართველოს დაცული ტერიტორიების 4 % - ს შეადგენს. აღნიშნული ტერიტორიების დაცვა მნიშვნელოვანია რამდენიმე სახეობის ჩლიქოსანისთვის (ჯიხვი და ნიამორი) თუმცა ზოგადად ბიომრავალფეროვნების სიმდიდრის, ენდემური სახეობების ან საფრთხეების მხრივ უფრო მნიშვნელოვანი შესაძლოა იყოს მესხეთის ქედი ან სამეგრელო - იმერეთის კირქვიანები. მნიშვნელოვანია ის ფაქტი რომ დაცული ტერიტორიების დაგეგმარების დროს არაა გათვალისწინებული ცოცხალ ორგანიზმთა ყველაზე მრავალფეროვანი ჯგუფი - უხერხემლო ცხოველები. ნაჩვენებია, რომ ვიდრე ხერხემლიანები, უხერხემლო ცხოველები ხშირად უფრო ეფექტურ ინდიკატორებს (კოსისტემების ფუნქციონალური გამართულობის) და სუროგატებს (მრავალფეროვნების) წარმოადგენენ. ამ მხრივ ცხოველთა ერთერთი საუკეთესო ჯგუფი ხმელეთის მოლუსკები არიან (Moritz et al., 2001; Lovel et al., 2007). სადისერტაციო სამუშაოს ნაწილი მიეძღვნა მოლუსკების ფაუნის კონსერვაციის საკითხებს. კერძოდ მე-VI ნაშრომში განხილულია ორი საკითხი; პირველი, საქართველოს რომელი რეგიონებია კავკასიის და საქართველოს ენდემური მოლუსკებით ყველაზე მრავალფეროვანი და მეორე - რამდენად საკმარისია დღევანდელი დაცული ტერიტორიების ქსელი იმისათვის რომ უზრუნველყოფილი

იყოს ენდემური მალაკოფაუნის ცენტრების დაცვა. საქართველოში ბინადარი ხმელეთის ენდემური (ენდემურები როგორც კავკასიისათვის ასევე საქართველოსათვის ცალცალკე) მოლუსკების მრავალფეროვნების და გავრცელების (მეთოდური დეტალები იხ. თავი II და პუბლიკაცია VI) ანალიზმა აჩვენა რომ ენდემური მოლუსკების ფაუნა (55 საქართველოს ხოლო 110 კავკასიის ენდემური სახეობა) არასაკმარისადაა დაცული. კერძოდ ენდემური მრავალფეროვნების ცენტრების 70%-ზე მეტი დაცული ტერიტორიების გარეთაა. სახეობათა დიდი ნაწილს ფრაგმენტული და ვიწრო არეალი აქვთ და შესაბამისად წარმოადგენენ მაღალი რისკის სახეობებს თუ მათი არეალი არ ხვდება დაცული ტერიტორიების ფარგლბში (VI). სამწუხაროდ, საქართველოს წითელ ნუსხაში ერთი სახეობის გარდა არცერთი მოლუსკი არაა შეტანილი. არ არსებობს წითელ ნუსხაში შესული სახეობებისათვის აქტიური - პრაქტიკული კონსერვაციული ღონისძიებების პრაქტიკა, რაც კიდევ უფრო ამძიმებს ენდემური მოლუსკების კონსერვაციის პერსპექტივას.

ლიტერატურა

ლეჟავა, გ. 1973. ხმელეთის მოლუსკები. საქართველოს ცხოველტა სამყარო, ტომი IV. მეცნიერება, თბილისი.

ჯაველიძე, გ. 1941. მასალები საქართველოში გავრცელებულ ხმელეთის ლოკოკინების ფაუნისა და *Helix lucorum* var. taurica Kryn, ბიოლოგია - ეკოლოგიის შესწავლისათვის. სადისერტაციო ნაშრომი. თბილისი

Aubry, S., Labaune, C., Magnin, F., Roche, P., & Kiss, L. (2006). Active and passive dispersal of an invading land snail in Mediterranean France. Journal of Animal Ecology, 75(3), 802-813.

Azanza, B., Alberdi, M. T., & Prado, J. L. (2000). Large mammal turnover pulses correlated with latest Neogene glacial trends in the northwestern Mediterranean region. Geological Society, London, Special Publications,181(1), 161-170.

Barrington, D. S., & Paris, C. A. (2007). Refugia and migration in the Quaternary history of the New England flora. Rhodora, 109(940), 369-386.

Brown, K. M., Lang, B., & Perez, K. E. (2008). The conservation ecology of North American pleurocerid and hydrobiid gastropods. Journal of the North American Benthological Society, 27(2), 484-495.

Cameron, R. A. D., Mylonas, M., Triantis, K., Parmakelis, A., & Vardinoyannis, K. (2003). Land-snail diversity in a square kilometre of Cretan maquis: modest species richness, high density and local homogeneity. Journal of Molluscan Studies, 69(2), 93-99.

Caro, T. M., & O'Doherty, G. (1999). On the use of surrogate species in conservation biology. Conservation biology, 13(4), 805-814.

Chape, S., Harrison, J., Spalding, M., & Lysenko, I. (2005). Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. Philosophical Transactions of the Royal Society B: Biological Sciences, 360(1454), 443-455.

Chiba, S. (1999). Accelerated evolution of land snails Mandarina in the oceanic Bonin Islands: evidence from mitochondrial DNA sequences. Evolution, 460-471.

Cowie, R. H. (1995). Variation in species diversity and shell shape in Hawaiian land snails: in situ speciation and ecological relationships. Evolution, 1191-1202.

Davison, A. (2002). Land snails as a model to understand the role of history and selection in the origins of biodiversity. Population Ecology, 44(3), 0129-0136.

Denk T, Frotzler N, Davitashvili N. 2001. Vegetational patterns and distribution of relict taxa in humid temperate forests and wetlands of Georgia Transcaucasia. Biological Journal of the Linnean Society 72: 287–332.

Douris, V., Cameron, R. A., Rodakis, G. C., & Lecanidou, R. (1998). Mitochondrial Phylogeography of the Land Snail Albinaria in Crete: Long-Term Geolgoical and Short-Term Vicariance Effects. Evolution, 116-125.

Dubois de Montpereux F. 1839. Voyage autour du Caucase, chez Tcherkesses et les Abkhases, en Colchide, en Georgie, en Armenie et en Crimee. Paris. T. 2: 1-462.

Dubois de Montpereux F. 1840. Voyage autour du Caucase, chez Tcherkesses et les Abkhases, en Colchide, en Georgie, en Armenie et en Crimee. Paris. T. 4: 1-562.

Falkner, G., Ripken, T. E. J. & Falkner, M. 2002. Mollusques continentaux de France. Liste de référence annotée et bibliographie. Patrimoines naturels, Paris. (Publications Scientifiques du M.N.H.N.) : 350 pages.

Fehér, Z., Németh, L., Nicoară, A., & Szekeres, M. (2013). Molecular phylogeny of the land snail genus Alopia (Gastropoda: Clausiliidae) reveals multiple inversions of chirality. Zoological Journal of the Linnean Society,167(2), 259-272.

Gaston, K. J., Jackson, S. F., Cantú-Salazar, L., & Cruz-Piñón, G. (2008). The ecological performance of protected areas. Annual Review of Ecology, Evolution, and Systematics, 39, 93-113.

Ghobad-Nejhad, M., Hallenberg, N., Hyvönen, J., & Yurchenko, E. (2012). The Caucasian corticioid fungi: level of endemism, similarity, and possible contribution to European fungal diversity. Fungal Diversity, 52(1), 35-48.

Glaubrecht, M. (2009). On "Darwinian Mysteries" or Molluscs as Models in Evolutionary Biology: From Local Speciation to Global Radiation*. American Malacological Bulletin, 27(1/2), 3-23.

Graham, R. W., & Grimm, E. C. (1990). Effects of global climate change on the patterns of terrestrial biological communities. Trends in Ecology & Evolution,5(9), 289-292.

Habel, J. C., Drees, C., Schmitt, T., & Assmann, T. (2010). Review Refugial Areas and Postglacial Colonizations in the Western Palearctic. In Relict Species (pp. 189-197). Springer Berlin Heidelberg.

Hayes, T. M. (2006). Parks, people, and forest protection: an institutional assessment of the effectiveness of protected areas. World Development,34(12), 2064-2075.

Hayes, K. A., Cowie, R. H., Jørgensen, A., Schultheiß, R., Albrecht, C., & Thiengo, S. C. (2009). Molluscan Models in Evolutionary Biology: Apple Snails (Gastropoda: Ampullariidae) as a System for Addressing Fundamental Questions*. American Malacological Bulletin, 27(1/2), 47-58.

Hewitt, G. M. (1999). Postglacial recolonization of European biota. Biological Journal of the Linnean Society, 68(1-2), 87-112.

Heywood, V. H. (1995). Global biodiversity assessment. Cambridge University Press.

Holland, B. S., & Cowie, R. H. (2009). Land Snail Models in Island Biogeography: A Tale of Two Snails*. American Malacological Bulletin, 27(1/2), 59-68.

James, A. N., Gaston, K. J., & Balmford, A. (1999). Balancing the Earth's accounts. Nature, 401(6751), 323-324.

James, A., Gaston, K. J., & Balmford, A. (2001). Can we afford to conserve biodiversity?. BioScience, 51(1), 43-52.

Jansson, R. (2003) Global patterns in endemism explained by past climatic changes. Proceedings of the Royal Society B: Biological Sciences, 270, 583–590.

Kikvidze Z, Ohsawa M. 1999. Adjara, East Mediterranean refuge of Tertiary vegetation. In: Ohsawa M, Wildpret W, Arco MD, eds. Anaga Cloud Forest, a comparative study on evergreen broad-leaved forests and trees of the Canary Islands and Japan. Chiba: Chiba University Publications, 297–315.

Lomolino, M.V., Riddle, B.R., & Brown, J.H. (2006). Biogeography. Sunderland, MA: Sinaver

Lovell, S., Hamer, M., Slotow, R., & Herbert, D. (2007). Assessment of congruency across invertebrate taxa and taxonomic levels to identify potential surrogates. Biological Conservation, 139(1), 113-125.

Lubell, D. 2004. Prehistoric edible land snails in the circum-Mediterranean: the archaeological evidence. In: Petits animaux et sociétés humaines du complément alimentaire aux resources utilitaires (Eds. J.P. Brugal and J. Desse). Éditions APDCA, Antibes.

Lydeard, C., Cowie, R. H., Ponder, W. F., Bogan, A. E., Bouchet, P., Clark, S. A., ... & Thompson, F. G. (2004). The global decline of nonmarine mollusks.BioScience, 54(4), 321-330.

Mienis HK, Rittner O (2010) On the presence of Helix lucorum Linnaeus, 1758 (Mollusca, Gastropoda, Helicidae) in Le Vesinet, a western suburb of Paris. MalaCo 6:266–267

Milne RI, Abbott RJ. 2002. The origin and evolution of Tertiary relict floras. Advances in Botanical Research 38: 281–314.

Mittermeier, R. A., Gil, P. R., Hoffmann, M., Pilgrim, J., T BROOKS, C. M., LAMOREUX, J., & DA FONSECA, G. A. B. (2004). Hotspots Revisted: Earth's Biologically Wealthiest and most Threatened Ecosystems. CEMEX, México DF.

Moritz, C., Richardson, K.S., Ferrier, S., Monteith, G.B., Stanisic, J., Williams, S.E. & Whiffin, W. 2001. Biogeographic concordance and efficiency of taxon indicators for establishing conservation priority for a tropical rainforest biota. Proceedings of the Royal Society: B, 268: 1875–1881.

Myers, N. (1988). Threatened biotas:" hot spots" in tropical forests.Environmentalist, 8(3), 187-208.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. Nature, 403(6772), 853-858.

Peltanová, A., Petrusek, A., Kment, P., & Juřičková, L. (2012). A fast snail's pace: colonization of Central Europe by Mediterranean gastropods. Biological Invasions, 14(4), 759-764.

Petit, R. J., Aguinagalde, I., de Beaulieu, J. L., Bittkau, C., Brewer, S., Cheddadi, R., ... & Vendramin, G. G. (2003). Glacial refugia: hotspots but not melting pots of genetic diversity. Science, 300(5625), 1563-1565.

Pfenninger, M., Nowak, C., & Magnin, F. (2007). Intraspecific range dynamics and niche evolution in Candidula land snail species. Biological Journal of the Linnean Society, 90(2), 303-317.

Pimm, S. L., & Raven, P. (2000). Biodiversity: extinction by numbers. Nature,403(6772), 843-845.

Pokryszko, B., & Cameron, R. (2005). Estimating the species richness and composition of land mollusc communities: problems, consequences and practical advice. Journal of Conchology, 38, 529.

Riedel, A. (1966). Zonitidae (excl. Daudebardiinae) der Kaukasusländer (Gastropoda). Państwowe Wydawnictwo Naukowe.

Rissler, L. J., & Apodaca, J. J. (2007). Adding more ecology into species delimitation: ecological niche models and phylogeography help define cryptic species in the black salamander (Aneides flavipunctatus). Systematic Biology,56(6), 924-942.

Rögl, F. (1998). Palaeogeographic considerations for Mediterranean and Paratethys seaways (Oligocene to Miocene). Ann. Naturhist. Mus. Wien A, 99, 279-310.

Rögl, F. (1999). Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to Miocene paleogeography (short overview). Geologica carpathica,50(4), 339-349.

Schütt, H. (2005). Turkish land snails. Solingen: Verlag Natur & Wissenschaft.

Sommer, R. S., & Zachos, F. E. (2009). Fossil evidence and phylogeography of temperate species:'glacial refugia'and post-glacial recolonization. Journal of Biogeography, 36(11), 2013-2020.

Steininger, F. F., & Rögl, F. (1984). Paleogeography and palinspastic reconstruction of the Neogene of the Mediterranean and Paratethys. Geological Society, London, Special Publications, 17(1), 659-668.

Stork NE. 1999. Estimating the number of species on Earth. Pages. 1-7. in Ponder WF, Lunney D, eds. The Other 99%: The Conservation and Biodiversity of Invertebrates. Mosman (Australia): Royal Zoological Society of New South Wales.

Sysoev, A. V., & Schileyko, A. A. (2005). Stylommatophora. In: Y. I. Kantor, & A. V. Sysoev (Eds.), Catalogue of molluscs of Russia and adjacent countries pp 228-308. Moscow: KMK Scientific Press. [In Russian].

Tarkhnishvili, D. N., Gokhelashvili, R. K., IUCN/SSC Declining Amphibian Populations Task Force. Regional Group for the Commonwealth of Independent States, & Institut problem ėkologii i ėvoliutsii im. AN Severtsova. (1999). The amphibians of the Caucasus. Pensoft.

Tarkhnishvili, D., Hille, A., & BÖHME, W. (2001). Humid forest refugia, speciation and secondary introgression between evolutionary lineages: differentiation in a Near Eastern brown frog, Rana macrocnemis. Biological Journal of the Linnean Society, 74(2), 141-156.

Tarkhnishvili, D., U. Kaya, A. Gavashelishvili, and I. Serbinova. 2008. Ecological Divergence between ewo Evolutionary Lineages of the Caucasian Salamander: Evidence from the GIS analysis. Herpetological Journal 18: 155‑163.

Tarkhnishvili, D., Serbinova, I., & Gavashelishvili, A. (2009). Modelling the range of Syrian spadefoot toad (Pelobates syriacus) with combination of GIS-based approaches. Amphibia-Reptilia, 30(3), 401-412.

Tarkhnishvili, D. N., R. S. Thorpe, and J. W. Artnzen. 2000. Pre-Pleistocene refugia and differentiation between populations of the Caucasian salamander (Mertensiella caucasica). Molecular Phylogenetics and Evolution 14: 414‑422.

Thompson, J.D. (2005) Plant evolution in the Mediterranean. Oxford University Press, Oxford.

Van Andel, T. H., & Tzedakis, P. C. (1996). Palaeolithic landscapes of Europe and environs, 150,000-25,000 years ago: an overview. Quaternary Science Reviews, 15(5), 481-500.

van Bruggen AC. 1995. Biodiversity of Mollusca: Time for a new approach. Pages. 1-19. in van Bruggen AC, Wells SM, Kemperman TCM, eds. Biodiversity and Conservation of the Mollusca. Oegstgeest-Leiden (The Netherlands): Backhuys.

Velichko AA, Kurenkova AA. 1990. Landscapes of the Northern Hemisphere during the Late Glacial Maximum. In: Soffer O, Gamble G, eds. The World at 18 000 BP. London: Unwin Hyman, 255–265.

Vitousek, P. M., D'Antonio, C. M., Loope, L. L., Rejmanek, M., & Westbrooks, R. (1997)a. Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology, 21(1), 1-16.

Vitousek, P. M., Mooney, H. A., Lubchenco, J., & Melillo, J. M. (1997)b. Human domination of Earth's ecosystems. Science, 277(5325), 494-499.

Welch, J.M. & Pollard.E., 1977. Review of current literature on the ecology and exploitations of the edible snail Helix pomatia. Malcological Review. 10, 1-6.

Wiktor, A. (2000). Agriolimacidae (Gastropoda: Pulmonata) a systematic monograph. Ann. zool. Warszawa, 49(3), 347-590.

Winston, J. E. (1999). Describing species: practical taxonomic procedure for biologists. Columbia University Press.

Zazanashvili, N., Sanadiradze, G. & Bukhnikashvili, A. 1999. Caucasus. In R.A. Mittermeier, N. Myers & C. Goettsch Mittermeier. (Eds.), *Hotspots – Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions*. Mexico City: CEMEX and Conservation International.

Лихарев, И.М., Виктор А.Й. Слизни фауны СССР и сопредельных стран (Gastropoda terrestria nuda) // Фауна СССР. – Т.3, вып.5. Нов. сер., № 122. – Л.: Наука, 1980. – 438 с.

Лихарев, И.М. Клаузилииды (Clausiliidae) // Фауна СССР. Моллюски. – Т.3, вып.4. Нов. сер., № 83. – М.-Л.: Наука, 1962. – 317 с

Лихарев, И. М., & Раммельмейер, Е. С. (1952). Наземные моллюски фауны СССР. Определители по фауне СССР, 43, 1-511.

Шилейко, А. А. (1978) Наземные моллюски надсемейства Helicoidea.Фауна СССР. Моллюски. – Т. 3, вып. 6. – Нов. сер. № 117. – Л.: Наука, 1978. – 384 с.

Шилейко, А.А. (1984) Наземные моллюски подотряда Pupillina фауны СССР (Gastropoda, Pulmonata, Geophila). Фауна СССР. № 130. Моллюски. Л.: Наука. Ленингр. Т. 3, вып. 3. 400 с.

დისერტაციის ფარგლებში მომზადებული პუბლიკაციები

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A NEW SPECIES OF THE GENUS *HELIX* FROM THE LESSER CAUCASUS (SW GEORGIA)

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Abstract Helix goderdziana *sp. nov. is described from the Lesser Caucasus, south-western Georgia. Its habitat is a humid montane forest. This is the largest species of* Helix *known so far.*

Key words *Land snails, Lesser Caucasus,* Helix, *new species.*

INTRODUCTION

The genus *Helix* Linnaeus, 1758 includes the largest snails of the family Helicidae, and probably the largest terrestrial pulmonates in western Eurasia. It is distributed in northern Africa and Eurasia. Three species of *Helix* have been so far recorded from Georgia: *H. lucorum* (Linnaeus, 1758) and *H. vulgaris* (Rossmässler, 1839), both widely distributed in western Eurasia, and *H. buchi* (L. Pfeiffer, 1853) which is endemic to the western part of the Caucasus Ecoregion sensu Mittermeier *et al*. (2004). A further five species are known from Asia Minor, the region southwest of the southern Caucasus: *H. figulina* (Ross, 1839), *H. pericalla* (Kobelt et Rolle, 1896), *H. cheikliensis* (Zilch, 1952), *H. cincta* (Muller, 1774), and *H. pomatia* (Linnaeus, 1758) (Schütt, 2001; http://www.biolib.cz/en/taxon/id269332); none of those, however, have been recorded from the north-eastern part of Turkey adjacent to Georgia.

Three very large helicid snails were collected on June 25th, 2006 by two of the authors (LM and DT) in south-western Georgia, at an elevation of between 1540 and 1595 m. a.s.l. (Fig. 1). *Helix buchi* or other known Caucasian representatives of the genus have never been recorded from this area. Our specimens differ from all other large members of the genus found in the Caucasus and Asia Minor and represent a new species which we describe below.

Helix goderdziana sp. nov. (Figs 2-4)

Holotype 1 shell (n10), Zoological Research Institute (ZRI), Tbilisi, Georgia.

Paratypes 2 specimens: subadult shell (n8) and shell + soft parts (n9): Zoological Research Institute (ZRI), Tbilisi, Georgia.

Type locality South-Western Georgia, just east of the Goderdzi Pass (see Fig. 1, 41°39’N, 42°36’E), the junction of the Meskheti and Shavsheti Ranges, basin of the Dzindzisu River (left tributary of the Mtkvari-Kura River).

Derivation of name The new species is named for its type locality - Goderdzi Pass.

Diagnosis Shell larger than in any other species of the genus *Helix*, somewhat similar to that of *Helix buchi* from which it differs in a taller shell (61 mm compared to at most 54 mm in *H. buchi*; Likharev & Rammelmeier, 1952) and light yellowish-brown foot (dark grey to almost black in *H. buchi*). Digitiform glands shorter than any other *Helix* from the Caucasus Region. Flagellum much longer than in

Fig. 1 Map showing the type locality of *Helix goderdziana* sp. nov.

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Fig. 2 From left to right: shells of *Helix goderdziana* sp. nov., holotype (ZRI n0010); paratype (ZRI n0009); *Helix buchi* from Borjomi Gorge, central Georgia (ZRI b0025); *Helix lucorum*, Tbilisi, Georgia (ZRI l0004).

Fig. 3 Left – live *Helix buchi*, right – live *Helix goderdziana* sp. nov. (paratype n0009)

Table 1 Shell measurements of the holotype and two paratypes of *Helix goderdziana* sp. nov. (all measurements in mm)

Specimen #	Shell height	Shell width	Aperture height	Aperture width
Holotype n0010	61	60	40	34
Paratype n0009	57	60	40	33
Paratype n0008 (subadult)	47	50	36	30

Fig. 4 *Helix goderdziana* sp. nov. genitalia (paratype n0009): left - full view, right - penial papilla.

H. buchi. Penial papilla larger than in *H. buchi*, spindle-shaped (for reproductive organs of *H. buchi* and other *Helix* species see Schileyko 1978).

Description Shell (Fig. 2), conic-globular, with 4.5 rapidly increasing whorls 1.5 of which form embryonic shell; apex blunt, conical; shell unevenly radially ribbed, sculpture similar to that of *Helix buchi*. Body whorl very wide, slightly descending. Aperture very large (height 40 mm, width 34 mm), short oval, oblique, resembling that of *H. buchi* but different from that of other *Helix* species of the region. Shell height up to 61 mm, shell width up to 60 mm (for measurements of the types see Table 1). Foot light yellowish-brown (Fig. 3). Penial papilla large, spindle-shaped. Flagellum 2.4 times as long as penis with epiphallus. Spermatheca diverticulum 1.75 times shorter than the section of the spermatheca duct beyond the bifurcation point (Fig. 4).

Ecology The macrohabitat is a montane spruce forest (dominant tree *Picea orientalis*), on the southern slopes of the Meskheti Mountain Range and the north-eastern slopes of the Shavsheti Mountain Range. It is a humid area, with the annual precipitation of ca 1200-1400 mm (Vladimirov *et al*., 1991). The microhabitat is a very damp vicinity of small montane brooks, mostly surrounded by alder trees (*Alnus barbata*), with logs and liverworts on the margins of the brooks (Fig.5). The snail is found in habitats different from those of *Helix buchi*: the latter species is found exclusively in broadleaf, mostly beach forests, away from from streams or brooks (Skarlato & Starobogatov, 1984).

Fig. 5 Type locality of *Helix goderdziana* sp. nov. habitat

ACKNOWLEDGEMENTS

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REFERENCES

LIKHAREV IM & RAMMELMEIER ES 1952 *Nazemnye Mollyuski Fauny SSSR* [Terrestrial Mollusks of the USSR Fauna]. USSR Acad. Sci. Publications 43, Moskva-Leningrad.

MITTERMAIER RA, GIL PG, HOFFMANN M, PILGRIM J, BROOKS T, MITTERMAIER CG, LAMOREUX J & DA FONSECA GAB 2004 *Hotspots Revisited: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions*. CEMEX/Agrupacion Sierra Madre, Mexico City. Toppan Printing Co., Japan.

PFEIFFER L 1853 *Monographia Helicorum Vivientum*. Vol. III. F. A. Brockhaus, Lipsiae.

SCHILEYKO AA 1978 *Nazemnye mollyuski nademeystva Helicoidea*. *Fauna USSR* 3 (6). Nauka, Leningrad.

SCHÜTT H 2001 Die Türkische Landschnechen 1758-2000. *Acta Biologica Benrodis* **Suppl. 4**: 1-550.

SKARLATO OA & STAROBOGATOV JI 1984. V*inogradnaya ulitka Bucha* [Buch's snail]. P. 369 In: Red Data Book of the USSR. Lesnaya Promyshlennost', Moscow.

VLADIMIROV LA, GIGINEISHVILI GN, DJAVAKHISHVILI AI, & ZAKHARASHVILI NN 1991 *Water balance of Caucasus and its geographic conformity to natural laws*. Tbilisi, Metsniereba, Tbilisi.

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Forest snail faunas from Georgian Transcaucasia: patterns of diversity in a Pleistocene refugium

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Thirty forest sites in Georgia were sampled to obtain inventories of their land snail faunas. The sites, in nine sampling areas, ranged from Batumi near the Turkish border to Lagodekhi near the Azerbaijan border, and included parts of both the Lesser and Greater Caucasus mountains and the Colchic lowlands. Abundance was generally low, and most sites held less than 20 species. Ninety species were found overall. Although sites within some sampling areas had very similar faunas, the overall levels of similarity among sites and sampling areas was low, especially when compared with similar forests from northern central Europe. Both climate and geographical position affected similarity: although these were correlated, independent effects of each were detected, and the effect of position alone was strongest. Despite this effect, most species have ranges extending into Turkey or Ciscaucasia, a few have very limited ranges, and there is no evidence of patterns of allopatric replacement among congeners. These patterns resemble those seen in faunas from forests in lower latitudes, and suggest a slow build-up of regional diversity by differentiation *in situ*, without the repeated restrictions to a multiplicity of small refugia that are characteristic of areas where fluctuations in aridity are important. The refugium has remained isolated, and has contributed little to the Holocene recolonization of areas further north. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, **102**, 239–250.

ADDITIONAL KEYWORDS: distance decay – land molluscs – species richness.

INTRODUCTION

Land snail faunas in Europe show a characteristic latitudinal gradient in regional richness that can be related to Pleistocene climatic fluctuations, and in particular to the glaciated or periglacial conditions prevailing north of the main mountain ranges at glacial maxima (Hausdorf & Hennig, 2003; Cameron, 2004; Cameron, Pokryszko & Horsák, 2010). Forest faunas in the north are essentially immigrant assemblages, with subsets and mixtures of faunas surviving in refuges further south. In Mediterranean and Balkan Europe, high diversity is associated with a multiplicity of small refuges; vicariance and short-distance dispersal across barriers promotes differentiation among congeners. Such differentiation is, however, most evident in open but calcareous habitats, and the structure of regional diversity seems to relate mainly to fluctuations in aridity, sea level, and the periodic isolation of montane and alpine habitats (Cameron *et al*., 2003). Within forest faunas, species richness at the level of small sites, termed alpha diversity by many authors (Magurran, 2004), does not vary greatly with latitude (Pokryszko & Cameron, 2005).

These patterns can be contrasted with some of those at lower or similar latitudes elsewhere, where although area and connectivity of forests varied, substantial areas of forest habitats remained within the region. Here, although there is evidence for speciation

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*Corresponding author. E-mail: r.cameron@sheffield.ac.uk as a result of the isolation of fragments of suitable habitats, regional diversity seems to have built up from isolation by distance alone (Solem, 1984; Barker, 2005): very few species have tightly restricted geographical ranges, and congeneric ranges overlap at the regional level. Local site diversities vary, but most are not much greater than those recorded for the immigrant faunas of northern European forests (Seddon *et al*., 2005; Stanisic *et al*., 2007). This runs counter to the general trend for site diversities of many organisms to be much greater at lower latitudes, other than in deserts (Ricklefs, 2004). Clearly, the balance and structure of local and regional diversity varies with the history of the regions concerned, and this raises questions about the assembly rules for local faunas.

For snails, these global comparisons are made less telling by the different spectra of taxonomic composition, size, and shape distribution, and known trophic status of snails between biogeographic realms (Cameron *et al*., 2005). Although the snail fauna of western Transcaucasia, including the extreme northeast of Turkey, contains many endemic species and genera (Schütt, 2005; Sysoev & Schileyko, 2009), the taxonomic composition of the forest snail fauna at family level and above is characteristically Western Palaearctic. The region is known to be one of the few places in the Western Palaearctic to have retained mixed broadleaf forests in large quantities throughout the Pleistocene, in either a single large refugium spreading along the south-eastern Black Sea Coast (van Andel & Tzedakis, 1996) or in multiple large and small refuges (Velichko & Kurenkova, 1990). Its flora is regarded as belonging to the broad Euro-Siberian assemblage, rather than to those of the Mediterranean or Irano-Turanian regions (Davis, 1971; Tumajanov, 1971). Although there were certainly shifts in climate sufficient to alter the altitudinal limits of some forest types by up to 1000 m (Tarasov *et al*., 2000), the combination of high mountains and exposure to warm and humid winds across the Black Sea evidently moderated the extremes of cold or aridity that characterized most of the region at glacial maxima (Denk, Frotzler & Davitashvili, 2001, and references therein). Areas to the north (Ciscaucasia), east, and south were, as now, dominated by arid conditions, with steppe vegetation predominating.

We report here on a survey of forest snail faunas in sites within refugial parts of the Caucasus, where forests persisted for millions rather than a few tens of thousands of years, along with others where most of the forests were likely to have been replaced by steppe at glacial maxima. We compare the patterns of richness and diversity found with those recorded elsewhere, and in particular with those from Poland and Transcarpathian Ukraine, typical of faunas established by northwards migration in the Holocene (Cameron, Pokryszko & Horsák, 2010). This gives us a deeper insight into the processes of the formation of the contemporary forest snail faunas and, more generally, to the dynamics of the refugial forests of the Caucasus ecoregion.

THE REGION AND SAMPLING SITES

Figure 1 shows the region, and the location of clusters of sampling sites (hereafter SA, sampling area) within it. Samples were made from just south of Batumi near the Turkish border in the west to Lagodekhi near the Azerbaijan border in the east. Denk *et al*. (2001) gave a detailed account of the region and of the types of forest flora to be found within it. Our SAs are mostly near named localities of their account. The region has sharp west-to-east gradients in rainfall, and in the contrast between summer and winter temperatures. Areas near Batumi have a very oceanic climate: January mean temperatures are above 0 °C, and rainfall in the mountains nearby can exceed 4000 mm year^{-1}. Further east the climate is more continental, with rainfall generally being in the range 760–2000 mm year^{-1}, and winters are colder. Natural forest cover is mainly of broad-leaved deciduous trees, principally beech, *Fagus orientalis*, and chestnut, *Castanea sativa*, with conifers, *Abies nordmanianna* and *Picea orientalis*, at higher altitudes, and with locally abundant alders, *Alnus barbata*, ash, *Fraxinus excelsior*, hornbeams, *Carpinus caucasica* and *Carpinus orientalis*, maples, *Acer* species, and elm, *Ulmus glabra*. Within each SA, sites were chosen to maximize the probability of obtaining a representative fauna, moderated by accessibility in difficult terrain. Details of location and descriptions are given in Appendix S1. Most accessible forests are subject to management resulting in near monocultures, and the combination of management, very steep slopes, and heavy rainfall over mainly acidic rocks (typically andesite volcanics) results in large areas in which land snail faunas are impoverished both in density and species richness. Typically, our sites were on less steep slopes with streams or run-off channels, with a greater than normal diversity in tree species. Although such sites have undoubtedly been subject to human disturbance (the presence of walnut *Juglans regia* being an indicator; Tumajanov, 1971), the presence of alders *Alnus barbata*, maples *Acer* species, and ash *Fraxinus excelsior* indicate soils with higher moisture and base status than those on the very steep and frequently unstable slopes around. Sites in the south-west (Batumi, Kintrisi, and Mtirala) frequently had *Rhododendron ponticum* as a dominant species in the understory: this species is missing in the easternmost parts of our survey area

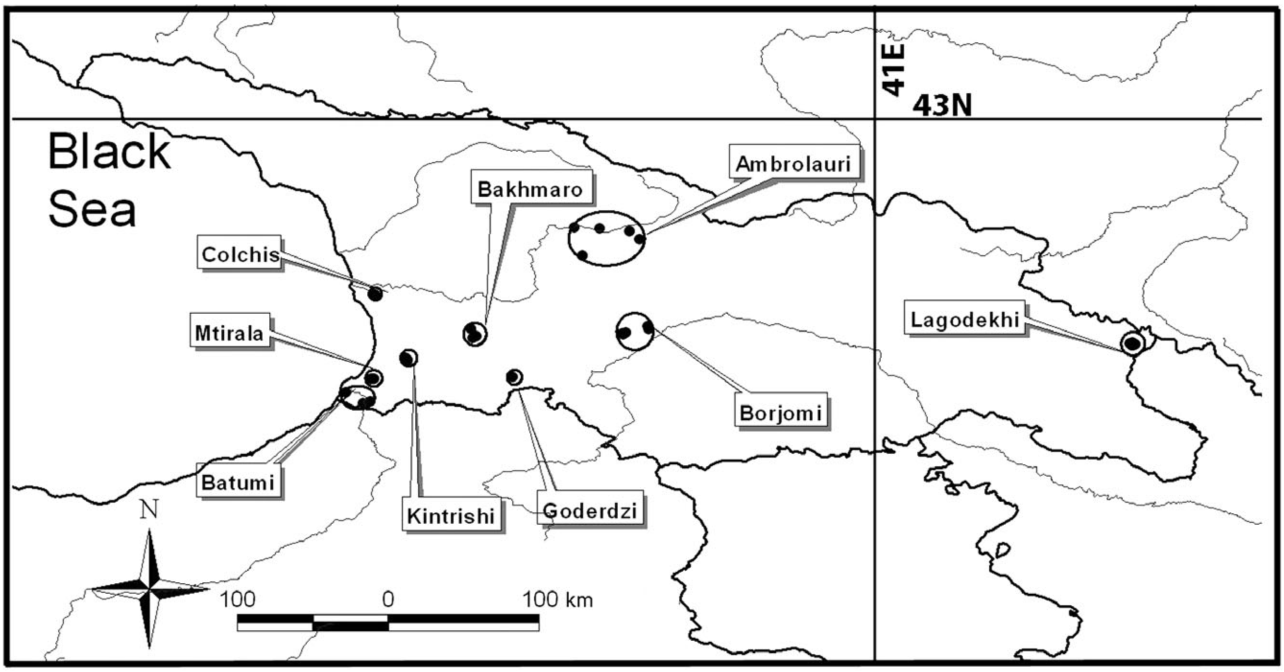

Figure 1. Map of the western Caucasus with sampling sites: black dots, sampling sites (as listed in Appendix S1); ellipses unify the sites into nine larger study areas (SAs).

(Tumajanov, 1971). One site at Ambrolauri (A1) was subject to much heavier and more destructive human disturbance than the remainder, a product of grazing by cattle. Only the sites at Ambrolauri (Fig. 1) had limestone as the underlying rock. Here, and at the Goderdzi Pass and at Bakhmaro, a few sites were sampled at elevations above 1400 m; the remainder were all below 1100 m. The Colchis site is unique in lying in swampy ground in the Colchic lowlands between the Lesser and Greater Caucasus.

MATERIAL AND METHODS

Sampling and identification

At each site, snails from an area of *c*. 400 m^2 were collected by hand in 5 person hours of searching; in addition, about 20 litres of litter was collected and sieved through 8-mm mesh sieves (Cameron & Pokryszko, 2005). Larger specimens were removed from the sieve, and material passing through the sieve was bagged, dried, and then sorted in the laboratory. Slugs (collected by hand in the field) were preserved separately, but, as in other studies (Cameron & Pokryszko, 2005), this method is not appropriate for obtaining a full inventory. Slug species found (identified by A. Wiktor) are listed by site in Appendix S2, but are excluded from our analyses. At each site location and altitude were determined by GPS (with the exception of sites at Batumi; see Appendix S1), and the dominance and occurrence of tree and understory shrubs were noted, as was the slope. Details are given in Appendix S1.

All living and empty but fresh shells were identified to species level as far as possible. Very eroded shells and unidentifiable juveniles are excluded from Appendix S2. Likharev (1962), Riedel (1966), Schileyko (1975, 1978, 1984), and Schütt (2005) were the principal sources for identification, supplemented by A. Riedel's collections of Zonitidae *s.l.* and others in the Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw. Nomenclature generally follows that of Sysoev & Schileyko (2009); authorities and deviations from their list are given in Appendix S2. In some cases our records mark a significant extension of geographical range, and a few species are not mentioned in their checklist. Voucher specimens are deposited in the Museum of Natural History, Wrocław, and in the Institute of Ecology, Ilia State University, Tbilisi.

Analyses and comparative data

Sampling efficiency (the completeness of inventories at each site) was assessed by using the Chao 1 estimator of missing species (Southwood & Henderson, 2000), as this appears to be one of the most reliable estimators (Walther & Moore, 2005). As standard errors of this estimator are very large when the number of singletons and doubletons are small, we have used the median value as an overall estimator (Cameron, Pokryszko & Long, 2006).

Several statistical approaches were used for estimating the overall site-specific species richness, the level of differentiation between the sites, and for associating these variables with geography and climate. The overall pattern in faunas was first exposed by detrended correspondence analysis (DCA), using log-transformed abundances, and without down-weighting rare species (Leps & Smilauer, 2003). In order to describe the climates of the individual sites, bioclimatic data from WorldClim v1.4 (http://www.worldclim.org/) was used. This is a set of 19 global climate layers (bioclimate grids, including means and yearly dynamics of temperature and precipitation) with a spatial resolution of 1 km^2 (Hijmans *et al.*, 2005). For all locations studied, the values of the bioclimatic variables were scored using ARCVIEW v.3.3 GIS software, and standardized in a way making the mean of each variable equal to zero and the standard deviation equal to unity. Two runs of canonical correspondence analysis (CCA; Manel *et al.*, 2003) were applied in order to detect association of faunas/species with: (1) climate and (2) geography. For individual species, the tolerance indexes inferred from CCA analyses were scored to estimate the species-specific breadth of climatic niche and extent of occurrence of a species. This was to identify the species for which distribution is directly limited by geography rather than by climate (i.e. the species positioned above the regression line connecting climatic and geographic tolerance), and those in which distribution is limited by climate rather than by geography (the species positioned below the regression line). The software used for DCA and CCA was CANOCO v4.5 (ter Braak & Smilauer, 2002).

'Climatic distances' between the sites were calculated as Euclidean distances based on the 19 standardized bioclimatic variables and geographic distances: i.e. as Euclidean distances based on the exact latitude and longitude of a site. Partial Mantel tests (Manly, 1997) were applied to test for the significance of association of faunal differences (estimated as the inverse value of Simpson's similarity indexes, 100-SI) with geographic distances and climatic differences between the sampling sites. The Simpson index of similarity is the proportion of species in common with those in the least rich of any pair, diminishing the effect of mere impoverishment or inadequate sampling. The significance of the relationship was estimated for the Mantel tests with 10 000 permutations, using IBD software (Bohonak, 2002).

Some direct comparisons were made with data from Polish and Transcarpathian Ukrainian forest sites sampled in the same way (Cameron, Pokryszko & Horsák, 2010). Many of the latter samples contained more individuals than found in any of those reported here. To reduce the effect of differing median sample sizes, comparisons are limited to samples from Poland and Transcarpathian Ukraine containing no more than the maximum number recorded here (530). There are 100 of these, spread unevenly over the whole region involved.

RESULTS

SITE SPECIES RICHNESS, SAMPLING ERROR, AND FREQUENCY OF OCCURRENCE

Ninety species of snail represented by 6993 individuals were found in 30 samples. Appendix S3 lists the numbers of each species found at each site. The basic statistics for the faunas are shown by SA in Table 1. In general, the numbers of individuals were smaller than those found (by comparable means) in Central European or British forests, and in nine cases they fall below the recommended minimum requirement of

Table 1. Basic data

SA	Sites	Mean numbers	Range numbers	Mean species	Range species	Total species	Unique species
Colchis	1	251	–	20	–	20	3
Batumi	3	117	85–140	14	12–16	25	4
Mtirala	3	309	67–449	16.2	13–19	24	2
Kintrisi	3	186	148–206	16.3	14–19	24	2
Bakhmaro	3	150	60–247	15.3	12–20	28	0
Goderdzi	1	151	–	17	–	17	2
Borjomi	5	251	78–385	16.5	14–21	29	2
Ambrolauri	5	283	170–530	18.2	13–21	52 (42)	20 (10)
Lagodekhi	6	272	167–417	12.7	8–16	25 (24)	6 (5)
TOTAL	30	233	60–530	15.9	8–21	90 (80)	

Figures in brackets represent totals after removal of subalpine and anthropochorous species (see text).

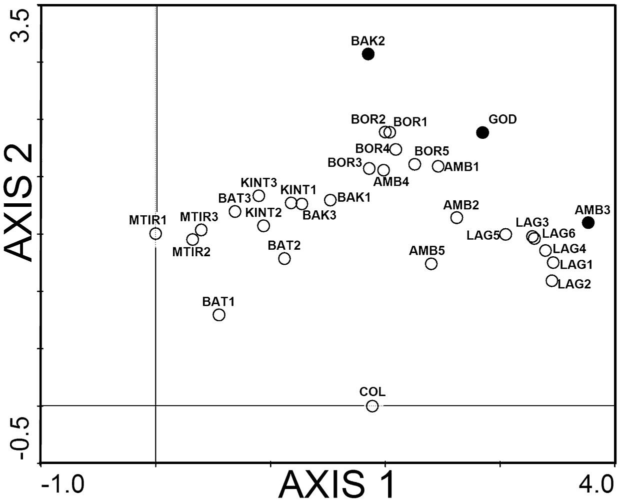

Figure 2. Positions of sites on a detrended correspondence analysis biplot: BAT, Batumi; MTIR, Mtirala; KINT, Kintrishi; COL, Colchis; BAK, Bakhmaro; GOD, Goderdzi; BOR, Borjomi; AMB, Ambrolauri; LAG, Lagodekhi; ●, BAK 2, GOD, and AMB 3, sites above 1400 m a.s.l.; AMB 1, disturbed site.

ten times as many individuals as species (Cameron & Pokryszko, 2005). Eight species are represented in the whole array by single individuals, 29 species (about one-third of the total species number) were recorded from a single SA, and 22 of those from a single site. There is a positive correlation between numbers of individuals and numbers of species ($R = 0.425$, $P < 0.05$), suggesting that species have been missed in some samples. The Chao 1 estimator of missing species gives widely varying estimates among samples (data not shown), but these do not correlate with the number of individuals per sample (Spearman's R on ranks, 0.165). The estimates are not normally distributed, with a few high values, but the median estimate is 1.1 missing species per site.

ECOLOGICAL DIFFERENTIATION AND CASUAL SPECIES

The favourable combination of mixed dominants among trees and gentle slopes has a significant effect on the number of individuals found (Spearman's R on ranks, 0.41, $P < 0.05$) (Appendix S1). Species richness, however, shows no significant association with any single environmental factor recorded at the site, nor with any combination of two or more factors regarded as favourable or the reverse on evidence from other studies. DCA analysis (Fig. 2) indicates the separation of faunas representing different longitudes (axis 1) and elevations (axis 2). Sites within the same study area tend to cluster together along both axes.

Table 2. Species found at Ambrolauri excluded from analyses of faunal similarity and distance decay

Species	Distribution	Habitat
Truncatellina cylindrica	Widespread	Open
*Poiretia mingrelica**	Transcaucasian	Generalist
*Xeropicta derbentina**	Widespread	Open
Phenacolimax annularis	Widespread	Alpine
Vitrina pellucida	Widespread	Here Alpine
*Paralaoma servilis**	Very widespread	Generalist
Sphyradium doliolum	Widespread	Here Alpine
*Zebrina detrita**	Widespread	Open
Pupilla triplicata	Widespread	Alpine
Vallonia pulchella	Widespread	Open

*Species associated with human activity.

It is evident (Table 1) that the aggregate fauna of Ambrolauri sites is far greater than those of other clusters containing more than one sample. This cluster also contains far more unique species than any other. Sites there include the highest and the most disturbed in the whole array. Table 2 lists species recorded uniquely in Ambrolauri that, on external evidence, are either characteristic of the subalpine zone (here recorded only in Ambrolauri 3) or are more typical of open habitats, and may be present as a result of grazing disturbance. These species have been eliminated from the analyses of faunal differentiation and distance decay, as has *Truncatellina strobeli* from Lagodekhi, represented by a single empty shell, which was possibly a product of flood transport. None are restricted endemics. Even with these eliminations, the aggregate fauna of Ambrolauri samples is richer than those from elsewhere. However, the span of distances within the Ambrolauri SA is similar to that for all Batumi, Kintrisi, and Mtirala samples combined. These have 41 species recorded compared with 42 within Ambrolauri.

FAUNAL SIMILARITIES AND THEIR DEPENDENCE ON GEOGRAPHY AND CLIMATE

All pairwise values of the Simpson index of similarity among sites are shown in Appendix S4. The faunas are strongly differentiated, and in four cases there are no species in common between pairs. Table 3 shows the mean values of the index in site-by-site comparisons within and among SAs. Although the numbers used in comparisons are limited, it is evident that the SAs at Mtirala, Kintrisi, Borjomi, and Lagodekhi are coherent, with much higher mean within-SA values in comparison with others. The single isolated sites at

Table 3. Mean values (%) of the Simpson index of similarity in site-by-site comparisons

	Col	Bat	Mti	Kin	Bak	God	Bor	Amb	Lag
Colchis	–	52.1	35.0	42.6	28.2	29.4	34.9	36.2	34.5
Batumi		**58.3**	56.1	53.7	41.1	16.6	39.0	30.2	27.8
Mtirala			**81.9**	50.5	40.1	16.9	34.0	32.5	16.0
Kintrisi				**81.8**	54.4	23.6	50.4	41.0	35.7
Bakhmaro					**59.8**	39.9	53.9	37.7	32.6
Goderdzi						–	44.0	36.2	20.9
Borjomi							**72.8**	49.6	39.4
Ambrolauri								**47.7**	38.4
Lagodekhi									**79.7**

Within-cluster values are given in bold; these values are not available for Colchis and Goderdzi, each represented by only one sample.

Table 4. Association of faunal dissimilarity between the sites (100 – Simpson's similarity index as a dependent variable) with geographic distance (Geodis) and distance based on the 19 normalized bioclimate variables (climdis) (independent variables): the output of partial Mantel tests

Independent variable	r	$P <$
Geodis	0.505694	0.0001
Climdis	0.350407	0.0001
Climdis controlled for Geodis	0.219106	0.0073
Geodis controlled for Climdis	0.438499	0.0001

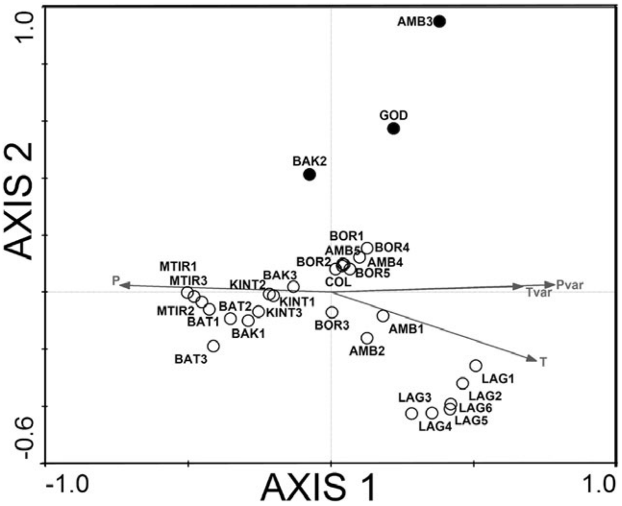

Figure 3. Ordination of the sites along the two canonical correspondence analysis axes determined by correlation between species abundances and standardized bioclimate variables. The four displayed bioclimatic variables are: T, mean annual temperature; T_{var}, temperature seasonality (standard deviation); P, annual precipitation; P_{var}, precipitation seasonality (coefficient of variation). The sites in the east are drier and more continental, but are warmer (in particular for Lagodekhi) than sites in south-west Georgia.

Colchis and Goderdzi are similarly well differentiated from the others, but for Bakhmaro, Batumi, and Ambrolauri, with the greatest range of altitude, habitat, and distance between sites, the within-SA values are lower: in the case of Ambrolauri it is exceeded in the comparison with Borjomi; the effects of disturbance and altitudinal range, as well as limestone substrate may be significant here. There is an apparent geographical structure in differentiation among SAs, seen most clearly in the low levels of similarity between Lagodekhi, the most isolated by distance, and all others, and by the coherence of the three adjacent SAs in the south-west, Batumi, Mtirala, and Kintrisi. Partial Mantel tests (Table 4) show that this structure depends both on the climatic differences and geographic distances between the sites. Importantly, climatic differences between the sites influence the differences in species composition, even if controlled for the geographic distances and *vice versa*.

The CCA based on the (log-transformed) species abundances, on the one hand, and geographic coordinates, on the other, shows an ordination of the sites reflecting a geographic pattern that does not differ much from the DCA output (results not shown). CCA based on the species abundances versus values of climatic variables showed a rather similar pattern (Fig. 3): although the first CCA axis reflected, to some extent, the eastern–western geographic gradient, the second axis separated the locations from different altitudes rather than those with different geography. There was significant ($P < 0.001$) correlation between species-specific geographic and climatic tolerances inferred from the CCA (Fig. 4). Twenty-two species showed climatic tolerances above the upper significance level ($P = 0.001$) of the regression line, indicating a more restricted geographical distribution than expected, and ten species had climatic tolerances

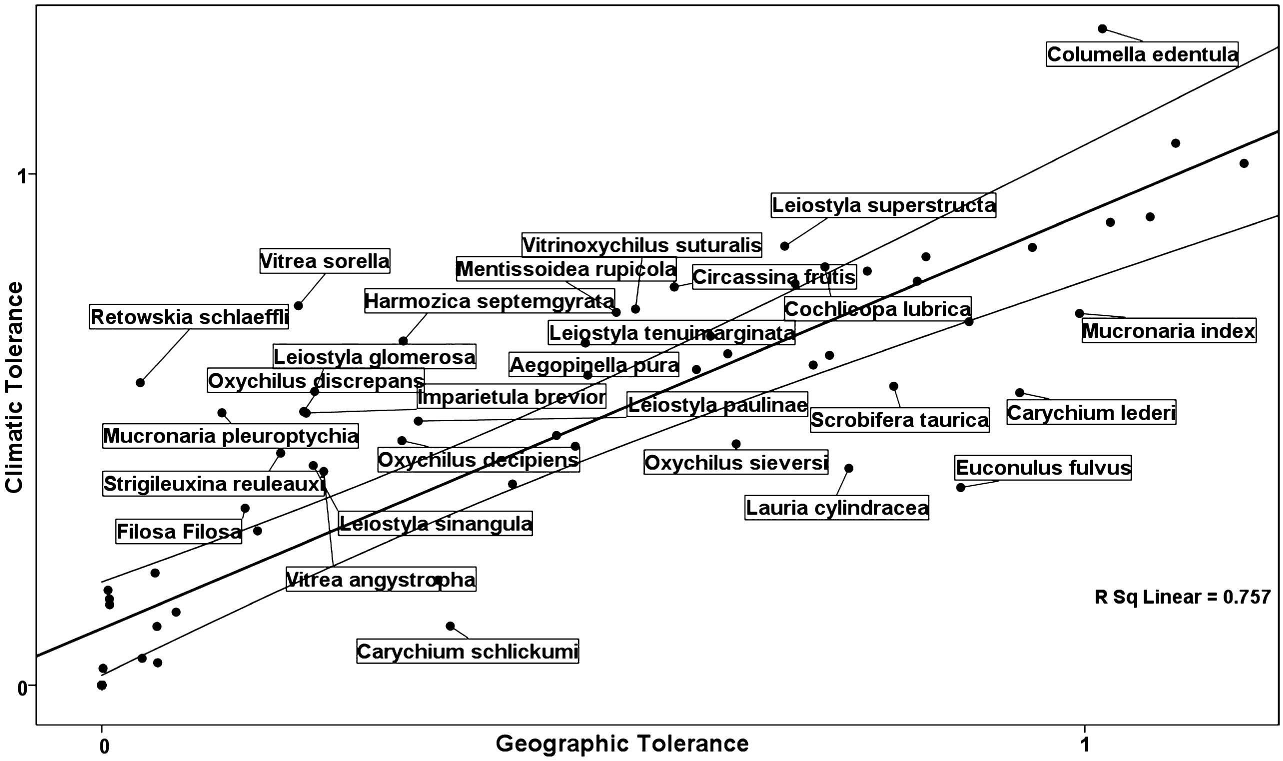

Figure 4. Regression line with $P = 0.001$ confidence limits, connecting species-specific 'geographic tolerance' (extent of occurrence of a species) and climatic tolerance. Species found at a single site (i.e. with zero tolerances) are not shown. Only names of the species that lie significantly above or below the regression line are shown.

below the lower significance level of the line, indicating a narrower climatic tolerance than expected from geographical range. It should be noted that some species were present in only two or three sites: it is the general trend rather than the precise position of each species that is meaningful. Of the 22 species apparently restricted by geography within our samples, 18 (86%) are also known from Turkey (see below), and three are widespread throughout the western Palaearctic.

Distance decay and biogeographical relationships

Analysis of the broader biogeographical pattern is hampered by the low intensity of previous sampling in the region. Many species are known only from scattered localities, and it would be premature to assume that all geographical ranges are adequately known. Several of our records (detailed in Appendix S2) represent significant range extensions. There are also some taxonomic uncertainties. Nevertheless, the extent to which differences among SAs are determined by limited geographical ranges can be examined by comparing the numbers and proportions of species known outside the area encompassed by our samples (Table 5). Nearly two-thirds (58) of all species recorded here are also known from Turkey. Thirty-one of these species recorded in Turkey are also known from Europe and/or Ciscaucasia: these include most of the anthropochoric and subalpine species. Only eight species not found in Turkey are previously recorded as confined to either the Lesser or Greater Caucasus, and two of these were found by us in a previously unrecorded range. The proportion of species also found in Turkey does not vary consistently or significantly with distance among groups of our samples, although it is slightly smaller in the Greater Caucasus than elsewhere (Table 5). Further evidence that actual ranges are not very restricted comes from considering the known distribution of the species found by us in only one cluster (Table 5). The proportion of such species also occurring in Turkey is lower, but is little different from that seen in the fauna as a whole.

Of the six species unallocated in Table 5, four raise taxonomic issues (Appendix S2). The remaining two are species of *Carychium*. The record of *Carychium lederi* from Colchis represents a major extension of known geographical range (southern Azerbaijan), and its presence also in Lagodekhi suggests a scattered but widespread distribution across Transcaucasia.

Table 5. Geographical distribution of species found in this study

A	Number of species	Europe	Ciscaucasia	Transcaucasia	Lesser + Black Sea	Greater	Unallocated
Also known in Turkey	58	19	12	6	17	3	1
Not known in Turkey	32	3	6	9 (11)	5 (4)	4 (3)	5
Total	90	22	18	15 (17)	22 (21)	7 (6)	6

B	Western Lesser Caucasus	Colchis	Borjomi	Greater Caucasus	Single SA
Known in Turkey	35 (73%)	14 (70%)	23 (79%)	38 (64%)	22 (54%)
Not known in Turkey	13 (27%)	6 (30%)	6 (21%)	21 (36%)	19 (46%)
Total	48	20	29	59	41

A, ranges of species: the column for Ciscaucasia (north of the Greater Caucasus watershed) indicates species found also in Transcaucasia; those for Transcaucasia, the Lesser Caucasus, and Black Sea coast, and for the Greater Caucasus indicate species known (outside Turkey) only in the regions named. Numbers in brackets take account of our findings (see text). For unallocated species see text. B, the representation of species known from Turkey in our samples, with clusters combined in groups, and ordered by distance from Pontic Turkey, and also for species recorded from only one sample area: Western Lesser Caucasus, Batumi, Mtirala, Kintrisi, Bakhmaro, and Goderdzi; Greater Caucasus, Ambrolauri and Lagodekhi. Distributional data from Schütt (2005), Likharev (1962), Sysoev & Schileyko (2009).

Table 6. The numbers of large and small species in different range categories, and the effect of *Leiostyla* species on the totals for small species

	Large	Small	*Leiostyla*	Small *ex Leiostyla*
Restricted	46 (85%)	21 (58%)	8 (100%)	13 (46%)
Widespread	8 (15%)	15 (42%)	0 (0%)	15 (54%)
Total	54	36	8	28

Widespread: ranging beyond the Caucasus and Pontic Turkey. The difference between large and small species is significant ($P < 0.01$) with or without *Leiostyla* (χ^2 tests).

Carychium schlickumi was previously known only as a Pliocene fossil, and, possibly, from beach debris on the Black Sea (Schütt, 2005): its occurrences in both Colchis and Borjomi also suggest a wide but discontinuous distribution within Transcaucasia.

In terms of overall distribution there is a clear difference between large and small species (Table 6), with the latter defined as those with a maximum shell dimension of less than 5 mm. (Hausdorf & Hennig, 2003): of the few widespread large species, three are probably present in forest as a result of human intervention (*Fruticicola fruticum*, *Xeropicta derbentina*, and *Zebrina detrita*). Inspection of differences among higher taxa reveals one singularity. Unlike the remainder, *Leiostyla* (Pupillidae) species show a clear difference in richness and occurrence between the Lesser and Greater Caucasus (seven and two species, respectively, one in common), with a peak of diversity at Mtirala, the wettest cluster within the array, where five species were found in a single site. Five of the eight species are also found in Turkey, but none are found outside the broad Caucasian region. The distribution of species in this genus runs counter to the general trend for small species.

COMPARISON WITH POLISH FOREST SNAIL FAUNAS

Table 7 shows comparisons of site species richness, overall similarity, and frequency of occurrence between the sites reported here and those from Poland, with no more than 530 individuals, a subset of those reported in Cameron, Pokryszko and Horsák (2010). Georgian forests are impoverished relative to those in Poland, with little more than half the median number of species. Median abundance is higher in Poland (even with a restriction to sites with less than 530 individuals) than in Georgia, but regressions of species on individuals over the same range of individuals per site (data not shown) confirm that the difference is not a product of differential sampling error: Polish sites are consistently richer for any given number of individuals. Species are also

Table 7. Comparative data on species richness, similarity, and frequency of occurrence between Georgian sites and those from Poland with less than 530 individuals per site

	Poland	Georgia
Samples	100	30
Species	101	90
Mean/median/site	25.2/26	15.9/15.5
Range	13–40	8–21
Median no. of individuals	333	233
Mean site-by-site Simpson index (±SE)	52.4 ± 0.28	41.4 ± 0.90
Overall Whittaker's index (S/α)	4.01	5.70
Species in less than 3.3% of sites	14 (14%)	30 (33.3%)

generally less frequent than in Poland: 33% of all species were recorded from only one site, compared with 14% found in the equivalent proportion of Polish sites (three or fewer). Faunal differentiation between sites and clusters is greater in Georgia than in Poland, despite the greater distances between clusters in the latter.

DISCUSSION

The snail faunas recorded in this study are characterized by relative poverty at the level of individual sites and by high levels of turnover among (and sometimes within) SAs, among which, however, there are only rather weak relationships between similarity and proximity. Although many species are endemic to the Caucasian region as a whole (including north-east Turkey), few have very restricted distributions, and although there are cases where congenerics have non-overlapping ranges, there is little sign of widespread allopatric or parapatric turnover of species within a genus. Detailed molecular studies would be needed to determine whether these parapatric or allopatric congeners were sister species diverging after confinement to separate refugia.

As in many studies of snail species richness and composition in tropical or subtropical forests (Emberton, Pearce & Randalana, 1996; de Winter & Gittenberger, 1998; Schilthuizen & Rutjes, 2001; Seddon *et al*., 2005; Tattersfield *et al*., 2006; Stanisic *et al*., 2007), densities are low, and even with considerable sampling effort full inventories of site faunas are difficult to achieve (Cameron & Pokryszko, 2005). Failure to achieve a full inventory affects both estimates of species richness and estimates of difference or similarity between sites and SAs. Although several of our samples do not meet the minimum requirements set out by Cameron & Pokryszko (2005), we note that the Chao estimator does not indicate gross deficiencies, and in comparison with Polish forests, over the same range of sample sizes, these samples from Georgia are both poorer at site level, and differ more among themselves, despite the shorter distances involved. Although the refugial status of the area is reflected in the high regional diversity (Sysoev & Schileyko, 2009), it does not result in locally richer faunas. Among tropical or subtropical study areas, in which at least patches of forest are thought to have survived throughout the Pleistocene, site richness varies considerably, but many have faunas that are no richer than those reported here. Within the limits of our choice of sites, richness appears unaffected by the features of the habitat recorded by us, although the numbers found increased in favourable conditions.

Among our samples, both the variation in climate and in position affect composition, although the latter effect is stronger, as shown both by the partial Mantel tests and by partial CCA; twice as many species appear constrained by location as by climate. However, a broader consideration of geographical ranges, using published information for the whole region, shows rather few cases of very restricted distributions; only 18 out of 90 species are known just from the area encompassed by our samples. Only slightly more than a third of all species are missing from the neighbouring part of Turkey (Schütt, 2005). Given the relatively low intensity of sampling in the region, even these proportions may be too high. Several species appear to have disjunct ranges (e.g. Turkey and the Greater Caucasus, but not in between), and our own sampling has extended the known ranges of a few species. The case of *Leiostyla*, where five out of eight species recorded were found in a single site, emphasizes the lack of neat patterns of allopatric replacement. A rather similar pattern is seen in the same genus in the forests of Madeira, another forest refugium through the Plio–Pleistocene climatic changes (Cameron, Cunha & Martins, 2007). As elsewhere, small species tend to be more widely distributed than large ones (Pokryszko & Cameron, 2005). *Leiostyla* is a conspicuous exception to this general trend.

These patterns stand in sharp contrast to those found in regions where there has been either repeated restriction to isolated refugia created by fluctuations in aridity, or where the whole forest fauna is a product of the colonization of previously glaciated or periglacial landscapes. In the former, families and genera with stenotypic species typically show very characteristic patterns of allopatric replacement; some species may have tiny geographical ranges, the most extreme case being reported by Solem (1988). Even within Turkey as a whole the influence of aridity and multiple, tiny refugia shows in the fact that around 25% of more than

100 clausiliid species are known only from, or very near, their type localities (Schütt, 2005). In the latter case, faunas are characterized by species with large geographical ranges and by very low rates of distance decay in similarity (Nekola & White, 1999; Pokryszko & Cameron, 2005; Cameron *et al*., 2010).

These various contrasts prompt consideration of the way in which regional diversity has developed in an area where forests have persisted, albeit with changes in character and connectivity, throughout the Pleistocene. In faunas from Africa, Australia, and New Zealand, it appears that several processes have been involved. Periodic isolation of optimal forest fragments have certainly played a part (Emberton *et al*., 1996; Moritz *et al*., 2001), and might account for some of the parapatric distributions noted above, as has the development of altitudinal differentiation (Stanisic, 1982; Tattersfield *et al*., 2006). There is, however, a substantial proportion of species that show patchy, more-or-less discontinuous distributions (Solem, 1984; Barker, 2005; Stanisic *et al*., 2007), for which isolation by distance alone, followed by back migration, with either niche separation or metapopulation dynamics allowing co-existence, seems the most robust explanation (Cameron *et al*., 2003). A general analysis is made more problematic by the differences in taxonomic composition, trophic levels, and ranges of size and shape among faunas.

In the case of Georgian forests, with a typically western Palaearctic fauna, high-altitude faunas, at least within the limits of our sampling, hold a number of species with wide geographical ranges but with alpine habitat preferences. More generally, although there are some species restricted to parts of the region where a combination of climate and geographical isolation may be involved, there are many that are distributed widely but are not found in all, or even most, samples. In this context, the contrasting hypotheses of multiple glacial forest refuges in the Caucasus (Velichko & Kurenkova, 1990), or of a single larger refugium at the Black Sea coast (van Andel & Tzedakis, 1996), are relevant. Some recent molecular genetic data on other organisms (Tarkhnishvili, Thorpe & Arntzen, 2000; Murtskhvaladze, Gavashelishvili & Tarkhnishvili, 2010) lend support to the former, and it is clear that a part of the pattern shown here stems from a combination of isolation and the strong east-to-west climatic gradient. However, the presence of a number of species confined to, but not restricted within, the region of north-east Turkey, the Lesser Caucasus, and the Black Sea coast suggests a rather large and long-standing refuge in which differentiation occurred. Most of the species with a limited distribution irrespective of estimated climate tolerance are found in south-west Georgia, close to the major glacial refugium, from Batumi to Bakhmaro, irrespective to the altitude and climate differences. The range of some of them, including the largest species *Helix goderdziana* (Mumladze, Tarkhnishvili & Pokryszko, 2008) extends to north-east Turkey, within the extent of the major refugium, but not to the rest of the Caucasus ecoregion. Forests persisted not only in the mountains, but also into the Colchic lowlands well into the Holocene (Connor, Thomas & Kvavadze, 2007).

Although our results tend to confirm that the pattern of diversification in forested regions, where forest has persisted with some connectivity over millions rather than tens of thousands of years, show similar patterns regardless of the details of faunal composition in terms of systematics, trophic levels, or size and shape spectra, there are two cautionary notes. First, although much work has been carried out, the region has not been surveyed intensively, and adequate sampling is made difficult by both low densities and difficult terrain. Patchy distributions may become less so, as more data is gained. Furthermore, a greater number of known sites would make the distinction between historic factors and present climatic limits much easier to disentangle. Second, and perhaps of more significance, we note that some recent molecular studies show that populations showing very little morphological differentiation may differ in genetic material, to the extent that isolation may be dated to the Pliocene. High morphological conservatism was shown, for instance, in Caucasian salamanders (*Mertensiella caucasica*), in which geographic populations isolated from at least the early Pliocene are not recognizable morphologically (Tarkhnishvili *et al*., 2000). Snail species are generally distinguished on morphological characters, especially of the shell, yet we know from studies elsewhere that relatively short periods of isolation can result in internal differentiation among externally similar populations (Martins, 2005).

The differential between large and small species in terms of geographical range reported here repeats a pattern found in other studies (Cameron *et al*., 2005; Cameron *et al*., 2010). It is even more pronounced when large species associated with human activity are excluded. Although this trend reflects the ease of passive dispersal in small species, we note that for small species with exacting requirements (*Leiostyla* species here, some charopids in Australia (Stanisic *et al*., 2007), range sizes may be very small without showing patterns of strict allopatry.

Finally, we note that the character of this forest refugium, reputedly the largest in the western Palaearctic, is one of relatively permanent isolation for forest snails. There is indeed an endemic fauna, one that appears to have played little part in the recolonization of northern Eurasia in the Holocene, unlike refuges around the Alps, the Carpathians, the

Balkans, and Iberia (Hausdorf & Hennig, 2003). Even the forest fauna of the southern Urals, closer to Transcaucasia than any strictly European refugium, has the character of early Holocene forests in Central Europe: the only species in common with our Georgian samples are those widespread across the whole western Palaearctic (Horsák *et al*., in press). The very high barrier of the Greater Caucasus and the predominance of steppe on all sides of the region appear to have constrained movement.

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REFERENCES

Barker GM. 2005. The character of the New Zealand land snail fauna and communities: some evolutionary and ecological perspectives. In: Cameron RAD, Nekola JC, Pokryszko BM, Wells FE, eds. *Pattern and process in land mollusc diversity*. Perth: Records of the Western Australian Museum, Supplement No. 68, 53–102.

Bohonak AJ. 2002. IBD (isolation by distance): a program for analyses of isolation by distance. *Journal of Heredity* **93:** 153–154.

ter Braak CJF, Smilauer P. 2002. *CANOCO reference manual and canodraw for windows user's guide: software for canonical community ordination (version 4.5)*. Ithaca, NY: Microcomputer Power.

Cameron RAD. 2004. From continents to quadrats: species/area relationships in land mollusc faunas. *Journal of Conchology Special Publication* **3:** 39–54.

Cameron RAD, Cunha RMT, Martins AMF. 2007. Chance and necessity: land-snail faunas of São Miguel, Azores, compared with those of Madeira. *Journal of Molluscan Studies* **73:** 11–21.

Cameron RAD, Mylonas M, Triantis K, Parmakelis A, Vardinoyannis K. 2003. Land snail diversity in a square kilometre of Cretan maquis: modest species richness, high density and local homogeneity. *Journal of Molluscan Studies* **69:** 93–99.

Cameron RAD, Nekola JC, Pokryszko BM, Wells FE, eds. 2005. *Pattern and process in land mollusc diversity. Records of the Western Australian Museum, Supplement 68*. Perth: Western Australian Museum.

Cameron RAD, Pokryszko BM. 2005. Estimating the species richness and composition of land mollusc communities: problems, consequences and practical advice. *Journal of Conchology* **38:** 529–548.

Cameron RAD, Pokryszko BM, Long DC. 2006. Snail faunas in southern English calcareous woodlands: rich and uniform, but geographically differentiated. *Journal of Conchology* **39:** 13–40.

Cameron RAD, Pokryszko BM, Horsák M. 2010. Land snail faunas in Polish forests: patterns of richness and composition in a post-glacial landscape. *Malacologia* **53:** 77–135.

Connor SE, Thomas I, Kvavadze EV. 2007. A 5600- yr history of changing vegetation, sea levels and human impacts from the Black Sea coast of Georgia. *The Holocene* **17:** 25–36.

Davis PH. 1971. Distribution patterns in Anatolia with particular reference to endemism. In: Davis PH, Harper PC, Hedge IC, eds. *Plant life of South-West Asia*. Edinburgh: Botanical Society of Edinburgh, 15–27.

De Winter AJ, Gittenberger E. 1998. The land snail fauna of a square kilometre patch of rainforest in southwestern Cameroon: high species richness, low abundance and seasonal fluctuations. *Malacologia* **40:** 231–250.

Denk T, Frotzler N, Davitashvili N. 2001. Vegetational patterns and distribution of relict taxa in humid temperate forests and wetlands of Georgia (Transcaucasia). *Biological Journal of the Linnean Society* **72:** 287–332.

Emberton KC, Pearce TA, Randalana R. 1996. Quantitatively sampling land snail species richness in Madagascan rainforests. *Malacologia* **38:** 203–212.

Hausdorf B, Hennig C. 2003. Nestedness of northwest European land snail ranges as a consequence of differential immigration from Pleistocene glacial refuges. *Oecologia* **135:** 102–109.

Hijmans RJ, Cameron SE Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated global terrestrial climate surfaces. *International Journal of Climatology* **25:** 1965–1978.

Horsák M, Chytrý M, Danihelka J, Kočí M, Kubešová S, Lasosová Z, Otypková Z, Tichý L. In press. Snail faunas in the southern Ural forests and their relations to vegetation: an analogue of the early Holocene assemblages of Central Europe? *Journal of Molluscan Studies*.

Leps J, Smilauer P. 2003. *Multivariate analysis of ecological data using CANOCO*. Cambridge: Cambridge University Press.

Likharev IM. 1962. *Klauziliidy (clausiliidae)*. Fauna of the USSR, 3 (4). Leningrad: Nauka, (in Russian).

Magurran AE. 2004. *Measuring biological diversity*. Oxford: Blackwell.

Manel S, Schwartz MK, Luikart G, Taberlet P. 2003. Landscape genetics: combining landscape ecology and population genetics. *Trends in Ecology and Evolution* **18:** 189–197.

Manly BJF. 1997. *Randomization, bootstrap and monte carlo methods in biology*, 2nd edn. London: Chapman and Hall.

Martins AFM. 2005. The shaping of a species: the Azorean *Drouetia* Gude (Pulmonata: Zonitidae: *Oxychilus*) as a model. In: Cameron RAD, Nekola JC, Pokryszko BM, Wells FE, eds. *Pattern and process in land mollusc diversity*. Perth: Records of the Western Australian Museum, Supplement No. 68, 143–157.

Moritz C, Richardson KS, Ferrier S, Monteith GB, Stanisic J, Williams SE, Whiffin T. 2001. Biogeographical concordance and efficiency of taxon indicators for establishing conservation priority in a tropical rainforest biota. *Proceedings of the Royal Society of London, B* **268:** 1875–1881.

Mumladze L, Tarkhnishvili D, Pokryszko BM. 2008. A new species of the genus *Helix* from the Lesser Caucasus (SW Georgia). *Journal of Conchology* **39:** 483–485.

Murtskhvaladze M, Gavashelishvili A, Tarkhnishvili D. 2010. Geographic and genetic boundaries of brown bear (*Ursus arctos*) population in the Caucasus. *Molecular Ecology* **19:** 1829–1841.

Nekola JC, White PS. 1999. Distance decay of similarity in biogeography and ecology. *Journal of Biogeography* **26:** 867–878.

Pokryszko BM, Cameron RAD. 2005. Geographical variation in the composition and richness of forest snail faunas in northern Europe. In: Cameron RAD, Nekola JC, Pokryszko BM, Wells FE, eds. *Pattern and process in land mollusc diversity*. Perth: Records of the Western Australian Museum, Supplement No. 68, 115–132.

Ricklefs RE. 2004. A comprehensive framework for global patterns in biodiversity. *Ecology Letters* **7:** 1–15.

Riedel A. 1966. Zonitidae (excl. Daudebardiinae) der Kaukasusländer (Gastropoda). *Annales Zoologici* **24:** 1–303.

Schilthuizen M, Rutjes HA. 2001. Land snail diversity in a square kilometre of tropical rainforest in Sabah, Malaysian Borneo. *Journal of Molluscan Studies* **67:** 417–423.

Schütt H. 2005. *Turkish land snails*. Solingen: Verlag Natur & Wissenschaft.

Seddon MB, Tattersfield T, Herbert DG, Rowson B, Lange CN, Ngereza C, Warui CM, Allen JA. 2005. Diversity of African forest mollusc faunas: what have we learnt since Solem (1984)? In: Cameron RAD, Nekola JC, Pokryszko BM, Wells FE, eds. *Pattern and process in land mollusc diversity*. Perth: Records of the Western Australian Museum, Supplement No. 68, 103–114.

Schileyko AA. 1975. Molluscs of the subfamily Lauriinae of the USSR fauna (Pulmonata, Pupillidae). *Zoologicheskji Zhurnal* **54:** 1767–1782. (in Russian).

Schileyko AA. 1978. *Terrestrial Molluscs of the Superfamily Helicoidea*. Fauna of the USSR, 3 (6). Leningrad: Nauka, (in Russian).

Schileyko AA. 1984. *Terrestrial molluscs of the suborder Pupillina of the USSR fauna (Gastropoda, Pulmonata, Geophila)*. *Fauna USSR* (new series): 130, Mollusca, III no. 3. Leningrad: Nauka, (in Russian).

Solem A. 1984. A world model of land snail diversity and abundance. In: Solem A, van Bruggen AC, eds, eds. *Worldwide snails: biogeographical studies on non-marine molluscs*. Leiden: Brill and Backhuys, 6–23.

Solem A. 1988. Maximum in the minimum: biogeography of land snails from the Ningbing Ranges and Jeremiah Hills, northeast Kimberley, Western Australia. *Journal of the Malacological Society of Australia* **9:** 59–113.

Southwood TRE, Henderson PA. 2000. *Ecological methods*. Oxford: Blackwell.

Stanisic J. 1982. The terrestrial molluscs. In: Anon, ed. *1981 Bellenden Ker Expedition, Interim Report*. Brisbane: Queensland Museum.

Stanisic J, Cameron RAD, Pokryszko BM, Nekola JC. 2007. Forest snail faunas from S.E. Queensland and N.E. New South Wales (Australia): patterns of local and regional richness and differentiation. *Malacologia* **49:** 445–462.

Sysoev A, Schileyko AA. 2009. *Land snails and slugs of Russia and adjacent countries*. Sofia and Moscow: Pensoft.

Tarasov PE, Volkova VS, Webb T III, Guiot J, Andreev AA, Bezusko LG, Bezusko TV, Bykova GV, Dorofayuk NI, Kvavadze EV, Psipova IM, Panova NK, Sevastyanov DV. 2000. Last glacial maximum biomes reconstructed from pollen and plant macrofossil data from northern Eurasia. *Journal of Biogeography* **27:** 609–620.

Tarkhnishvili DN, Thorpe RS, Arntzen JW. 2000. Pre-Pleistocene refugia and differentiation between populations of the Caucasian salamander (*Mertensiella caucasica*). *Molecular Phylogenetics and Evolution* **14:** 414–422.

Tattersfield P, Seddon MB, Ngereza C, Rowson B. 2006. Elevational variation in diversity and composition of land-snail faunas in a Tanzanian forest. *African Journal of Ecology* **44:** 47–60.

Tumajanov II. 1971. Changes of the Great Caucasus forest vegetation during the Pleistocene and Holocene. In: Davis PH, Harper PC, Hedge IC, eds. *Plant life of South-West Asia*. Edinburgh: Botanical Society of Edinburgh, 73–88.

Van Andel TH, Tzedakis PC. 1996. Palaeolithic landscapes of Europe and environs: 150 000–25 000 years ago: an overview. *Quaternary Science Reviews* **15:** 481–500.

Velichko AA, Kurenkova AA. 1990. Landscapes of the Northern Hemisphere during the Late Glacial Maximum. In: Soffer O, Gamble G, eds. *The World at 18 000 BP*. London: Unwin Hyman, 255–265.

Walther BA, Moore JL. 2005. The concepts of bias, precision and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. *Ecography* **28:** 815–829.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Details of location and habitat of samples.
Appendix S2. List of species found with authorities, taxonomic notes, and details of known geographical ranges.
Appendix S3. Species/sites matrix for the samples used in this study.
Appendix S4. All pairwise Simpson indices of similarity (%) for samples used in this study.

Sites	Date	Long	Lat	alt (metres)	rhodo	alder	mdw	conifer	fag/cast	slope	Species	Individuals
Colchis	10-Jul	41.7816	42.152	5	0	2	1	0	0	0	20	251
Batumi 1 x	05-Jul	41.6136	41.566	117	2	2	1	0	0	2	16	140
Batumi 2 x	05-Jul	41.714	41.503	111	0	0	2	0	1	2	14	85
Batumi 3 x	05-Jul	41.7556	41.515	95	0	1	2	0	1	2	12	127
Mtirala 1	06-Jul	41.7775	41.6502	865	2	1	1	0	2	2	13	67
Mtirala 2	06-Jul	41.7684	41.6469	640	0	0	2	0	1	1	18	410
Mtirala 3	06-Jul	41.7647	41.6502	600	1	0	2	0	1	1	17	449
Kintrisi 1	08-Jul	41.9792	41.7582	380	1	1	1	0	1	1	14	148
Kintrisi 2	08-Jul	41.9789	41.7639	400	2	0	0	0	2	2	16	206
Kintrisi 3	08-Jul	41.9692	41.773	250	1	1	2	0	1	1	20	203
Bakhmaro 1	04-Jul	42.3527	41.9475	350	1	2	1	0	0	2	14	247
Bakhmaro 2	04-Jul	42.3683	41.8902	1470	0	1	0	1	0	2	12	60
Bakhmaro 3	04-Jul	42.388	41.9046	750	2	0	0	0	2	2	20	144
Goderdzi	07-Jul	42.6051	41.6585	1475	0	1	0	2	0	2	17	151
Borjomi 1	14-Jul	43.2554	41.9177	670	1	1	2	0	1	2	18	329
Borjomi 2	14-Jul	43.2598	41.9155	675	1	1	2	0	1	2	21	385
Borjomi 3	14-Jul	43.2768	41.9211	550	1	0	1	0	2	2	15	261
Borjomi 4	15-Jul	43.4097	41.9478	810	0	0	0	2	2	2	15	78
Borjomi 5	15-Jul	43.4045	41.9611	700	0	0	2	1	1	2	14	204
Ambrolauri 1	11-Jul	43.122	42.5406	718	0	0	1	0	2	2	15	252
Ambrolauri 2	11-Jul	42.9688	42.5477	650	0	0	2	0	1	2	18	170
Ambrolauri 3	12-Jul	43.3546	42.4766	2050	0	0	2	0	0	0	21	530
Ambrolauri 4	12-Jul	43.2975	42.527	1100	0	2	1	0	1	2	18	179
Ambrolauri 5	13-Jul	43.0183	42.3821	1000	1	1	1	0	2	1	21	285
Lagodekhi 1	20-Jul	46.2685	41.8584	800	0	0	1	0	2	1	16	284
Lagodekhi 2	20-Jul	46.2855	41.8662	890	0	0	1	0	2	1	8	167
Lagodekhi 3	21-Jul	46.2834	41.8469	600	0	0	1	0	1	0	14	417
Lagodekhi 4	21-Jul	46.2928	41.8487	620	0	0	1	0	2	0	10	263
Lagodekhi 5	21-Jul	46.3001	41.8552	680	0	0	1	0	2	0	14	198
Lagodekhi 6	21-Jul	46.2996	41.8563	705	0	1	2	0	1	2	16	303

APPENDIX S1. Site details. See next page for key.

NOTES:

1. Batumi sites had false GPS readings (well into Turkey); locations determined from maps.
2. Altitudes are approximate, estimated from map for Bakhmaro 3
3. Environment: vegetation: 0, absent; 1, present but not dominant; 2, dominant.
   rhodo, *Rhododendron* spp, usually *R. ponticum* (understory)
   alder, *Alnus* spp.
   mdw, mixed broadleaf trees (*Fraxinus, Carpinus, Ulmus, Acer*)
   conifer, *Picea* and/or *Abies.*
   fag/ cast, *Fagus* and/or *Castanea,* occasionally *Quercus.*
4. Environment: slope: 0, flat or nearly so; 1, moderate slopes; 2. steep slopes (30° +)

APPENDIX S2. List of species found. Nomenclature follows Sysoev and Schileyko (2009), except where names are in bold font. Species not listed in their work are asterisked. All *Leiostyla* species here are assigned by them to *Euxinolauria*. Comments on distribution come mainly from Schütt (2005) and Sysoev and Schileyko (2009).

Species	**Comments**
Pomatias rivulare (Eichwald, 1829)	As far west as Moldova and Romania
Caspicyclotus sieversi (L. Pfeiffer, 1871)	Eastern Transcaucasia only
Acicula limbata Reuss,1860	Transcaucasia
Carychium tridentatum (Risso, 1826)	Widespread
Carychium minimum Westerlund, 1897	Widespread
Carychium lederi O.Boettger,1880	Previously only in Lenkoran & Talysh (E. Transcaucasia) **Our records extend range westwards.** Unallocated in Table 5.
*Carychium schlickumi Strauch, 1977	**Previously known only as fossil and possibly from shoreline debris, Black Sea (Schütt, 2005). Our records are the first of living animals.** Unallocated in Table 5
Cochlicopa lubrica (Müller, 1774)	Widespread
Pilorcula trifilaris (Mousson, 1856)	Broad Caucasian, including Turkey.
Sphyradium doliolum (Bruguière, 1792)	Widespread. In Caucasus at high altitude.
Columella edentula (Draparnaud, 1805)	Widespread
Truncatellina cylindrica (Férussac, 1807)	Widespread, generally open habitats
*Truncatellina strobeli (Gredler,1853)	**Widespread, montane, generally open habitats. Schütt (2005) includes Transcaucasia in its range, but not listed in S & S.**
Vertigo sieversi (O. Boettger, 1879)	Western Cis- and Trans- Caucasia
Pupilla triplicata (Studer, 1820)	Widespread, high altitudes.
Lauria cylindracea (Da Costa, 1778)	Widespread
*Lauria sp	**Undetermined, but clearly not _L. cylindracea._** Unallocated in Table 5
Leiostyla sinangula (Schileyko, 1975)	**Batumi and NE Turkey**
Leiostyla glomerosa (Suvarov & Schileyko, 1991)	**SW. Transcaucasia, not Turkey**
Leiostyla zonifera (Pilsbry, 1934)	**W. Transcaucasia, not Turkey**
Leiostyla superstructa (Mousson, 1876)	**W. Transcaucasia to Novo rossiysk and Turkey**
Leiostyla tenuimarginata (Pilsbry, 1922)	**Extreme NE Turkey and around Batumi**
Leiostyla silicea (Schileyko, 1975)	**W. Great Caucasus. Our record extends geographical range eastwards**
Leiostyla paulinae (Lindholm, 1913)	**SW Transcaucasia and extreme NE Turkey**
Leiostyla rectidentata (Schileyko, 1975)	**Extreme SW Transcaucasia, possibly adjacent Turkey.**
Vallonia pulchella (Müller, 1774)	Widespread
Acanthinula aculeata (Müller, 1774)	Widespread
Imparietula brevior (Mousson, 1876)	Armenia, NE Turkey and Lesser Caucasus
Akramowskiella umbrosa (Mousson, 1873)	Broadly Caucasian, including NE Turkey
Retowskia schlaefflii (Mousson, 1863)	Transcaucasia, not Turkey
Andronakia catenulata (Lindholm, 1913)	Extreme SW Transcaucasia and NE Turkey
Zebrina detrita (Müller, 1774)	Widespread
Poiretia mingrelica (O. Boettger, 1881)	Transcaucasia
*Paralaoma servilis (Shuttleworth, 1852)	Cosmopolitan, introduced widely.
Punctum pygmaeum (Draparnaud, 1801)	Widespread
Vitrina pellucida (Müller, 1774)	Widespread
Phenacolimax annularis (Studer, 1820)	Widespread, high altitude. (Generic synonym*: Gallandia*)
Vitrea contortula (Krynicki, 1837)	Caucasia generally, including NE Turkey
Vitrea sorella (Mousson, 1863)	Turkey and W. Greater Caucasus
Vitrea praetermissa Riedel, 1988	SW Transcaucasia, not Turkey
Vitrea angystropha (O. Boettger, 1880)	W & C Transcaucasia, also into Turkey
Vitrea retowskii (Lindholm, 1914)	**As “_Oxychilus”_ in S & S. Lesser Caucasus and Armenia**
Vitrea pygmaea (O. Boettger, 1880)	Widespread
Aegopinella pura (Alder, 1830)	Widespread
Nesovitrea hammonis (Strøm, 1765)	**Widespread. As _Perpolita hammonis_ in S & S**
Oxychilus decipiens (O. Boettger, 1886)	Great Caucasus and Borjomi
Oxychilus koutaisanus (Mousson, 1863)	Caucasia generally, including NE Turkey
Oxychilus discrepans (Retowski, 1889)	SW Transcaucasia and NE Turkey
Oxychilus sieversi (O. Boettger, 1879)	**As _Conulopolita sierversi_ in S &S. Wide Caucasian but not Turkey**
Oxychilus oschtenicus (O. Boettger, 1888)	Greater Caucasus and Ciscaucasia
Oxychilus sucinacius (O. Boettger, 1883)	Transcaucasia and NE Turkey

Oxychilus duboisi (Charpentier in Mousson, 1863)	Kutaisi (Transcaucasia) only
Discoxychilus lindholmi Riedel, 1966	Extreme SW Transcaucasia and N.E. Turkey
Vitrinoxychilus suturalis (O. Boettger, 1881)	Transcaucasia and NE Turkey
Sieversia lederi (O. Boettger, 1881)	W Caucasus (including Ciscaucasia) and NE Turkey
Euconulus fulvus (Müller,1774)	Widespread
Caspiophaedusa perlucens (O. Boettger, 1877)	Eastern Transcaucasia only
Pontophaedusa funiculum (Mousson, 1863)	Black Sea Coastal from Sochi into NE Turkey
Pravispira semilamellata (Mousson, 1863)	Transcaucasia, also NE Turkey
Filosa filosa (Mousson, 1863)	SW Transcaucasia and NE Turkey
Serrulina serrulata (L. Pfeiffer, 1847)	Widespread, west to Romania
Scrobifera taurica (L. Pfeiffer, 1848)	Caucasia, except SW corner. Also in NE Turkey
Strigileuxina reuleauxi (O. Boettger, 1887)	SW Transcaucasia and NE Turkey
__*Strigileuxina lindholmi* (Kobelt in Lindholm, 1912)__	**Apparently only in Gt Caucasus (Lagodekhi) and also in NE Turkey Listed as *Kazancia lindholmi* in S & S**
Elia derasa derasa (Mousson, 1863)	Widespread in Caucasia, also NE Turkey
__*_Elia derasa suanetica_ (O. Boettger, 1883)__	**Taxon not recognised by S & S, regarded as distinct here on conchological characters. Transcaucasian.**
Elia ossetica (Mousson, 1863)	C & E Caucasia; Turkey near Kars, not Pontic coast
Mucronaria duboisi (Charpentier, 1852)	Widespread in Caucasia and NE Turkey
Mucronaria strauchi (O. Boettger, 1878)	Central Transcaucasia
Mucronaria pleuroptychia (O. Boettger, 1878)	Apparently in Gt Caucasus (Trans only), but also in NE Turkey
Mucronaria acuminata (Mousson, 1876)	Only near Armenian border of Georgia. **Our record extends range**. Unallocated in Table 5.
Mucronaria index (Mousson, 1863)	W Transcaucasia only, mostly coastal.
Mentissoidea rupicola rupicola (Mortillet, 1854)	Black Sea coast from Sukhumi to NE Turkey
Mentissoidea rupicola litotes (A. Schmidt, 1868)	Ciscaucasia and C & E Transcaucasia to Armenia
Quadriplicata quadriplicata (A. Schmidt, 1868)	E. & C Caucasia.
Quadriplicata subaggesta (Retowski, 1887)	SW Transcaucasia and NE Turkey
Quadriplicata lederi (O. Boettger, 1879)	Transcaucasia
Fruticicola fruticum (Müller, 1774)	Widespread, often introduced.
Circassina fruitis (L. Pfeiffer, 1859)	Caucasia and NE Turkey. We have not distinguished subspecies
__*_Caucasocressa dasilepida_ (Mabille, 1881)__	**Not listed in S & S** Here, Greater Caucasus (Ambrolauri). Unallocated in Table 5.
__*Harmozica maiae* (Hudec & Lehzawa, 1969)__	__*As Stenomphalia maiae* in S & S.__ Extreme SW Transcaucasus and NE Turkey
__*Harmozica selecta* (Klika, 1894)__	**Gt. Caucasus including Ciscaucasia. Also Turkey. As *Stenomphalia selecta* in S & S.**
__*_Harmozica septemgyrata_ (Mousson, 1876)__	**Not listed in S & S. Possibly NE Turkey and Transcaucasia.** Unallocated in Table 5.
__*Harmozica appeliana* (Mousson, 1876)__	**As *Euomphalia appeliana* in S & S. W Gt Caucasus (Cis- & Trans-)**
Caucasigena eichwaldi (L. Pfeiffer, 1846)	E. Gt Caucasus (Cis- & Trans-)
Kokotschaschvilia holotricha (O. Boettger, 1884)	Western Gt Caucasus (Trans-)
Xeropicta derbentina (Krynicki, 1836)	Widespread, frequently introduced.
Caucasotachea calligera (Dubois de Montpéreux, 1840)	Transcaucasia
Helix buchi (Dubois de Montpéreux, 1839)	Transcaucasia and NE Turkey
__*Helix goderdziana* Mumladze, Tarknishvili & Pokryszko, 2008__	One site in Lesser Caucasus, also NE Turkey**. S & S regard it as a form of *H. buchi***
SLUGS	
Gigantomilax lederi (O. Boettger, 1883)	Transcaucasia & NE Turkey
Eumilax brandti (Martens, 1880)	Transcaucasia & NE Turkey
Krynckillus melanocephalus Kaleniczenko, 1851	All Caucasia, NE Turkey, Iran and Ukraine
Trigonochlamys imitatrix O. Boettger, 1881	Lesser Caucasus, NE Turkey, Iran and Armenia

TAXON/LOCALITY/SITE	COL	BAT 1	BAT 2	BAT 3	MTI 1	MTI 2	MTI 3	KIN 1	KIN 2	KIN 3	BAK 1	BAK 2	BAK 3	GOD
Pomatias rivulare			18					2	4	4	46	2	1	
Caspicyclotus sieversi														
Acicula limbata			6	15	1	1	6	3	2		1		3	2
Carychium tridentatum	5		4	15		6	26			5	10		11	
Carychium minimum				14										
Carychium lederi	4													
Carychium schlickumi	57													
Cochlicopa lubrica	2	1												2
Pilorcula trifilaris	1	2							2	1	62			
Sphyradium doliolum														
Columella edentula						1							1	
Truncatellina cylindrica														
Truncatellina strobeli														
Vertigo sieversi														
Pupilla triplicata														
Lauria cylindracea	2													
Lauria sp						1								
Leiostyla sinangula	1	39	2	2	5	41	15				2			
Leiostyla glomerosa					4	26	15						3	
Leiostyla zonifera										11				
Leiostyla superstructa							15						1	18
Leiostyla tenuimarginata	3	20		33		42	52	19	6	33				
Leiostyla silicea														
Leiostyla paulinae		7	23			15	22			19	34		73	
Leiostyla rectidentata			2											
Vallonia pulchella														
Acanthinula aculeata		1		4		3				4		2	1	7
Imparietula brevior														
Akramowskiella umbrosa														2
Retowskia schlaeffli												36		12
Andronakia catenulata		3												
Zebrina detrita														
Poiretia mingrelica														
Paralaoma servilis														
Punctum pygmaeum	46	11						12	15	2	30		3	25
Vitrina pellucida														
Phenacolimax annularis														
Vitrea contortula	10	5	5	9	8	7	18		2	2			8	
Vitrea sorella														
Vitrea praetermissa		1			16		13							
Vitrea angystropha											6	3	1	
Vitrea retowskii														
Vitrea pygmaea														
Aegopinella pura														12
Nesovitrea hammonis	3													3
Oxychilus decipiens											2	3	1	7
Oxychilus koutaisanus										2		1		14
Oxychilus discrepans	2				2	24	4	2	13	6		7		
Oxychilus sieversi														
Oxychilus oschtenicus	3	2	2	1	1	12		1	2					
Oxychilus sucinacius														
Oxychilus duboisi							3							
Discoxychilus lindholmi					6									

TAXON/LOCALITY/SITE	COL	BAT 1	BAT 2	BAT 3	MTI 1	MTI 2	MTI 3	KIN 1	KIN 2	KIN 3	BAK 1	BAK 2	BAK 3	GOD
Vitrinoxychilus suturalis		2	5	7	14	64	1	10	5	7	17	1	4	
Sieversia lederi					1	1	2							
Euconulus fulvus														4
Caspiophaedusa perlucens														
Pontophaedusa funiculum			1											
Pravispira smilamellata								2					3	4
Filosa filosa		5		20	1	54	228	2	47	57				
Serrulina serrulata						1					1			
Scrobifera taurica													5	
Strigileuxina reuleauxi						8		4	7	7			3	
Strigileuxina lindholmi										1		2	1	
Elia derasa derasa	2													9
Elia derasa suanetica														
Elia ossetica														
Mucronaria duboisi			5					13	2	4		1		
Mucronaria strauchi														
Mucronaria pleuoptychia														
Mucronaria acuminata														
Mucronaria index	11													
Mentissoidea rupicola												1		3
Mentissoidea litotes	71													
Quadriplicata quadriplicata				4				67	71	28	1		5	
Quadriplicata subaggesta		32			3	83	21							
Quadriplicata lederi														
Fruticicola fruticum										1				
Circassina frutis	6		3		5	20	4	10	20	8	33	1	13	17
Caucasocressa dasilepida														
Harmozica maiae									4	1				
Harmozica selecta														
Harmozica septemgyrata	4	7	2											
Harmozica appeliana	1													
Caucasigena eichwaldi														
Kokotschaschvilia holotricha														
Xeropicta derbentina														
Caucasotachea calligera	17	2	7	3			4	1	4		2		3	
Helix buchi														
Helix goderziana														10
Individuals	251	140	85	127	67	410	449	148	206	203	247	60	144	151
Species	20	16	14	12	13	19	17	14	16	19	14	12	20	17
Slugs														
Gigantomilax lederi			x	x	x		x	x				x		
Eumilax brandti			x		x			x	x			x		x
?Krynickillus melanocephalus	x													
Trigonochlamys imitatrix							x		x					
Limax ecarinatus														

APPENDIX S3. Species/Sites matrix. A: Colchis (COL), Batumi (BAT), Mtirala (MTI), Kintrisi (KIN), Bakhmaro (BAK), Goderdzi (GOD).

TAXON/LOCALITY/SITE	BOR1	BO R2	BO R3	BO R4	BO R5	AM B1	AM B2	AM B3	AM B4	AM B5	LA G1	LA G2	LA G3	LA G4	LA G5	LA G6
Pomatias rivulare	36	33	18	10	110	51	54		54	7	3		17	8	19	27
Caspicyclotus sieversi											40	13	115	174	19	78
Acicula limbata	27	29	18	2					2	3	1				2	
Carychium tridentatum		18	17	4					12	17			13			
Carychium minimum																
Carychium lederi											23					29
Carychium schlickumi				6												
Cochlicopa lubrica					1		1	89	1	2						2
Pilorcula trifilaris	33	15	16	14	4	112	34		39	74						
Sphyradium doliolum								24								
Columella edentula								2			1					
Truncatellina cylindrica						20	1									
Truncatellina strobeli													1			
Vertigo sieversi										2						
Pupilla triplicata								1								
Lauria cylindracea								1			3	2	8	5	1	2
Lauria cf. cylindracea																
Leiostyla sinangula																
Leiostyla glomerosa																
Leiostyla zonifera																
Leiostyla superstructa	49	21		2	14			10		3	5					
Leiostyla tenuimarginata	7	28	23													
Leiostyla silicea																4
Leiostyla paulinae																
Leiostyla rectidentata																
Vallonia pulchella							1									
Acanthinula aculeata	2		3				4		4		16		20		4	15
Imparietula brevior				3				37								
Akramowskiella umbrosa																
Retowskia schlaeffli																
Andronakia catenulata																
Zebrina detrita						2										
Poiretia mingrelica						3			6							
Paralaoma servilis						25										
Punctum pygmaeum		13	3				11	77	6	60	125	41	102	7	70	23
Vitrina pellucida								26								
Phenacolimax annularis								97								
Vitrea contortula	19	3	14		3		1		2	1		3		5	6	27
Vitrea sorella		1						17	4							
Vitrea praetermissa																
Vitrea angystropha				1												
Vitrea retowskii		1														
Vitrea pygmaea									1							
Aegopinella pura	5	2						13	2							
Nesovitrea hammonis								26								
Oxychilus decipiens		5	2	3												
Oxychilus koutaisanus	26	49		3		13	5	45								7
Oxychilus discrepans																
Oxychilus sieversi							4									5
Oxychilus oschtenicus									4							
Oxychilus sucinacius											2			2	2	

TAXON/LOCALITY/SITE	BOR1	BOR2	BOR3	BOR4	BOR5	AMB1	AMB2	AMB3	AMB4	AMB5	LAG1	LAG2	LAG3	LAG4	LAG5	LAG6
Oxychilus duboisi							11		4							
Discoxychilus lindholmi																
Vitrinoxychilus suturalis	29	30	17	7	2					4						
Sieversia lederi									4							
Euconulus fulvus								20			5		7			
Caspiophaedusa perlucens											5	9	9	4	12	10
Pontophaedusa funiculum																
Pravispira smilamellata	1	1			2					2						
Filosa filosa																
Serrulina serrulata	1		8	2							6	75	7		1	
Scrobifera taurica	9	3	5		3	12	6			7	47	22	21	21	29	49
Strigileuxina reuleauxi																
Strigileuxina lindholmi																
Elia derasa derasa	3	10			6					1						
Elia derasa suanetica								20								
Elia ossetica													9			
Mucronaria duboisi	11	2	105	7	40		17		1	2			85	36	31	10
Mucronaria strauchi										7						
Mucronaria pleuoptychia								3		75						
Mucronaria acuminata								8								
Mucronaria index																
Mentissoidea rupicola					1			2								
Mentissoidea litotes																
Quadriplicata quadriplicata															1	1
Quadriplicata subaggesta																
Quadriplicata lederi	26	41	3	8	5											
Fruticicola fruticum						1	3			3						
Circassina frutis	44	76	9	6	3	7		8	29	4						
Caucasocressa dasilepida								4								
Harmozica maiae																
Harmozica selecta							5			1						
Harmozica septemgyrata																
Harmozica appeliana																
Caucasigena eichwaldi										3						
Kokotschaschvilia holotricha						3	4									
Xeropicta derbentina						1	3									
Caucasotachea calligera	1				10	2	5			7	2	2	3	1	1	
Helix buchi		4							4							14
Helix goderziana																
Individuals	329	385	261	78	204	252	170	530	179	285	284	167	417	263	198	303
Species	18	21	15	15	14	13	18	21	18	21	15	8	14	10	14	16
Slugs																
Gigantomilax lederi					x											
Eumilax brandti	x			x	x									x		
?Krynickillus melanocephalus					x											
Trigonochlamys imitatrix																
Limax ecarinatus												x				

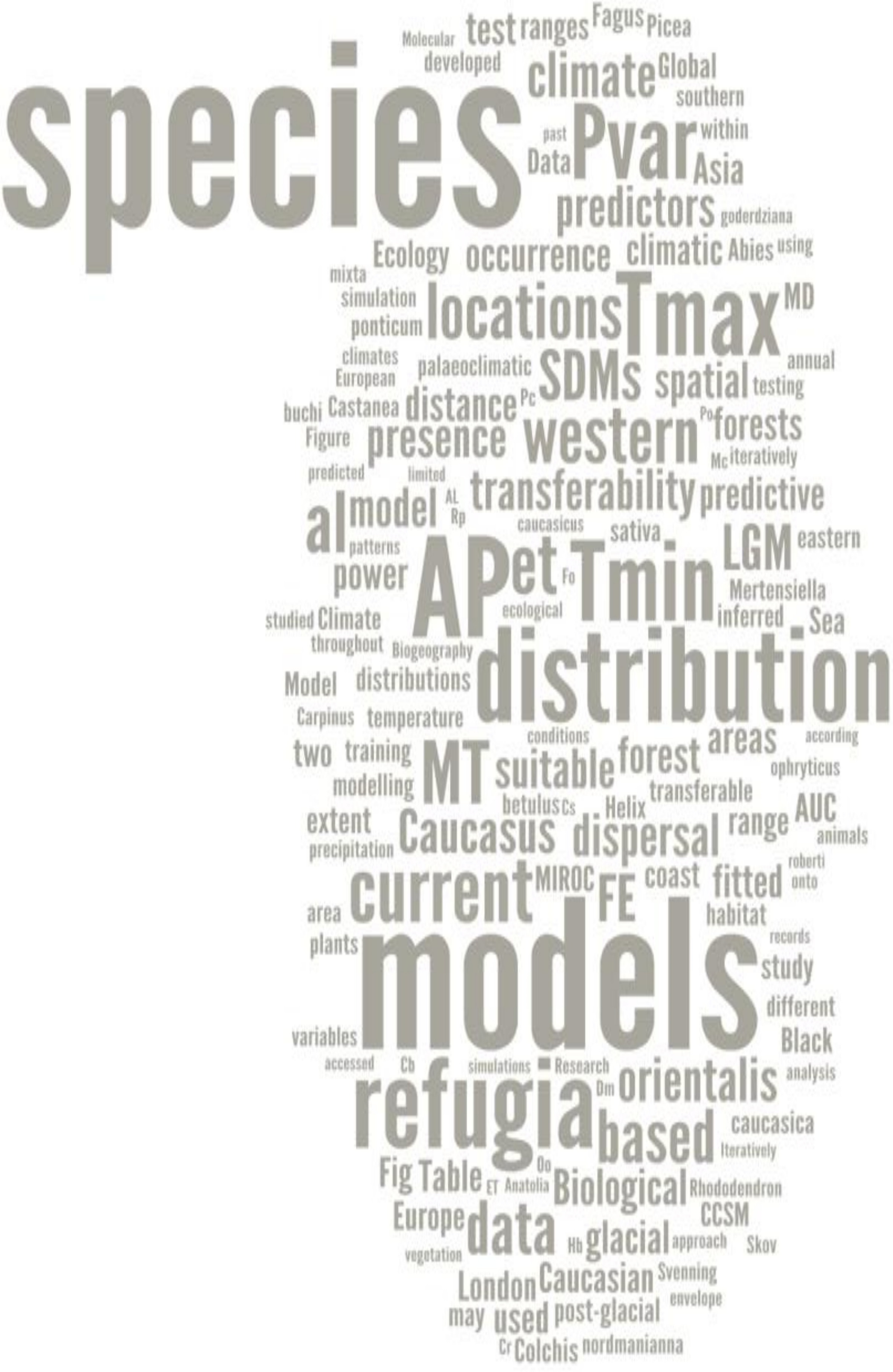
APPENDIX S3. Species/Sites matrix. B: Borjomi (BOR), Ambrolauri (AMB), Lagodekhi (LAG)

APPENDIX S4

Simpson Indices (%) of similarity between all pairs of samples

	Species		BAT1	BAT2	BAT3	MTIR1	MTIR2	MTIR3	KINT1	KINT2	KINT3	BAK1	BAK2	BAK3	GOD	BOR1	BOR2	BOR3	BOR4	BOR5	AMB1	AMB2	AMB3	AMB4	AMB5	LAG1	LAG2	LAG3	LAG4	LAG5	LAG6
COL	20	1	56.3	50.0	50.0	25.0	38.9	41.2	42.9	50.0	35.0	42.9	16.7	25.0	29.4	30.0	35.0	40.0	26.7	42.9	37.5	33.3	29.4	41.2	40.0	26.7	50.0	30.8	40.0	28.6	31.3
BAT1	16	2		50.0	66.7	43.8	56.3	56.3	42.9	50.0	50.0	42.9	16.7	37.5	18.8	37.5	31.3	40.0	13.3	35.7	25.0	40.0	12.5	37.5	37.5	20.0	37.5	23.1	30.0	28.6	25.0
BAT2	14	3			58.3	42.9	57.1	57.1	50.0	57.1	50.0	57.1	33.3	57.1	14.3	50.0	50.0	50.0	42.9	42.9	37.5	28.6	7.1	50.0	57.1	21.4	25.0	30.8	40.0	35.7	21.4
BAT3	12	4				50.0	75.0	66.7	58.3	66.7	58.3	50.0	16.7	58.3	16.7	50.0	41.7	50.0	25.0	25.0	12.5	25.0	0.0	41.7	41.7	25.0	25.0	25.0	20.0	41.7	25.0
MTIR1	13	5					84.6	84.6	46.2	53.8	38.5	30.8	25.0	38.5	15.4	30.8	30.8	30.8	23.1	23.1	12.5	7.7	7.7	38.5	30.8	7.7	12.5	0.0	10.0	15.4	7.7
MTIR2	18	6						76.5	57.1	56.3	55.6	50.0	33.3	55.6	17.6	38.9	33.3	53.3	33.3	21.4	12.5	13.3	11.8	41.2	27.8	26.7	25.0	23.1	10.0	28.6	12.5
MTIR3	17	7							50.0	50.0	47.0	50.0	25.0	52.9	17.6	41.2	41.2	40.0	33.3	35.7	25.0	20.0	11.8	35.3	41.2	20.0	25.0	15.4	20.0	21.4	6.3
KINT1	14	8								92.9	71.4	50.0	41.7	64.3	28.6	57.1	57.1	50.0	35.7	42.9	37.5	28.6	14.3	42.9	57.1	28.6	25.0	30.8	40.0	42.9	28.6
KINT2	16	9									81.3	57.1	41.7	56.3	18.8	56.3	56.3	60.0	40.0	50.0	50.0	40.0	12.5	50.0	56.3	26.7	37.5	30.8	50.0	50.0	31.3
KINT3	20	10										57.1	66.7	55.0	23.5	45.0	50.0	66.7	46.7	42.9	62.5	53.3	17.6	47.1	45.0	20.0	25.0	38.5	40.0	42.9	43.8
BAK1	14	11											41.7	78.6	28.6	50.0	57.1	64.3	64.3	35.7	50.0	28.6	14.3	42.9	57.1	35.7	37.5	38.5	30.0	42.9	21.4
BAK2	12	12												58.3	50.0	50.0	50.0	50.0	58.3	41.7	37.5	33.3	25.0	33.3	33.3	16.7	0.0	25.0	20.0	25.0	0.0
BAK3	20	13													41.2	55.6	55.0	66.7	53.3	57.1	50.0	40.0	23.5	41.2	55.0	53.3	50.0	46.2	50.0	57.1	37.5
GOD	17	14														47.1	52.9	33.3	33.3	42.9	25.0	26.7	52.9	35.3	41.2	33.3	12.5	23.1	10.0	21.4	25.0
BOR1	18	15															83.3	80.0	66.7	85.7	75.0	53.3	23.5	47.1	66.7	46.7	50.0	46.2	50.0	57.1	37.5
BOR2	21	16																86.7	73.3	78.6	62.5	46.7	35.3	64.7	61.9	33.3	37.5	38.5	50.0	42.9	43.8
BOR3	15	17																	66.7	57.1	50.0	46.7	13.3	60.0	66.7	40.0	50.0	53.8	50.0	57.1	40.0
BOR4	15	18																		50.0	50.0	26.7	26.7	40.0	53.3	26.7	12.5	30.8	20.0	28.6	20.0
BOR5	14	19																			62.5	50.0	28.6	42.9	85.7	28.6	37.5	30.8	50.0	35.7	35.7
AMB1	8	20																				87.5	25.0	37.5	75.0	37.5	25.0	37.5	37.5	37.5	37.5
AMB2	15	21																					20.0	53.3	66.7	33.3	50.0	46.2	60.0	50.0	60.0
AMB3	17	22																						29.4	29.4	33.3	25.0	23.1	20.0	14.3	25.0
AMB4	17	23																							52.9	26.7	25.0	38.5	40.0	42.9	43.8
AMB5	21	24																								40.0	50.0	46.2	60.0	50.0	37.5
LAG1	15	25																									87.5	76.9	80.0	78.6	53.3
LAG2	8	26																										87.5	87.5	100.0	75.0
LAG3	13	27																											80.0	76.9	61.5
LAG4	10	28																												100.0	80.0
LAG5	14	29																													71.4

III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The LINNEAN SOCIETY of London BIOLOGICAL Journal of the Linnean Society

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Palaeoclimatic models help to understand current distribution of Caucasian forest species

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Spatial and temporal constraints on dispersal explain the absence of species from areas with potentially suitable conditions. Previous studies have shown that post-glacial recolonization has shaped the current ranges of many species, yet it is not completely clear to what extent interspecific differences in range size depend on different dispersal rates. The inferred boundaries of glacial refugia are difficult to validate, and may bias spatial distribution models (SDMs) that consider post-glacial dispersal constraints. We predicted the current distribution of 12 Caucasian forest plants and animals, factoring in the effective geographical distance from inferred glacial refugia as an additional predictor. To infer glacial refugia, we tested the transferability of the current SDMs based on the distribution of climatic variables, and projected the most transferable ones onto two climate scenarios simulated for the Last Glacial Maximum (LGM). We then calculated least-cost distances from the inferred refugia, using elevation as a friction surface, and recalculated the current SDMs incorporating the distances as an additional variable. We compared the predictive powers of the initial with the final SDMs. The palaeoclimatic simulation that best matched the distribution of species was assumed to represent the closest fit to the true palaeoclimate. SDMs incorporating refugial distance performed significantly better for all but one studied species, and the Model for Interdisciplinary Research on Climate (MIROC) climatic simulation provided a more convincing pattern of the LGM climate than the Community Climate System Model (CCSM) simulation. Our results suggest that the projection of suitable habitat models onto past climatic conditions may yield realistic boundaries of glacial refugia, and that the current distribution of forest species in the study region is strongly associated with locations of former refugia. We inferred six major forest refugia throughout western Asia: (1) Colchis; (2) western Anatolia; (3) western Taurus; (4) the upper reaches of the Tigris River; (5) the Levant; and (6) the southern Caspian basin. The boundaries of the modelled refugia were substantially broader than the refugia boundaries inferred solely from pollen records. Thus, our method could be used to: (1) improve models of current species distributions by considering the dispersal histories of the species; and (2) validate alternative reconstructions of palaeoclimate with current distribution data. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, **105**, 231–248.

ADDITIONAL KEYWORDS: forests – fuzzy envelopes – Mahalanobis distance – post-glacial dispersal – range modelling – reconstruction of palaeoclimate – variable selection – western Asia.

INTRODUCTION

Spatial and temporal constraints on dispersal may be important in shaping the ranges of species, in addition to habitat suitability (Pulliam, 2000; Guisan & Thuiller, 2005). Species may be absent from suitable habitats because of limited dispersal ability, preventing full recolonization after historical reduction of their ranges (Pulliam, 2000; Araújo *et al.*, 2005; Guisan & Thuiller, 2005; Marsico, 2009).

The Last Glacial Maximum [LGM; *c.* 21 thousand years (ky) BP] was a crucial event that determined the current landscape and species diversity throughout the Earth. In temperate zones, forests were confined to isolated refugia during the LGM (Van Andel & Tzedakis, 1996), and their current distribution reflects post-glacial expansion from these refugia. One can expect that the expansion rates of different species were dependent on several factors, such as

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*Corresponding author. E-mail: davitar@gmail.com dispersal ability, physiological tolerances and competitive ability. It has been suggested that post-glacial dispersal patterns should be considered when explaining current distributions (Svenning & Skov, 2004; Graham, Moritz & Williams, 2006). The analysis of the distribution of multiple forest plant species shows that the distance from glacial refugia may be more important than the current climatic conditions in explaining species diversity (Willner, Di Pietro & Bergmeier, 2009).

The incorporation of post-glacial dispersal patterns into current spatial distribution models (SDMs) requires a good knowledge of the geographical ranges of species during the LGM. Traditional methods for the reconstruction of ancient ranges, based on the analyses of fossils, provide a limited and biased picture, because dead organisms tend to decompose, and conditions favouring fossilization are unevenly distributed in space and time (e.g. Signor, 1985). This is particularly true for the reconstruction of glacial refugia: they can often be overlooked if molecular genetic data are not considered (Provan & Bennett, 2008; Tarkhnishvili *et al.*, 2008). Since gridded palaeoclimatic data became widely available (Braconnot *et al.*, 2007), researchers have been trying to reconstruct ancient distributions of plants and animals by projecting SDMs, based on present occurrence data, onto past conditions (Graham *et al.*, 2006; Martínez-Meyer & Peterson, 2006; Davies, Purvis & Gittleman, 2009). Palaeovegetation data suggest that, since the LGM, the ecological requirements of long-lived, temperate tree species have not changed considerably (Martínez-Meyer & Peterson, 2006), and the projection of current SDMs onto past conditions may provide a realistic output.

The consideration of dispersal history may improve current distribution models for plants (Svenning, Normand & Skov, 2008; Willner *et al.*, 2009; Normand *et al.*, 2011). Because the precision of the shape, size and location of glacial refugia was not the primary objective of these studies, the authors did not discuss different palaeoclimatic simulations, or species–climate modelling algorithms, and the studies were applied at coarse spatial resolutions. Normand *et al.* (2011), who inferred glacial refugia and included as many as 1016 plant species in their study, only indicated the consistency of the results without addressing the issue of model transferability before inferring the location of glacial refugia.

Nogués-Bravo (2009) emphasized that the majority of palaeodistribution reconstructions have not been tested using independent data. Indeed, it is difficult to validate the models inferring future or past distributions because of a lack of test occurrence locations. Sometimes palaeodistribution data, e.g. pollen records, are used for validation (Martínez-Meyer & Peterson, 2006), but known occurrences may not capture the full extent or climatic diversity of the ancient range, leading to poor predictive performance.

Palaeodistribution models can be validated indirectly through an examination of which of the competing LGM climate simulations best explains the current distribution of the species. This approach considers the incorporation of the spatio-temporal autocorrelation of an inferred ancient distribution into current distribution models, followed by a test of the predictive power of a corrected current SDM.

In this article, we predict the current distribution of several plants and animals in the Caucasus and western Asia at a high spatial resolution by the incorporation of the least-cost distance from the inferred species-specific location of glacial refugia as an additional predictor in the modelling of species distributions. We infer the glacial refugia by projecting the current species–climate models onto available palaeoclimatic simulations. We assume that the palaeoclimatic simulation that best matches the species distributions represents the closest fit to the true palaeoclimate. Thus, our method could be used to: (1) improve models of current species distributions by considering the distribution histories of the species; and (2) validate palaeoclimatic simulations using current distribution data.

METHODS

Study area and target species

The Caucasus Ecoregion and surrounding parts of western Asia and eastern Europe (latitudinal range, 32–48°N; longitudinal range, 26–54°E) were selected as a study area. Most of this region has a dry continental or Mediterranean-type climate and a forestless landscape. Forests are associated with distinct areas of mesic climates. The largest continuous mesic forest landscapes are located along the southern and eastern Black Sea coast, north-west of the Greater Caucasus, and along the southern coast of the Caspian Sea (Fig. 1). They support biological communities with several dominant trees, including oriental beech (*Fagus orientalis*) (Denk *et al.*, 2002). The area harbours multiple glacial relict populations, which survived the LGM in forest refugia (Kikvidze & Ohsawa, 1999; Denk, Frotzler & Davitashvili, 2001; Milne & Abbott, 2002). The ranges of many forest plants and animals overlap, either throughout western Asia, or in its larger subsections, although the extent of such overlap varies from species to species.

For our study, we selected 12 species for which we had sufficiently accurate distribution data and that only coexist in the eastern Black Sea region known as Colchis. Selecting the species from the Colchis, which

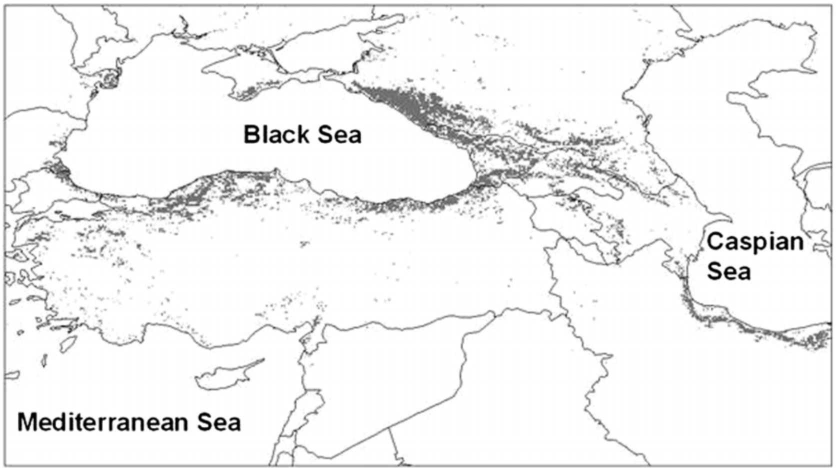


Figure 1. Current distribution of forests in western Asia, extracted from Land Cover Type 1 of the MODIS Land Cover Yearly L3 Global 500-m dataset coded MCD12Q1 (EOS Data Gateway, 2010).

is traditionally associated with glacial refugia, made it possible to compare the extents of post-glacial dispersal for diverse life forms. The selected species represent taxonomic groups with different life cycles, physiologies, reproduction and dispersal potential. The list includes five trees typical for the Caucasian forests (*Abies nordmanianna*, *Picea orientalis*, *Castanea sativa*, *Fagus orientalis*, *Carpinus betulus*), common rhododendron (*Rhododendron ponticum*), an endemic snail (*Helix buchi*), Caucasian salamander (*Mertensiella caucasica*), northern banded newt (*Ommatotriton ophryticus*), Caucasian parsley frog (*Pelodytes caucasicus*), Ajarian lizard (*Darevskia mixta*) and Robert's snow vole (*Chionomys roberti*). *Helix buchi* and *D. mixta* have parapatric sister species with very similar habitat requirements: *H. goderdziana* and *D. clarkorum*, respectively (Murphy *et al*., 2000; Mumladze *et al*., 2008). In our analyses, each pair of sister species was treated as a single taxon. For each of these study taxa, our datasets included 31–1000 presence locations covering the extent of occurrence of each taxon throughout the Caucasus. The datasets of species occurrence were from published data, the Soviet military topographical maps at a scale of 1 : 50 000 (for data on tree species) and field data collected by the authors since the early 1980s (Darevskii, 1967; Tarkhnishvili & Gokhelashvili, 1999; Tarkhnishvili *et al.*, 2008; Bukhnikashvili, 2004; Kryštufek & Vohralík, 2004. Supporting Information Table S1 and Fig. S1).

We paid particular attention to the accuracy of the presence locations of the studied species (Table S1). In mountain areas such as the Caucasus, climate changes abruptly with horizontal distance, and inaccurate locations can strongly bias the modelling output. This explains the relatively small number of species used in our analyses.

GENERAL METHODOLOGICAL REMARKS

Niche-based SDMs with the best predictive power are commonly based on many predictors and consider interactions among them (McPherson, Jetz & Rogers, 2006; Cordellier & Pfenninger, 2009). A number of commonly used modelling techniques, including logistic regression (Hosmer & Lemeshow, 1989), maximum entropy (Phillips & Dudik, 2008), neural networks (Fitzgerald & Lees, 1992) and simple or partitioned Mahalanobis distance (MD) (Rotenberry, Preston & Knick, 2006; Griffin *et al*., 2010) estimate the strength and type of association between predictors. Some of these methods help to estimate the relative importance of predictors in distinguishing between presence and absence locations.

However, these methods have major limitations that result in poor transferability of the respective models. SDMs rarely perform well outside the extent of training locations (Barry & Elith, 2006; Hijmans & Graham, 2006), and one could expect similar problems with SDMs projected into different geological periods. There are two potential reasons for this issue. First, the association between environmental predictors may be specific to a particular area (Pearson & Dawson, 2003; Randin *et al*., 2006), causing loss of model accuracy elsewhere. Second, predictors that separate presence and absence locations within the extent of training data may be unimportant elsewhere (Guisan & Thuiller, 2005). To estimate the transferability of SDMs, several approaches have been applied (Thomas & Bovee, 1993; Randin *et al*., 2006; Vanreusel *et al*., 2006), based on a comparison of SDM predictive power within and outside the extent of training locations.

There are also ways of increasing transferability. It has been suggested that only mechanistic SDMs, based on an a priori knowledge of the ecophysiological requirements of a species, provide a reliable basis for the potential niche (Kearney & Porter, 2004; McPherson *et al*., 2006; Zarnetske, Edwards & Moisen, 2007), although relevant knowledge is very limited (Guisan & Thuiller, 2005). If an SDM is based on empirical occurrence data, one should expect higher transferability for simple models, not including assumptions whose relevance is difficult to test – such as interactions between the predictors. One example of this simple approach is climatic envelope analysis (Hijmans & Graham, 2006; Pearson *et al*., 2006), a straightforward methodology linking the suitability of a habitat with empirically identified tolerance limits, or its modifications, such as fuzzy envelope (FE) analysis (Skov & Svenning, 2004; Svenning & Skov, 2004). Bioclimatic envelope models provide a good first approximation on large geographical scales (Pearson & Dawson, 2003). In addition, transferable SDMs should be based only on the environmental predictors whose impact on a species has a simple and straightforward explanation.

We applied two approaches for inferring sufficiently powerful and, simultaneously, transferable suitable habitat models, prior to correcting the models using the post-glacial dispersal constraints: one focused on the increasing predictive power of a model within the training extent, and the other on a simple intuitive approach, based on fixed, expert-selected environmental predictors.

The purposes of our study included: (1) the development of sufficiently transferable suitable habitat models of the study species, based on the current distribution of climates; (2) the projection of the models for each species onto LGM conditions, according to two different palaeoclimatic simulations, and inferring the extent of LGM refugia; (3) refinement of the current SDMs by the incorporation of post-glacial dispersal constraints; and (4) testing of the predictive power of the refined SDMs, based on different palaeoclimatic simulations, within the geographical extent of the analysis, in order to identify which palaeoclimatic simulation was in better accordance with current species distributions (Fig. 2).

SELECTION OF THE MOST TRANSFERABLE DISTRIBUTION MODELS

As environmental predictors for SDM development, we used climatic grids downloaded from WorldClim Version 1.4 (http://www.worldclim.org/), a set of global climate layers with a spatial resolution of 5 km^2, which provide various parameters of temperature and precipitation at a global scale (Hijmans *et al*., 2005).

We applied two algorithms requiring presence-only datasets: FE analysis (Skov & Svenning, 2004) and the MD method (Clark, Dunn & Smith, 1993).

The analyses were based on two alternative approaches – an 'iterative' approach and an approach based on the expert selection of environmental predictors. In the 'iterative' approach, multiple models were developed, based on various combinations of climatic variables, with MD considering correlations among the predictors and FE excluding these correlations. For the iterative approach, we used six predictors: (1) mean annual temperature; (2) isothermality; (3) maximum temperature of the warmest month; (4) minimum temperature of the coldest month; (5) annual precipitation; and (6) precipitation seasonality. We developed multiple models including one to all six climatic variables in different combinations, such that all combinations with two or more predictors included at least one that described temperature (1, 2, 3, 4) and at least one that represented precipitation (5, 6). Thus, we had 45 combinations in total (Appendix). Based on each predictor combination, we developed 90 spatial models for each combination of the predictors and selected the MD and FE models with the highest predictive power for the training extent (hereafter referred to as 'iteratively fitted models') for further analyses.

As an alternative approach, we selected three predictors with a straightforward impact on the ecological performance of a wide range of biological species and applied the FE algorithm based on these predictors (fixed-predictor models). The predictors were the maximum temperature of the warmest month, minimum temperature of the coldest month and annual precipitation. Annual precipitation is routinely used as an important predictor in spatial models developed for both animals and plants. Temperature extremes may have lethal effects, and may be important at long time intervals (Barry & Elith, 2006).

Three-quarters of the occurrence locations of each species (training locations) were used for the development of the models, and the remaining presence locations (test locations) were used for model validation at a local scale. In order to test the predictive power of the derived models, we estimated the area under the curve (AUC) of the receiver operating characteristic (ROC) curve (Fielding & Bell, 1997; Hand & Till, 2001) based on the predicted probabilities of presence for test occurrence locations and 5000 random ('pseudo-absence') locations, generated within the study extent using the random point generator extension for ArcView GIS 3.x (Jenness, 2004). We applied shuffling (1000 permutations) to randomly subdivide the original occurrence datasets into test vs. training locations, and selected subsets of the test pseudo-absence locations equal in size to a set of test presence locations. For each permutation, the predicted probabilities of the test presence and test pseudo-absence locations and respective AUC values

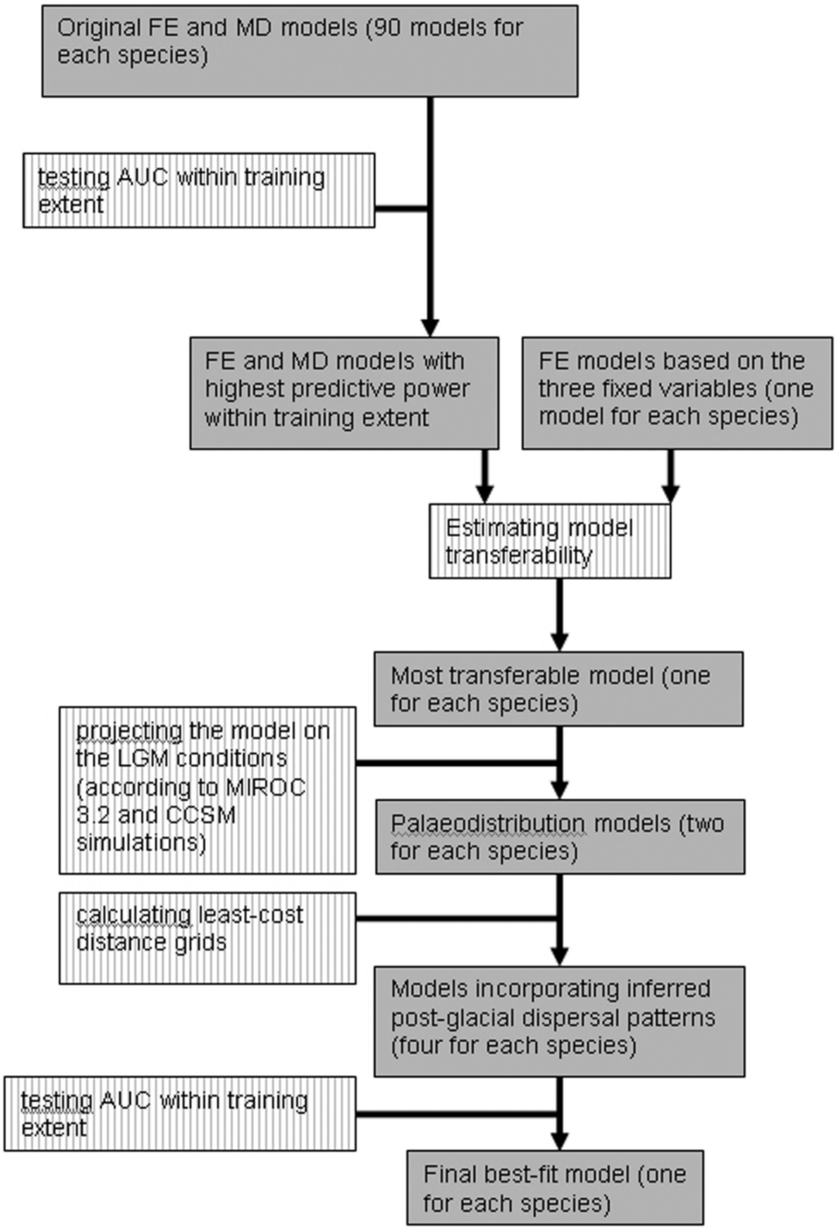


Figure 2. Diagram showing sequential steps in the modelling (see Methods section for explanations). AUC, area under the curve; CCSM, Community Climate System Model; FE, fuzzy envelope; LGM, Last Glacial Maximum; MD, Mahalanobis distance; MIROC, Model for Interdisciplinary Research on Climate.

were estimated, using Microsoft Excel; the mean AUC value over 1000 permutations was used as a final output. For the permutation procedure, we used 'shufflerows' and 'MonteCarlo methods' options in the Microsoft Excel application PopTools (Hood, 2010).

Based on test presence data from Europe, we tested the transferability level of iteratively fitted MD and FE models with the highest predictive power, and that of the fixed-predictor models. This was performed in order to select the model with the best transferability – that is, that which performed best in areas distant from the training extent. The best transferable model in space would be highly likely to retain its predictive power over time, which is important when considering making inferences in the remote past, typically with no validation data.

As a test European dataset, we downloaded or generated occurrence locations of the target species and their closest relatives/ecological counterparts (Supporting Information Table S2). *Abies alba*, *Picea abies*, *Fagus sylvatica*, *Helix pomatia* and *Chioglossa lusitanica* are closest or very close relatives of *A. nor-*

dmanianna, *P. orientalis*, *F. orientalis*, *H. buchi* + *H. goderdziana* and *M. caucasica*, respectively (Farjon, 1990; Veith *et al*., 1998; Denk *et al*., 2002; Schütt, 2005), and were used as their ecological counterparts in Europe. *Castanea sativa*, *C. betulus* and *R. ponticum* form natural or invasive populations in Europe. We did not test the transferability of the SDMs for *P. caucasicus*, *O. ophryticus*, *D. mixta* and *C. roberti*, because they do not have single, unequivocal ecological counterparts in the regions remote from western Asia. Because the test occurrence locations from Europe did not always cover the entire ranges of the species or their equivalents, we did not apply AUC analysis, but used omission error as an indicator of SDM transferability. We calculated median probability values and applied a Kruskall–Wallis nonparametric test in order to compare mean ranks of estimated probabilities for test European locations, based on the three competing models. A model with the highest mean rank/highest median value was assumed to be the most transferable. The significance of the difference between the competing models of the same species was tested with the Mann–Whitney nonparametric test.

Model projections were visualized using the ArcView GIS module *Spatial Analyst* (ESRI, Redlands, CA, USA) and the MD extension for ArcView GIS 3.x (Jenness, 2003).

Consideration of post-glacial dispersal patterns

We identified the 95th percentile cut-off of the most transferable models and projected the output onto LGM climatic conditions to infer the spatial distribution of glacial refugia. We used grids based on two palaeoclimatic models downscaled to a resolution of 5 km^2: the Community Climate System Model (CCSM) and the Model for Interdisciplinary Research on Climate (MIROC) (Braconnot *et al*., 2007). We selected these two climate models because of their high resolution and availability at the time of our study. The areas suitable for the target species under LGM conditions were defined as 'refugia'. Subsequent analyses were based on the incorporation of spatio-temporal autocorrelation into the current, most transferable models by including the distance from the boundaries of the refugia as an additional predictor in order to explain the current distribution of the study species.

Two sets of polygons of potential post-glacial dispersal sources were used for each species: (1) all continuous refugia throughout western Asia and the Caucasus region; and (2) only the refugia that fell within, overlapped or were geographically closest to the current distribution of the species. We derived least-cost distances from refugial polygons (hereafter referred to as REFDIST) based on the cost-distance algorithm in the ArcGIS module *Spatial Analyst* (ESRI). This algorithm considers a friction or cost grid that is a raster map in which each cell indicates the relative difficulty (cost) of moving through that cell. A least-cost path minimizes the sum of frictions of all cells along the path, and this sum is the least-cost distance (Adriaensen *et al*., 2003). In the calculation of cost-distances, we incorporated information about climate suitability to provide more realistic distances regarding the dispersal. We used elevation (source: the SRTM 1-km grid of elevation available at Global Land Cover Facility, 2010) as the surrogate for climate at a regional level to derive the cost-distance from the refugia. We assumed that the cost-distance between a refugium and a certain point accounted for not only the straight-line distance, but also the additional effort made by the species population to expand through inclement terrain to reach or colonize that point. The cost-distance grids were calculated separately for each studied species, and for CCSM and MIROC palaeoclimatic models. We developed one-sided fuzzy envelopes for REFDIST at four different settings for each studied species (Table 1). We tested a set of each of the four REFDIST predictors and climatic variables included in potential climatic niche models to validate our SDMs against the current distributions of the study species.

Finally, we estimated AUC of the spatial models by incorporating spatio-temporal autocorrelation, using the described permutation procedure. The models were not tested with the occurrence data outside the study extent, because distributions of the studied species in distant geographical areas relate to glacial refugia outside the western Asian region.

Figure 2 shows the interrelations between the sequential steps of the analysis.

RESULTS

Predictive power and transferability of iteratively fitted models

For most species, the highest AUC value at the training extent was obtained for either the MD or FE model that included three or more predictors. For each species, different combinations of the predictors produced the best statistically fitted models (Table 1, Appendix).

However, the transferability of most of the iteratively fitted FE and MD models was moderate or low (Table 1), as the respective spatial projections onto the whole of Europe and western Asia underpredicted the presence of the species in many regions in which they or their closest relatives occurred (Supporting Information Fig. S2). The omission error was particularly high for the MD-based models, but also substantial for iteratively fitted FE models (Table 1).

Table 1. Predictive power (area under the curve, AUC) and transferability (mean rank, MR, according to a Kruskall–Wallis test, and median probability, MP) of suitable spatial distribution models (SDMs) of the studied species inferred from a fixed-predictor fuzzy envelope (FE) model, iteratively fitted FE model and iteratively fitted Mahalanobis distance (MD) model

Model	*An*	*Po*	*Cs*	*Cb*	*Fo*	*Rp*	*Hb*	*Mc*	*Pc*	*Oo*	*Dm*	*Cr*
Fixed FE (variables)	T_{max} T_{min} AP	T_{max} T_{min} AP	T_{max} T_{min} AP	T_{max} T_{min} AP	T_{max} T_{min} AP	T_{max} T_{min} AP	T_{max} T_{min} AP	T_{max} T_{min} AP	T_{max} T_{min} AP	T_{max} T_{min} AP	T_{max} T_{min} AP	T_{max} T_{min} AP
Iteratively fitted FE (variables)	IT T_{max} AP	MT IT AP $\mathrm{P}_{\mathrm{var}}$	T_{min} AP $\mathrm{P}_{\mathrm{var}}$	MT IT AP $\mathrm{P}_{\mathrm{var}}$	T_{min} IT AP $\mathrm{P}_{\mathrm{var}}$	IT T_{max} $\mathrm{P}_{\mathrm{var}}$	T_{max} IT AP $\mathrm{P}_{\mathrm{var}}$	IT T_{max} $\mathrm{P}_{\mathrm{var}}$	IT T_{max} AP	IT T_{max} AP	IT AP $\mathrm{P}_{\mathrm{var}}$	IT T_{max} AP
Iteratively fitted MD (variables)	MT IT T_{min} $\mathrm{P}_{\mathrm{var}}$	MT IT T_{max} AP $\mathrm{P}_{\mathrm{var}}$	MT IT T_{min} AP	MT IT T_{max} T_{min} AP $\mathrm{P}_{\mathrm{var}}$	MT IT T_{max} T_{min} AP $\mathrm{P}_{\mathrm{var}}$	MT IT T_{max} T_{min} AP	MT IT T_{max} T_{min} $\mathrm{P}_{\mathrm{var}}$	MT IT T_{max} T_{min} P_{var}	MT IT T_{min} AP	MT IT T_{max} T_{min} AP	IT T_{min} AP	MT IT AP $\mathrm{P}_{\mathrm{var}}$
Fixed FE (AUC)	0.892	0.884	0.840	0.661	0.709	0.823	0.836	0.829	0.852	0.878	0.851	0.860
Iteratively fitted FE (AUC)	0.923	0.938	0.914	0.749	0.784	0.857	0.864	0.881	0.856	0.893	0.886	0.875
Iteratively fitted MD (AUC)	0.896	0.911	0.898	0.815	0.806	0.845	0.885	0.855	0.836	0.881	0.865	0.867
Fixed FE (MR)	14 497	11 202	5275	12 906	26 171	3693	8232	1039				
Iteratively fitted FE (MR)	6737	8524	4619	10 848	24 232	3583	7118	271				
Iteratively fitted MD (MR)	6226	9794	2487	3801	8404	1504	3471	772				
Fixed FE (MP)	0.497	0.134	0.396	1.000	1.000	1.000	0.499	1.000				
Iteratively fitted FE (MP)	0.000	0.100	0.286	1.000	0.950	1.000	0.236	0.000				
Iteratively fitted MD (MP)	0.000	0.001	0.000	0.000	0.001	0.000	0.000	0.000				

An, *Abies nordmanianna*; *Cb*, *Carpinus betulus*; *Cr*, *Chionomys roberti*; *Cs*, *Castanea sativa*; *Dm*, *Darevskia mixta* + *D. clarkorum*; *Fo*, *Fagus orientalis*; *Hb*, *Helix buchi* + *H. goderdziana*; *Mc*, *Mertensiella caucasica*; *Oo*, *Ommatotriton ophryticus*; *Pc*, *Pelodytes caucasicus*; *Po*, *Picea orientalis*; *Rp*, *Rhododendron ponticum*. Climatic predictors: 1, mean annual temperature (MT); 2, isothermality (IT); 3, maximum temperature of warmest month (T_{max}); 4, minimum temperature of coldest month (T_{min}); 5, annual precipitation (AP); 6, precipitation seasonality ($\mathrm{P}_{\mathrm{var}}$).

FIXED-PREDICTOR FE MODELS

The AUC values of the fixed-predictor FE models, based on the maximum temperature of the warmest month, minimum temperature of the coldest month and annual precipitation, exceeded 0.82 for all studied species except *F. orientalis*, but were lower than those of the iteratively fitted models (Table 1). Even minor differences were highly significant ($P < 0.001$), given 1000 permutations.

However, the transferability index of the FE models, based on the three fixed predictors, was higher than that of the iteratively fitted models (Table 1). The differences were significant for all studied species ($P < 0.001$, Mann–Whitney test).

Visually, the predicted suitable areas for the selected species covered the entire ranges of the studied species in western Asia and Europe, although the presence of some species or their relatives was overpredicted in northern and/or eastern Europe (Fig. S2).

In addition, spatial projection of the models onto the Caucasus and western Asia showed large areas beyond the actual distribution of some species, expanding the predicted ranges eastwards and southwards from their actual ranges (Fig. 4, left panel).

PROJECTION OF THE MOST TRANSFERABLE MODELS ONTO LGM CONDITIONS

The refugia, defined as projections of the most transferable models onto LGM land surfaces, showed similar ranges for all studied species. Throughout the Caucasus and western Asia, a large refugium with a suitable climate was concentrated along the southern and eastern Black Sea coast (Colchis), and smaller refugia occurred in the southern Caspian basin, at the eastern Mediterranean coast (the Levant) and throughout different parts of Anatolia (Fig. 3). The refugia were more fragmented according to the MIROC model than the CCSM model. The MIROC model, unlike the CCSM model, identified large refugia in western Anatolia, the westernmost Taurus Mountains and the upper reaches of the Tigris River, but showed fewer refugial areas at the southern Black Sea coast (Fig. 3).

MOST TRANSFERABLE MODELS INCORPORATING SPATIO-TEMPORAL AUTOCORRELATION

The inclusion of refugial distance in the most transferable models increased significantly the values of AUC for most of the species, relative to the original models. The AUC gain was particularly high when the distance was calculated from the refugia that spatially matched the current distributions (Table 2).

The REFDIST calculated from MIROC-based refugia yielded a greater increase in model predictive power than that based on the CCSM-based refugia. The increase in the predictive power of the SDMs, incorporating the distance from the MIROC-based refugia, was significant ($P < 0.001$) in all species except *O. ophryticus*; the corrected models of *A. nordmanianna*, *P. orientalis* and *C. sativa* had the highest predictive power. The increase in the predictive power of SDMs incorporating the distance from the CCSM-based refugia was not significant for *R. ponticum*, *P. caucasicus* and *O. ophryticus*, and the predictive power of all corrected models (except *O. ophryticus*) was lower than the models corrected using MIROC-based refugia.

Comparison of the models with the actual distribution maps (Fig. S1) showed qualitative improvement of the most transferable models with spatio-temporal autocorrelation, when compared with the models in which autocorrelation was not incorporated (Fig. 4). For all species, the SDMs incorporating refugial distance based on the MIROC climatic simulation showed higher specificity than the models that incorporated refugial distance based on the CCSM climatic simulation. The models calculated from the CCSM-based refugia overpredicted the presence of animals endemic to the Caucasus (*H. buchi* + *H. goderdziana*, *M. caucasica*, *P. caucasicus*, *D. mixta* + *D. clarkorum*, *C. roberti*) on the south-western Black Sea coast, whereas the models based on the MIROC simulation did not (Fig. 5).

DISCUSSION

The potential niche of a species, which defines the spatial distribution of suitable environments, only partly explains the observed distribution patterns (Pulliam, 2000; Guisan & Thuiller, 2005). In order to increase the predictive power of SDMs based on the analysis of abiotic environmental predictors, we should consider biotic interactions, metapopulation dynamics and dispersal limitations (Legendre, 1993; Gavashelishvili, 2004; Hampe, 2004; Svenning & Skov, 2004; Barry & Elith, 2006). The last two factors can be incorporated into SDMs by accounting for spatial or temporal autocorrelation patterns (Lichstein *et al*., 2002; Araújo *et al*., 2005; Randin *et al*., 2006). Our results show that factoring in a few environmental predictors and modelling post-glacial dispersal patterns improves the predictive power of spatial models for Caucasian forest species, whose ranges were reduced during glacial advances in the Pleistocene. The results also suggest that the distribution models based on different simulations of palaeoclimate are not equally powerful in explaining current distribution patterns, and that forest distri-

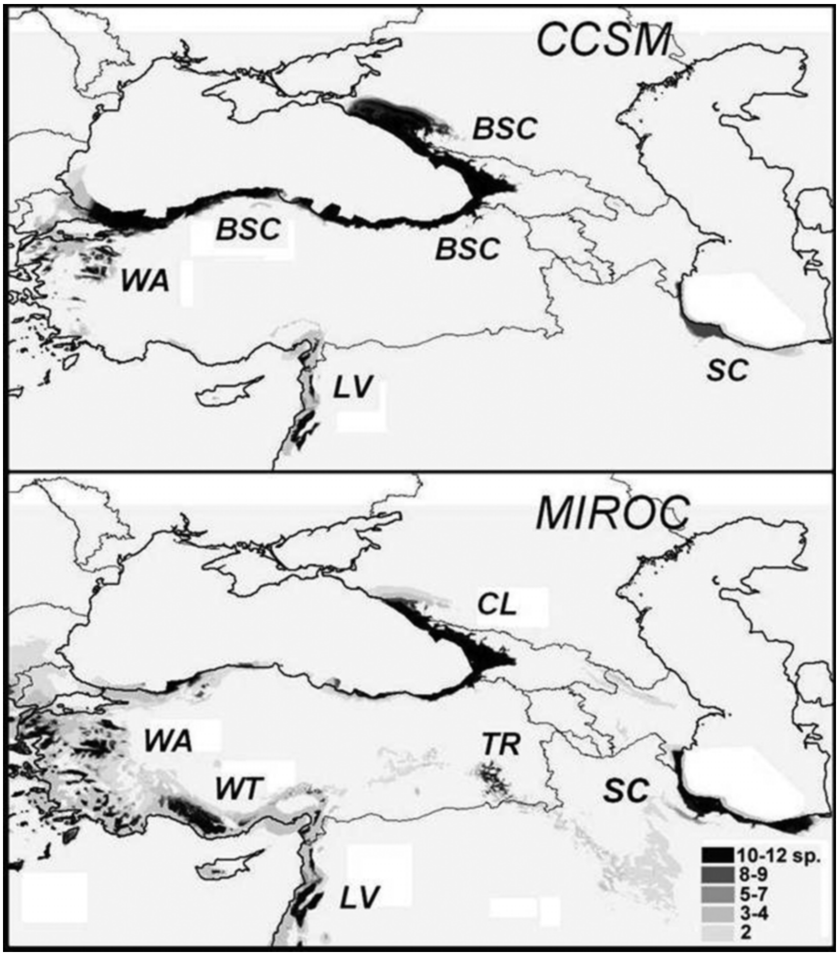


Figure 3. The distribution of climates suitable for the 12 forest plants and animals during the Last Glacial Maximum (LGM) throughout the Caucasus and western Asia. Shade intensity indicates the number of species out of the 12 for which the LGM climate was suitable. Our data show that the Model for Interdisciplinary Research on Climate (MIROC) climatic simulation provides a more realistic pattern of the LGM climate than the Community Climate System Model (CCSM) simulation. The CCSM-based inference indicates a large refugium throughout most of the Black Sea coast (BSC) and smaller refugia in western Anatolia (WA), the southern Caspian basin (SC) and the Levant (LV). The MIROC-based inference suggests that major refugia existed in Colchis (CL), the southern Caspian basin (SC), western Anatolia (WA), the western Taurus Mountains (WT), the upper reaches of the River Tigris (TR) and the Levant (LV). Contours in the maps show the current sea surface line and political borders.

Table 2. Predictive power (area under the curve, AUC) of the most transferable models (MTMs), based solely on habitat suitability and corrected by incorporating the post-glacial dispersal pattern. The Community Climate System Model (CCSM) and Model for Interdisciplinary Research on Climate (MIROC) are two different reconstructions of the palaeoclimate (see the text for details); 'alref' refers to all inferred continuous refugia for one species, whereas 'specref' refers to those refugia that overlap with the current range of the species. See Table 1 for abbreviations of the studied species. The standard error is below 0.001 for all cases at 1000 permutations. The highest AUC values are shown in bold type

Model	*An*	*Po*	*Cs*	*Cb*	*Fo*	*Rp*	*Hb*	*Mc*	*Pc*	*Oo*	*Dm*	*Cr*
MTM	0.892	0.884	0.840	0.661	0.709	0.823	0.836	0.829	0.852	**0.878**	0.851	0.860
CCSM_alref	0.909	0.894	0.872	0.746	0.732	0.806	0.841	0.863	0.858	0.874	0.863	0.870
MIROC_alref	0.911	0.897	0.864	**0.762**	**0.787**	0.820	0.832	0.873	0.845	0.870	0.863	0.858
CCSM_specref	0.912	0.913	0.891	0.746	0.732	0.818	0.869	0.870	0.857	0.872	0.881	0.879
MIROC_specref	**0.918**	**0.920**	**0.904**	**0.762**	**0.787**	**0.833**	**0.883**	**0.883**	**0.870**	0.870	**0.885**	**0.885**

Figure 4. Spatial projection of the most transferable models on the Caucasus and western Asia under current climatic conditions: left, uncorrected models; right, models corrected with the refugial distance. Dotted outlines indicate the areas in which the presence of a species is overpredicted. *An*, *Abies nordmanianna*; *Cb*, *Carpinus betulus*; *Cr*, *Chionomys roberti*; *Cs*, *Castanea sativa*; *Dm*, *Darevskia mixta* + *D. clarkorum*; *Fo*, *Fagus orientalis*; *Hb*, *Helix buchi* + *H. goderdziana*; *Mc*, *Mertensiella caucasica*; *Oo*, *Ommatotriton ophryticus*; *Pc*, *Pelodytes caucasicus*; *Po*, *Picea orientalis*; *Rp*, *Rhododendron ponticum*.

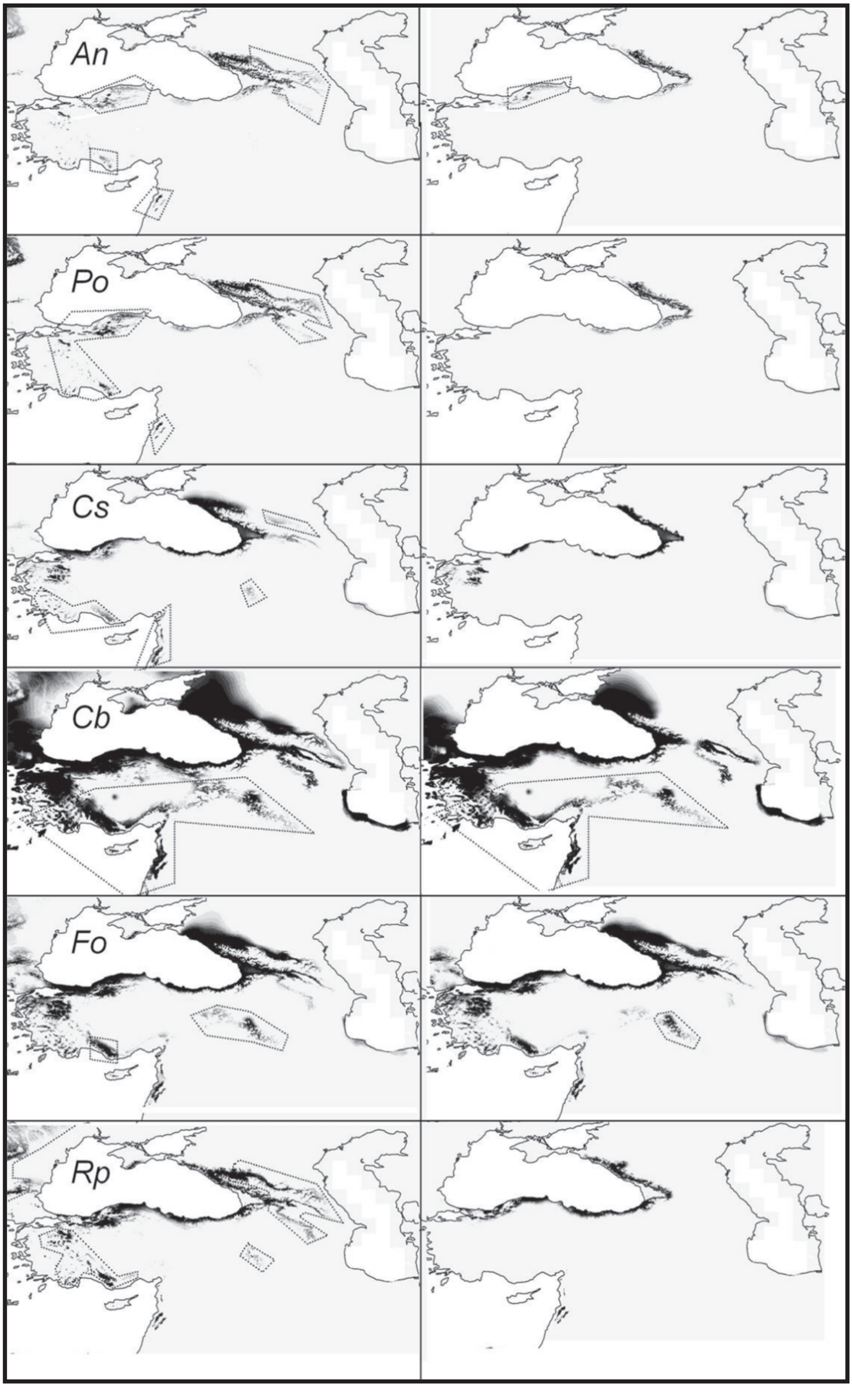
bution in western Asia during the LGM was considerably broader than is reflected in the existing pollen record (Van Andel and Tzedakis, 1996; Arslanov, Dolukhanov & Gei, 2007; Connor & Kvavadze, 2008).

FE models, which do not consider interactions between variables, had a higher predictive power within the training extent than the models that considered these interactions for all species except *F. orientalis* and *H. buchi* (Table 1). Fixed-predictor FE models had a higher transferability than the iteratively fitted models, but somewhat lower predictive power within the training extent. Apparently, this outcome is a result of overfitting of the training dataset. The selection of predictors based on expert ecological knowledge has clear advantages (Midgley *et al*., 2002; Kearney & Porter, 2004). This approach is commonly used for modelling suitable habitats (Hijmans & Graham, 2006; Pearson *et al*., 2006). Increased interest in the models of ancient ranges (Martínez-Meyer & Peterson, 2006; Davies *et al*., 2009) requires the availability of environmental variables for a sufficiently wide temporal and spatial scale. Climatic variables important for the survival of species (Midgley *et al*., 2002; Skov & Svenning, 2004) are not always available for distant geological periods. The three simple predictors selected for this study have an obvious impact on a broad range of living organisms, and the respective climatic grids are freely available for both present and glacial time (as well as for the predicted future).

Although the fixed-predictor FE models had only moderate predictive power on a local spatial scale, the incorporation of palaeoclimatic information into these models provided a reasonable improvement. The explanations of the observed distribution patterns, based on the dispersal hypothesis, appear to be more plausible in many cases than those based on complex hypotheses on the interaction between an organism and its environment. The Caucasian ranges of *R. ponticum*, *A. nordmanianna* and *P. orientalis* extend only slightly east to the boundaries of the inferred Colchis refugium. In contrast, the ranges of *F. orientalis* and *C. betulus* go far beyond this area, to the eastern Caucasus (Nakhutsrishvili, 1999). The forests of Colchis (where all listed species are sympatric) generally have a higher annual rainfall than the forests of eastern Georgia, where only beech and hornbeam are found. One can obtain an impression that the last two species are more resistant to the lack of humidity than the others. This is not true. The areas in the southern Black Sea coast west of Trabzon, where all five species coexist, have lower annual rainfall and colder winters than many areas of the eastern Caucasus. This also applies to variables more directly reflecting summer drought, including the ratio of the rainfall level to the sum of positive temperatures throughout the year. The simplest explanation of the observed distribution patterns is that all included species survived during the LGM at the Black Sea coast, but some failed to recolonize the central and eastern Caucasus during the Holocene.

In general, the diversity of species increases rapidly near the sources of post-glacial dispersal. The expansion of forests in the Caucasus was directed from the west to the east (Connor & Kvavadze, 2008), and more competitive trees and shrubs might have prevented the dispersal of the less competitive ones. This is in line with the suggestion that the distribution of plants typical for temperate rainforests, such as rhododendrons, is largely limited by the presence of competitors (Vetaas, 2002). Similarly, congeneric species have a substantial impact on the realized niche of *D. mixta* (Tarkhnishvili *et al*., 2010), and this may explain why this species failed to recolonize the areas east of the LGM refugium.

MIROC climatic grids better describe the current distribution patterns than do CCSM grids. Although the former model suggests the presence of isolated refugia in Colchis, the latter expands the boundaries of suitable climates west to the Bosporus with limited interruptions (Fig. 4). Consequently, the CCSM model fails to explain the presence of multiple species endemic to the western Caucasus (Zazanashvili *et al*., 2004), whereas the MIROC model explains this phenomenon well. Molecular genetic data also support the presence of isolated refugia in the western Caucasus. A number of Caucasian endemics have been isolated from their relatives throughout the world since the Pliocene, such as the Caucasian rhododendron (Milne, 2004), Caucasian salamander (Weisrock *et al*., 2001), Caucasian parsley frog (Garcia-Paris, Buchholz & Parra-Olea, 2003) and Caucasian grouse (Lucchini *et al*., 2001). All of these species have sister taxa in distant parts of Europe, East Asia and North America, but none in geographically close and potentially suitable habitats in western Turkey. A broad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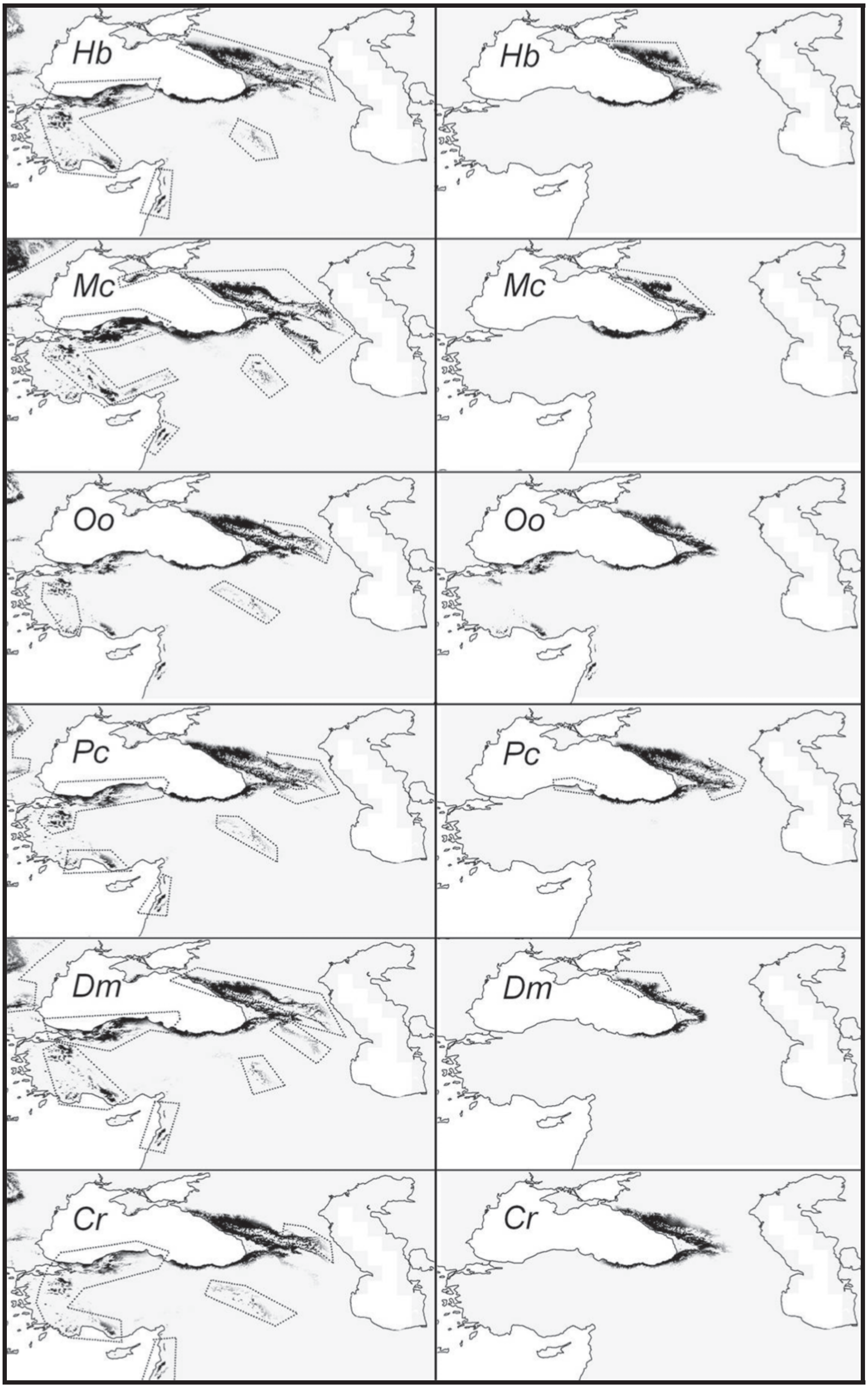

Figure 4. *Continued*

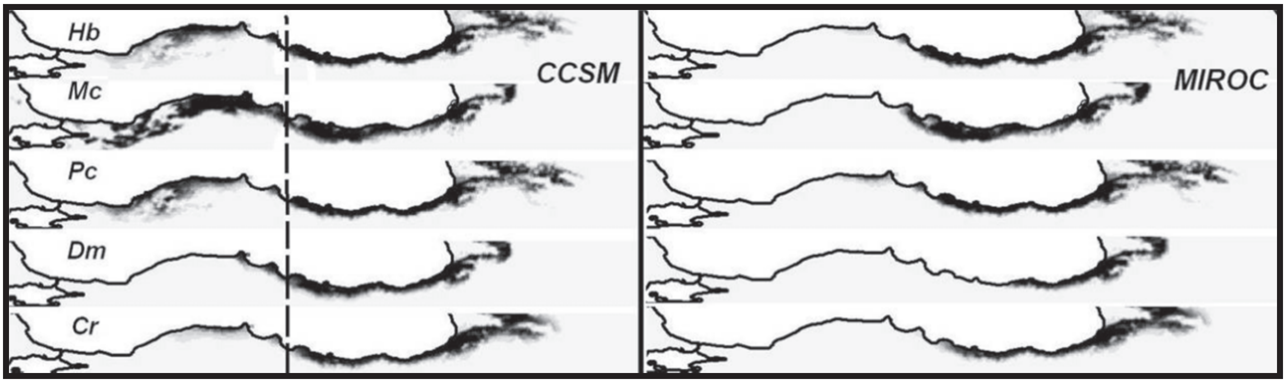

Figure 5. Southern coast of the Black Sea, with the predicted distribution of five endemic Caucasian animals, incorporating the distance from the Last Glacial Maximum (LGM) refugia, according to Community Climate System Model (CCSM) and Model for Interdisciplinary Research on Climate (MIROC) climate simulations. For abbreviations see Figure 3. The broken line indicates the current westernmost limit of the distribution of the species. CCSM simulation overpredicts the presence of all species at the south-western Black Sea coast, whereas MIROC simulation does not.

gap with unfavourable climate, which existed between the Colchis and western Anatolia during the LGM according to our MIROC-based model (Fig. 4), explains the limited current distribution of the listed species. Currently, a dry segment of the southern Black Sea coast between Ordu and Sinop in Turkey, where annual rainfall at the coast is below 700 mm and forest vegetation is scarce (Fig. 1), hinders the dispersal of the Caucasian endemics into north-western Anatolia. However, if the CCSM-based model is considered, we should expect a continuous distribution of suitable habitats along the southern Black Sea coast in LGM, and the absence of a number of Caucasian endemics from the south-western Black Sea coast becomes difficult to explain.

The reconstruction of the ancient suitable areas provides us with improved insight into the spatial position of glacial refugia, where forest-associated biological communities could survive the glacial period. Palynology suggests the presence of forests during the LGM in limited parts of Europe and western Asia (van Andel & Tzedakis, 1996). These areas are concentrated in the Alps, the Carpathians and along the south-eastern Black Sea coast. Beyond these major refugia, pollen records (Arslanov *et al*., 2007; Connor & Kvavadze, 2008) provide evidence of uninterrupted forest cover at the north-eastern Black Sea coast. However, there is a lack of pollen diagrams which could either confirm or reject the occurrence of forests in the rest of the modelled Colchis refugium earlier than 10 ky BP (Connor & Kvavadze, 2008). Did the forests actually occur in the areas predicted by the palaeodistribution models? Genetic studies support a pattern in line with the modelling results. *Mertensiella caucasica*, which is found exclusively in forests or near the timberline, has two evolutionary lineages isolated from each other since pre-glacial time (Tarkhnishvili *et al*., 2000, 2008). The eastern lineage is limited to the eastern part of the western Caucasus, i.e. the area outside the palynologically confirmed refugia. The same applies to *D. mixta* (Murphy *et al*., 2000). This means that the allopatric evolutionary lineages of the salamander and rock lizard independently survived the LGM in the south-western and eastern parts of the western Caucasus, and that the east of the inferred Colchis refugium had forests undetected so far in pollen profiles. The genetic data suggest that the actual distribution of forests in Colchis was more fragmented than predicted by the palaeodistribution models, but confirm that forests did exist in parts of Colchis, where palynological evidence is still lacking.

Our inference of the broader distribution of forests than that obtained from the available pollen records is in accordance with the outcomes of phylogeographical and vegetation studies. Van Zeist & Bottema (1991) postulated the presence of woodland during the LGM in parts of the Near East where the current forest distribution is limited (e.g. Levantine Mountains), based on the analysis of the current distribution of plants and the synthesis of palaeoecological data. The presence of multiple cryptic refugia in Europe (Provan & Bennett, 2008) and the isolation of evolutionary lineages of forest frogs and banded newts from the southern Caspian area and the Levant from their close relatives in Colchis since the Tertiary period support the presence of multiple, mesic, glacial refugia in western Asia (Veith *et al*., 2003; Litvinchuk *et al*., 2005). Our study suggests that, in all potential refugia, shown in Figure 4B, suitable climates existed during the LGM for temperate forest species, and this pattern provides a plausible explanation for their current distributions.

A comparison of the current distribution of suitable climates (Fig. 3) with the actual distribution of forests in western Asia (Fig. 1) suggests that the area of the potentially suitable climates for some tree species, including beech and hornbeam, is wider than the actual distribution. Even distribution models for these two species, corrected by the post-glacial dispersal constraints (Fig. 3, right panel), predict their presence in the western Tarsus and in the upper reaches of the Tigris. The most likely explanation of their absence in the indicated areas is deforestation caused by human activity, especially in the areas in which the human population has remained dense for thousands of years. In particular, the inferred refugium in the upper reaches of the Tigris River, where mesic forests are currently absent, is located in the specific small region of the Fertile Crescent, which has been suggested to be the cradle of agriculture (Diamond, 1997; Abbo, Lev-Yadun & Gopher, 2010). The human-caused deforestation in the Caucasus was less extensive in the past than in the south of the Middle East, although substantial transformation of forests in the historical past has been suggested for this area as well (Dolukhanov, 1966). The palynological record of the mid-Holocene suggests that forests existed in many potentially suitable, but nowadays treeless, agricultural areas (Connor & Kvavadze, 2008). The current vegetation of areas such as the upper reaches of the Tigris does not encourage vegetation scientists to hypothesize the presence of forest refugia there. Conversely, spatial modelling suggests the presence of a climate suitable for forest vegetation in a number of currently treeless regions.

The results of the present study suggest that, during the LGM, climates suitable for forest vegetation existed in six regions of western Asia: Colchis, western Anatolia, western Taurus, the upper reaches of the Tigris River, Levant and the southern Caspian basin. Figure 4B roughly outlines the spatial positions of these forest refugia, which could help to better understand the geographical distribution of plants and animals throughout the Near and Middle East. Further palaeobiological and phylogeographical studies may verify the exact position of the predicted refugia and add more details to the inferred pattern.

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REFERENCES

Abbo S, Lev-Yadun S, Gopher A. 2010. Agricultural origins: centers and noncenters; a near eastern reappraisal. *Critical Reviews in Plant Sciences* **29:** 317–328.

Adriaensen F, Chardon JP, De Blust G, Swinnen E, Villalba S, Gulinck H, Matthysen E. 2003. The application of 'least-cost' modelling as a functional landscape model. *Landscape and Urban Planning* **64:** 233–247.

Araújo MB, Whittaker RJ, Ladle R, Erhard M. 2005. Reducing uncertainty in projections of extinction risk from climate change. *Global Ecology and Biogeography* **14:** 529–538.

Arslanov KA, Dolukhanov PM, Gei NA. 2007. Climate, Black Sea levels and human settlements in Caucasus littoral 50 000–9000 BP. *Quaternary International* **167–168:** 121–127.

Barry S, Elith J. 2006. Error and uncertainty in habitat models. *Journal of Applied Ecology* **43:** 413–423.

Braconnot P, Otto-Bliesner B, Harrison S, Joussaume S, Peterschmitt J-Y, Abe-Ouchi A, Crucifix M, Driesschaert E, Fichefet T, Hewitt CD, Kageyama M, Kitoh A, Laîné A, Loutre M-F, Marti O, Merkel U, Ramstein G, Valdes P, Weber SL, Yu Y, Zhao Y. 2007. Results of PMIP2 coupled simulations of the Mid-Holocene and Last Glacial Maximum – Part 1: experiments and large-scale features. *Climate of the Past* **3:** 261–277.

Bukhnikashvili A. 2004. *On cadastre of small mammals Insectivora, Chiroptera, Lagomorpha, Rodentia of Georgia*. Tbilisi: Universal.

Clark JD, Dunn JE, Smith KG. 1993. A multivariate model of female black bear habitat use for a geographic information system. *Journal of Wildlife Management* **57:** 519–526.

Connor SE, Kvavadze EV. 2008. Modelling late Quaternary changes in plant distribution, vegetation and climate using pollen data from Georgia, Caucasus. *Journal of Biogeography* **36:** 529–545.

Cordellier M, Pfenninger M. 2009. Inferring the past to predict the future: climate modelling predictions and phylogeography for the freshwater gastropod *Radix balthica* Pulmonata, Basommatophora. *Molecular Ecology* **18:** 534–544.

Darevskii IS. 1967. *Rock lizards of the Caucasus: systematics, ecology and phylogenesis of the polymorphic groups of Caucasian rock lizards of the subgenus Archaeolacerta*. Leningrad: Nauka (in Russian, English translation published by the Indian National Scientific Documentation Centre, New Delhi, 1978).

Davies TJ, Purvis A, Gittleman JL. 2009. Quaternary climate change and the geographic ranges of mammals. *American Naturalist* **174:** 298–307.

Denk T, Frotzler N, Davitashvili N. 2001. Vegetational patterns and distribution of relict taxa in humid temperate forests and wetlands of Georgia Transcaucasia. *Biological Journal of the Linnean Society* **72:** 287–332.

Denk T, Grimm G, Stιgerer K, Langer M, Hemleben V. 2002. The evolutionary history of Fagus in western Eurasia: evidence from genes, morphology and the fossil record. *Plant Systematics and Evolution* **232:** 213–236.

Diamond J. 1997. Location, location, location: the first farmers. *Science* **278:** 1243–1244.

Dolukhanov AG. 1966. Rastitel'nyi Pokrov (Vegetation cover). In: Dumitrashko NV, ed. *Kavkaz*. Moscow: Nauka, 223–251. (in Russian).

EOS DATA GATEWAY. 2010. Available at: http://www.landcover.org/data/ (accessed at 11 October 2011).

Farjon A. 1990. Piinaceae, Drawings and Descriptions of the Genera: Abies, Cedrus, Pseudolarix, Keteleeria, Nothotsuga, Tsuga, Cathaya, Pseudotsuga, Larix and Picea. *Regnum Vegetabile*, Volume **121**. Koenigstein, Germany: Koeltz Scientific Books.

Fielding AH, Bell JF. 1997. A review of methods for the assessment of prediction errors in conservation presence–absence models. *Environmental Conservation* **24:** 38–49.

Fitzgerald RW, Lees BG. 1992. The application of neural networks to the floristic classification of remote sensing and GIS data in complex terrain. In: American Society of Photogrametry and Remote Sensing (ASPRS), ed. *Proceedings of the XVII Congress of ASPRS*. Bethesda, MD: ASPRS, 570–573.

Garcia-Paris M, Buchholz DR, Parra-Olea G. 2003. Phylogenetic relationships of Pelobatoidea re-examined using mtDNA. *Molecular Phylogenetics and Evolution* **28:** 12–23.

Gavashelishvili A. 2004. Habitat selection by East Caucasian tur *Capra cylindricornis*. *Biological Conservation* **120:** 391–398.

Global Land Cover Facility. 2010. Available at: http://www.landcover.org (accessed 11 October 2011).

Graham CH, Moritz C, Williams SE. 2006. Habitat history improves prediction of biodiversity in a rainforest fauna. *Proceedings of the National Academy of Sciences of the United States of America* **103:** 632–636.

Griffin SC, Taper ML, Hoffman R, Mills LS. 2010. Ranking Mahalanobis distance models for predictions of occupancy from presence-only data. *Journal of Wildlife Management* **74:** 1112–1121.

Guisan A, Thuiller W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* **8:** 993–1009.

Hampe A. 2004. Bioclimate envelope models: what they detect and what they hide. *Global Ecology and Biogeography* **13:** 469–471.

Hand DJ, Till RJ. 2001. A simple generalisation of the area under the ROC curve for multiple class classification problems. *Machine Learning* **45:** 171–186.

Hijmans RJ, Cameron SE, Parra JL, Jonesc PG, Jarvisc A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25:** 1965–1978.

Hijmans RJ, Graham C. 2006. The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology* **12:** 2272–2281.

Hood GM. 2010. PopTools version 3.2.3. Available on the internet. Available at: http://www.poptools.org (accessed 11 October 2011).

Hosmer D, Lemeshow S. 1989. *Applied logistic regression*. New York: John Wiley and Sons.

Jenness J. 2003. *Mahalanobis distances mahalanobis.avx. extension for ArcView 3.x. Jenness Enterprises*. Available at: http://www.jennessent.com/arcview/mahalanobis.htm (accessed 11 October 2011).

Jenness J. 2004. *Random point generator randpts.avx. extension for ArcView 3.x. Jenness Enterprises*. Available at: http://www.jennessent.com/arcview/random_points.htm (accessed 11 October 2011).

Kearney M, Porter WP. 2004. Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology* **85:** 3119–3131.

Kikvidze Z, Ohsawa M. 1999. Adjara, East Mediterranean refuge of Tertiary vegetation. In: Ohsawa M, Wildpret W, Arco MD, eds. *Anaga Cloud Forest, a comparative study on evergreen broad-leaved forests and trees of the Canary Islands and Japan*. Chiba: Chiba University Publications, 297–315.

Kryštufek B, Vohralík V. 2004. *Mammals of Turkey and Cyprus. Rodentia I: Sciuridae, Dipodidae, Gliridae, Arvicolinae*. Koper: Univerza na Primorskem.

Legendre P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* **74:** 1659–1673.

Lichstein JW, Simons TR, Shriner SA, Franzreb KE. 2002. Spatial autocorrelation and autoregressive models in ecology. *Ecological Monographs* **72:** 445–463.

Litvinchuk SN, Zuiderwijk A, Borkin LJ, Rosanov JM. 2005. Taxonomic status of *Triturus vittatus* Amphibia: Salamandridae in western Turkey: trunk vertebrae count, genome size and allozyme data. *Amphibia-Reptilia* **26:** 305–323.

Lucchini V, Hoglund J, Klaus S, Swenson J, Randi E. 2001. Historical biogeography and a mitochondrial DNA phylogeny of grouse and ptarmigan. *Molecular Phylogenetics and Evolution* **20:** 149–162.

Marsico TD. 2009. *Post-glacial migration, limitations to poleward range expansion, and growth responses to future climates of plants in the Garry oak ecosystem*. Notre Dame, IN: University of Notre Dame.

Martínez-Meyer E, Peterson AT. 2006. Conservatism of ecological niche characteristics in North American plant species over the Pleistocene-to-Recent transition. *Journal of Biogeography* **33:** 1779–1789.

McPherson JM, Jetz W, Rogers DJ. 2006. Using coarse-grained occurrence data to predict species distributions at finer spatial resolutions – possibilities and limitations. *Ecological Modelling* **192:** 499–522.

Midgley GF, Hannah L, Millar D, Rutherford MC, Powerie LW. 2002. Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Global Ecology and Biogeography* **11:** 445–451.

Milne RI. 2004. Phylogeny and biogeography of *Rhododendron* subsection *Pontica*, a group with a Tertiary relict distribution. *Molecular Phylogenetics and Evolution* **33:** 389–401.

Milne RI, Abbott RJ. 2002. The origin and evolution of

Tertiary relict floras. *Advances in Botanical Research* **38:** 281–314.

Mumladze L, Tarkhnishvili D, Pokryszko B. 2008. A new species of the genus *Helix* from south-western Georgia. *Journal of Conchology* **39:** 483–485.

Murphy RW, Fu J, MacCulloch RD, Darevsky IS, Kupriyanova LA. 2000. A fine line between sex and unisexuality: the phylogenetic constraints on parthenogenesis in lacertid lizards. *Zoological Journal of the Linnean Society* **130:** 527–549.

Nakhutsrishvili G. 1999. *Vegetation of Georgia*. Camerano: Braun-Blanquetia.

Nogués-Bravo D. 2009. Predicting the past distribution of species climatic niches. *Global Ecology and Biogeography* **18:** 521–531.

Normand S, Ricklefs RE, Skov F, Bladt J, Tackenberg O, Svenning J-C. 2011. Postglacial migration supplements climate in determining plant species ranges in Europe. *Proceedings of the Royal Society B*. DOI 10.1098/rspb.2010.2769.

Pearson RG, Dawson TP. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* **12:** 361–371.

Pearson RG, Thuiller W, Araújo MB, Brotons L, Martínez-Meyer E, McClean C, Miles L, Segurado P, Dawson TP, Lees D. 2006. Model-based uncertainty in species' range prediction. *Journal of Biogeography* **33:** 1704–1711.

Phillips SJ, Dudik M. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* **31:** 161–175.

Provan J, Bennett KD. 2008. Phylogeographic insights into cryptic glacial refugia. *Trends in Ecology and Evolution* **23:** 564–571.

Pulliam HR. 2000. On the relationship between niche and distribution. *Ecology Letters* **3:** 349–361.

Randin CF, Dirnböck T, Dullinger S, Zimmermann NE, Zappa M, Guisan A. 2006. Are niche-based species distribution models transferable in space? *Journal of Biogeography* **33:** 1689–1170.

Rotenberry JT, Preston CL, Knick AS. 2006. Gis-based niche modeling for mapping species' habitat. *Ecology* **87:** 1458–1464.

Schütt H. 2005. *Turkish land snails*. Solingen: Natur und Wissenschaft.

Signor PW. 1985. The geological history of diversity. *Annual Review of Ecology, Evolution, and Systematics* **21:** 509–539.

Skov F, Svenning J-C. 2004. Potential impact of climatic change on the distribution of forest herbs in Europe. *Ecography* **27:** 366–380.

Svenning JC, Normand S, Skov F. 2008. Postglacial dispersal limitation of widespread forest plant species in nemoral Europe. *Ecography* **31:** 316–326.

Svenning J-C, Skov F. 2004. Limited filling of the potential range in European tree species. *Ecology Letters* **7:** 565–573.

Tarkhnishvili D, Gavashelishvili A, Avaliani A, Murtskhvaladze M, Mumladze L. 2010. Unisexual rock lizard might be outcompeting its bisexual progenitors in the Caucasus. *Biological Journal of the Linnean Society* **101:** 447–460.

Tarkhnishvili D, Gokhelashvili R. 1999. *The Amphibians of the Caucasus*. Sofia: Pensoft Publications.

Tarkhnishvili D, Kaya U, Gavashelishvili A, Serbinova I. 2008. Ecological divergence between two evolutionary lineages of the Caucasian salamander: evidence from the GIS analysis. *Herpetological Journal* **18:** 155–163.

Tarkhnishvili D, Thorpe RS, Arntzen JW. 2000. Pre-Pleistocene refugia and differentiation between populations of the Caucasian salamander (*Mertensiella caucasica*). *Molecular Phylogenetics and Evolution* **14:** 414–422.

Thomas JA, Bovee KD. 1993. Application and testing of a procedure to evaluate transferability of habitat suitability criteria. *Regulated Rivers: Research and Management* **8:** 285–294.

Van Andel TH, Tzedakis PC. 1996. Palaeolithic landscapes of Europe and environs: 150 000–25 000 years ago: an overview. *Quaternary Science Reviews* **15:** 481–500.

Vanreusel W, Maes D, Van Dyck H. 2006. Transferability of species distribution models: a functional habitat approach for two regionally threatened butterflies. *Conservation Biology* **21:** 201–212.

Veith M, Schmidtler JF, Kosuch J, Baran I, Seitz A. 2003. Palaeoclimatic changes explain Anatolian mountain frog evolution: a test for alternating vicariance and dispersal events. *Molecular Ecology* **12:** 185–199.

Veith M, Steinfartz S, Zardoya R, Seitz A, Meyer A. 1998. A molecular phylogeny of 'true' salamanders (family Salamandridae) and the evolution of terrestriality of reproductive modes. *Journal of Zoological Systematics and Evolutionary Research* **36:** 7–16.

Vetaas OR. 2002. Realized and potential climate niches: a comparison of four rhododendron tree species. *Journal of Biogeography* **29:** 545–554.

Weisrock DW, Macey JR, Urugtas IH, Larson A, Papenfuss TJ. 2001. Molecular phylogenies and historical biogeography among salamandrids of the 'True' salamander clade: rapid branching of numerous highly divergent lineages in *Mertensiella luschani* associated with the rise of Anatolia. *Molecular Phylogenetics and Evolution* **18:** 434–448.

Willner W, Di Pietro R, Bergmeier E. 2009. Phytogeographical evidence for post-glacial dispersal limitation of European beech forest species. *Ecography* **32:** 1011–1018.

Zarnetske PL, Edwards TC Jr, Moisen GG. 2007. Habitat classification modeling with incomplete data: pushing the habitat envelope. *Ecological Applications* **17:** 1714–1726.

Zazanashvili N, Sanadiradze G, Bukhnikashvili A, Kandaurov A, Tarkhnishvili D. 2004. Caucasus. In: Mittermaier RA, Gil PG, Hoffmann M, Pilgrim J, Brooks T, Mittermaier CG, Lamoreux J, da Fonseca GAB, eds. *Hotspots revisited, Earth's biologically richest and most endangered terrestrial ecoregions*. Sierra Madre: CEMEX/Agrupacion Sierra Madre, 148–153.

van Zeist W, Bottema S. 1991. *Late Quaternary vegetation of the Near East*. Weisbaden: Reichert.

APPENDIX

AREA UNDER THE CURVE (AUC) VALUES FOR FUZZY ENVELOPE AND MAHALANOBIS DISTANCE MODELS BASED ON THE DIFFERENT NUMBERS AND COMBINATIONS OF CLIMATIC VARIABLES

Maximum values for both methods in shaded cells, as well as AUC values for the models based on the three bioclimatic variables: minimum and maximum annual temperatures (T_{min} and T_{max}, respectively) and annual precipitation (AP)

							Hb												*Hb*					
Variable	*An*	*Po*	*Cs*	*Cb*	*Fo*	*Rp*	FE	*Mc*	*Pc*	*Oo*	*Dm*	*Cr*	*An*	*Po*	*Cs*	*Cb*	*Fo*	*Rp*	MD	*Mc*	*Pc*	*Oo*	*Dm*	*Cr*
MT	0.802	0.825	0.537	0.308	0.442	0.411	0.437	0.459	0.382	0.432	0.472	0.462	0.839	0.849	0.529	0.317	0.439	0.406	0.491	0.456	0.341	0.425	0.466	0.469
IT	0.662	0.316	0.520	0.201	0.326	0.230	0.478	0.554	0.408	0.573	0.671	0.533	0.778	0.776	0.794	0.420	0.573	0.408	0.751	0.763	0.658	0.778	0.810	0.700
T_{max}	0.862	0.829	0.799	0.485	0.596	0.796	0.724	0.799	0.750	0.780	0.757	0.798	0.871	0.851	0.804	0.359	0.620	0.788	0.736	0.813	0.752	0.791	0.792	0.764
T_{min}	0.130	0.694	0.291	0.100	0.153	0.111	0.087	0.090	0.161	0.073	0.016	0.045	0.697	0.743	0.495	0.110	0.374	0.324	0.500	0.293	0.151	0.326	0.269	0.402
AP	0.785	0.022	0.839	0.031	0.611	0.698	0.796	0.711	0.809	0.843	0.807	0.813	0.818	0.786	0.817	0.181	0.668	0.378	0.766	0.090	0.718	0.637	0.457	0.808
$\mathrm{P}_{\mathrm{var}}$	0.753	0.706	0.761	0.517	0.594	0.684	0.622	0.677	0.538	0.663	0.680	0.627	0.738	0.726	0.770	0.482	0.597	0.690	0.651	0.665	0.568	0.655	0.732	0.642
MT,AP	0.860	0.867	0.864	0.695	0.672	0.738	0.818	0.752	0.823	0.843	0.817	0.829	0.835	0.842	0.843	0.412	0.736	0.804	0.824	0.783	0.791	0.816	0.811	0.828
MT,$\mathrm{P}_{\mathrm{var}}$	0.850	0.825	0.766	0.290	0.592	0.688	0.621	0.678	0.521	0.647	0.759	0.640	0.846	0.870	0.733	0.514	0.544	0.596	0.629	0.647	0.491	0.578	0.681	0.633
IT,AP	0.853	0.779	0.839	0.661	0.666	0.721	0.822	0.799	0.823	0.860	0.852	0.832	0.845	0.834	0.813	0.585	0.747	0.597	0.816	0.748	0.757	0.822	0.821	0.832
IT,$\mathrm{P}_{\mathrm{var}}$	0.884	0.338	0.872	0.179	0.743	0.766	0.827	0.860	0.769	0.851	0.876	0.819	0.850	0.841	0.843	0.730	0.746	0.775	0.830	0.807	0.766	0.808	0.858	0.812
T_{max},AP	0.879	0.858	0.881	0.747	0.678	0.812	0.838	0.823	0.856	0.880	0.851	0.863	0.840	0.845	0.834	0.432	0.726	0.788	0.830	0.794	0.797	0.829	0.828	0.822
T_{max},$\mathrm{P}_{\mathrm{var}}$	0.885	0.831	0.859	0.471	0.673	0.843	0.774	0.833	0.758	0.815	0.794	0.810	0.842	0.848	0.847	0.570	0.695	0.799	0.734	0.815	0.733	0.793	0.824	0.802
T_{min},AP	0.792	0.855	0.851	0.625	0.641	0.719	0.798	0.722	0.811	0.831	0.807	0.813	0.841	0.842	0.856	0.407	0.755	0.790	0.825	0.742	0.800	0.818	0.813	0.832
T_{min},$\mathrm{P}_{\mathrm{var}}$	0.756	0.699	0.790	0.079	0.623	0.703	0.630	0.681	0.555	0.660	0.661	0.620	0.791	0.809	0.783	0.557	0.579	0.612	0.652	0.549	0.439	0.598	0.697	0.649
MT,IT,AP	0.907	0.935	0.860	0.707	0.720	0.771	0.854	0.813	0.831	0.862	0.837	0.865	0.882	0.905	0.868	0.682	0.761	0.803	0.833	0.812	0.818	0.857	0.856	0.857
MT,IT,$\mathrm{P}_{\mathrm{var}}$	0.901	0.885	0.867	0.468	0.749	0.774	0.809	0.833	0.746	0.836	0.850	0.820	0.877	0.899	0.878	0.752	0.733	0.757	0.850	0.815	0.772	0.844	0.847	0.845
MT,T_{max},AP	0.880	0.870	0.882	0.635	0.692	0.812	0.829	0.816	0.839	0.868	0.838	0.851	0.870	0.897	0.860	0.736	0.772	0.828	0.837	0.832	0.811	0.843	0.841	0.845
MT,T_{max},$\mathrm{P}_{\mathrm{var}}$	0.884	0.826	0.857	0.289	0.671	0.833	0.761	0.831	0.741	0.807	0.802	0.799	0.860	0.891	0.857	0.707	0.763	0.800	0.792	0.814	0.759	0.808	0.813	0.814
MT,T_{min},AP	0.867	0.890	0.874	0.660	0.687	0.742	0.821	0.755	0.820	0.836	0.816	0.832	0.871	0.886	0.865	0.721	0.758	0.825	0.847	0.813	0.806	0.829	0.828	0.839
MT,T_{min},$\mathrm{P}_{\mathrm{var}}$	0.859	0.850	0.792	0.344	0.632	0.697	0.653	0.691	0.535	0.646	0.755	0.642	0.871	0.898	0.840	0.732	0.761	0.780	0.801	0.812	0.707	0.776	0.806	0.791
IT,T_{max},AP	0.923	0.782	0.868	0.610	0.724	0.814	0.853	0.859	0.856	0.893	0.874	0.875	0.886	0.894	0.880	0.683	0.753	0.797	0.858	0.824	0.811	0.858	0.852	0.852
IT,T_{max},$\mathrm{P}_{\mathrm{var}}$	0.908	0.337	0.866	0.179	0.749	0.857	0.833	0.881	0.805	0.871	0.883	0.848	0.874	0.879	0.886	0.732	0.742	0.828	0.854	0.832	0.798	0.847	0.862	0.846
IT,T_{min},AP	0.854	0.787	0.838	0.636	0.695	0.737	0.816	0.793	0.806	0.845	0.844	0.829	0.885	0.898	0.864	0.678	0.771	0.788	0.845	0.801	0.826	0.874	0.865	0.851
IT,T_{min},$\mathrm{P}_{\mathrm{var}}$	0.880	0.371	0.866	0.243	0.757	0.772	0.815	0.842	0.763	0.838	0.862	0.811	0.883	0.901	0.873	0.759	0.747	0.739	0.848	0.809	0.770	0.838	0.849	0.833
T_{max},T_{min},AP	0.892	0.884	0.840	0.661	0.709	0.823	0.836	0.829	0.852	0.878	0.851	0.860	0.871	0.889	0.865	0.755	0.773	0.821	0.847	0.825	0.819	0.848	0.836	0.847
T_{max},T_{min},$\mathrm{P}_{\mathrm{var}}$	0.887	0.852	0.858	0.512	0.681	0.837	0.774	0.823	0.763	0.804	0.781	0.816	0.861	0.894	0.857	0.733	0.771	0.807	0.806	0.828	0.746	0.808	0.815	0.817
MT,AP,$\mathrm{P}_{\mathrm{var}}$	0.888	0.861	0.905	0.686	0.730	0.799	0.846	0.790	0.841	0.858	0.857	0.844	0.871	0.892	0.877	0.714	0.761	0.840	0.830	0.837	0.818	0.832	0.857	0.840
IT,AP,$\mathrm{P}_{\mathrm{var}}$	0.890	0.776	0.883	0.649	0.772	0.829	0.853	0.855	0.854	0.878	0.886	0.862	0.883	0.880	0.873	0.732	0.778	0.756	0.843	0.807	0.793	0.839	0.846	0.851
T_{max},AP,$\mathrm{P}_{\mathrm{var}}$	0.893	0.854	0.868	0.739	0.729	0.844	0.860	0.839	0.853	0.882	0.863	0.871	0.880	0.883	0.868	0.689	0.758	0.812	0.814	0.819	0.810	0.840	0.832	0.838
T_{min},AP,$\mathrm{P}_{\mathrm{var}}$	0.847	0.849	0.914	0.613	0.742	0.800	0.849	0.808	0.847	0.865	0.862	0.851	0.861	0.896	0.854	0.741	0.775	0.838	0.832	0.810	0.823	0.838	0.855	0.842
MT,IT,T_{max},AP	0.848	0.882	0.866	0.464	0.736	0.814	0.846	0.843	0.838	0.875	0.843	0.869	0.885	0.913	0.889	0.798	0.786	0.831	0.854	0.837	0.818	0.861	0.850	0.861
MT,IT,T_{max},$\mathrm{P}_{\mathrm{var}}$	0.901	0.928	0.864	0.620	0.755	0.844	0.823	0.848	0.777	0.849	0.855	0.847	0.883	0.909	0.890	0.768	0.781	0.815	0.848	0.839	0.797	0.850	0.841	0.854
MT,IT,T_{min},AP	0.904	0.887	0.857	0.523	0.732	0.772	0.839	0.821	0.829	0.862	0.836	0.859	0.894	0.908	0.898	0.771	0.780	0.825	0.855	0.827	0.836	0.867	0.847	0.863
MT,IT,T_{min},$\mathrm{P}_{\mathrm{var}}$	0.898	0.929	0.865	0.657	0.752	0.760	0.816	0.839	0.762	0.835	0.854	0.827	0.896	0.914	0.895	0.779	0.774	0.796	0.858	0.836	0.782	0.836	0.862	0.843
MT,T_{max},T_{min},AP	0.888	0.844	0.889	0.367	0.698	0.813	0.832	0.820	0.840	0.882	0.845	0.850	0.875	0.912	0.874	0.755	0.782	0.841	0.843	0.833	0.824	0.873	0.831	0.844
MT,T_{max},T_{min},$\mathrm{P}_{\mathrm{var}}$	0.890	0.907	0.858	0.561	0.685	0.826	0.775	0.830	0.746	0.852	0.806	0.807	0.867	0.911	0.861	0.732	0.769	0.817	0.830	0.832	0.786	0.834	0.823	0.831
IT,T_{max},T_{min},AP	0.919	0.350	0.865	0.257	0.749	0.826	0.850	0.858	0.842	0.872	0.867	0.868	0.888	0.912	0.891	0.794	0.783	0.828	0.857	0.831	0.820	0.865	0.845	0.862
IT,T_{max},T_{min},$\mathrm{P}_{\mathrm{var}}$	0.903	0.706	0.866	0.563	0.761	0.855	0.826	0.866	0.804	0.850	0.868	0.847	0.893	0.907	0.885	0.776	0.785	0.817	0.865	0.841	0.797	0.849	0.852	0.851
MT,IT,AP,$\mathrm{P}_{\mathrm{var}}$	0.902	0.938	0.878	0.749	0.771	0.819	0.851	0.835	0.829	0.869	0.862	0.865	0.890	0.919	0.889	0.752	0.759	0.835	0.843	0.824	0.820	0.860	0.862	0.867
MT,T_{max},AP,$\mathrm{P}_{\mathrm{var}}$	0.886	0.905	0.903	0.702	0.730	0.830	0.847	0.831	0.844	0.871	0.835	0.860	0.885	0.914	0.879	0.790	0.798	0.842	0.831	0.836	0.812	0.847	0.852	0.842
MT,T_{min},AP,$\mathrm{P}_{\mathrm{var}}$	0.885	0.916	0.901	0.718	0.738	0.798	0.848	0.786	0.831	0.842	0.861	0.849	0.895	0.931	0.874	0.775	0.779	0.835	0.841	0.838	0.798	0.828	0.851	0.842
IT,T_{max},AP,$\mathrm{P}_{\mathrm{var}}$	0.909	0.834	0.874	0.703	0.768	0.850	0.864	0.867	0.854	0.889	0.870	0.869	0.891	0.919	0.878	0.741	0.757	0.820	0.847	0.832	0.810	0.854	0.847	0.855
IT,T_{min},AP,$\mathrm{P}_{\mathrm{var}}$	0.888	0.834	0.880	0.718	0.784	0.821	0.851	0.852	0.843	0.855	0.879	0.862	0.883	0.912	0.883	0.762	0.780	0.830	0.845	0.817	0.830	0.871	0.862	0.859
T_{max},T_{min},AP,$\mathrm{P}_{\mathrm{var}}$	0.893	0.893	0.912	0.717	0.743	0.848	0.854	0.847	0.854	0.870	0.869	0.864	0.889	0.914	0.873	0.797	0.796	0.830	0.843	0.837	0.808	0.844	0.854	0.847
MT,IT,T_{max},T_{min},AP	0.912	0.927	0.863	0.709	0.751	0.813	0.841	0.839	0.835	0.872	0.848	0.870	0.885	0.921	0.893	0.797	0.803	0.845	0.851	0.844	0.815	0.881	0.841	0.859
MT,IT,T_{max},T_{min},$\mathrm{P}_{\mathrm{var}}$	0.898	0.880	0.860	0.463	0.757	0.833	0.829	0.854	0.790	0.846	0.844	0.844	0.888	0.910	0.896	0.777	0.795	0.829	0.885	0.855	0.813	0.861	0.856	0.863
MT,IT,T_{max},AP,$\mathrm{P}_{\mathrm{var}}$	0.904	0.875	0.873	0.438	0.769	0.837	0.841	0.839	0.838	0.869	0.840	0.866	0.886	0.911	0.883	0.809	0.798	0.840	0.848	0.835	0.807	0.873	0.845	0.862
MT,IT,T_{min},AP,$\mathrm{P}_{\mathrm{var}}$	0.899	0.879	0.878	0.506	0.778	0.813	0.837	0.838	0.831	0.855	0.861	0.866	0.893	0.929	0.886	0.793	0.789	0.832	0.854	0.841	0.808	0.869	0.853	0.865
MT,T_{max},T_{min},AP,$\mathrm{P}_{\mathrm{var}}$	0.888	0.838	0.901	0.346	0.738	0.828	0.851	0.822	0.845	0.865	0.854	0.864	0.883	0.930	0.865	0.800	0.800	0.840	0.840	0.836	0.816	0.861	0.852	0.845
IT,T_{max},T_{min},AP,$\mathrm{P}_{\mathrm{var}}$	0.901	0.344	0.874	0.234	0.779	0.843	0.851	0.855	0.844	0.864	0.866	0.867	0.889	0.910	0.882	0.809	0.800	0.834	0.858	0.839	0.818	0.871	0.848	0.857
MT,IT,T_{max},T_{min},AP,$\mathrm{P}_{\mathrm{var}}$	0.895	0.909	0.867	0.739	0.776	0.829	0.842	0.837	0.826	0.864	0.847	0.860	0.678	0.865	0.880	0.815	0.806	0.838	0.859	0.851	0.813	0.872	0.843	0.860

An, *Abies nordmanianna*; *Cb*, *Carpinus betulus*; *Cr*, *Chionomys roberti*; *Cs*, *Castanea sativa*; *Dm*, *Darevskia mixta* + *D. clarkorum*; *Fo*, *Fagus orientalis*; *Hb*, *Helix buchi* + *H. goderdziana*; *Mc*, *Mertensiella caucasica*; *Oo*, *Ommatotriton ophryticus*; *Pc*, *Pelodytes caucasicus*; *Po*, *Picea orientalis*; *Rp*, *Rhododendron ponticum*. IT, isothermality; MT, mean annual temperature; $\mathrm{P}_{\mathrm{var}}$, precipitation seasonality.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Maps of occurrence locations for 12 plants and animals, used as training locations for spatial modelling. *An*, *Abies nordmanianna*; *Cb*, *Carpinus betulus*; *Cr*, *Chionomys roberti*; *Cs*, *Castanea sativa*; *Dm*, *Darevskia mixta* + *D. clarkorum*; *Fo*, *Fagus orientalis*; *Hb*, *Helix buchi* + *H. goderdziana*; *Mc*, *Mertensiella caucasica*; *Oo*, *Ommatotriton ophryticus*; *Pc*, *Pelodytes caucasicus*; *Po*, *Picea orientalis*; *Rp*, *Rhododendron ponticum*.

Figure S2. Iteratively fitted and fixed-predictor models of suitable climates for four plant and two animal species projected on Europe: *A*, iteratively fitted Mahalanobis distance models; *B*, iteratively fitted fuzzy envelope (FE) models; *C*, fixed-predictor FE models; *D*, European range of a species or its ecological equivalent. *1*, *Abies nordmanianna*; *2*, *Picea orientalis*; *3*, *Castanea sativa*; *4*, *Carpinus betulus*; *5*, *Fagus orientalis*; *6*, *Rhododendron ponticum*; *7*, *Helix buchi* + *H. goderdziana*; *8*, *Mertensiella caucasica*. See Table 1 for transferability estimates.

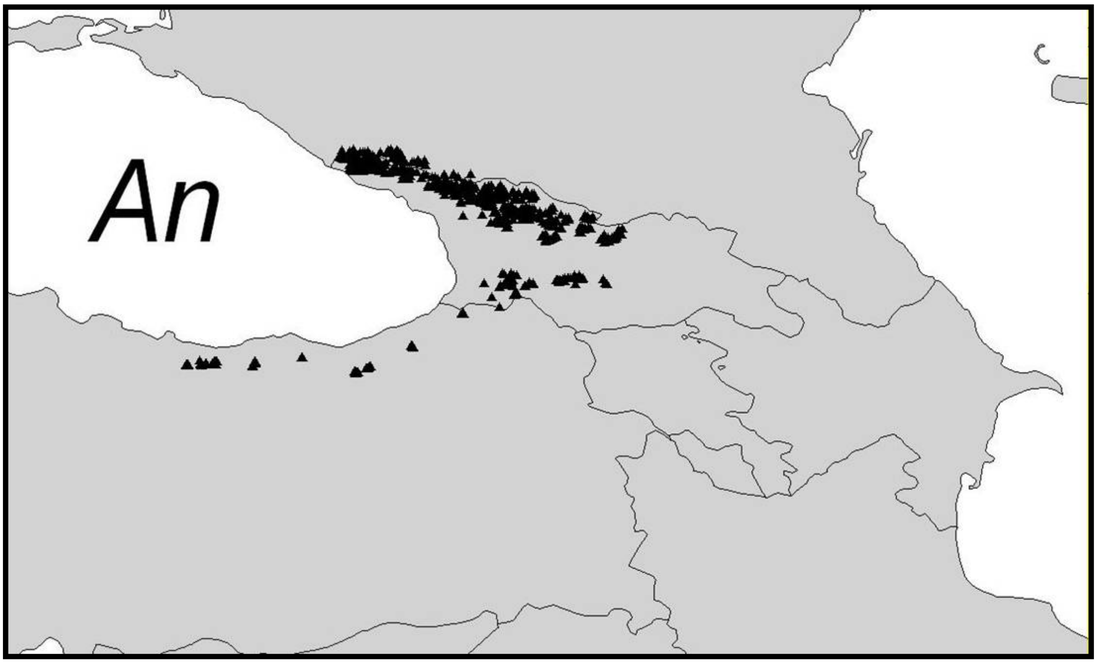
Table S1. Species occurrence data from the Caucasus Ecoregion.

Table S2. Data sources for testing model transferability (occurrence data for the target species or their ecological equivalents from Europe).

Table S1. Species occurrence data from the Caucasus Ecoregion.

Species	Sample size of locations	source
Abies nordmanianna (An)	671	Locations accurate to < 500 m, extracted from the 1:50,000 Soviet Military Topographic maps (Headquarters of Geodesy and Cartography under the Council of Ministers of the USSR. 1955-1976, Facility No. 11); Authors' GPS records (NE Turkey; 2007-2010).
Picea orientalis (Po)	500	
Castanea sativa (Cs)	189	
Carpinus betulus (Cb)	1000	
Fagus orientalis (Fo)	282	
Rhododendron ponticum (Rp)	42	Authors' GPS records (2006-2010).
Helix buchi + H. goderdziana (Hb)	42	Authors' GPS records (2006-2010).
Mertensiella caucasica (Mc)	52	GPS locations (Tarkhnishvili *et al*. 2008)
Ommatotriton ophryticus (Oo)	31	Locations accurate to < 500 m (Tarkhnishvili & Gokhelashvili 1999); Authors' GPS records (1983-2010)
Pelodytes caucasicus (Pc)	56	
Darevskia mixta + D. clarkorum (Dm)	34	Locations accurate to < 2 km (Darevskii 1967) ; Authors' GPS records (2008-2010)
Chionomys roberti (Cr)	78	Locations accurate to < 5 km (Bukhnikashvili 2004; Kryštufek & Vohralík 2004)

Fig. S1. Maps of occurrence locations for 12 plants and animals, used as training locations for spatial modeling. *An - Abies nordmanianna, Pc – Picea orientalis, Cs - Castanea sativa, Cb – Carpinus betulus, Fo - Fagus orientalis, Rp - Rhododendron ponticum, Hb - Helix buchi+goderdziana, Mc - Mertensiella caucasica, Pc - Pelodytes caucasicus, Oo - Ommatotriton ophryticus, Dm - Darevskia mixta+ clarkorum, Cr - Chionomys roberti.*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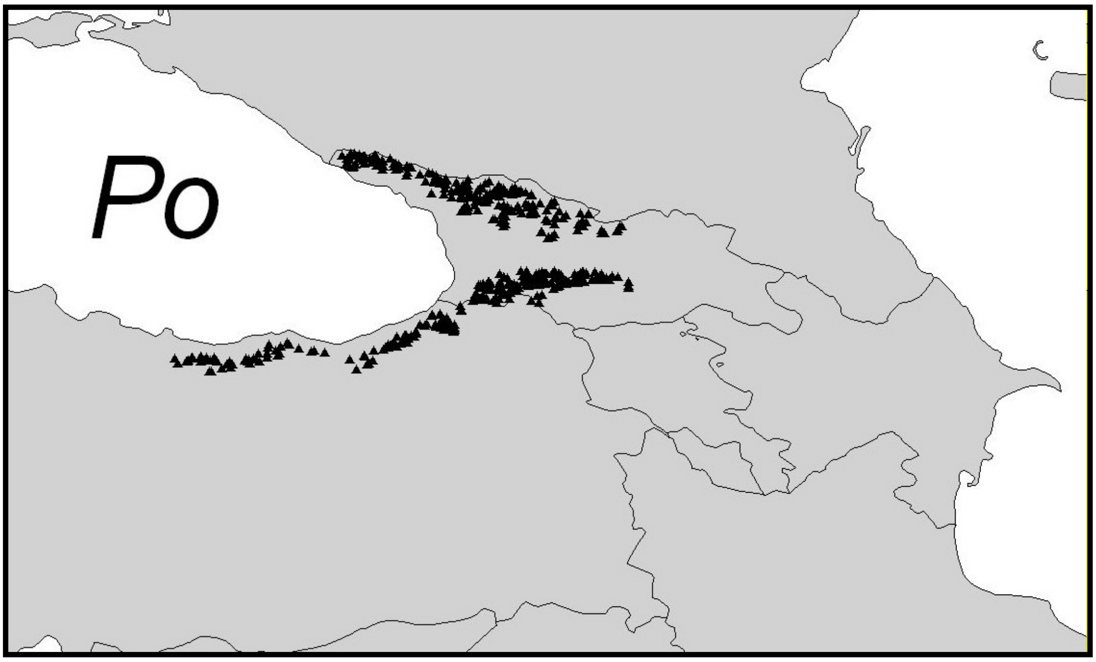
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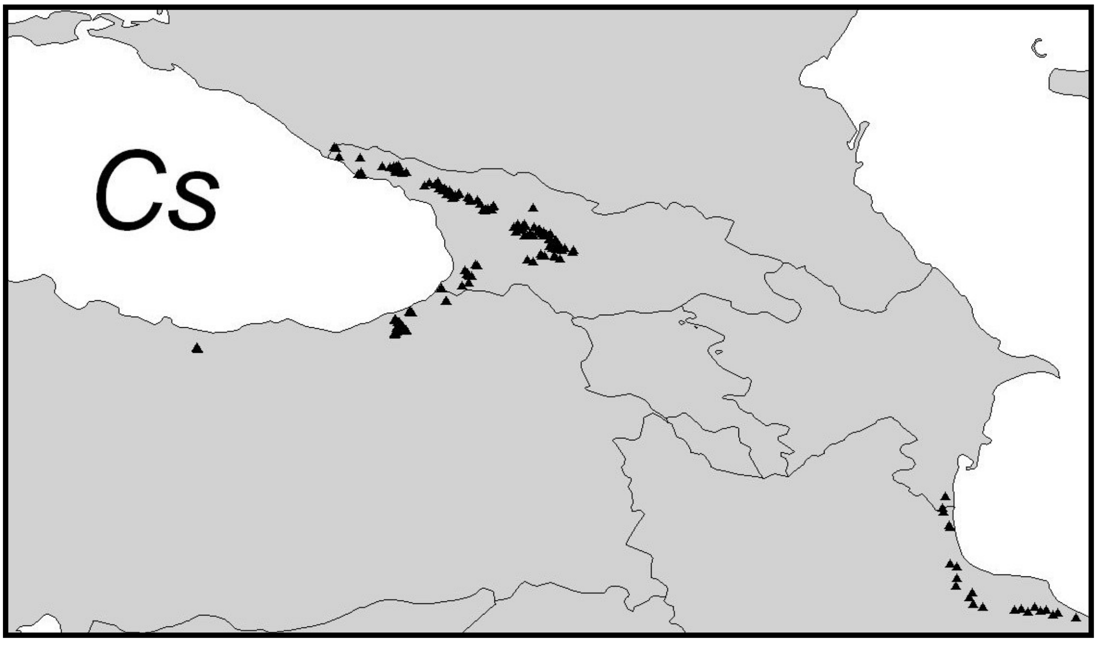
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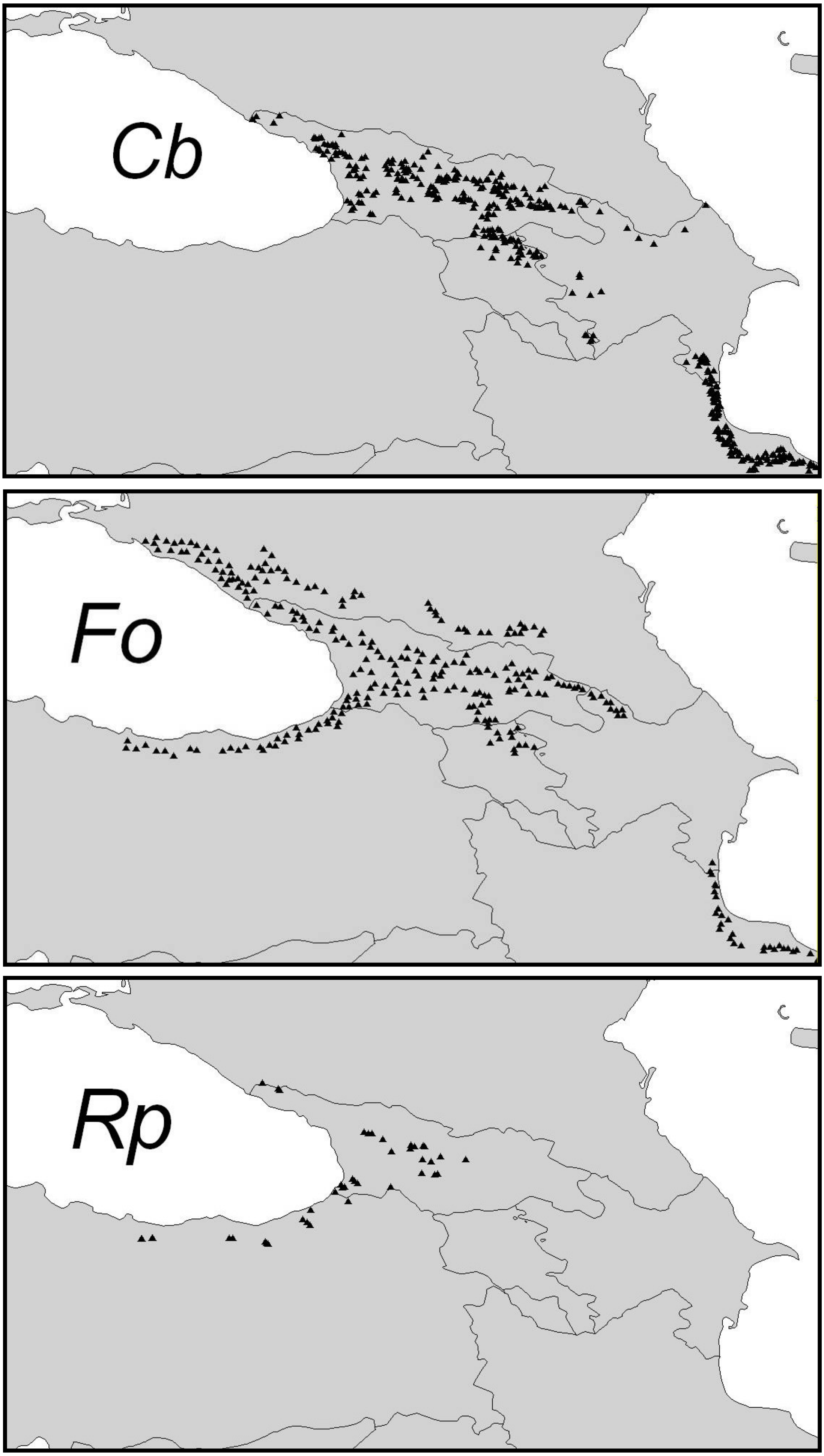
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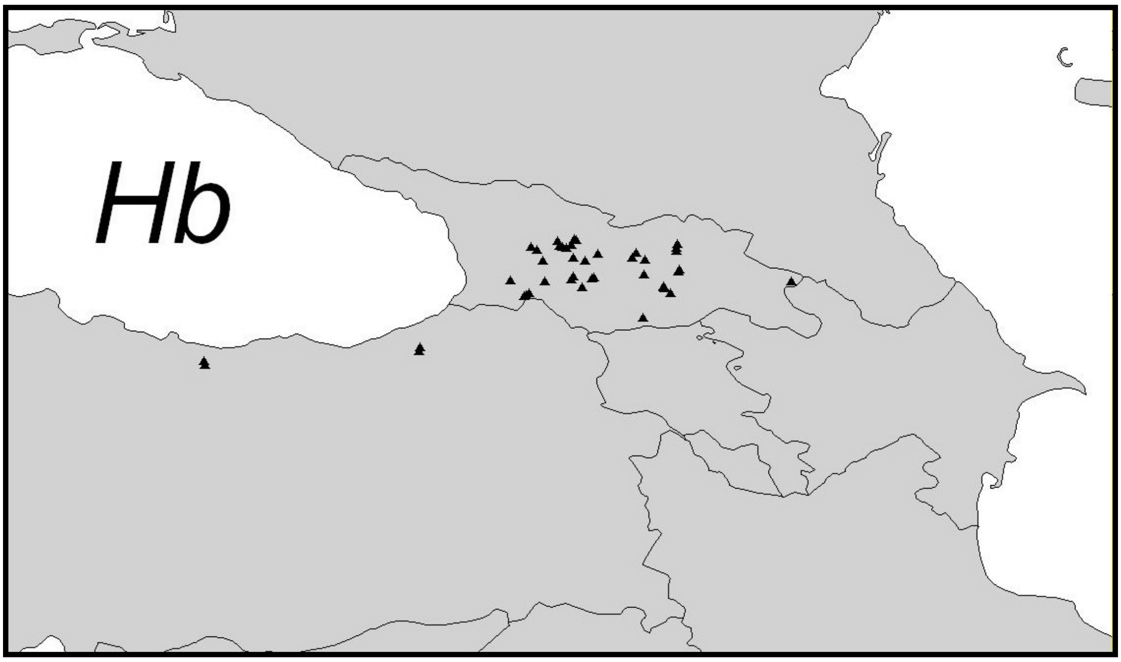

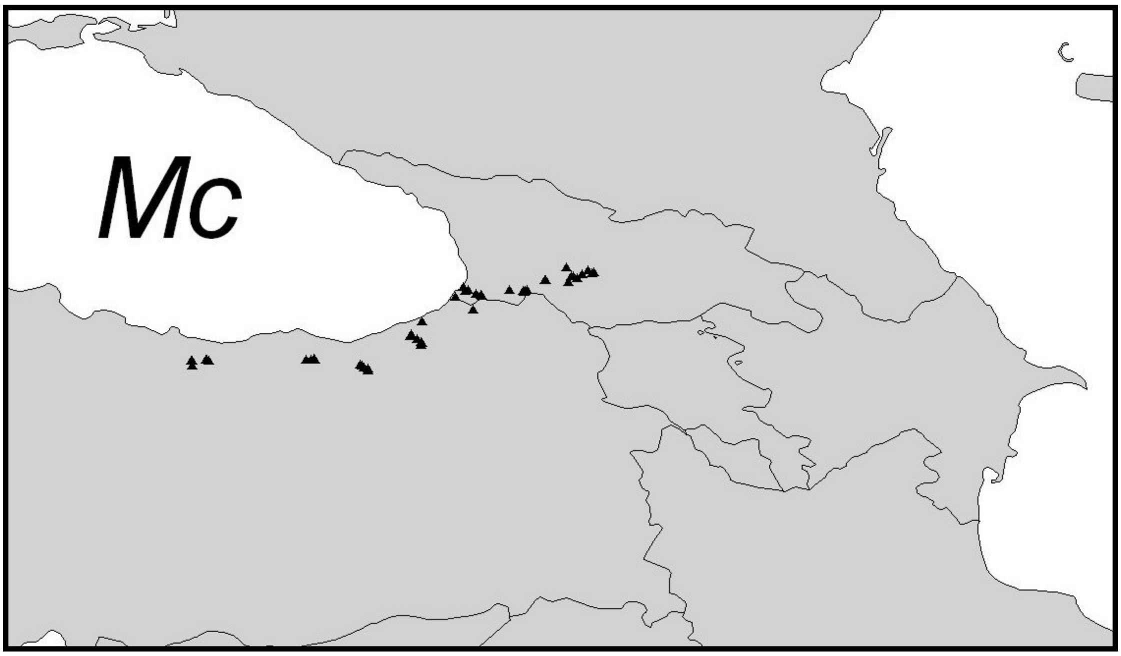

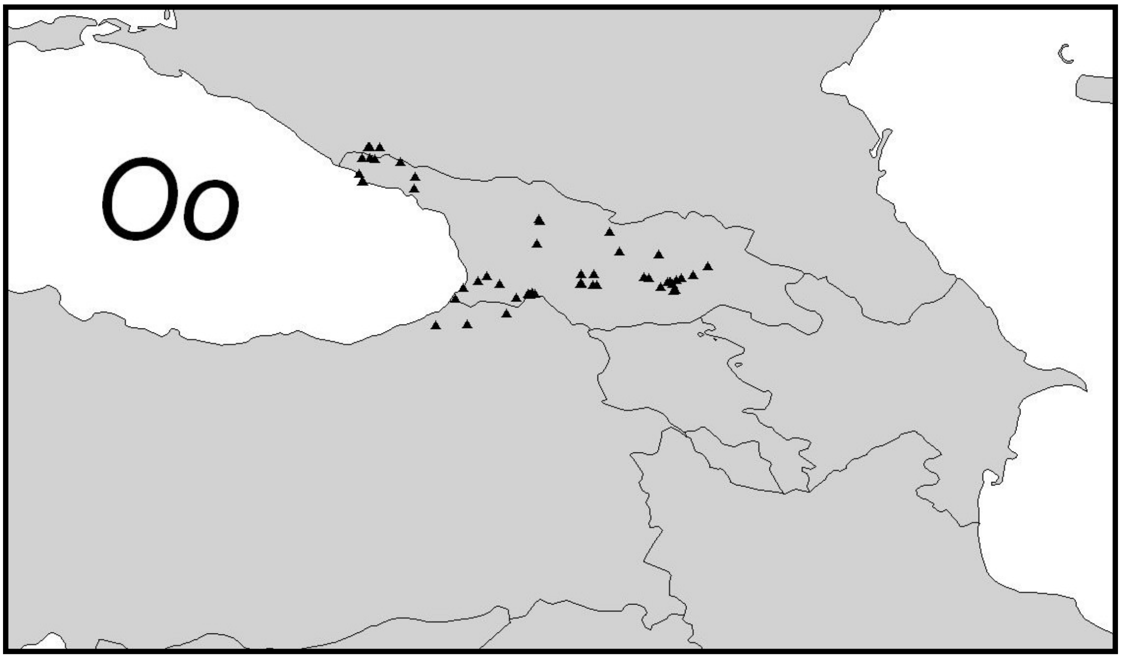

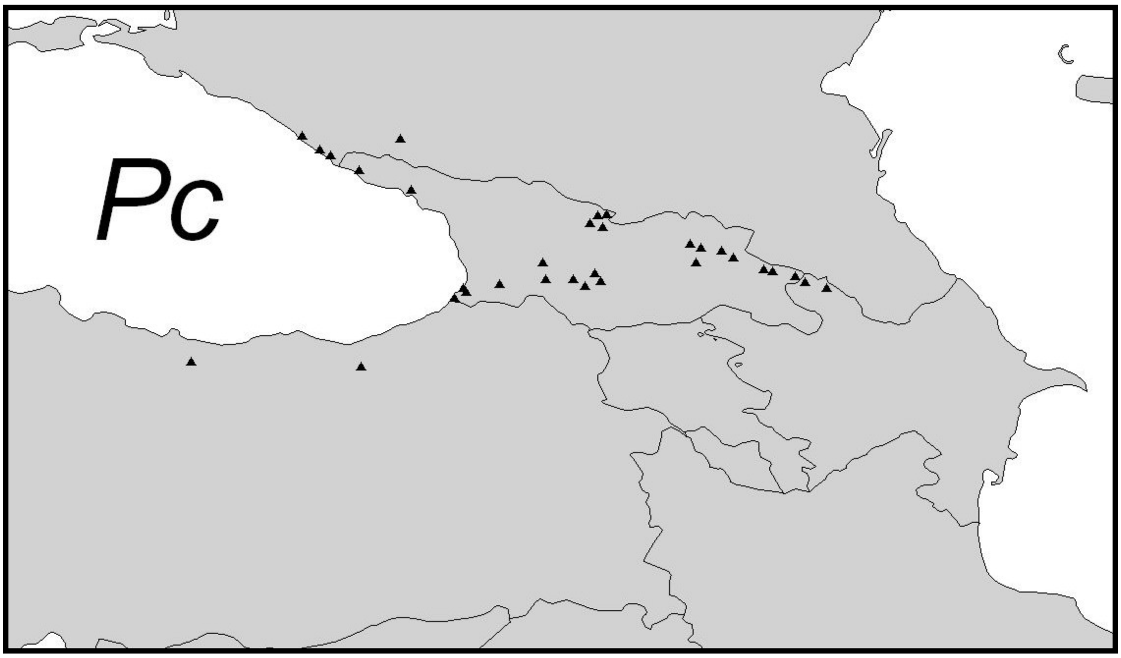
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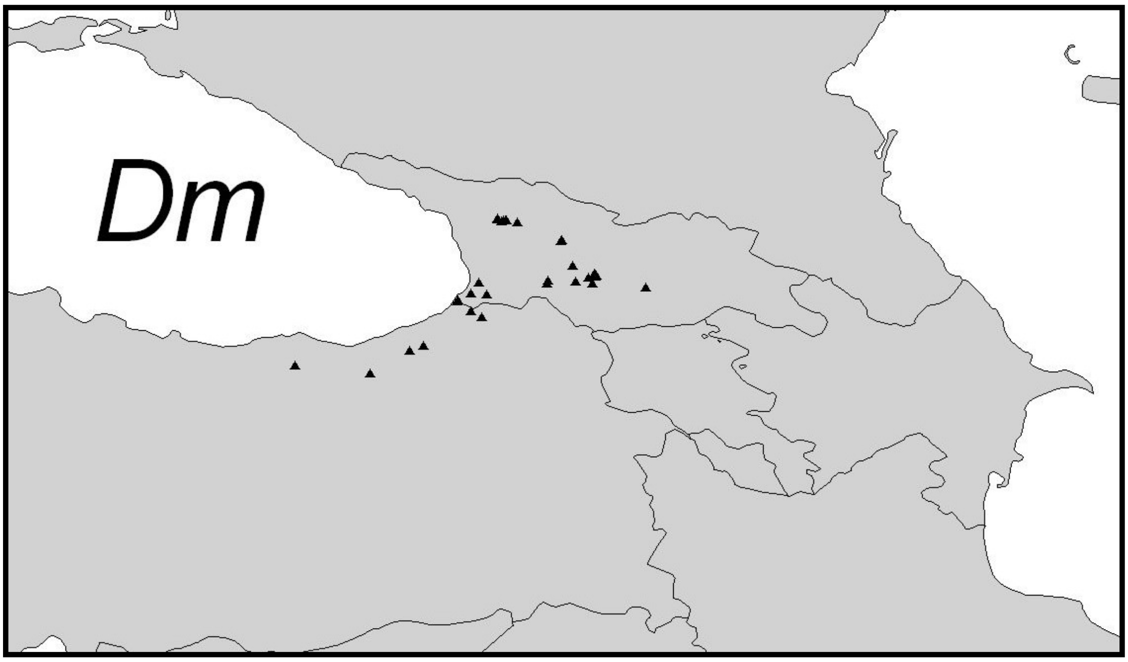
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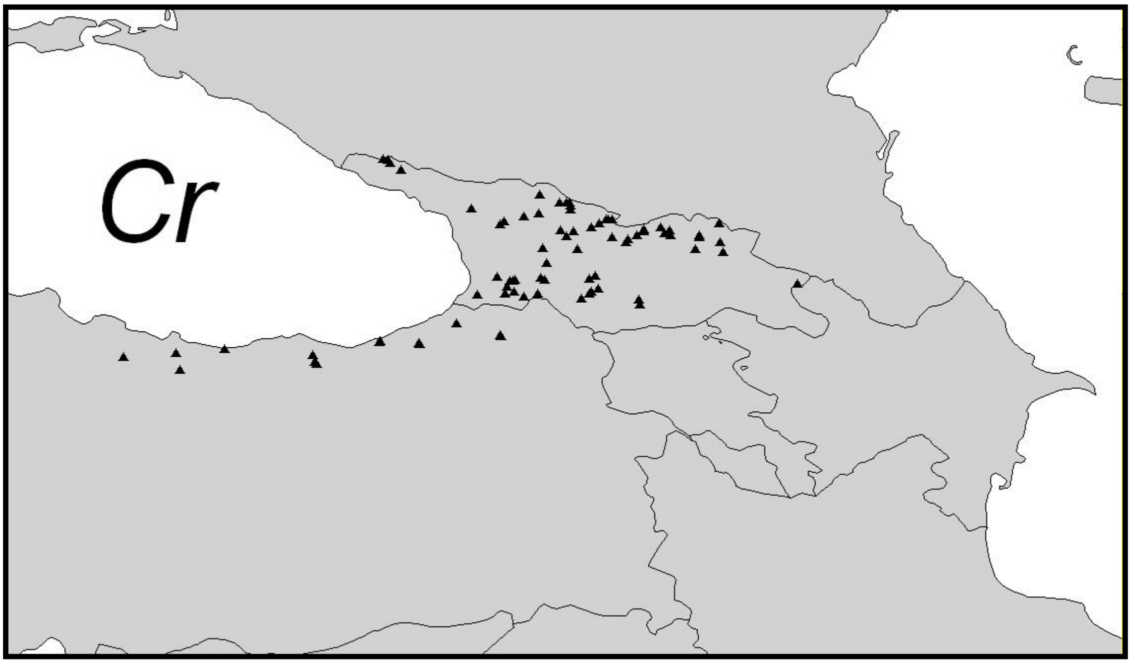
Cr

Fig. S2. Iteratively-fit and fixed-predictor models of suitable climates for four plant and two animal species projected on Europe. *A* - iteratively-fit Mahalanobis Distance models; *B* - iteratively-fit Fuzzy Envelope models; *C* - fixed-predictor FE models; *D* – European range of a species or its ecological equivalent. *1- Abies nordmanianna, 2 – Picea orientalis, 3 - Castanea sativa, 4 – Carpinus betulus, 5 - Fagus orientalis, 6 - Rhododendron ponticum, 7 - Helix buchi+goderdziana, 8 - Mertensiella caucasica.* See Table 1 for transferability estimates.

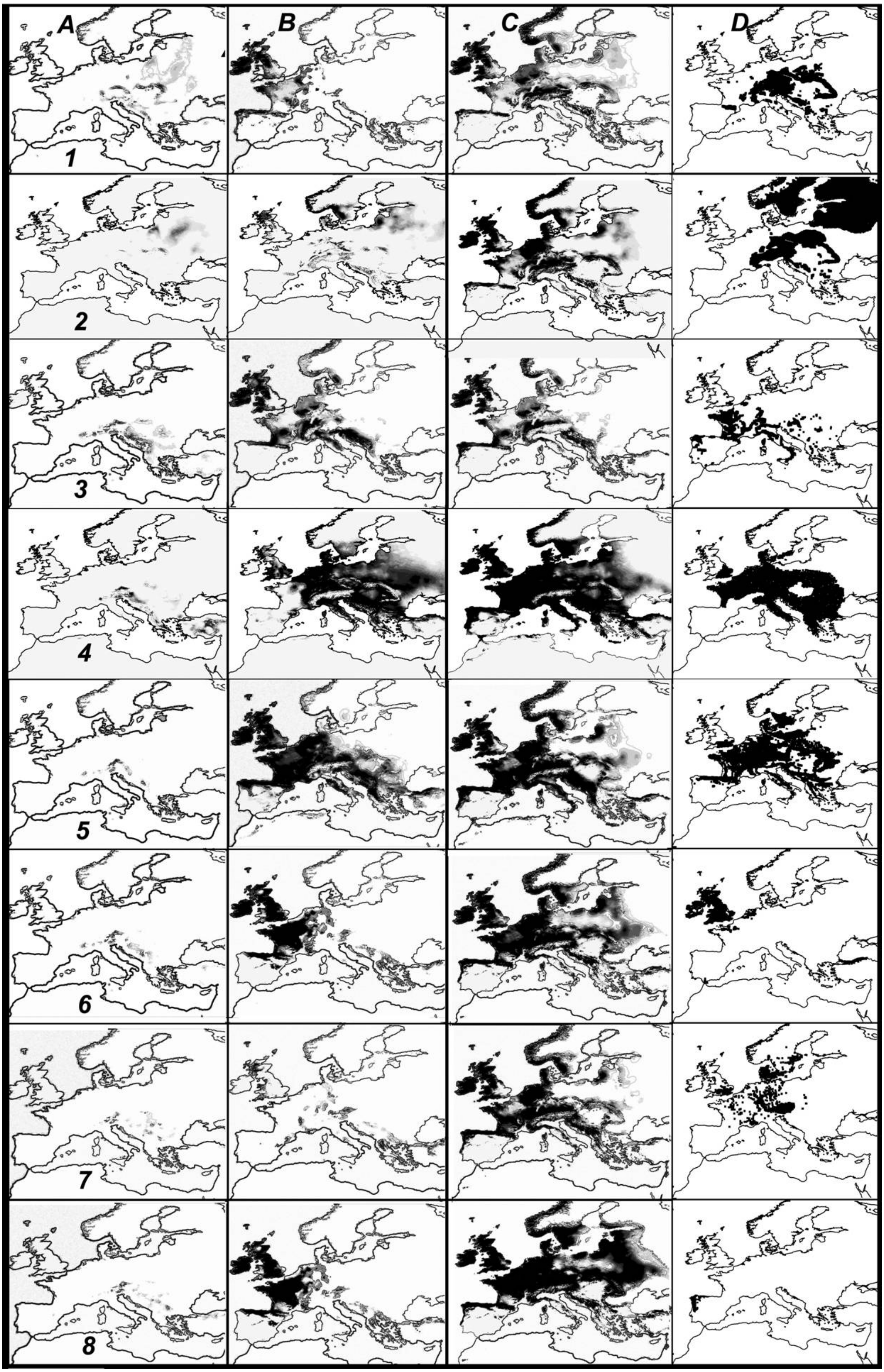

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Table S3. Data sources for testing model transferability (occurrence data for the target species or their ecological equivalents from Europe)

1. Data for testing transferability of SDMs developed for *Abies nordmanianna*: 6103 locations generated within the European range of *Abies alba,* according to: Wolf, H. 2003. EUFORGEN Technical Guidelines for genetic conservation and use for Silver fir (*Abies alba*). International Plant Genetic Resources Institute, Rome, Italy. 6 p.

2. Data for testing transferability of SDMs developed for *Picea orientalis*: 7000 locations generated within the European range of *Picea abies,* according to: Skrøppa, T. 2003. EUFORGEN Technical Guidelines for genetic conservation and use for Novrey spruce (*Picea abies*). International Plant Genetic Resources Institute, Rome, Italy. 6 p.

3. Data for testing transferability of SDMs developed for *Castanea sativa*: 2772 locations generated within the European range of *Castanea sativa,* according to: Josefa Fernandez-Lopez, J and Alia, R. 2003. EUFORGEN Technical Guidelines for genetic conservation and use for chestnut (*Castanea sativa*). International Plant Genetic Resources Institute, Rome, Italy. 6 p.

4. Data for testing transferability of SDMs developed for *Carpinus betulus*: 6147 locations of *Carpinus betulus*, extracted from Global Biodiversity Information Facility (GBIF) Data Portal (accessed through www.gbif.org, 2011-01-20).

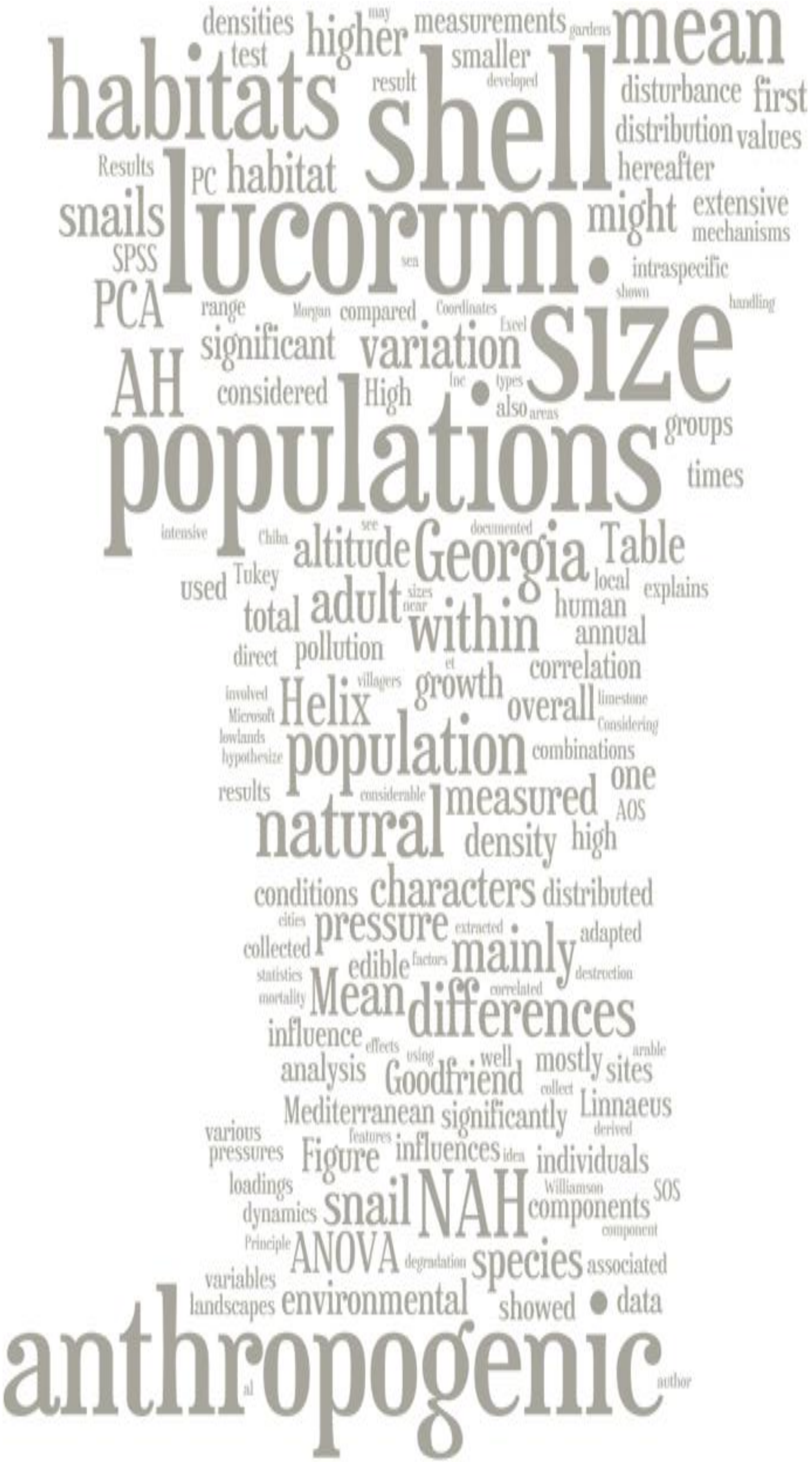
5. Data for testing transferability of SDMs developed for *Fagus orientalis*: 12963 locations generated within the European range of *Fagus sylvatica,* according to: von Wühlisch, G. 2003. EUFORGEN Technical Guidelines for genetic conservation and use for European beech (*Fagus sylvatica*). International Plant Genetic Resources Institute, Rome, Italy. 6 p.

6. Data for testing transferability of SDMs developed for *Rhododendron ponticum*: 2226 wild locations of the species from Britain, France, and Spain, downloaded from Global occurrence data were provided by Global Biodiversity Information Facility (GBIF) Data Portal (accessed through www.gbif.org, 2011-01-20).

7. Data for testing transferability of SDMs developed for *Helix buchi* + *H. goderdziana*: 4690 wild locations of *Helix pomatia*, downloaded from Global occurrence data were provided by Global Biodiversity Information Facility (GBIF) Data Portal (accessed through www.gbif.org, 2011-01-20).

8. Data for testing transferability of SDMs developed for *Mertensiella caucasica*: 496 locations of *Chioglossa lusitanica*, downloaded from Global occurrence data were provided by Global Biodiversity Information Facility (GBIF) Data Portal (accessed through www.gbif.org, 2011-01-20), and generated within the range of the species published in: Arntzen, J.W., Teixeira, J. (2006): History and new

developments in the mapping and modelling of the distribution of the golden-striped salamander, *Chioglossa lusitanica.* Zeitschr. Feldherpetol. (Suppl.) **10**: 113-126.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Shell size differences in *Helix lucorum* Linnaeus, 1758 (Mollusca: Gastropoda) between natural and urban environments

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Abstract: *Helix lucorum* Linnaeus, 1758 is a large helicid snail widespread in Georgia. While its occurrences are mainly associated with human activity, it is frequently impacted by strong direct pressure, which could cause local extinctions of populations. Instead, *H. lucorum* populations in anthropogenic landscapes are usually dense and apparently well adapted. Morphometric studies were carried out on 12 populations from both anthropogenic and more natural habitats in a wide range of altitudes and climatic regimes in Georgia to investigate the effects of human pressure. Populations in more anthropogenic habitats have smaller adult shells independently of any effects of climate, altitude, or density. *H. lucorum* appears to adapt to anthropogenic pressures by changes in population dynamics, ceasing growth at a smaller size.

Key words: *Helix lucorum*, shell, size, adaptation, plasticity, Georgia

1. Introduction

Helix lucorum Linnaeus, 1758 is an abundant snail with a Mediterranean distribution. It is an edible snail, well adapted to human-modified landscapes such as gardens, parks, and arable land. In Georgia, *H. lucorum* is widely distributed and mostly found within or near settlements and in agricultural territory, while in natural habitats it is not very common – to date, only a few populations are documented in natural habitats, mainly in limestone areas of Georgia (Lejava, 1973; author's observation). This abundance in anthropogenic habitats is despite the heavy pressures associated with these habitats. In the lowlands of Georgia where intensive agriculture is developed (mainly winery, market gardening, and apple orchards), snails are considered one of the worst pests. Gardeners and villagers collect *H. lucorum* and burn or crush them several times per year (such influences are considered as a direct human impact throughout the text). In the cities, *H. lucorum* is mostly subject to accidental mechanical destruction and various other anthropogenic influences, such as pollution and habitat degradation. Clearly, there must be considerable differences in the dynamics of *H. lucorum* populations between anthropogenic and more natural habitats. Surprisingly, there is no research on the mechanisms involved in the survival and distribution of *H. lucorum* under such anthropogenic influence.

It is known that adult shell size and shape vary among populations of the same species of snail. There are marked responses in shell features to variation in environmental conditions, such as intraspecific competition, predation, parasitism, and environmental influence (for reviews see Goodfriend, 1986; Ożgo, 2008). High population density can restrict growth (Williamson et al., 1976; Cameron and Carter, 1979). This variation in shell characters undoubtedly has both hereditary and ecophenotypic components (Cook and Cain, 1980; Goodfriend, 1986; Baur, 1984, 1988), and it may have adaptive significance to local conditions (Chiba, 2009).

The present study explores whether shell characters of *H. lucorum* are correlated with anthropogenic disturbance. Considering edible snails (mainly *Helix* species) in general, Lubell (2004) suggested that the larger size of such species at prehistoric sites around the Mediterranean is a result of less disturbance and pollution than in modern times. We might hypothesize that if adult mortality is high, snails might mature at a younger age and smaller size. High densities might also limit growth. To test this idea, I compared shell sizes from 2 types of habitats, the first being undisturbed natural and anthropogenic habitat (NAH hereafter) where there is no extensive pressure by humans, and the other being anthropogenic habitat (AH hereafter) with extensive pressure.

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2. Materials and methods

2.1. Data collection and measurements

I collected samples of adult *H. lucorum* from NAH and AH sites during 2011 and 2012 (Figure 1, Table 1.). Brief descriptions of each site are as follows:

Pop1: Botanical garden, southwest outskirts of Tbilisi. Leghvtakhevi River ravine with polydominant forest and rocky slopes.

Pop2: 1 km west from Daba village with undisturbed alder forest.

Pop3: East outskirts of Katskhi village. Hornbeam (*Carpinus caucasica*) and beech (*Fagus orientalis*) mixed forest with limestone rocks. Very little grazing.

Pop4: Ateni village. Yard of Ateni church with old orchard. No disturbance.

Pop5: 2 km east from Sakramulo village. Dry hornbeam forest with limestone. Very little grazing or no disturbance.

Pop6: 600 m east from Igoeti village. Artificial mixed forest of 70–80 years old near the main road. Little or no disturbance.

Pop7: Tbilisi; parts of former garden with intensive littering and building.

Pop8: Outskirts of Tbilisi. Orchards. Owners of gardens collect snails every year and kill them.

Pop9: 1.5 km south of Broliskedi village. Forest of *Zelkova* (*Zelkova carpinifolia*) with limestone. Very intensive grazing.

Pop10: Tbilisi; Vakisparki garden. Artificial poplar (*Populus* sp.) trees. Very abundant population with very intensive physical destruction by humans.

Pop11: 700 m southwest of Aradeti village. Apple orchard. Villagers are physically destroying snails several times per year.

Pop12: Borjomi. City center, around the railway line. Various factors resulting in mechanical destruction.

In order to objectively assess shell size measurements, a strict definition of adult status was needed, but there are no earlier studies on this issue specifically for *H. lucorum*. However, Pollard (1973) regarded *H. pomatia* as fully adult when the lip of the aperture is reflected, after which it becomes thicker, with only a tiny increase in overall diameter. Based on this knowledge, only live snails with reflected lips were sampled at each point. In the laboratory 4 shell characters – shell height (SH), shell width (SW), aperture height (AH), and aperture width (AW) – were measured (Figure 2) using digital Vernier calipers with 0.05 precision. Two new variables expressing shell overall size (SOS) and aperture overall size (AOS) were derived by summing absolute height and width for shell and aperture, respectively.

2.2. Statistical analysis

For practical reasons, populations were selected for sampling only if density was sufficient to obtain an adequate number of adults within a 10 × 10 m plot. To investigate any density effect on shell sizes, I estimated densities using the following method: within each site where snails were found, each plot was divided into numbered subplots of 1 m^2. Three of these were selected at random at each site, and the number of adults found in each was used to estimate density per square meter (Table 1). Mean annual temperature and humidity values were extracted for each sampling point using ArcGIS 9.3. Climatic data were downloaded from http://worldclim.org (Hijmans et al., 2005).

Pearson's correlation was used to estimate the relationship between density and mean shell characters, and correlation analyses were also used to explore the influence of climate on shell size.

One-way ANOVA (with Tukey's post hoc test for multiple comparisons) was used to test the variation in

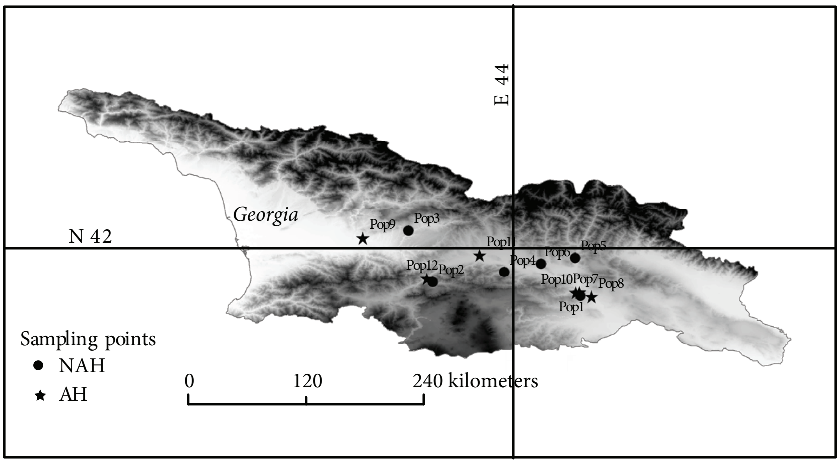

Figure 1. Map of the sampling localities in Georgia.

Table 1. Summary table of the collected data. Coordinates of sampling localities, altitude, mean density, number of sampled individuals, and the mean values (mm) of measured variables (with standard error of the mean) are shown.

Group	Pop ID	Coordinates	Altitude	Mean density	Measured individuals	Mean SH	Mean AH	Mean SW	Mean AW	Mean SOS	Mean AOS
NAH	Pop1	N41.684110 E044.792231	553	3.33	37	42.6 (0.4)	27.3 (0.2)	43.2 (0.3)	24.2 (0.2)	85.8 (0.7)	51.5 (0.4)
	Pop2	N41.811820 E043.438890	966	7.67	33	44.7 (0.3)	28.6 (0.4)	46.4 (0.3)	26.2 (0.2)	91.1 (0.7)	54.8 (0.6)
	Pop3	N42.284732 E043.217104	629	3.33	21	42.2 (0.6)	28.1 (0.4)	46.1 (0.6)	26.6 (0.2)	88.2 (1.2)	54.7 (0.7)
	Pop4	N41.904453 E044.094441	746	1.67	24	41.3 (0.3)	26.9 (0.2)	42.6 (0.3)	24.2 (0.2)	83.9 (0.7)	51 (0.5)
	Pop5	N42.034424 E044.744869	653	7.33	38	41.1 (0.2)	25.8 (0.1)	42.7 (0.2)	24.2 (0.1)	83.7 (0.5)	49.9 (0.3)
	Pop6	N41.979957 E 44.432056	711	9.67		44 (0.3)	27.9 (0.1)	44.5 (0.2)	25.6 (0.1)	88.4 (0.5)	53.5 (0.3)
AH	Pop7	N41.716093 E044.784564	433	7	29	38.5 (0.3)	24.6 (0.2)	39.7 (0.3)	22.7 (0.2)	78.2 (0.7)	47.2 (0.4)
	Pop8	N41.676460 E044.893970	426	7.33	23	38.3 (0.4)	25.3 (0.3)	40.5 (0.5)	23.2 (0.2)	78.7 (1)	48.5 (0.6)
	Pop9	N42.215146 E042.798710	130	2.33	31	35.8 (0.5)	23.8 (0.3)	39.5 (0.4)	23.2 (0.2)	75.2 (1)	47 (0.6)
	Pop10	N41.711319 E044.749842	488	6.67	51	36.7 (0.2)	23.2 (0.1)	38 (0.3)	22.3 (0.1)	74.6 (0.5)	45.4 (0.3)
	Pop11	N42.057500 E043.869400	676	3.67	35	36 (0.3)	23.3 (0.2)	38.1 (0.3)	21.6 (0.3)	74.1 (0.8)	44.8 (0.5)
	Pop12	N41.841969 E43.385347	794	10.33	36	38.2 (0.2)	24 (0.1)	40.1 (0.2)	23.3 (0.1)	78.2 (0.5)	47.2 (0.3)

size measurements between and within groups (NAH and AH) (Sokal and Rohlf, 1995). Principle component analysis (PCA) based on the correlation matrix (Joliffe and Morgan, 1992) was used to visualize shell size differences between populations using 4 empirical measurements. For data handling and correlation analysis, a spreadsheet (Microsoft Excel) was used. ANOVA and PCA were performed in SPSS 16.0 (SPSS Inc., Chicago, IL, USA).

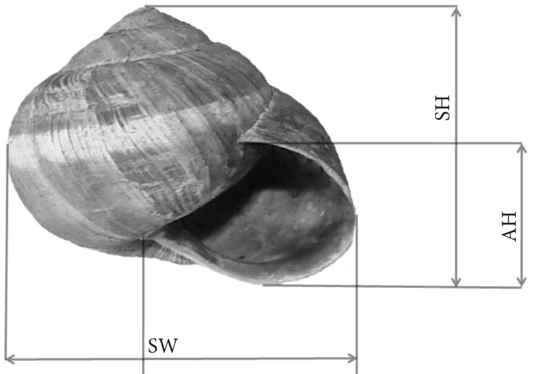

Figure 2. Measurements of the shells of *Helix lucorum* used in the analysis: SH, shell height; SW, shell width; AH, aperture height; AW, aperture width.

3. Results

In total, 412 adult individuals (207 from 6 NAH and 205 from 6 AH populations) were collected and measured (Table 1). Sampling sites are distributed within an altitude range from 130 m to 966 m above sea level (Figure 1). Pearson's r statistics showed no significant correlations between measured shell characters and population densities, altitude, mean annual temperature, or mean annual humidity (for all combinations $P > 0.05$).

After ANOVA, every NAH population had a significantly higher mean overall size (SOS) than AH populations (Tukey's HSD post hoc test), whereas populations within each of the groups showed no significant differences (Table 2, Figure 3). Almost identical results were derived for the AOS variable except one: Pop5 does not have a significantly higher mean apertural overall size than Pop8.

The PCA extracted 2 components with eigenvalues exceeding unity. The first PC explains 89% of total variation

Table 2. Results of Tukey's multiple tests after ANOVA. Bold-italic font denotes significant results. Positive values above the diagonal indicate that the population on the left of the chart (column 1) has a higher mean value compared to respective population at the top of the table (row 1), and vice versa for values below the diagonal. Highlighted values show that overall size for shell and aperture is consistently higher in NAH populations.

	Pop1	Pop2	Pop3	Pop4	Pop5	Pop6	Pop7	Pop8	Pop9	Pop10	Pop11	Pop12
Pop1	0	***-0.33***	***-0.33***	0.05	0.15	***-0.2***	***0.42***	***0.3***	***0.45***	***0.61***	***0.66***	***0.43***
Pop2	***-0.06***	0	0.01	***0.38***	***0.48***	0.13	***0.75***	***0.63***	***0.78***	***0.94***	***1***	***0.76***
Pop3	-0.03	0.03	0	***0.37***	***0.48***	0.13	***0.75***	***0.63***	***0.77***	***0.93***	***0.99***	***0.76***
Pop4	0.02	***0.08***	0.05	0	0.11	***-0.24***	***0.38***	***0.26***	***0.4***	***0.56***	***0.62***	***0.39***
Pop5	0.02	***0.08***	***0.05***	0.01	0	***-0.35***	***0.27***	0.15	***0.29***	***0.46***	***0.51***	***0.28***
Pop6	-0.03	0.03	-0.01	***-0.05***	***-0.06***	0	***0.62***	***0.5***	***0.65***	***0.81***	***0.86***	***0.63***
Pop7	***0.09***	***0.15***	***0.12***	***0.07***	***0.07***	***0.12***	0	-0.12	0.02	0.19	***0.24***	0.01
Pop8	***0.09***	***0.15***	***0.11***	***0.07***	***0.06***	***0.12***	-0.01	0	0.15	***0.31***	***0.36***	0.13
Pop9	***0.13***	***0.19***	***0.16***	***0.11***	***0.11***	***0.16***	0.04	0.05	0	0.16	***0.22***	-0.02
Pop10	***0.14***	***0.2***	***0.17***	***0.12***	***0.12***	***0.17***	***0.05***	***0.05***	0.01	0	0.06	-0.18
Pop11	***0.15***	***0.21***	***0.18***	***0.13***	***0.12***	***0.18***	***0.06***	***0.06***	0.02	0.01	0	***-0.23***
Pop12	***0.09***	***0.15***	***0.12***	***0.07***	***0.07***	***0.12***	-0.01	0.01	-0.04	***-0.05***	***-0.06***	0

Above the diagonal: **AOS**, $F_{11,400} = 65.03$, $P < 0.0001$; Below the diagonal: **SOS**, $F_{11,400}$ = 73.17.03, $P < 0.0001$.

where all 4 measured variables have high positive loadings and the ratios have small negative loadings. In contrast, the second PC explains 6% of total variations, and neither of the variables have high positive or negative loadings (Table 3). A result of ANOVA and PCA suggests that increasing any one dimension of the shell also increases the other. The differences between NAH and AH populations along the first and second PC are shown in Figure 4.

4. Discussion

Variations in shell size and form in helicoid snails have been extensively investigated and mechanisms underlying this variation are attributed to combinations of various environmental factors, inter- or intraspecific interactions, and genetic processes (Goodfriend, 1986). However, there are no data on how *H. lucorum* responds in shell size to external factors or on the heritability of shell size

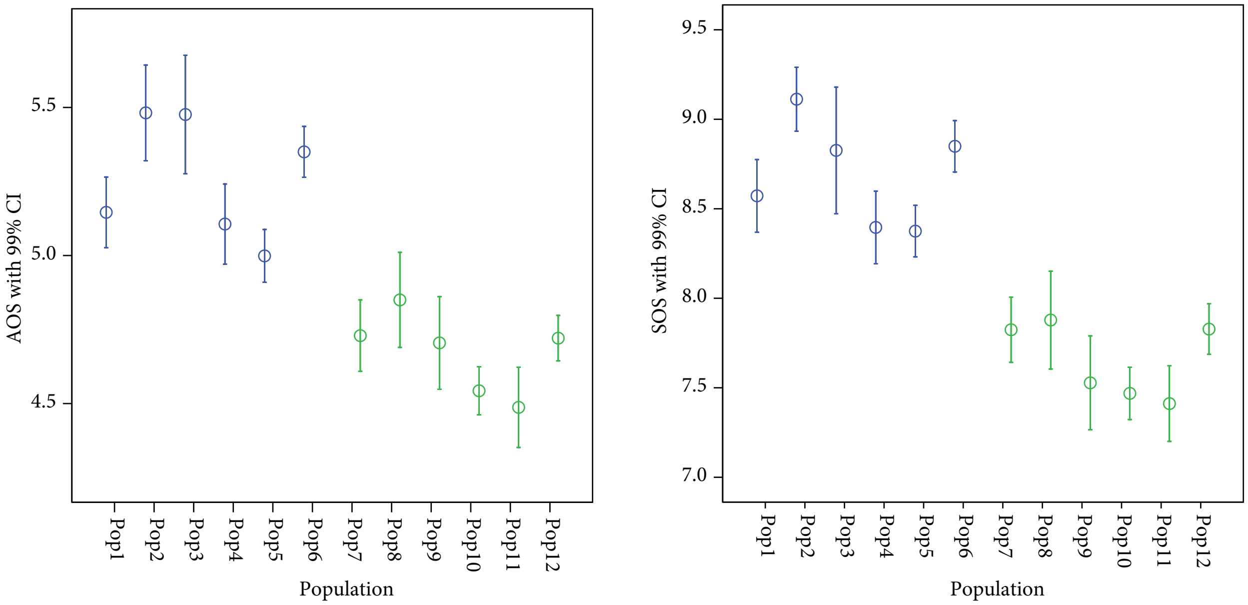

Figure 3. Error bars of mean values of SOS and AOS variables are shown with 99% confidence intervals.

Table 3. PCA loadings are shown for PC with eigenvalues exceeding unity.

Variable	PC1	PC2
SH	0.935	–0.293
AH	0.954	–0.120
SW	0.979	0.042
AW	0.920	0.377

differences. Only a few published papers are available concerning the life cycle, genital anatomy, growth, reproduction, and activity of *H. lucorum* (Lazaridou-Dimitriadou and Saunders, 1985; Staikou et al., 1987; Lazaridou-Dimitriadou and Bailey, 1991; Osselaer and Tursch, 2000).

The results shown here indicate that shell size in *H. lucorum* is influenced by factors associated with human activity, to the extent that other potentially important factors such as climate and population density appear irrelevant. I have no means at present to determine the extent to which this influence is direct and ecophenotypic or the result of hereditary adaptation to the prevailing conditions. Work on other species suggests that this balance may vary among species and circumstances (Goodfriend, 1986; Baur, 1988). In many studies, large adult size is correlated with rapid growth (Williamson et al., 1976; Baur, 1984; Gould, 1984; Goodfriend, 1986), but we have yet to establish this connection in *H. lucorum*. The lack of any direct relationship between size and density is particularly noteworthy, as this has been reported in many species (Goodfriend, 1986), and, in general, AH habitats support higher densities than NAH in Georgia. A greater range of densities might demonstrate a link.

Whatever the causes, these results show a form of adaptability in *H. lucorum* populations of a kind not yet reported in other snails. We can hypothesize that high adult mortality may put a premium on early maturity and reproduction where potentially long-lived adults have less chance of surviving from year to year. Alternatively, in populations where direct human impact (i.e. collecting and killing snails) is very strong, snails are smaller in size because it is easier for them to hide effectively. In this context, humans can be considered as predators; Bantock and Bayley (1973) demonstrated that predators selected larger individuals in *Cepaea* populations. Changes or differences in shell morphology as a result of adaptations are well known for other snails (Konuma and Chiba, 2007; Chiba, 2009). However, populations in anthropogenically heavily impacted habitats (e.g., big cities where snails are not considered pests and hence are not collected deliberately to be killed) are revealing similar size distribution to the populations under direct human impact in contrast to natural ones.

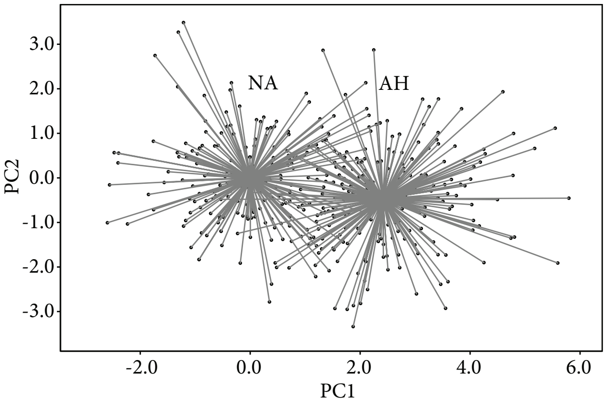

Figure 4. Individual scores of the *Helix lucorum* along the first 2 PCA axes defined by size variables and 2 ratios.

Certainly, this study provides no evidence that some factors influential in other species, for example crowding or interspecific competition (Williamson et al., 1976; Baur, 1988), are strong enough to override the effects of human activity. *H. lucorum* is a widespread species, undoubtedly spread by humans, originally for food (Lubell, 2004). Responses to pressures of this kind are likely to be common to most populations, rather than a consequence of specific adaptations evolved independently in each. More research, perhaps especially on the population dynamics and growth patterns of *H. lucorum* and other large, edible helicids, might shed light on the specific factors involved.

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References

Bantock, C.R. and Bayley, J.A. 1973. Visual selection for shell size in *Cepaea* (Held.). J. Anim. Ecol. 42: 247–261.

Baur, B. 1984. Shell size and growth rate differences for alpine populations of *Arianta arbustorum* (L.) (Pulmonata: Helicidae). Rev. Suisse Zool. 91: 37–46.

Baur, B. 1988. Microgeographical variation in shell size of the land snail *Chondrina clienta*. Biol. J. Linn. Soc. 35: 247–259.

Cameron, R.A.D. and Carter, M.A. 1979. Intra- and interspecific effects of population density on growth and activity in some helicid land snails (Gastropoda: Pulmonata). J. Anim. Ecol. 48: 237–246.

Chiba, S. 2009. Morphological divergence as a result of common adaptation to a shared environment in land snails of the genus *Hirasea*. J. Mollus. Stud. 75(3): 253–259.

Cook, L.M. and Cain, A.J. 1980. Population dynamics, shell size and morph frequency in experimental populations of the snail *Cepaea nemoralis* (L.). Biol. J. Linn. Soc. 14: 259–292.

Goodfriend, G.A. 1986. Variation in land-snail shell form and size and its causes: a review. Syst. Biol. 35(2): 204–223.

Gould, S.J. 1984. Covariance sets and ordered geographic variation in *Cerion* from Aruba, Bonaire, and Curaçao: a way of studying nonadaptation. Syst. Zool. 33(2): 217–237.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. and Jarvis, A. 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25: 1965–1978.

Joliffe, I.T. and Morgan, B.J. 1992. Principal component analysis and exploratory factor analysis. Stat. Methods Med. Res. 1: 69–95.

Konuma, J. and Chiba, S. 2007. Trade-offs between force and fit: extreme morphologies associated with feeding behavior in carabid beetles. Am. Nat. 170: 90–100.

Lazaridou-Dimitriadou, M. and Bailey, S.E.R. 1991. Growth, reproduction and activity rhythms in 2 species of edible snails, *Helix aspersa* and *Helix lucorum*, in non 24-hour light cycles. J. Zool. 225: 381–391.

Lazaridou-Dimitriadou, M. and Saunders, D.S. 1985. The influence of humidity, photoperiod, and temperature on the dormancy and activity of *Helix lucorum* L. (Gastropoda, Pulmonata). J. Mollus. Stud. 52(3): 180–189.

Lejava, G. 1973. Animal World of Georgia, Tom IV. Metsniereba, Tbilisi (in Georgian).

Lubell, D. 2004. Prehistoric edible land snails in the circum-Mediterranean: the archaeological evidence. In: Petits animaux et sociétés humaines du complément alimentaire aux resources utilitaires (Eds. J.P. Brugal and J. Desse). Éditions APDCA, Antibes.

Osselaer, C.V. and Tursch, B. 2000. Variability of the genital system of *Helix pomatia* L., 1758 and *H. lucorum* L., 1758 (Gastropoda: Stylommatophora). J. Mollus. Stud. 66: 499–515.

Ożgo, M. 2008. Current problems in the research of *Cepaea* polymorphism. Folia Malacologica 16(2): 55–60.

Pollard, E. 1973. Growth classes in the adult Roman snail (*Helix pomatia* L.). Oecologia 12: 209–212.

Sokal, R.R. and Rohlf, F.J. 1995. Biometry: The Principles and Practice of Statistics in Biological Research. W. H. Freeman and Company, New York.

Staikou, A., Lazaridou-Dimitriadou, M. and Farmakis, N. 1987. Aspects of the life cycle, population dynamics, growth and secondary production of the edible snail *Helix lucorum* Linnaeus, 1758 (Gastropoda, Pulmonata) in Greece. J. Mollus. Stud. 54(2): 139–155.

Williamson, P., Cameron, R.A. and Carter, M.A. 1976. Population density affecting adult shell size of snail *Cepaea nemoralis* L. Nature 263: 496–497.

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Systematics and evolutionary history of large endemic snails from the Caucasus (*Helix buchii,* and *H. goderdziana*) (Helicidae)

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Abstract. Two species of genus *Helix* Linnaeus, 1758 (Mollusca: Gastropoda: Helicidae) endemic to the Caucasus region are known from Georgia and northeastern Turkey: *Helix buchii* Dubois de Montpereux, 1839 and the recently-described but disputed *Helix goderdziana* Mumladze, Tarkhnishvili and Pokryszko, 2008. The latter species is the largest land snail throughout non-tropical Eurasia. We compared shell shapes and genital morphology of the two species. We analyzed mitochondrial COI and nuclear 18S ribosomal RNA and ITS1 gene fragments in 39 specimens of *H. buchii* and *H. goderdziana* from ten locations from the entire distribution range of these species, together with 13 specimens of the widespread *H. lucorum* Linnaeus, 1758 and *H. pomatia* Linnaeus, 1758. Based on shell morphology alone, most of the individuals of the two species can be discriminated using multivariate approaches. The species have different flagellum/diverticulum ratios, and the foot coloration is a fully diagnostic morphological character. Molecular genetic analysis revealed little variation in 18S+ITS1 fragment, and eleven COI haplotypes. Phylogenetic analyses support reciprocal monophyly of *H. buchii* and *H. goderdziana*. The genetic distances significantly correlate with the geographic and morphological distances; correlation of morphological distances with geography is insignificant. The basal lineages of both species are found within two distinct glacial refugia, a result which matches the separation of eastern and western evolutionary lineages of other relicts of the Western Caucasus. The present distribution of *H. goderdziana* coincides with the expected refugial borders, whereas *H. buchii* is likely to have extended its geographical range since the last glaciation.

Key words: Mollusca, phylogeography, DNA, Caucasus, refugia

Helix Linnaeus, 1758 (Gastropoda: Helicidae) are the largest land snails of northern Eurasia. The genus includes over 25 species (Schütt 2005, Welter-Schultes 2009). *Helix buchii* Dubois de Montpereux, 1839, (Figs. 1A, 1C) until recently known as the largest land snail of the western Palaearctic, is an endemic of the mountain broadleaf forests of the Caucasus ecoregion (Zazanashvili *et al.* 2004), which harbor numerous Tertiary relict species and habitats (Tuniyev 1990, Röhrig 1991, Mai 1995, Veith *et al*. 1998, Kikvidze and Ohsawa 1999, Denk *et al.* 2001, Milne and Abbott 2002, Milne 2004, 2006, Zazanashvili *et al.* 2004, Tarkhnishvili *et al.* 2012).

Another large snail, *Helix goderdziana* Mumladze, Tarkhnishvili and Pokryszko, 2008 (Figs. 1B, 1D), has been recently-described from southwestern Georgia near Goderdzi pass (Mumladze *et al.* 2008). This snail is even larger: the shell diameter in some individuals reaches 68 mm (this paper). The distribution ranges of both species overlap, although *H. goderdziana* is limited to the western Lesser Caucasus and is known from only two localities (Fig. 2). Sysoev and Shileyko (2009) disputed the taxonomic status of *H. goderdziana*, suggesting that the traits used in the original description (foot coloration, shell size, and flagellum length) may vary broadly within a species. Indeed, morphological traits in *Helix* are highly variable, and species-level taxonomy is regularly disputed (Schütt 2005, Neubert and Bank 2006, Sysoev and Shileyko 2009).

Delineating species is a common problem in systematics (De Queiroz 2007, Mallet *et al.* 2007, Hausdorf 2010, Mallet 2010), but distinguishing between similar species is a core step to assess and maintain biodiversity (Bickford *et al.* 2006). There is a lack of comprehensive studies on systematics, distribution and conservation of Caucasian *Helix* species. In order to clarify the evolutionary history and taxonomic status of *H. goderdziana* and *H. buchii* (from here onwards – *Endemic Caucasian Helix*, *ECH*), we applied a combination of molecular genetics and morphometric approaches to the samples collected throughout the range of both species. In addition, we provide brief information on the two known localities of *H. goderdziana* to address its conservation status.

MATERIAL AND METHODS

Sampling

During 2008–2010, we collected adult specimens (individuals with well-developed lip) of *Helix buchii* and *H. goderdziana* from Georgia and NE Turkey (Fig. 2). One to twelve *H. buchii* from eight locations, and two to five *H. goderdziana* from both known locations of this species were sampled. The small samples of *H. goderdziana* reflect its rarity. As outgroups for genetic and morphological studies, the widespread species

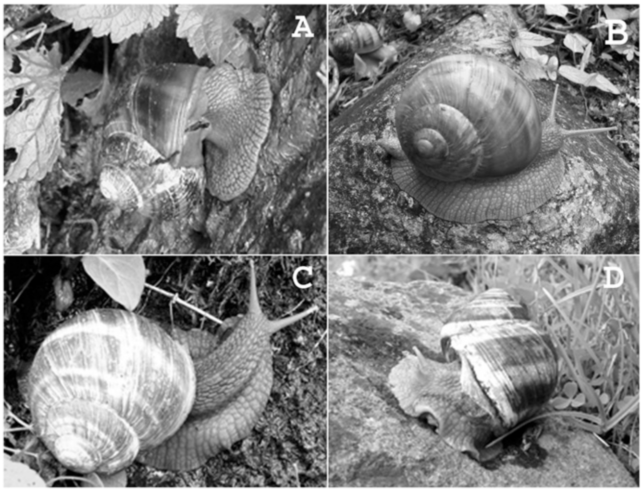

Figure 1. *Endemic Caucasian Helix (ECH).* **A,** subadult *H. buchii*; **B,** subadult *H. goderdziana*; **C,** adult *H. buchii*; **D,** adult *H. goderdziana.*

Helix lucorum Linnaeus, 1758 and *Helix pomatia* Linnaeus, 1758 were used: eight and five adult specimens, respectively (Table 1). Geographic coordinates of each location were recorded with a Garmin Etrex 12 Channel GPS unit (Garmin Corp., Olathe, Kansas, U.S.A.). Live individuals were drowned in water and then preserved and stored in 96% alcohol for further processing. The genitalia were dissected and measured for five *H. buchii*, three *H. goderdziana,* one *H. lucorum,* and one *H. pomatia*. Pieces of muscular tissue of collected individuals were used for DNA extraction and processing. Alcohol-stored specimens and shells are deposited in the collection of Zoological Institute of Ilia State University under accession numbers h1–h59.

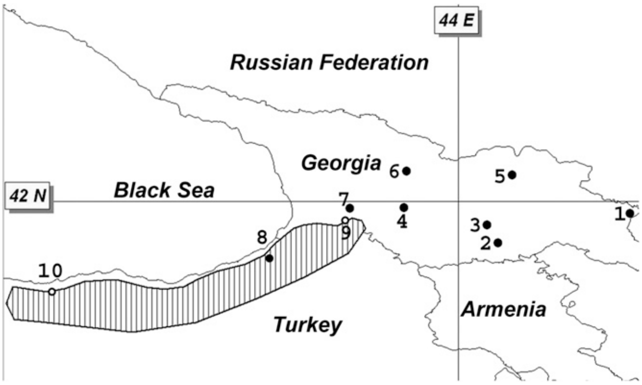

Figure 2. Sampled locations of *Helix buchii* (black dots) and *H. goderdziana* (open circles): **1,** Lagodekhi (eastern Greater Caucasus); **2,** Dmanisi; **3,** Didgori; **4,** Borjomi (central Lesser Caucasus); **5,** Khevsha; **6,** Mokhva (central Greater Caucasus); **7,** Bakhmaro (western Lesser Caucasus); **8,** Jamilikhemshin (Kackar Mountains); **9,** Goderdzi Pass (western Lesser Caucasus, type locality of *H. goderdziana*); **10,** Kovanlyk. Outlined area: borders of the Major Forest Refugium (see discussion), *sensu* van Andel and Tzedakis (1996).

Morphology

The shells of adult specimens (thirteen *Helix buchii*, seven *H. goderdziana*, four *H. pomatia*, and four *H. lucorum*) were scanned using a 3D scanner (Roland PICZA 3D Laser Scanner LPX-600). Nineteen landmarks were selected: L0 = intersection of the main axis and the columellar part of lip; L3 = junction of the lip with the body whorl; L6 = apex; other landmarks were positioned using the junctions of two perpendicular planes, the first crossing the landmarks L0, L3, and L6 and the second adjusted perpendicularly to the first so that landmarks L0 and L6 were common to both (Fig. 3). Placing landmarks and extracting coordinates were performed with software Landmark v2.0 (Wiley *et al.* 2005). Geometric morphometry methods are commonly used for the analysis of snail shells (Conde-Padín *et al.* 2007) when landmark data can be captured. However, if the landmarks do not meet true homology criteria, the interpretation of the analysis results might be misleading (Zelditch *et al.* 2004). Because our landmarks (except L3 and L6) cannot be assumed as homologous, we used a "traditional" Principal Component Analysis (PCA; Joliffe 1992, MacCallum *et al.* 1999) for describing shell shape differences using between landmark distances, which are easier to interpret (Blackith and Reyment 1971, Richtsmeier *et al.* 2002).

To maximally approximate the assumptions of PCA and to maintain sufficiently high sample/ variable ratio, we had to reduce the available set of distance measures to few distance variables. Based on visual observations on *Helix buchii* and *H. goderdziana*, most obvious differences in shell shape are due to the shape of shell spire. Consequently, we used the following eight distance measures describing shell spire: L4–L6, L5–L6, L5–L7, L6–L8, L6–L9, L6–L16, L6–L17, L11–L15, L12–L16, and L13–L17 (Fig. 3). In order to meet a normality assumption and minimize size influence and allometric effect, the distances were log-transformed and then standardized residuals of the regression of each character on the distance between shell apex and most proximate distance of outer lip (L1–L6) were calculated, as recommended by Thorpe and Leamy (1983). Standardized residuals calculated for the 10 variables were subjected to Principal Component Analysis (PCA) with components extracted at eigenvalues over 1.

We dissected five adult specimens of *Helix buchii,* three of *H. goderdziana,* one of *H. lucorum*, and one of *H. pomatia* in order to compare qualitative and quantitative traits of their genital morphology. We measured length of flagellum, length of penis + epiphallus, length of bursa tract, diverticulum, maximum length of mucus gland, and length of dart sac of each dissected individual (Fig. 4). All statistical analysis was

Table 1. Sampling locations with GPS coordinates and number of sampled specimens. Abbreviation in brackets for first column stands for: Geo, Georgia; Tu, Turkey; Pol, Poland.

Sampling location	GPS coordinates	Species	DNA samples	Shell samples	Genital samples
Lagodekhi (Geo)	41.85N, 46.29E	*Helix buchii*	1	1	-
Dmanisi (Geo)	41.33N, 44.35E	*H. buchii*	6	2	-
Didgori (Geo)	41.78N, 44.51E	*H. buchii*	7	2	1
Borjomi (Geo)	41.91N, 43.25E	*H. buchii*	2	1	-
Khevsha (Geo)	42.40N, 44.69E	*H. buchii*	1	1	-
Mokhva (Geo)	42.43N, 43.30E	*H. buchii*	12	2	2
Bakhmaro (Geo)	41.89N, 42.37E	*H. buchii*	2	2	-
Jamilihamshin (Tu)	41.14N, 40.93E	*H. buchii*	3	2	2
Goderdzi (Geo)	42.57N, 41.63E	*H. goderdziana*	2	4	2
Kovanlik (Tu)	38.14N, 40.68E	*H. goderdziana*	3	3	1
Tbilisi (Geo)	41.72N, 44.65E	*H. lucorum*	8	4	1
Wroclaw (Pol)	51.11N, 17.01E	*H. pomatia*	5	4	1

performed using SPSS v.16 for Windows (SPSS Inc. Chicago, Illinois, U.S.A.).

DNA analysis and inferring relations between haplotypes

Total cellular DNA was extracted from a small piece of the hind part of the foot of individual snails. Extraction was performed using QIAGEN® QIAamp DNA Mini Kit followed by a slightly modified standard protocol provided by QIAamp DNA Mini Kit Handbook (QIAGEN, Hilden, Germany). Partial sequences of mitochondrial gene COI and fragments of nuclear 18S ribosomal RNA gene and internal transcribed spacer 1b (18S+ITS1) were amplified and sequenced for 34 *Helix buchii,* five *H. goderdziana,* eight *H. lucorum,* and five *H. pomatia*. Amplification conditions and temperature profiles are given in Appendix 1. The amplicons were sequenced on the automatic sequencer ABI 3130 (Applied Biosystems, Foster City, California). Single-stranded sequencing was performed with polymerase chain reaction primers, using the Big-Dye Terminator v3.1 (Applied Biosystems, Foster City, California). DNA sequences were edited using SEQSCAPE v2.5 (Applied Biosystems Inc. Foster City, California); only unique COI and 18S+ITS1 haplotypes were deposited in GenBank (accession # GU784797–GU784807). The alignment of the sequences was performed with BioEdit v7.0 (Hall 1999). Phylogenetic analyses were performed for high-quality sequence fragments including 364 bp for COI (the obtained sequences of COI were not readable in the end of 3′ direction) and 473 bp for 18S+ITS1.

The sequences were aligned with the six most similar GenBank sequences, as shown by BLAST output *Lozekia deubeli* (Kimakowicz, 1890) (COI; GenBank accession # EU182503), *Marmorana scabriuscula* (Deshayes, 1830) (COI; # EU189930), *Arianta arbustorum* Linnaeus, 1758 (both genes; # AF296946 and AY546455), species of *Satsuma* H. Adams, 1868 (both genes; #AB242535 and AB481049), and *Iberus* Montfort, 1810 spp. (both genes; # EF440266 and EU446026), and *Caucasotachea calligera* (Dubois de Montpereux, 1840) (18S+ITS1; # GU784810 – sequenced by authors specifically for this manuscript). Unfortunately, no homologous DNA fragments of other *Helix* are available from GenBank). Phylogenetic relationships between the individual COI haplotypes were inferred

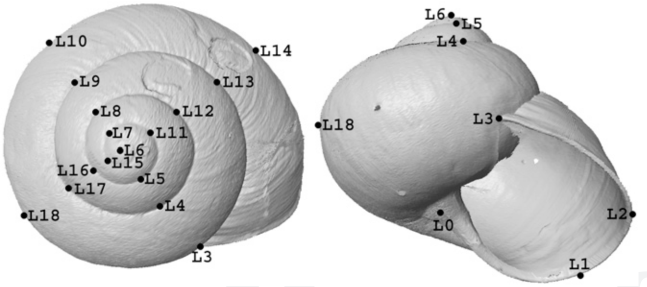

Figure 3. The position of the landmarks used for morphometric analysis of shells of the studied species.

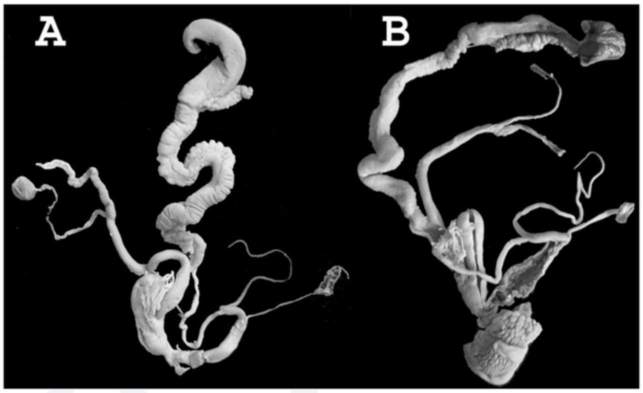

Figure 4. Overall view of genital organs. **A,** *Helix goderdziana*; **B,** *H. buchii*.

with neighbor-joining (NJ), maximum parsimony (MP), and Bayesian algorithms. NJ and MP trees were inferred using MEGA v5 (Tamura *et al.* 2011) with applying default settings (all positions included, 1000 bootstrap replications, Max-mini branch-and-bound for MP). Bayesian phylogenetic analysis was performed using the software BEAST v1.5.1 (Drummond and Rambaut 2007). Posterior distributions of parameters were approximated using Markov Chain Monte Carlo (MCMC) with length of chain 3×10^7 that harvested effective sample size (ESS) > 100 for each parameter. The best model was identified by the model comparison procedure based on the marginal likelihood, using a code written for BEAST (Suchard *et al.* 2001). Prior to this analysis, we tested the molecular clock hypothesis (Hasegawa *et al.* 1985) and found the best model of nucleotide substitution using Bayesian Information Criterion (BIC) using software MEGA v5 (Tamura *et al.* 2011). All possible evolutionary pathways among the obtained haplotypes of *H. buchii* and *H. goderdziana* were reconstructed using Median-Joining (MJ) algorithm (Donnelly and Tavare 1986, Bandelt *et al.* 1999) using the software Network 4.6.1 (Bandelt *et al.* 1999). The GenGIS software (Parks *et al.* 2009) was used for plotting the phylogenetic tree on a geographic map (Fig.7).

Because 18S+ITS1 sequences were identical for three out of four studied species (see results), they were not subjected to the detailed phylogenetic analyses.

To explore to what extent morphological variability among *ECH* individuals is associated with their evolutionary differentiation we applied partial Mantel test (Manel *et al.* 2003) with 10,000 permutations, using IBD software (Bohonak 2002). All 20 studied *ECH* individuals were included in the analysis, without *a priori* attribution to *Helix buchii* or *H. goderdziana*. To perform Mantel test genetic distances between individual COI sequences were estimated according to Kimura (1980) using MEGA v5.

Morphological distances (shell shape) were estimated as Euclidean distances based on individual scores from all PCA axes with eigenvalues exceeding unity. We explored whether: (I) genetic distances between the individuals of *Helix buchii* and *H. goderdziana* significantly correlated with geographic distances between the locations; (II) morphological distances significantly correlated with (a) genetic distances between the individuals, and (b) geographic distances between the locations.

RESULTS

Morphometry

The output of PCA based on the shell measurements is shown in Table 2 and Fig. 5. Two PCA axes were extracted with eigenvalues > 1. All included variables had a high communality values (> 0.8), indicating that the result can be used in a meaningful way (Table 2). The first PCA axis (72% of the total variation and 10% for second PCA axis) had similar positive loading for all the variables which implies that increasing score values along the axis marks higher shells with broader spire (wider apical whorls) relative to the shell size. Adult individuals of *Helix lucorum* have the highest scores along this axis, and *H. buchii* and *H. pomatia* have the lowest scores. *Helix goderdziana* keeps an intermediate position between *H. buchii* and *H. lucorum*, but the overlap is higher with the latter species (Fig. 5). The interspecific differences in the average values of the first PCA scores are significant

Table 2. Loadings of individual shell dimensions on the PCA axes. PCs with eigenvalues exceeding unity are shown. All variables are standardized residuals of the corresponding measurements from the regression line on lnL1–L6. Last column contains Communality (indicating a percent of variance accounted by the PCs) values for each distance variable.

Distances	PC1	PC2	Communalities
L4–L6	0.91	-0.27	0.894
L5–L7	0.88	-0.20	0.811
L5–L6	0.82	-0.34	0.779
L12–L16	0.83	0.50	0.932
L6–L8	0.90	0.09	0.813
L6–L9	0.91	-0.05	0.828
L6–L15	0.65	-0.21	0.465
L6–L16	0.88	-0.26	0.837
L6–L17	0.90	-0.18	0.838
L11–L15	0.88	0.34	0.897
L13–L17	0.75	0.63	0.956

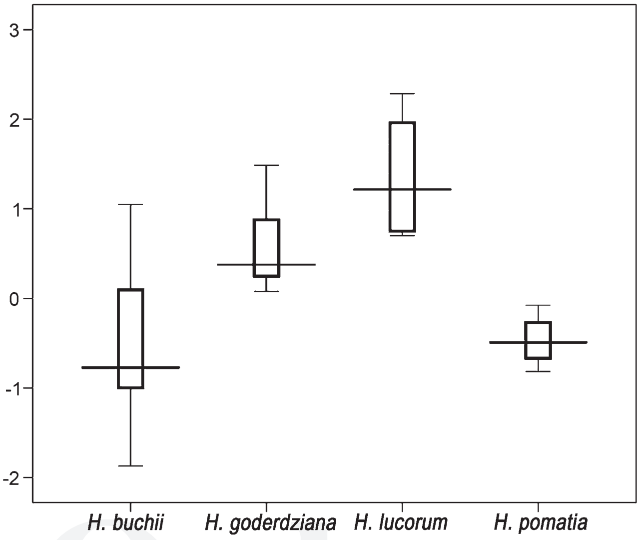

Figure 5. Box plots of individual scores of the four studied *Helix* species along the first PCA axis defined by shape of the shell spire.

Table 3. Multiple pairwise comparison (with Bonferroni adjustment) after One-way ANOVA based on individual scores for first PCA axis. Numbers indicate the mean differences. Numbers in bold represent significant results at 0.05 significance level.

	H. goderdziana	*H. lucorum*	*H. pomatia*
Helix buchii	**-1.14**	**-1.87**	0.42
H. goderdziana		-0.76	1.07
H. lucorum			**1.82**

(One-way ANOVA, $F_{3,26} = 8.9$, $P < 0.001$). Mean differences are significant ($P < 0.05$ after Bonferroni adjustment) between *H. lucorum* and *H. buchii*, *H. lucorum* and *H. pomatia*, *H. buchii* and *H. goderdziana*; the differences are not significant ($P > 0.05$) between *H. goderdziana* and *H. lucorum*, *H. pomatia* with *H. buchii*, and *H. pomatia* with *H. goderdziana* (Table 3).

Most of the genitalia measurements did not show obvious differences neither between *Helix buchii* and *H. goderdziana*, nor among *ECH* and the two other *Helix* species (Fig. 6). However, the flagellum/diverticulum ratio in the studied individuals of *H. goderdziana* was significantly lower than in *H. buchii* and much shorter in *ECH* than in either *H. lucorum* or *H. pomatia*.

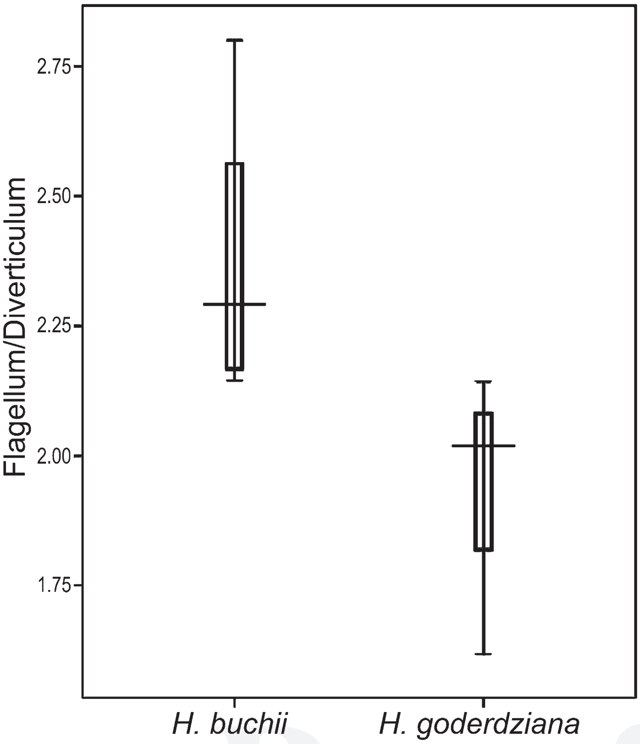

Figure 6. Box plots of flagellum/diverticulum ratios for *Helix buchii* and *H. goderdziana*.

Phylogenetic relations of the studied species

The sequenced fragment of nuclear 18S+ITS1 was identical for *Helix goderdziana, H. buchii* and *H. lucorum*. Five substitutions separate these species from *H. pomatia.* The sequenced COI fragment had 92 informative sites for all 52 obtained sequences of four *Helix* species. The lowest BIC value was shown for Hasegawa-Kishino-Yano model (HKY) with gamma distribution (HKY+G). Five haplotypes of *H. buchii*, two of *H. goderdziana,* three of *H. lucorum* and one of *H. pomatia* were identified. Individual haplotypes of *ECH* differed by 1–15 substitutions. NJ, Bayesian, and MP consensus tree (Fig. 7) supported (1) monophyletic origin of *ECH*, with respect to the outgroup taxa (*H. pomatia, H. lucorum,* one hygromiid and four helicids downloaded from the GenBank) and (2) reciprocal monophyly of *H. buchii* and *H. goderdziana*. The MJ network (Fig. 8) showed a single possible path connecting *H. goderdziana* and *H. buchii.* Six out of the seven unique haplotypes inferred within *ECH* are geographically distinct. Two haplotypes of *H. goderdziana* are attributed to NE Turkey (Kovanlyk) and SW Georgia (Goderdzi), respectively; two haplotypes of *H. buchii* are attributed to the Central Greater Caucasus (Mokva, Khevsha) and to the Lesser and Eastern Greater Caucasus (Borjomi, Didgori, Dmanisi, Lagodekhi) respectively. Three remaining basal haplotypes of *H. buchii* mark individual locations in the Western Lesser Caucasus (Jamili, Bakhmaro). Only the latter location had two closely-related haplotypes, individuals from other studied ECH locations did not differ genetically. The hypothesis of a molecular clock was supported (LRT = 56.8, $P < 0.001$) for the sequenced fragment of COI, without considering the codon position.

Relationships between morphology, genetics, and geography

A Mantel test showed significant correlation between genetic and geographic distances for *ECH* samples ($r_{xy} = 0.41$, $P < 0.001$). The morphological distance (distance between the individuals based on the first two PCA axes for shell measurements) significantly correlates with genetic distance (COI sequence) between the corresponding individuals, if controlled for geographic distance ($r_{xy} = 0.22$, $P = 0.02$) between the locations but no correlation of morphological distance with geography was detected.

DISCUSSION

Systematics and Taxonomic inference

This study suggests that *Helix buchii* and *H. goderdziana* are two distinct, reciprocally-monophyletic evolutionary lineages. Morphological differences between these species are slight but obvious. Foot coloration, albeit variable in most

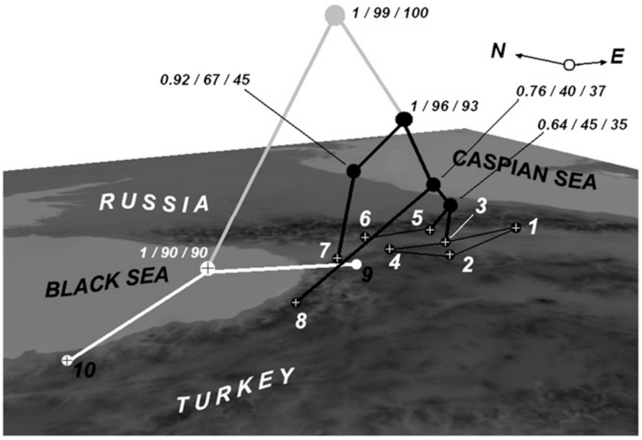

Figure 7. Phylogenetic relations between the *ECH* from different parts of the range; consensus tree based on the BA, NJ, and MP analyses. *Helix buchii*: black lines and circles; *H. goderdziana*: white lines and circles. The numbers attributed to individual nodes are Bayesian posterior probabilities / bootstrap supports for NJ tree nodes / bootstrap supports for MP tree nodes. Numbering of the sites (smaller crossed circles on the map) as in Fig. 2. The sites with identical haplotypes of *H. buchii* (1–4 and 5–6) are connected with narrower lines. Note that site 7 unites two haplotypes (see results).

land snails (Sysoev and Schileyko 2009), is the fully diagnostic character. In over 100 observed live individuals of *H. buchii*, the foot is dark, from grey to black, whereas over 20 adult and juvenile *H. goderdziana* found in both natural locations had light-colored yellowish foot, similar to that of the widespread *H. lucorum* (not all the observed specimens were used in the analysis, see Table 1). *Helix goderdziana* have in average larger shells with relatively broader spires than *H. buchii*, being more similar in shell shape to *H. lucorum* than to its sister species, if size and allometry factors are assumed. At last, *H. goderdziana* have lower flagellum/diverticulum ratio than *H. buchii*, and both *ECH* species have substantially lower diverticulum/flagellum ratio than *H. lucorum* or *H. pomatia.*

Long-running debates on the species criteria focus on some questions, on which an expert consensus perhaps never will be achieved (*e.g.*, Mayden 1977, Hey 2001, Avise 2004, de Queiroz 2007, Hausdorf 2010, Mallet 2010). Incipient species commonly exchange genes for millions of years, although this might not prevent progressive divergence (Mallet *et al.* 2007, Hausdorf 2010). We follow the suggestion of Mallet (2010) and refrain from the puritanical approach to species definition, deciding the nomenclatural questions dependent on the practical appropriateness. *Helix goderdziana* and *H. buchii* are morphologically, ecologically and geographically distinct and they are marked with reciprocally-monophyletic mitochondrial haplo-groups. These facts convince the authors that the differential species names are practically applicable to the studied taxa.

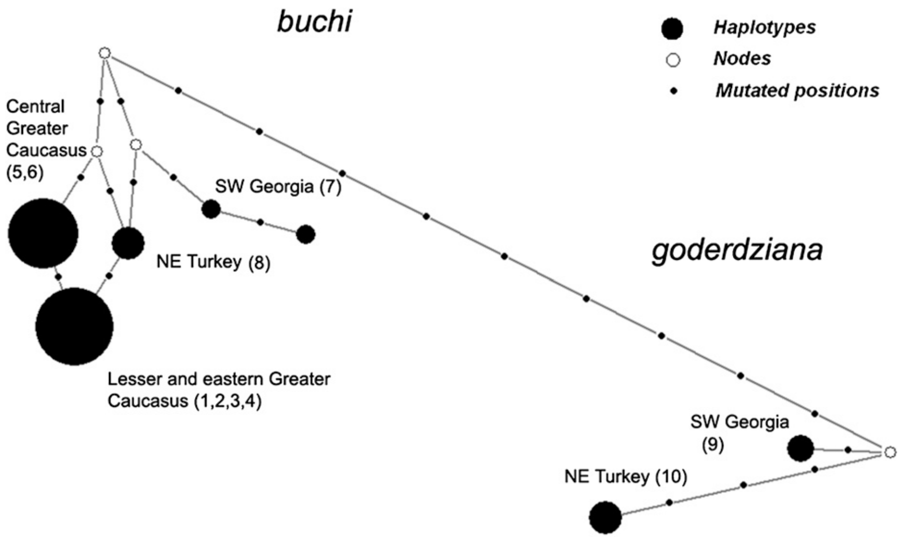

Figure 8. Median-joining network connecting inferred haplotypes of *Helix goderdziana* (Goderdzi and Kovanlyk) and *H. buchii* (all others). Numbers in parenthesis represent location numbers (see Fig. 2). Size of the circles marking haplotypes is proportional to the number of respective individuals.

Evolutionary history of Endemic Caucasian Snails

If we consider morphological similarity, geographic closeness, and monophyly (based on COI sequence) of *ECH* relative to the analyzed widespread *Helix* species, *H. buchii* and *H. goderdziana* are likely to be sister taxa, although this assumption needs additional genetic data for more representatives of the genus.

Helix lucorum (and not the superficially more similar *H. pomatia*) is genetically closer to the *ECH* clade. This is supported by both phylogenetic inference based on the mitochondrial COI and structural identity of the sequenced fragment of nuclear 18S+ITS1. As opposed to the suggestion of Steinke *et al.* (2004), the fragment is less variable among the included outgroup of Helicidae than the sequenced fragment of COI: the mean proportion of pairwise differences among *H. buchii*, *H. lucorum*, and species of the outgoup reach 0.12 for the homologous 18S+ITS1 fragment but 0.23 for homologous fragment of mitochondrial COI.

The outcome of the partial Mantel test suggests that size and shape of shell correlates with genetic distance for *ECH* rather than by short-term/reversible adaptations to local climates. The extant range of *Helix goderdziana* is restricted to the western Lesser Caucasus in SW Georgia and NE Turkey. Paleontological data suggests that this area supported a major forest refugium (MFR) during the last glacial maxima (Zeist and Bottema 1988, Van Andel and Tzedakis 1996). Molecular genetic study of the salamander *Mertensiella caucasica* (Waga, 1876) (Tarkhnishvili *et al.* 2000) revealed presence of two distinct evolutionary lineages of the salamanders isolated since pre-glacial time. The range of the western lineage coincides with the MFR and, hence, with the distribution range of *H. goderdziana*; the range of the eastern lineage is restricted to a small area in central Georgia. This finding supports the hypothesis of existence of multiple forested refugia east of MFR (Velichko and Kurenkova 1990, Tarkhnishvili *et al.* 2012). The geographic line separating MFR from the habitats supporting the eastern lineage of the salamander and the basal haplotype of *H. buchii* coincides with a belt of dry climate crossing the Meskheti Mountains in SW Georgia (Tarkhnishvili *et al.* 2008). The present geographic distribution of the climates was shaped ca. 6 MYBP (million years before present) (Fortelius *et al.* 2002, but see Micheels *et al.* 2009). Data on the rates of molecular evolution in COI in mollusks are controversial. Marko (2002) suggests 1.21% substitution rates per MY, but later studies of snail divergence in Europe (Gittenberger *et al.* 2004, Haase and Misof 2008) indicate that the molecular evolution can be much faster. If Marko's calibration is considered, the average split time between *H. buchii* and *H. goderdziana* may be 3.36 MYBP (95% confidence interval 1.7–4.5 MYBP). However, one cannot exclude that the lineages have been separated much later, in middle or even late Pleistocene. One can suppose that the "dry belt", limiting the eastern range of *H. goderdziana*, was an insuperable barrier for the spread of mesophylic species with limited dispersal ability during glacial maxima. This may have triggered the original split between the two snail lineages. The ancestral lineage of *H. buchii* survived in the refugia far from the Black Sea with a more continental climate, and the ancestors of *H. goderdziana* survived in MFR.

Habitat preferences and conservation

There are remarkable ecological differences between the two *ECH* species. *Helix buchii* is found in a wide habitat spectrum, mainly broadleaf forest litter away from the water sources but never in coniferous forest. This species is relatively common in primary forests of Caucasian mountain, whereas both known locations of *H. goderdziana* lay in exceedingly damp habitats along the brooks in mixed or broadleaf forest (*Alnus barbata* and *Picea orientalis*). The only known Georgian locality of *H. goderdziana* is currently under intensive anthropogenic pressure. In the last 5 years, the habitat was repeatedly littered and damaged (most of trees were cut down), and water in the brooks was polluted by sawdust and waste. We were unable to find *H. goderdziana* in 2010 and 2011 at the type locality. The disappearance of the species may be related either to the changing of microclimatic conditions at the brooks or the water pollution. The potential solution for the future is creation of a mini-reserve in the area, but this needs immediate attention from the relevant governmental bodies and international conservation community.

ACKNOWLEDGMENTS

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REFERENCES

Armbruster, G. F. J., C. H. M. Van Moorsel, and E. Gittenberger. 2000. Conserved sequence patterns in non-coding ribosomal ITS1 of distantly related snail taxa. *Journal of Molecular Studies* **66**: 570–573.

Bandelt, H., P. Forster, and A. Rohl. 1999. Median-joining networks for inferring intraspecific phylogenies. *Molecular Biology and Evolution* **16**: 37–48

Bickford, D., D. J. Lohman, N. S. Sodhi, P. K. L. Ng, R. Meier, K. Winker, K. K. Ingram, and I. Das. 2006. Cryptic species as a window on diversity and conservation. *Trends in Ecology and Evolution* **22**: 148–155.

Blackith R. and R. A. Reyment. 1971. *Multivariate Morphometrics*. Academic Press, New York.

Bohonak, A. J. 2002. IBD (Isolation By Distance): A program for analyses of isolation by distance. *Journal of Heredity* **93**: 153–154.

Conde-Padín, P., J. W. Grahame, and E. Rolán-Alvarez. 2007. Detecting shape differences in species of the *Littorina saxatilis* complex by morphometric analysis. *Journal of Molluscan Studies* **73**: 147–154.

Denk, T., N. Frotzler, and N. Davitashvili. 2001. Vegetational patterns and distribution of relict taxa in humid temperate forests and wetlands of Georgia (Transcaucasia). *Biological Journal of the Linnean Society* **72**: 287–332.

Donnelly, P. and S. Tavare. 1986. The age of alleles and a coalescent. *Advances in Applied Probability* **18**: 1–19.

De Queiroz, K. 2007. Species concepts and species delimitation. *Systematic Biology* **56**: 879–886.

Drummond, A. J. and A. Rambaut. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* **7**: 214. doi:10.1186/1471-2148-7-214

Folmer, O., M. Black, W. Heah, R. Lutz, and R. Vrijenhoek. 1994. DNA primers for amplification of mitochondrial cytochrome C oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3**: 294–299.

Fortelius, M., J. Eronen, J. Jernvall, L. Liu, D. Pushkina, J. Rinne, A. Tesakov, I. Vislobokova, Z. H. Zhang, and L. Zhou. 2002. Fossil mammals resolve regional patterns of Eurasian climate change over 20 million years. *Evolutionary Ecology Research* **4**: 1005–1016.

Gittenberger, E., W. H. Piel, and D. S. J. Groenenberg. 2004. The Pleistocene glaciations and the evolutionary history of the polytypic snail species *Arianta arbustorum* (Gastropoda, Pulmonata, Helicidae). *Molecular Phylogenetics and Evolution* **30**: 64–73.

Haase, M. and B. Misof. 2009. Dynamic gastropods: Stable shell polymorphism despite gene flow in the land snail *Arianta arbustorum*. *Journal of Zoological Systematics and Evolutionary Research* **47**: 105–114.

Hall, T. A. 1999. BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* **41**: 95–98.

Hasegawa, M., H. Kishino, and T. Yano. 1985. Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. *Journal of Molecular Evolution* **22**: 160–174.

Hausdorf, B. 2010. Progress toward a general species concept. *Evolution* **64**: 923–931.

Joliffe, I. T. and B. J. Morgan. 1992. Principal component analysis and exploratory factor analysis. *Statistical Methods in Medical Research* **1**: 69–95.

Kikvidze, Z. and M. Ohsawa. 1999. Adjara, East Mediterranean refuge of tertiary vegetation. *In*: M. Ohsawa, W. Wildpret, and M. D. Arco, eds., *Anaga Cloud Forest, a Comparative Study on Evergreen Broad-leaved Forests and Trees of the Canary Islands and Japan*. Chiba University Publications, Chiba, Japan.

Kimura, M. 1980. A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* **16**: 111–120.

MacCallum, C. R., K. F. Widaman, S. Zang, and S. Hong. 1999. Sample size in factor analysis. *Psychological Methods* **4**: 84–99.

Mai, D. H. 1995. *Tertiäre Vegetationsgeschichte Europas*. Gustav Fischer Verlag, Jena, Germany. [In German]

Mallet, J. 2010. Why was Darwin's view of species rejected by twentieth century biologists? *Biology and Philosophy* **25**: 497–527.

Mallet, J., M. Beltrán, W. Neukirchen, and M. Linares. 2007. Natural hybridization in heliconiine butterflies, the species boundary as a continuum. *BMC Evolutionary Biology* **7**: 28. doi:10.1186/1471-2148-7-28

Manel, S., M. K. Schwartz, G. Luikart, and P. Taberlet. 2003. Landscape genetics: Combining landscape ecology and population genetics. *Trends in Ecology and Evolution* **18**: 189–197.

Marko, P. 2002. Fossil calibration of molecular clocks and divergence times of geminate species pairs separated by the Isthmus of Panama. *Molecular Biology and Evolution* **19**: 2005–2021.

Micheels, A., A. Bruch, and V. Mosbrugger. 2009. Miocene climate modeling sensitivity experiments for different CO_2 concentrations. *Palaeontologia Electronica* **12**: 1–20.

Milne, R. I. and R. J. Abbott. 2002. The origin and evolution of Tertiary relict floras. *Advances in Botanical Research* **38**: 281–314.

Milne, R. I. 2004. Phylogeny and biogeography of *Rhododendron* subsection *Pontica*, a group with a Tertiary relict distribution. *Molecular Phylogenetics and Evolution* **33**: 389–401.

Milne, R. I. 2006. Northern hemisphere plant disjunctions: A window on Tertiary land bridges and climate change? *Annals of Botany* **98**: 465–472.

Mumladze, L., D. Tarkhnishvili, and B. M. Pokryszko. 2008. A new species of the genus *Helix* from the Lesser Caucasus (SW Georgia). *Journal of Conchology* **39**: 483–485.

Neubert, E. and A. R. Bank. 2006. Notes on the species of *Caucasotachea* C. Boettger 1909 and *Lindholmia* P. Hesse 1919, with annotations to the Helicidae. *Archiv für Molluskenkunde* **135**: 101–132.

Parks, D. H., M. Porter, S. Churcher, S. Wang, C. Blouin, J. Whalley, S. Brooks, and R. G. Beiko. 2009. GenGIS: A geospatial information system for genomic data. *Genome Research* **19**: 1896–1904.

Richtsmeier, J. T., V. B. Deleon, and S. R. Lele. 2002. The promise of geometric morphometrics. *Yearbook of Physical Anthropology* **45**: 63–91.

Röhrig, E. 1991. Deciduous forests of the Near East. *In*: E. Röhrig and B. Ulrich, eds., *Ecosystems of the World*. Elsevier, Amsterdam, Netherlands. Pp. 165–174.

Schütt, H. 2005. *Turkish Land Snails*. Verlag Natur and Wissenschaft, Solingen, Germany.

Suchard, M. A., E. W. Robert, and J. S. Sinsheimer. 2001. Bayesian selection of continuous-time Markov chain evolutionary models. *Molecular biology and Evolution* **18**: 1001–1013.

Sysoev, A. and A. Schileyko. 2009. *Land Snails and Slugs of Russia and Adjacent Countries*. Pensoft, Sofia-Moscow, Russia.

Tamura, K., D. Peterson, N. Peterson, G. Stecher, M. Nei, and S. Kumar. 2011. MEGA v5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution.* **28**: 2731–2739.

Tarkhnishvili, D., A. Gavashelishvili, and L. Mumladze. 2012. Palaeoclimatic models help to understand current distribution of Caucasian forest species. *Biological Journal of the Linnean Society* **105**: 231–248.

Tarkhnishvili, D., U. Kaya, A. Gavashelishvili, and I. Serbinova. 2008. Ecological Divergence between two Evolutionary Lineages of the Caucasian Salamander: Evidence from the GIS analysis. *Herpetological Journal* **18**: 155–163.

Tarkhnishvili, D. N., R. S. Thorpe, and J. W. Artnzen. 2000. Pre-Pleistocene refugia and differentiation between populations of the Caucasian salamander (*Mertensiella caucasica*). *Molecular Phylogenetics and Evolution* **14**: 414–422.

Thorpe, R. S. and L. Leamy. 1983. Morphometric studies in inbred and hybrid house mice (*Mus* sp.): Multivariate analysis of size and shape. *Journal of Zoology* **199**: 421–432.

Tuniyev, B. S. 1990. On the independence of the Colchic center of amphibian and reptile speciation. *Asiatic Herpetological Research* **3**: 67–84.

Van Andel, T. H. and P. C. Tzedakis. 1996. Palaeolithic landscapes of Europe and environs, 150,000–25,000 years ago: An overview. *Quaternary Science Reviews* **15**: 481–500.

Veith, M., S. Steinfartz, R. Zardoya, A. Seitz, and A. Meyer. 1998. A molecular phylogeny of 'true' salamanders (family Salamandridae) and the evolution of terrestriality of reproductive modes. *Journal of Zoological Systematic and Evolutionary Research* **36**: 7–16.

Velichko, A. A. and A. A. Kurenkova. 1990. Landscapes of the Northern Hemisphere during the Late Glacial Maximum. *In*: O. Soffer and G. Gamble, eds., *The World at 18,000 BP*. Unwin Hyman, London, United Kingdom. Pp. 255–265.

Welter-Schultes, F. 2009. Species in genus *Helix*. Available from www.animalbase.uni-goettingen.de (version 21-01-2009), accessed 2 June 2012.

Wiley, D. F., N. Amenta, D. A. Alcantara, D. Ghosh, Y. J. Kil, E. Delson, W. Harcourt-Smith, F. J. Rohlf, K. St. John, and B. Hamann. 2005. Evolutionary morphing. *Proceedings of the IEEE Visualization* (VIS'05). 431–438.

Zazanashvili, N., G. Sanadiradze, A. Bukhnikashvili, A. Kandaurov, and D. Tarkhnishvili. 2004. Caucasus. *In*: R. A. Mittermaier, P. G. Gil, M. Hoffmann, J. Pilgrim, T. Brooks, C. G. Mittermaier, J. Lamoreux, and G. A. B. Da Fonseca, eds., *Hotspots Revisited, Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions*. CEMEX/Agrupación Sierra Madre, Mexico.

Zeist, W. V. and S. Bottema. 1988. Late Quaternary vegetational and climatic history of southwest Asia. *Proceedings of the Indian National Science Academy* **54**: 461–480.

Zelditch, M. L., D. L. Swiderski, H. D. Sheets, and W. L. Fink. 2004. *Geometric Morphometrics for Biologists: A Primer*. Elsevier Academic Press, San Diego, California.

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Appendix 1.

Source	Primer sequence	Amplification conditions	Temperature profile
COI universal (Folmer *et al*. 1994)	5′-GGTCAACAATCATAAAGATATTGG-3′ 5′-TAAACTTCAGGGTGACCAAAAAATCA-3′	20µl total volume, with: 2 µl template DNA 1.5U of Taq polymerase (Promega) 1x Promega buffer 1.5 µm of $MgCl_2$ 0.1 µm of each dNTP, 0.1 µm primer concentrations	1 cycle of 3 min @ 95 °C 25 cycles: 40s @ 94 °C 40s @ 50 °C 1min @ 72 °C 1 cycle of 10 min @ 72 °C
18S+ITS1 mollusc-specific (Armbruster *et al*. 2000; van Moorsel *et al*. 2000)	5′-TAACAAGGTTTCCGTAGGTGAA-3′ 5′-GCTGCGTTCTTCATCGATGC-3′	20 µl total volume, with: 3 µl template DNA 1U of Taq polymerase(Promega) 1x romegabuffer 1.5 µm of $MgCl_2$ 0.1 µm of each dNTP, 0.1 µm primer concentrations	1 cycle of 3 min @ 95 °C 25 cycles: 40s @ 94 °C 30s @ 56 °C 0.3 °C each cycle) 1min @ 72 °C 1 cycle of 10 min @ 72 °C

VI

პუბლიკაცია გაგზავნილია ჟურნალში *Journal of Molluscan Studies*

Endemic Land Molluscs in Georgia (Caucasus): how well are they protected by existing reserves and National Parks?

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ABSTRACT

The globally significant Caucasus hotspot for biological diversity holds a rich and largely endemic fauna of land molluscs. Georgia holds the majority of these regional endemics. Land molluscs are particularly sensitive indicators of habitat quality and faunal diversity. In this study, we examine the extent to which the existing network of protected areas within Georgia captures the hotspots of endemic molluscan diversity. We collected and mapped the records of Georgian and Caucasian endemic species onto a 20 x 20 km square UTM grid to identify the most important endemic areas in Georgia. We related these to the existing network of protected areas. Less than half of the richest grid cells included significant protected areas. Although those endemics with the smallest known ranges were better protected than the remainder, the incomplete state of knowledge means that our estimates of existing protection are surely optimistic. To date, the designation of protected areas in Georgia has not used distributional data for invertebrates, although they have been shown elsewhere to be an effective aid to planning and management for conservation. Further surveys of molluscs and their monitoring in existing protected areas can and should inform a systematic conservation strategy in Georgia.

Keywords: Molluscs, Georgia, Caucasus, Richness, Conservation, Reserve selection

INTRODUCTION

The Caucasus Ecoregion is one of the 34 hotspots of biological diversity recognized as of global importance (Zazanashvili et al. 2004). It is one of the most significant West-Palaearctic refugia in which forest fauna and flora survived through the climatic oscillations of the Pleistocene, and has a high proportion of endemic taxa, some with very restricted distributions. Unfortunately, only 12.7% of its area is currently protected (Caucasus Ecoregion: http://wwf.panda.org/; data retrieved 01.02.2012). Georgia is situated in the centre of this region, constituting only 12% of its area, but including most of its climatic zones and vegetation types, especially in the variety of forests. Currently, only 7.3% of Georgia is subject to legal protection (Fig.1).

The granting of protected status in the region has been based largely on the distribution of vegetation and of charismatic vertebrates, and has been an *ad hoc* selection not based on detailed distribution data. The most important disadvantage of such a selection is that it may not protect all or even most of the endemic invertebrate fauna (Pressey 1994; Kerr 1997; Bakarr and Lockwood 2006), especially in those taxa where geographical ranges are very restricted (Cameron 1998). One problem in applying more rigorous approaches to the designation of protected areas (PA) is the lack of adequate distributional data for many invertebrates; in some cases even alpha taxonomy and reliable identification are inadequate. Where such data are available, the use of modern quantitative methods has proved effective in identifying the extent to which existing protected areas safeguard the fauna; an excellent example is given by Sólymos (2007) for the land mollusc fauna of Hungary.

Land molluscs are particularly useful in identifying hotspots of endemic invertebrate diversity (Moritz et al. 2001). The Caucasus region in general and Georgia in particular have exceptionally rich land mollusc faunas with high levels of endemism (Schütt 2005; Sysoev and Schileyko 2009). Many species have very restricted distributions within the region. While studies on this fauna started early in the 19th century (Dubois de Montpereux 1839, 1840), and have continued thereafter, sustained by visiting Soviet scientists, they diminished in the late 20th century, and have only recently resumed. The new stage in malacological research in Georgia was started by the author in collaboration with foreign malacologists (Mumladze et al. 2008,2013; Mumladze 2013; Pokryszko et al. 2011; Hausdorf and colleagues in progress). While there is no doubt that knowledge of distributions and even of taxonomy are incomplete, the combination of the new data obtained with data obtained from older accounts and from museum collections makes it possible to present a more rigorous, if provisional, analysis of the extent to which existing protections safeguard the mollusc fauna.

This study used the collated data from all reliable sources to map the distribution of endemic mollusc species within Georgia, and to detect the hotspots of greatest endemic diversity. It considers both species endemic to Georgia itself and those others endemic to the region. Ultimately protection of the former depends entirely on national policies, at least in those areas where they can be implemented. For the latter, policies elsewhere also affect protection, but the central position of Georgia in the region places particular emphasis on protection within it. The distributions are related to protected areas to estimate the extent to which they safeguard the fauna. While it is certain that the knowledge of distributions is incomplete, further information is likely to weaken the link between protection and the distribution of endemic species, as it is National Parks that receive the most attention. The estimate thus gives the most optimistic view of the extent to which the endemic fauna is protected.

MATERIALS AND METHODS

The most up-to-date catalogue of the land molluscs of Georgia is provided by Sysoev and Schileyko (2009). Except in the cases of species known only from their type localities, however, they give only very general descriptions of range. Far more detail is given by Lezhava (1973), but many species listed by him have subsequently been eliminated by synonymy with others, and others have been newly-described or found in further localities. These data have therefore been supplemented by information in Riedel (1966), Hausdorf (2000, 2001, 2003), Egorov and Greke (2005), Sysoev and Schileyko (2005), Schütt (2005), Neubert and Bank (2006) and Pokryszko et al. (2011). Many of these draw also on earlier museum records. Nomenclature generally follows that of Sysoev and Schileyko (2009) with some exceptions (Riedel 1966; Neubert and Bank 2006). Authorities are given in Online Resource 1.

The records of Caucasian (CE) and Georgian (GE) endemic mollusc species, with locations, were entered in a database (All the following analyses were performed separately for GE and CE species groups). Using ArcGIS v. 9.3 (ESRI Inc., Redlands, CA, USA), a 20 x 20 km net based on UTM grid cells was superimposed on a map of Georgia and for each grid cell endemic species presence data were attached. The choice of UTM grid cell size was made to enable the maximum use of bibliographic data with minimal bias. Occurrence records (often place names) generally fell within a maximum 20 km square spatial error range. Marginal cells with more than 50% situated outside Georgia were excluded from the analysis, which thus used 244 cells in total. Since distribution data is incomplete, we tested for the influence of site accessibility on records by examining linear correlations between both raw and weighted richness (see below) and the distance from large towns.

Based on the endemic species distributional data associated with this 20 x 20 km UTM grid, we calculated raw (RR) and weighted species (WR) richness for each cell. Raw species richness was assessed as the sum of all endemic species occurring in each grid cell. To calculate weighted richness firstly each species was down-weighted by its range size. Range size for each species was assessed as the total number of cells of its occurrence within Georgia. For each cell in which the species was present its contribution to weighted richness was the reciprocal of the range size. Thus for each cell weighted richness was the sum of such scores (Williams and Humphries 1994; Crisp et al. 2001; Linder 2001). For Caucasian endemics, this weighting reflects only the Georgian range. While this overestimates the weighting that such species merit in a regional assessment, it reflects their status within Georgia itself, a useful indicator for national conservation planning.

We used two approaches to assess the protection status of endemic species (PSS). First, we determined what proportion of the richest 5% of cells (12 out of 244 UTM squares) had at least 10% of their area subject to protection. These are deemed to be protected. The 5% selection is an arbitrary but frequently used threshold (Prendergast et al. 1993; La Ferla et al. 2002; López-Pujol et al. 2011). Second, in order to derive a single threshold independent measure of general protection status of endemic species (gPSS) we calculated an average of percent of occupied grid cells that included protected areas for each species (where grid cell value is either 0 or 1 and at least 10% is covered by the protected areas). Analyses were performed with the help of ArcGIS v. 9.3 and SPSS v. 16.0 (SPSS Inc. Chicago, IL, USA) software packages.

RESULTS

At least 255 species of land slugs and snails are recorded in Georgia (Sysoev and Schileyko, 2009). 165 (64%) are endemic to the Caucasus region (Online Resource 1). Of these endemic species, six (indicated in Online Resource 1) are excluded from analysis as we were unable to locate records in Georgia with the required degree of accuracy. Of the 159 remaining, 55 are endemic to Georgia (GE), while 104 are also found elsewhere in the Caucasus (CE).

While there is no means of assessing the intensity of collecting effort across the country, it is clear from published accounts that areas now designated as National Parks have been searched most thoroughly. More generally, there is a slight but significant negative association between the endemic richness of a cell and its mean distance from a large centre of population ($-0.19 > r^2 > -0.31$, $P < 0.001$ for both richness measures (RR and WR) within either species group (GE and CE)), the easiest surrogate available for accessibility.

Figure 2 shows the frequency distributions of GE and CE endemic species by number of cells occupied within Georgia. It is evident that GE species are generally more restricted within Georgia than those also known from elsewhere in the region (CE species). Not all restricted ranges are represented by adjacent cells. For GE species there is a modest positive correlation between RR and WR scores (Fig. 3). For RR scores, only three out of the 12 cells with the highest scores contain at least 10% of their area under protection, a PSS score of 25%. For WR scores, the situation is improved, with six cells involved (PSS 50%); the most restricted species are nominally better protected. This is confirmed by considering the PSS status of each species in relation to its range size. There is a loose but significant negative association between range size and species specific PSS score (Fig. 4), but 11 GE and 7 CE species have ranges entirely outside protected areas (Online Resource 1). It is noticeable also that 5 of 6 troglobiont species (Online Resource 1) with very narrow ranges (three of them known only from type localities) are inside the PAs under our criterion. These PAs may have been established for geological reasons. Removing them from the dataset does not have any significant influence on the richness patterns.

For Caucasian endemics not restricted to Georgia (CE), a broadly similar pattern occurs, and there is a positive correlation between RR scores for each kind of endemic among cells (Figs. 3, 5a,c). The patterns do not, however, coincide completely. WR patterns show a weaker association (Figs. 3, 5b,d). These regional endemics are rather better protected within Georgia, with a PSS score of 50% based on RR, and 58% on WR. In this analysis, confined to Georgia, the combined data for GE and CE species gives PSS scores of 50% for RR, and 58% for WR, the same values as for CE species alone.

The threshold independent measures of overall protection status (gPSS) gave values of 43% for CE and 46% for GE species; the overall value (GE + CE) was 44.5%. Although the richness patterns of GE and CE species are not identical, the overall distribution of high diversity is similar in each. The most species-rich cells are found mainly in the west and centre of Georgia, while cells in the east and south-east are generally poor. Three regions: Eastern Abkhasia, west Adjaria and the centre of Borjomi district harbour significant concentrations of endemic species (both GE and CE). The north-western part of Imereti region, the mountainous north of Mingrelia and southern Racha (these are adjacent areas) are also important endemic areas where high ground connects the Greater and Lesser Caucasus Mountains (Figs. 1, 5).

DISCUSSION

Molluscan hotspots and protected areas

Both Caucasia as a whole and Georgia within it are recognised hotspots of biodiversity, rich in endemic species (Kikvidze and Ohsawa 1999; Denk et al. 2001; Milne and Abbott 2002; Zazanashvili et al. 2004). Recent work (Tarkhnishivili et al. 2012) shows that this endemic richness is the product of the existence of multiple forest refugia and their varying connectedness over the Pliocene and Pleistocene. The best signals of these refugia are found among organisms with poor powers of dispersal, often with very restricted ranges. Snails typify such organisms, and their use in identifying small forest refugia was pointed out by Moritz et al. (2001). They therefore also act as indicators of areas requiring protection.

Despite the large number of endemic snail species, some with very small recorded ranges, only one, *Helix buchii* Dubios de Montpereux, 1839 is currently included in the Georgian Red List (with the status of Data Deficient). It is certainly not the rarest species in the region, though perhaps the best known. The first author has documented several cases of rapid population decline of *H. buchii* in the last decade (unpublished data), accompanied by habitat fragmentation and loss (NR - 2010). Given the incomplete knowledge of snail distributions it is unlikely that the case for protection can be made by proposing more candidates for high-risk categories within the IUCN framework, a complex task requiring data that are hard to obtain for invertebrates (Bouchet and Gargominy 1998). For the same reason, we have chosen to look at the overall trends, rather than identify those species least protected. Sólymos (2007) was able to do the latter for the better known Hungarian fauna. We note, however, that eleven Georgian endemics (including one troglobiont species) are not known from any protected area (Online Resource 1).

Hence, it was appropriate to use all the available data on Georgian endemic snails to identify hotspots of diversity, and to examine the extent to which they were protected. The proportions of ranges, and indeed the number of species found in existing protected areas will no doubt alter as more data are acquired. For Georgian endemics only a quarter of the richest cells identified here had more than 10% of their area subject to protection. Although the WR index, emphasising species with the smallest known ranges, gives a more positive picture, half the cells with the highest values have no significant protection. For other Caucasian endemics the situation is marginally better, as it is for the endemic fauna as a whole.

While there are minor differences between GE and CE species, the richest areas extend from the west along the Lesser and Greater Caucasus chains, up to and including the Likhi range – the only connecting ridge between them. Further east, the endemic fauna is generally poor, with the exception of the Lagodekhi National Park (PA 22 in Figure 1). This pattern is clearly a result of the distribution of the primary forests of Caucasia represented mainly by beech (*Fagus orientalis*), hornbeam (*Carpinus caucasicus*), sweet chestnut (*Castanea sativa*), linden trees (*Tilia carpinifolia*), Nordmann Fir (*Abies normanniana*) Caucasian spruce (*Picea orientalis*) and several oak species (*Quercus spp*) (Denk et al. 2001). The numbers of endemic species known from each PA reflects this pattern (Table 1). The hotspot of Adjaria in the south-west near Batumi (Lesser Caucasus) now has a number of protected areas containing a number of rare endemics (Fig. 1). The north-west Greater Caucasus, Abkhasia, (*de facto* outside Georgian control) is less intensively protected. Elsewhere, the only major protected areas matching a hotspots are Borjomi (Table 1; Fig. 1) in the northern Javakheti region and, to a lesser extent, Lagodekhi as mentioned above. Nearby hotspots in the north-western part of Imereti region, the north mountainous Mingrelia and southern Racha districts are unprotected, although containing calcareous substrates and humid mountain forests - preferred habitats for molluscs. These areas are constantly represented with high endemic richness for both CE and GE species, and should be considered for protection (see below). Overall, more than half of the cells with at least 10% of their area under protection contain fewer endemics than many unprotected cells (Table 1; Fig. 5). We note that in the north-eastern part of Georgia only the relatively well-studied Lagodekhi national reserve is a hotspot for snails; it contains one of the most wild and conserved part of Caucasian forests. Its flora indicates that it has been on the fringe of the forest refugium (Denk et al. 2001).

Informing conservation planning

The Caucasian diversity hotspot results from the survival of certain habitats over long periods and from their periodic splitting into multiple refugia (Velichko and Kurenkova 1990; Van Andel and Tzedakis 1996; Tarkhnishvili et al. 2012). Where ranges are small as a result, the total area protected is of less significance than the choice of which areas to protect. Where, as for snails, there are many small and often non-overlapping ranges, but species are able to survive in relatively small areas (Cameron 1998), this choice is crucial. According to the last national report (NR-2010) to CBD, habitat (especially forest habitat) destruction is still continuing and is the main threat for native biodiversity (Conservation International 2009; Myers 2000). In the absence of any successful conservation project for any single species or habitat in Georgia, the establishment of protected areas (PA) is the only conservation activity available, and new areas have indeed been designated. A network of such areas can perform well if it matches the patterns of biodiversity in the target area (Hunter 1996; Margules et al. 2002). Unfortunately, designation of protected areas in Georgia is not informed by any science based preliminary assessment report or on an estimate of protection gained across all taxa. The recently established Javakheti protected area (established in 2011) was created as an important bird area whereas other vertebrates, invertebrates and plants were rather poorly represented there (Table 1). In general invertebrate animals are ignored during the planning process of PAs in Georgia.

Our study shows that there are a number of hotspots for molluscs, often containing different range-restricted endemics. While the use of surrogates or indicators, inevitable in designing a conservation strategy, may not always yield the best results, there is evidence that such poor dispersers may serve this function better than larger, more mobile and more charismatic species (Moritz et al. 2001). While not all areas deserving of immediate protection will be molluscan hotspots, molluscs can contribute significantly to systematic conservation planning based on a range of taxa (Margules and Pressey 2000).

The overall gPSS estimate for endemic molluscs (44.5%) provided here is probably an overestimate. Richness pattern (both RR and WR) are significantly correlated with proximity to populated areas which can be considered as a sign of insufficient or biased sampling. Coverage is uneven, and much less complete than in more developed countries of similar size (c.f. Sólymos' (2007) account for Hungary). Even at this level the current PA network is not sufficient to cover even 50 % of most species-rich areas for regional endemic molluscs. Molluscs are one of the animal groups most vulnerable to environmental changes (Lydeard et al. 2004). The national conservation strategy in Georgia is to expand the PA network (NEAP - National Environmental Action Programme of Georgia 2012 –2016; http://moe.gov.ge/index.php?sec_id=32&lang_id=ENG). The size and shape of PAs should be based on biodiversity data rather than a simple area target (Rodrigues et al. 2003). Endemic molluscs can provide such data, and can assist the managers and decision makers for upcoming PAs to incorporate the main principles (complementarity, irreplaceability and vulnerability) for systematic area prioritization (Margules and Pressey 2000; Sarkar 2006; Margules and Sarkar et al. 2007). Further surveys and the monitoring of molluscs in existing PAs will certainly improve the quality of decisions made in this context.

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REFERENCE

Bakarr MI, Lockwood M (2006) Establishing protected areas. In: Lockwood M, Worboys GL, Kothari A (eds) Managing protected areas—a global guide. Earthscan Publications Ltd, Camden, pp 195-222

Bouchet P, Gargominy O (1998) Action plan formulation for molluscan conservation: getting the facts together for a global perspective. J Conchol 2:45-50

Cameron RAD (1998) Dilemmas of rarity: biogeography ical insights and conservation priorities for land mollusca. J Conchol 2:51–60

Conservation International (2009) Biodiversity hotspots-resources-maps and GIS data. http://www.biodiversityhotspots.org/ Accessed 9 Sept 2010. Accessed 15 January 2013

Crisp MD, Laffan S, Linder HP, Monro A (2001) Endemism in the Australian flora. J Biogeogr 28:183–198

Denk T, Frotzler N, Davitashvili N (2001) Vegetational patterns and distribution of relict taxa in humid temperate forests and wetlands of Georgia Transcaucasia. Biol J Linn Soc 72:287–332

Dubois de Montpereux F (1839) Voyage autour du Caucase, chez Tcherkesses et les Abkhases, en Colchide, en Georgie, en Armenie et en Crimee. Librairie de Gide, Paris

Dubois de Montpereux F (1840) Voyage autour du Caucase, chez Tcherkesses et les Abkhases, en Colchide, en Georgie, en Armenie et en Crimee. Librairie de Gide, Paris

Egorov RV, Greke K (2005) Treasure of Russian Shells, Orculoidea, Orculidae, Strobilopsida. Colus-doverie LTD, Moscow

Hausdorf B (2000) The genus *Monacha* in the Western Caucasus (Gastropoda: Hygromiidae). J Nat Hist 34:1575-1594

Hausdorf B (2001) A systematic revision of *Circassina* from the Western Caucasus region (Gastropoda: Hygromiidae). J Mollus Stud 67:425-446

Hausdorf B (2003) Revision of the genus *Caucasocressa* from the eastern Pontic Region (Gastropoda: Hygromiidae). J Nat Hist 37:2627-2646

Hunter ML (1996) Fundamentals of Conservation Biology. Blackwell, Cambridge

Kerr JT (1997) Species Richness, Endemism, and the Choice of Areas for Conservation. Conserv Biol 11:1091-1100

Kikvidze Z, Ohsawa M (1999) Adjara, East Mediterranean refuge of Tertiary vegetation. In: Ohsawa M, Wildpret W, Arco MD (eds) Anaga Cloud Forest, a comparative study on evergreen broad-leaved forests and trees of the Canary Islands and Japan. Chiba University Publications, Chiba, pp 297–315

La Ferla B, Taplin J, Ockwell D, Lovett JC (2002) Continental scale patterns of biodiversity: can higher taxa accurately predict African plant distributions? Bot J Linn Soc 138:225–235

Lezhava G (1973) Terrestrial and freshwater molluscs. Animal world of Georgia, v IV [In Georgian]

Linder HP (2001) Plant diversity and endemism in sub-Saharan tropical Africa. J Biogeogr 28:169–182

Lydeard C, RH Cowie, Ponder WF, Bogan AE, Bouchet P, Clark SA, Cummings KS, Frest TJ, Gargominy O, Herbert DG, Hershler R, Perez KE, Roth B, Seddon M, Strong EE, Thompson FG (2004) The global decline of nonmarine mollusks. BioScience 54:321–330

López-Pujol J, Zhang FM, Sun HQ, Ying TS, Ge S (2011) Centres of plant endemism in China: places for survival or for speciation? J Biogeogr 38:1267–1280

Margules CR, Pressey RL (2000) Systematic conservation planning. Nature 405:243-253

Margules CR, Pressey RL, Williams PH (2002) Representing biodiversity: Data and procedures for identifying priority areas for conservation. J Biosci 27:09-326

Margules CR, Sarkar S (2007) Systematic conservation planning. Cambridge University Press, Cambridge

Milne RI, Abbott RJ (2002) The origin and evolution of Tertiary relict floras. Adv Bot Res 38:281–314

Moritz C, Richardson KS, Ferrier S, Monteith GB, Stanisic J, Williams SE, Whiffin W (2001) Biogeographic concordance and efficiency of taxon indicators for establishing conservation priority for a tropical rainforest biota. Proc R Soc B 268:1875–1881

Mumladze L, Tarkhnishvili D, Pokryszko BM (2008) A New Species of the Genus *Helix* From The Lesser Caucasus (SW Georgia). J conchol 39:483-485

Mumladze L (2013) Shell size differences in *Helix lucorum* Linnaeus, 1758 (Mollusca: Gastropoda) between natural and urban environments. Turk J Zool 37:1-6

Mumladze L, Tarkhnishvili D, Murtskhvaladze M (2013) Distribution and taxonomy of the Caucasian endemic *Helix* (Gastropoda: Helicidae) with remarks on the conservation status of *Helix goderdziana*. Am Malacol Bull (In Press)

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Neubert E, Bank RA (2006) Notes on the species of *Caucasotachea* C. Boettger, 1909 and *Lindholmia* P. Hesse, 1919, with annotations to the Helicidae (Gastropoda: Stylommatophora: Helicidae). Arch Molluskenkd 135:101-132

NR – 2010 (2010) Fourth National Report to the United Nations Convention on Biological Diversity: Georgia. http://www.cbd.int/doc/world/ge/ge-nr-04-en.pdf. Accessed 12 December 2012

Pokryszko BM, Cameron RAD, Mumladze L, Tarkhnishvili D (2011) Forest snail faunas from Georgian Transcaucasia: patterns of diversity in a Pleistocene refugium. Biol J Linn Soc 102:239–250

Prendergast JR, Quinn RM, Lawton JH, Eversham BC, Gibbons DW (1993) Rare species, the coincidence of diversity hotspots and conservation strategies. Nature 365:335–337

Pressey RL (1994) *Ad Hoc* Reservations: Forward or Backward Steps in Developing Representative Reserve Systems? Conserv Biol 8:662–668

Riedel A (1966) Zonitidae (excl. Daudebardiinae) der Kaukasusländer (Gastropoda). An Zool 24:1–303

Rodrigues ASL, Andelman SJ, Bakarr MI, Boitani L, Brooks TM, Cowling RM, Fishpool LDC, da Fonseca GAB, Gaston KJ, Hoffmann M, Long JS, Marquet PA, Pilgrim D, Pressey RL, Schipper J, Sechrest W, Stuart SN, Underhill LG, Waller RW, Watts MEJ, Yan X (2003) Global gap analysis towards a representative network of protected areas. Adv Ap Biodivers Sci 5:1–98

Sarkar S, Pressey RL, Faith D et al (2006) Biodiversity conservation planning tools, present status and challenges for the future. Annu Rev Environ Resour 31:123–159

Schütt H (2005) Turkish land snails. Verlag Natur & Wissenschaft, Solingen

Solymos P (2007) Are current protections of land snails in Hungary relevant to conservation? Biodivers Conserv 16:347–56

Sysoev AV, Schileyko AA (2005) Stylommatophora. In: Kantor YuI, Sysoev AV (eds) Catalogue of molluscs of Russia and adjacent countries. KMK Scientific Press, Moscow, pp 228-308 [In Russian]

Sysoev AV, Schileyko AA (2009) Land snails and slugs of Russia and adjacent countries. Pensoft, Sofia

Tarkhnishvili D, Gavashelishvili A, Mumladze L (2012) Palaeoclimatic models help to understand current distribution of Caucasian forest species. Biol J Linn Soc 105:231–248

Van Andel TH, Tzedakis PC (1996) Palaeolithic landscapes of Europe and environs: 150 000–25 000 years ago: an overview. Quat Sci Rev 15:481–500

Velichko AA, Kurenkova AA (1990) Landscapes of the Northern Hemisphere during the Late Glacial Maximum. In: Soffer O, Gamble G (eds) The World at 18 000 BP. Unwin Hyman, London, pp 255–265

Williams PH, Humphries CJ (1994) Biodiversity, taxonomic relatedness, and endemism in conservation. In: Forey PL, Humphries CJ, Vane-Wright RI (eds) Systematics and conservation evaluation. Oxford University Press, Oxford, pp 269–287.

Zazanashvili N, Sanadiradze G, Bukhnikashvili A, Kandaurov A, Tarkhnishvili D (2004) Caucasus. In: Mittermaier RA, Gil PG, Hoffmann M, Pilgrim J, Brooks T, Mittermaier CG, Lamoreux J, da Fonseca GAB (eds) Hotspots revisited, Earth's biologically richest and most endangered terrestrial ecoregions. CEMEX/ Agrupacion, Sierra Madre, pp 148–153

Table 1. The RR and WR scores for GE and CE species (and also totals) are provided for each PA. The *PA_ID* stand for protected area number as reported in the Fig.1.

PA_ID	***1***	***2***	***3***	***4***	***5***	***6***	***7***	***8***	***9***	***10***	***11***	***12***	***13***	***14***	***15***	***16***	***17***	***18***	***19***	***20***	***21***	***22***
PA Area	164	364	364	6	238	137	157	86	4	49	825	221	76	71	66	84	981	38	10	139	323	89
RR_GE	6	9	13	8	2	7	10	5	8	7	12	3	1	5	1	5	5	6	1	3	0	3
RR_CE	17	27	41	39	0	33	42	36	22	26	39	10	5	26	7	16	18	22	15	17	6	26
RR_total	**23**	**36**	**54**	**47**	**2**	**40**	**52**	**41**	**30**	**33**	**51**	**13**	**6**	**31**	**8**	**21**	**23**	**28**	**16**	**20**	**6**	**29**
WR_GE	1.23	1.29	1.29	2.26	0.34	1.67	3.95	3.45	2.86	0.46	1.10	0.28	0.13	0.68	0.08	0.65	0.72	1.06	0.20	0.13	0.00	1.76
WR_CE	0.32	0.86	1.12	0.86	0.31	1.30	2.81	2.69	0.60	0.34	0.74	0.17	0.09	0.58	0.07	0.49	0.28	0.38	0.14	0.11	0.08	1.17
WR_total	**1.55**	**2.15**	**2.41**	**3.12**	**0.65**	**2.97**	**6.76**	**6.14**	**3.46**	**0.80**	**1.84**	**0.45**	**0.23**	**1.26**	**0.15**	**1.14**	**1.00**	**1.44**	**0.33**	**0.24**	**0.08**	**2.93**

Figures

Fig.1 General map of Georgia. There are shown: Main districts of Georgia (A - Abkhasia, B - Svanetia, C - Mingrelia, D - Guria, E - Ajaria, F – Racha, G - Imereti, H - Javakheti, I – Shida Kartli, J – Qvemo Qartli, K - Tianeti, L - Tbilisi, M - Kakheti), PAs (1 - Ritsa, 2 – Pskhu, 3 - Gumista, 4 - Miusera, 5 - Kolkheti, 6 - Kintrishi, 7 - Mtirala, 8 - Machakhela, 9 - Sataplia, 10 - Ajameti, 11 – Borjom-kharagauli, 12 – Ktsia-Tabatskuri, 13 - Javakheti, 14 - Algeti, 15 - Liakhvi, 16 - Kazbegi, 17 - Tusheti, 18 - Babaneuri, 19 - Mariamjvari, 20 – Iori-Chachuna, 21 – Vashlovani, 22 - Lagodekhi) and grid of 20X20 sq km cells

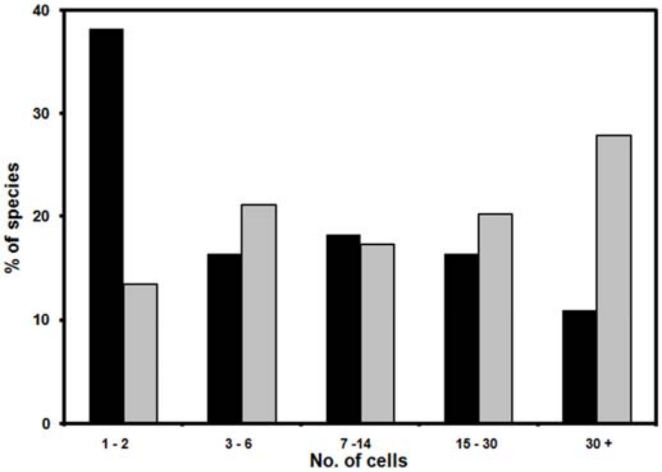

Fig.2 Frequency distribution of range sizes of endemic species. Black bars – GE, Gray bars – CE. Frequencies (Ordinate) is reported as a percentage of species numbers

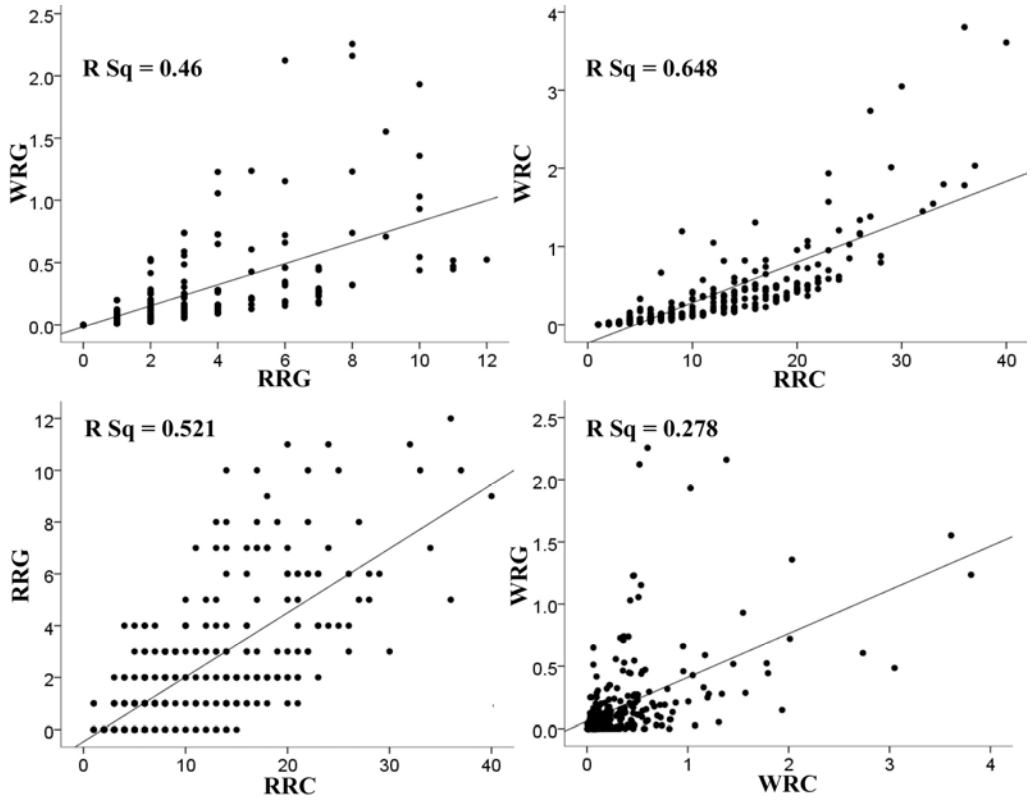

Fig.3 Scatter plots showing the relationships between of RR and WR for GE and CE species. Abbreviations: WRG - weighted richness of Georgian endmeics, RRG - raw richness of Georgian endmeics, WRC – weighted richness of Caucasian endmeics, RRC – raw richness of Caucasian endmeics. All relationships are positive and highly significant (*P*<0.0001)

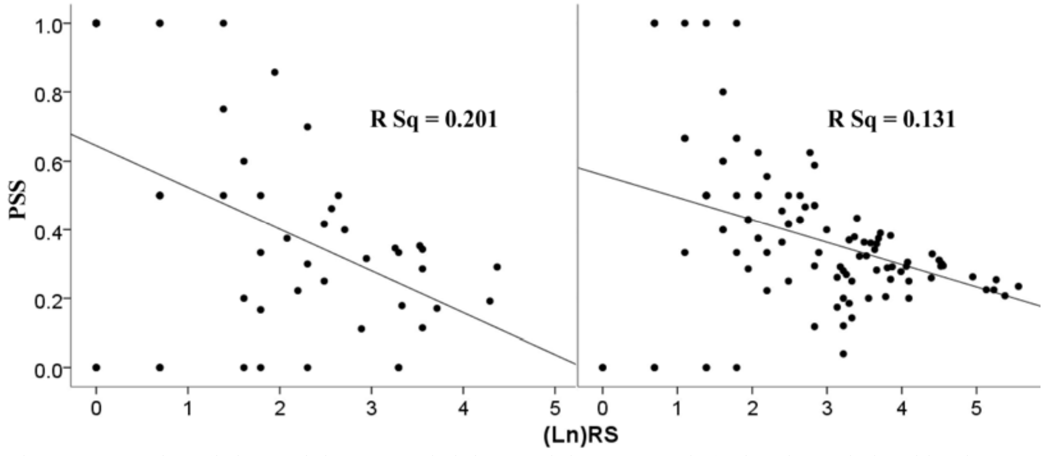

Fig.4 Scatter plots (left panel for GE and right panel for CE species) showing relationships between range size (RS) and species specific protection status (PSS). PSS is significantly (*P*<0.001) and negatively related to the range size. 11 and 7 species are outside of PAs (i.e. their PSS equals to zero) for GE and CE species respectively. Several of them have the same value of RS and PSS and hence are overlaid (see Table 1)

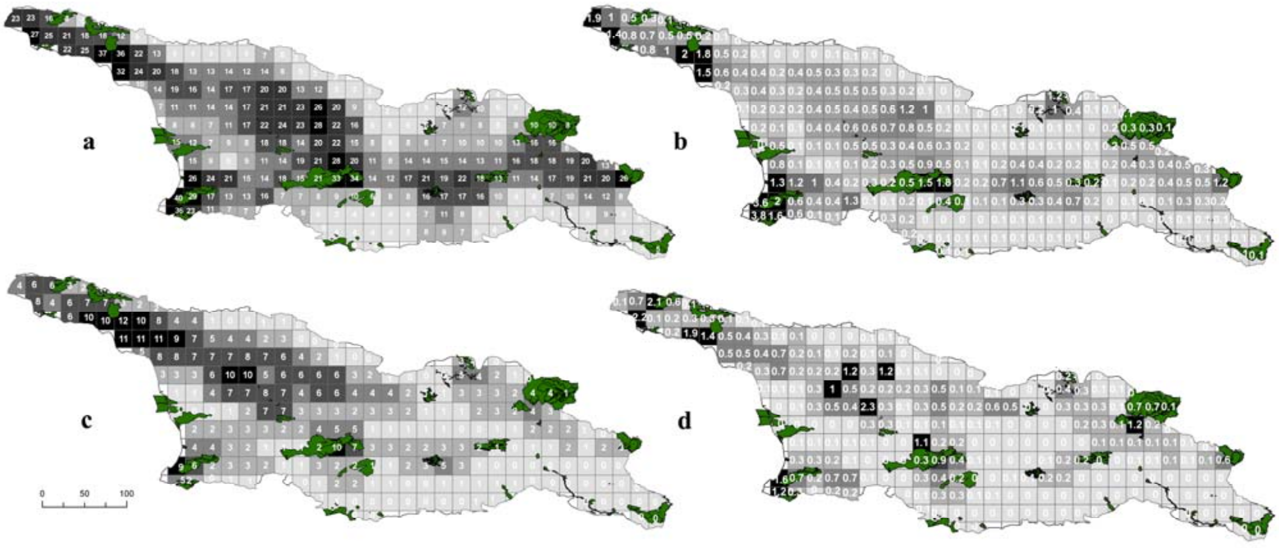

Fig.5 Maps indicating the richness distribution of endemic species. Black indicates 5% - top most rich sites. a – RR-CE (in this case there are 14 black square instead of 12 as the least three richest square contains the same number (26) of endemic species), b – WR-CE, c – RR-GE, d – WR-GE. Green shapes represent existing PAs. The number in each cell indicates numbers of endemic species

Appendix

Endemic Land Molluscs in Georgia (Caucasus): how well are they protected by existing reserves and National Parks?

Biodiversity and Conservation

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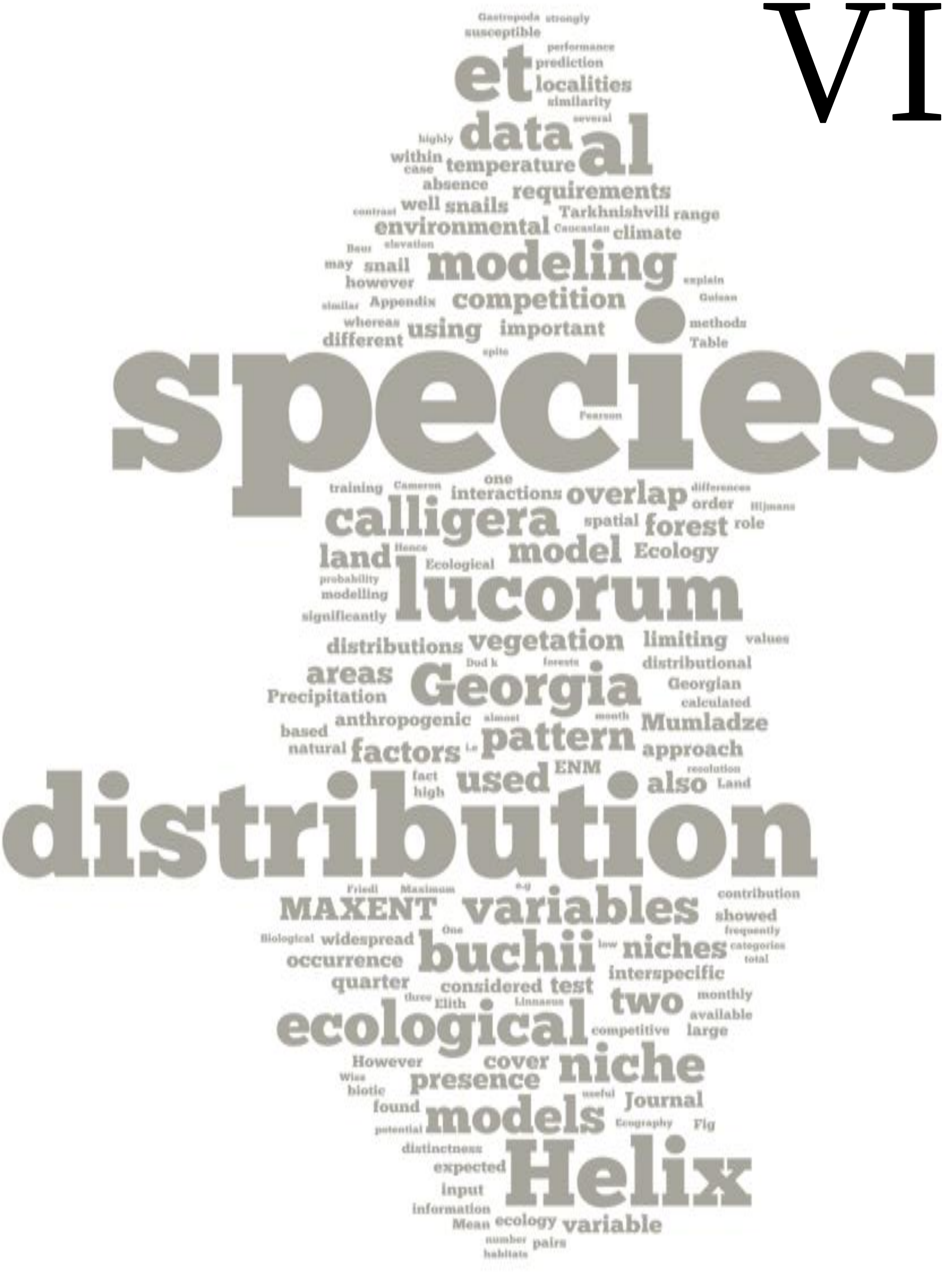
Supplement1. Georgian and Caucasian endemic species list with range size (RS), protection status (PSS) and protected areas (PA) where species does occurs (the number indicates PAs which are described in the main text in Figure 1). Troglobiont species are underlined, and species not recorded from any protected area are named in bold font.

Species		Endemism	RS	PSS	PA
Acicula moussoni	O. Boettger, 1879	GE	78	0.29	2,3,4,10,11,14,15,16,17,18,20,22
Acrotoma baryshnikovi	Likharev and Schileyko, 2007	GE	2	0	-
Acrotoma claussi	Nordsieck, 1977	GE	2	0.5	1
Acrotoma gegica	Suvorov, 2002	GE	1	1	1
Acrotoma juliae	Suvorov, 2002	GE	2	1	1
Acrotoma komarowi	(O. Boettger, 1881)	GE	31	0.29	1,2,3,4
Acrotoma laccata	(O. Boettger, 1881)	GE	12	0.42	2,3
Adzharia renschi	Hesse, 1933	GE	2	0	-
Akramowskiella andronakii	(Lindholm, 1913)	CE	6	0.63	6,7,8
Akramowskiella umbrosa	(Kobelt, 1902)	CE	26	0.37	10,11,14,18,19,22
Andronakia catenulata	(Lindholm, 1914)	CE	2	1	7,8
Armenica gracillima	(Retowski, 1889)	CE	3	0.6	7,8
Armenica griseofusca	(Mousson, 1676)	GE	26	0.35	6,7,11,12,14
Armenica unicristata	(O. Boettger, 1877)	CE	2	0	14
Boettgerilla compressa	Simroth, 1910	GE	10	0.3	2,3,9,10
Caspicyclotus sieversi	(L. Pfeiffer, 1871	CE	12	0.42	17,18,20,22
Caspiophaedusa perlucens	(O. Boettger, 1877)	CE	24	0.36	17,20,21,22
Caucasicola raddei	(Kobelt, 1880)	CE	20	0.4	1,2,3,4
Caucasigena abchasica	(Lindholm, 1927)	CE	6	0.33	2,4
Caucasigena armeniaca	(L. Pfeiffer, 1846)	CE	3	1	16
Caucasigena eichwaldi	(L. Pfeiffer, 1846)	CE	30	0.34	15,16,17,18,22
Caucasigena thalestris	(Lindholm, 1927)	CE	24	0.38	2,3,4,9,10
Caucasocressa dasilepida	(Mabille, 1881)	CE	2	0	-
Caucasocressa ibera	Hausdorf, 2003	GE	4	0.75	11
Caucasocressa joannis	(Mortillet, 1854)	CE	6	0.56	6,7,8
Caucasolimax caucasicus	(Simroth, 1898)	GE	11	0.46	16,22
Caucasotachea atrolabiata	(Krynicki, 1833)	CE	11	0.36	1,2,3,4
Caucasotachea calligera	(Dubois de Montpereux, 1840)	CE	88	0.29	6,7,8,9,10,11,14,17,18,19,20,21,22
Chondrula sunzhica	Steklov, 1962	GE	9	0.22	18,19
Circassina frutis	(L. pfeiffer, 1859)	CE	156	0.22	1,2,3,4,6,7,8,9,10,11,12,14,15,16
Circassina pachnodes	(O. Boettger, 1884)	CE	2	0	-
Circassina pergranulata	Hausdorf, 2001	GE	1	0.5	4
Circassina stephaniae	(Hudec et Lezhawa, 1970)	GE	1	0	-
Clausilioides filifer	(Lindholm, 1913)	GE	2	0.5	7,8
Conulopolita cavatica	(Riedel, 1966)	CE	13	0.47	1,2,3,4
Conulopolita raddei	(O. Boettger, 1879)	GE	15	0.4	1,2,3,4
Conulopolita sieversi	(O. Boettgeri, 1879)	CE	39	0.36	2,4,6,11,14,16,17,18,19

Daudebardia nivea	Schileyko, 1988	GE	1	1	9
Deroceras osseticum	(Simroth, 1901)	CE	10	0.25	2,4,7,8,10
Discoxychilus lindholmi	Reidel, 1966	CE	5	0.5	1,1,1
Drilolestes retowskii	(O. Boettger, 1884)	CE	15	0.47	2,4,9,10,14,22
Elia derasa	(Mousson, 1863)	CE	32	0.32	2,4,9,10,11
Elia ossetica	(Mousson, 1863)	CE	38	0.39	11,14,16,17,18,20,22
Elia somchetica	(L. Pfeiffer, 1846)	CE	37	0.38	11,14,16,17,18,20,22
Elia tuschetica	Likharev et Lezhawa, 1961	GE	2	1	17
Euchondrus acutior	(Lindholm, 1922)	CE	1	0.33	8
Eumilax brandti	(Martens, 1880)	CE	59	0.25	1,2,3,4,11,18,19,22
Eumilax intermittens	(O. Boettger, 1883)	CE	35	0.28	2,4,17,18,20,22
Euomphalia appeliana	(Mousson, 1876)	CE	2	0.67	3
Euomphalia aristata	(Krynicki, 1836)	CE	36	0.36	9,10,11,16
Euxinastra hamata	(O. Boettger, 1888)	CE	5	0.5	6,7,8
Euxinolauria caucasica	(L. pfeiffer, 1857)	GE	14	0.5	16,17,18,20
Euxinolauria glomerosa	Suvorov et Schileyko, 1991	GE	6	0.5	6,7
Euxinolauria honesta	Suvorov et Schileyko, 1991	GE	4	0	-
Euxinolauria nemethi	(Hausdorf, 1996)	CE	4	0.4	2,4
Euxinolauria paulinae	(Lindholm, 1913)	CE	9	0.42	6,7,8
Euxinolauria pulchra	(Retowski, 1883)	GE	25	0.18	5,6,7,8
Euxinolauria rectidentata	Schileyko, 1975	GE	2	1	7,8
Euxinolauria silicea	Schileyko, 1975	GE	2	0.5	22
Euxinolauria sinangula	Schileyko, 1975	CE	4	0.6	4,7
Euxinolauria superstructa	(Mousson, 1876)	CE	42	0.29	6,7,8,11,12,22
Euxinolauria tenuimarginata	(Pilsbry, 1922)	CE	15	0.63	5,6,7,11
Euxinolauria zonifera	(Pilsbry, 1934)	CE	37	0.26	2,3,4,5,6,7,8
Filosa filosa	(Mousson, 1863)	CE	5	0.38	6,7,8
Fruticocampylaea kobiensis	(O. Boettger, 1883)	GE	6	0.17	16
Fruticocampylaea narzanensis	(Krynicki, 1836)	CE	168	0.25	2,3,4,9,10,11,12,14,15,16,17,18,19,20,21,22
Georginapaeus hohenackeri	(L. Pfeiffer, 1848)	CE	35	0.2	11,14
Gibbulinopsis interrupta	(Reinhardt in Martens, 1876)	CE	42	0.38	11,14,18,19,20,21
Gigantomilax koenigi	(Simroth, 1912)	CE	4	0.67	6,7,8
Gigantomilax lederi	(O. Boettger, 1883)	CE	80	0.26	1,2,3,4,6,7,8,10,11,14
Gigantomilax monticola	(O. Boettger, 1881)	CE	49	0.28	6,7,8,11,12,13,14
Helix buchii	(Dubios de Montpereux, 1839)	CE	57	0.29	6,7,8,9,10,11,14,22
Helix goderdziana	Mumladze et al., 2008	CE	1	0	-
Hyrcanolestes velitaris	(Martens, 1880)	CE	14	0.43	9,10,11,14
Imparietula brevior	(Mousson, 1876)	CE	225	0.23	1,2,3,4,6,7,8,10-22
Inguria wagneri	(Rosen, 1911)	CE	27	0.19	2,3,4
Kalitinaia crenimargo	(L. Pfeiffer, 1848)	CE	53	0.31	14,18,19,20,21
Kalitinaia perspectiva	Hausdorf, 1993	CE	4	0	-
Kalitinaia tiflisiana	(Lindholm, 1913)	CE	2	0.67	16
Kazancia lindholm	(Kobelt in Lindholm, 1912)	CE	4	0.8	8,22
Kokotschashvilia eberhardi	Schileyko, 1978	CE	2	1	16
Kokotschashvilia holotricha	(O. Boettger, 1884)	CE	20	0.17	2,3,4
Kokotschashvilia makvalae	(Hudec et Lezhawa, 1969)	GE	10	0	-
Kokotschashvilia tanta	Schileyko, 1978	GE	1	0	-
Lesticulus nocturnus	Schileyko, 1988	GE	1	1	9
Lindholmia christophi	(O. Boettger, 1881)	CE	2	0.5	1,1
Lindholmia nordmanni	(Mousson, 1854)	CE	8	0.22	11,13
Ljudmilena sieversi	(Mousson, 1873)	CE	14	0.29	6,7,8
Ljudmilena tricolis	(Mousson, 1876)	GE	11	0.25	7,11,12,13
Mentissoidea rupicola	(Mortillet, 1854)	CE	147	0.22	1,2,3,4,6,7,8,9,10,11,12,13,14,18,19,22
Metalimax elegans	Simroth, 1901	GE	27	0	-
Metalimax varius	(O. Boettger, 1884)	CE	13	0.43	1,2,3,4
Micropontica closta	(O. Boettger, 1881)	GE	2	0.5	4
Milax caucasicus	Simroth, 1912	CE	2	1	11
Monacha perfrequens	(Hesse, 1914)	CE	27	0.43	1,2,3,4,6,7,9,10
Monacha roseni	(Hesse, 1914)	CE	8	0.45	1,2,3,4
Monacha subcarthusiana	(Lindholm, 1913)	CE	1	0	-
Mucronaria acuminata	(Mousson, 1876)	GE	6	0.33	12
Mucronaria duboisi	(Chrapentier, 1852)	CE	176	0.21	1,2,3,4,6,7,8,9,10,11,14,15,16,17,18,19,20,22
Mucronaria index	(Mousson, 1863)	GE	21	0.33	5,6,7,9,10,11
Mucronaria pleuroptychia	(O. Boettger, 1878)	CE	25	0.04	9,10
Mucronaria strauchi	(O. Boettger, 1878)	GE	8	0.38	14,18,20
Oscarboettgeria euages	(O. Boettger, 1883)	CE	7	0.29	2,4
Oxychilus andronakii	(Lindholm, 1914)	CE	4	0.67	6,7,8
Oxychilus birsteini	Tzvetkov, 1940	GE	1	1	2,3

Oxychilus crenimargo	(Retowskii, 1889)	CE	2	0.5	7,8
Oxychilus decipiens	(O. Boettger, 1886)	CE	12	0.5	7,8,11
Oxychilus difficilis	(O. Boettger, 1888)	CE	13	0.59	1,2,3,4
Oxychilus discrepans	(Retowski, 1889)	CE	19	0.29	6,7,8
Oxychilus duboisi	(Charpentier in Mousson, 1863)	GE	34	0.35	2,3,6,7,9,10,11,14
Oxychilus imperator	Reidel, 1966	GE	30	0.34	1,2,3,4
Oxychilus Koutaisanus	(Mousson, 1863)	CE	75	0.33	1,2,3,4,7,9,10,11,14,18,19,22
Oxychilus lederi	(O. Boettger, 1880)	GE	1	1	17,18
Oxychilus oschtenicus	(O. Boettger, 1888)	CE	44	0.29	2,3,4,6,7,8
oxychilus retowskii	(Lindholm, 1914)	CE	20	0.14	11,13
Oxychilus suaneticus	(O. Boettgeri, 1883)	CE	24	0.12	2,4
Oxychilus sucinaceus	(O. Boettger, 1883)	CE	25	0.27	10,11,14
Peristoma boettgeri	(Clessin, 1883)	GE	19	0.32	2,3,9,10,11
Peristoma lanceum	Schileyko, 1984	GE	1	1	4
Pilorcula aspinosa	Hausdorf, 1996	GE	2	0	-
Pilorcula pusilla	Hausdorf, 1996	GE	7	0.86	11,17,18
Platytheba mingrelica	(Hesse, 1921)	GE	18	0.11	2,3
Platytheba prometheus	(O. Boettger, 1883)	GE	27	0	-
Poiretia mingrelica	(O. Boettger, 1881)	GE	41	0.17	2,3,4,9,10
Pontophaedusa funiculum	(Mousson, 1863)	CE	21	0.32	2,3,4,6,7,8
Pravispira semilamellata	(Mousson, 1863)	CE	93	0.3	2,4,6,7,8,9,10,11,12,14,17,18,19,20
Pseudochondrula lederi	(O. Boettger, 1883)	CE	3	1	2,4,11,12
Pseudochondrula sinistrosa	Kokotschashvili et Schileyko, 1984	GE	1	1	11
Pseudochondrula tetrodon	(Mortillet, 1854)	CE	12	0.5	9,10,11
Pseudochondrula tuberifera	(O. Boettger, 1879)	CE	7	0.43	11,16
Pupilla inops	(Reinhardt, 1877)	CE	6	1	11,17,18
Quadriplicata aggesta	(O. Boettger, 1879)	CE	12	0.47	1,2,3,4
Quadriplicata dipolauchen	(O. Boettger, 1881)	GE	6	0	-
Quadriplicata lederi	(O. Boettger, 1879)	GE	73	0.19	2,3,9,10,11,14
Quadriplicata pumiliformis	(O. Boettger, 1881)	CE	18	0.26	2,3,4
Quadriplicata quadriplicata	(A. Schmidt, 1868)	CE	58	0.2	6,7,15,16,17,18,19,20,22
Quadriplicata subaggesta	(Retowski, 1887)	CE	5	0.5	6,7,8
Retowskia schlaeflii	(Mousson, 1863)	CE	8	0.38	2,4,11
Schileykula batumensis	(Retowski, 1889)	GE	4	1	6,7,8
Scrobifera taurica	(L. Pfeiffer, 1848)	CE	136	0.26	1,2,3,4,9,10,11,12,14,15,16,17,18,19,20,22
Selenochlamys pallida	O. Boettger, 1883	CE	17	0.12	9,10
Serrulina sieversi	Likharev, 1962	CE	6	0.33	22
Shileykoia daghestana	(Kobelt, 1877)	CE	12	0.33	17,20,22
Sieversia heydeni	(O. Boettger, 1879)	CE	25	0.2	2,4,11
Stenomphalia maiae	(Hudec et Lezhava, 1969)	CE	2	0.5	7,8
Stenomphalia selecta	(Klika, 1894)	CE	89	0.29	2,4,7,9,10,11,12,14,16,17,18,19,20,21
Strigileuxina lindholmi	(Lindholm, 1912)	CE	4	0.5	6,7,22
Strigileuxina reuleauxi	(O. Boettger, 1887)	CE	6	0.43	6,7,8
Szuchumiella jetschini	(A. Wagner, 1895)	GE	33	0.11	2,3
Toffoletia lederi	(O. Boettger, 1881)	CE	44	0.2	1,2,3,4,9,10
Trigonochlamys imitatrix	O. Boettger, 1881	CE	25	0.28	6,7,9,11
Trochovitrina lederi	(O. Boettger, 1879)	GE	9	0.7	11,16
Vertigo sieversi	(o. Boettger, 1879)	CE	6	0	-
Vitrea contortula	(Krynicki, 1837)	CE	84	0.31	2,4,6,7,8,9,10,11,14,17,18,20,22
Vitrea praetermissa	Reidel, 1988	GE	3	0.6	6,7,8
Vitrea rhododendronis	Reidel, 1966	GE	1	0	-
Vitrea sorella	(Mousson, 1863)	GE	5	0.2	11
Vitrinoxychilus subsuturalis	(O. Boettger, 1888)	CE	5	0.4	2,3,4
Vitrinoxychilus suturalis	(O. Boettger, 1881)	CE	26	0.25	6,7,8,11
Euchondrus acutior	(Rossmassler, 1859)	Not included			
Improvisa pupoides	(Krynicki, 1833)	Not included			
Serrulinella senghanensis	(Germain, 1933)	Not included			
Teberdina flavolimbata(O.	(O. Boettger, 1883)	Not included			
Caucasigena rengarteni	(Lindholm, 1913)	Not included			
Caucasigena schaposchnikovi	(Rosen, 1911)	Not included			

VII



პუბლიკაცია გაგზავნილია ჟურნალში *Journal of Molluscan Studies*.

Sympatry without co-occurrence: exploring the pattern of the distribution of two *Helix* species in Georgia using ecological niche modeling approach

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Two species of the genus *Helix* (Mollusca: Gastropoda) are widespread in Georgia. One species *Helix lucorum* has Mediterranean distribution whereas the other – *Helix buchii* is Caucasian endemic typically associated with broadleaf forest. In spite of their sympatry within Georgia, they never co-occur. Furthermore, in contrast with *H. buchii*, *H. lucorum* is manly found in areas subject to human disturbance. With these two con-generics there is another large helicoid species (*C. calligera*) which also is widespread in Georgia. *C. calligera* is usually found with both species of *Helix*. Based on the pattern of distribution these three species it can be assumed that interspecific competition might play a pivotal role in shaping the distribution of two *Helix* species. In order to test this hypothesis, I used predictive ecological niche models (ENM) based on the Maximum Entropy algorithm. ENMs showed that the niches of these species in Georgia are significantly different but not fully separated (~15-36% overlap). The distributional pattern of *H. lucorum* should not be considered truly natural in Georgia and may be a synanthropic phenomenon. The fact that these two *Helix* species never co-occur could be a result of competitive relationship and the lack of natural habitats for *H. lucorum* whereas *H. buchii* usually avoids anthropogenic disturbance. However the competition remains most useful informative assumption to explain the distributional pattern of *H. lucorum*.

Key words: Georgia, *Helix*, distribution, niche, modeling, co-existence

INTRODUCTION

Two large helicid (Mollusca: Gastropoda) species - *Helix lucorum* Linnaeus 1758 and *Helix buchii* Dubios De Montpereux, 1839 are common in Georgia. *H. lucorum* is typical circum Mediterranean snail (probably coming from the areas around the Adriatic Sea), and approaches the Caspian Sea in its eastern range. *H. lucorum* is slowly expanding its range to Northern and Western parts of Europe, previously unoccupied by this species. It is usually one of the most common and abundant snails within its native distribution area (Yildirim et al., 2004). *H. lucorum* is widespread in Georgia as well. According to Lubel (2004a, b) this species is probably introduced by human and occupied Caucasian region during the late last glaciations or even in Holocene. *H. lucorum* is found in almost all kinds of habitats near or within human modified landscapes and can be considered as synanthrop species (Salgado et al., 2010; Henk & Rittner, 2010; Peltanová et al., 2012; Mumladze, 2013).

In contrast to *H. lucorum,* the second species - *H. buchii* is typical Caucasian species mainly attributing humid broadleaf (mainly beech) mountain forests between the Black and Caspian Seas (except north-western Georgian mountains). It also occurs (but is not common) in some subalpine and anthropogenic areas (Mumladze et al., 2013 and this study). In fact, these two species are distributed sympatrycaly, and the boundary of their distribution ranges are almost completely overlapped within Georgia (Fig.1). Several years of personal observation showed that in Georgia *H. lucorum* avoids pure natural habitats, which are mostly selected by other large helicoid species (*H. buchii*, *Helix goderdziana* Mumladze, Tarkhnishvili et Pokryszko, 2008, *H. albescens* Rossmassler, 1839, *Lindholmia nordmanni* (Mousson, 1854), *L. christophi* (O. Boettger, 1881) and *Caucasotachea calligera* (Dubios De Montpereux, 1840)). The most intriguing fact in the distribution of *Helix* spp. in Georgia is that they never co-occur (i.e. they have prapatric spatial pattern within sites) whereas e.g. *C. calligera* is frequently found together with both *Helix* species. Similar sympatric distribution of another *Helix* pair (*Helix pomatia* Linnaeus, 1758 and *Helix lutescens* Rossmässler, 1837) without co-occurrence was reported from Poland, however, without attempt to explain the mechanisms underlying the pattern (Koralewska-Batura, 1999). The pattern described above arise a question about the possible role of interspecific interactions and species specific ecological requirements as possible drivers of the distribution of con-generic *Helix* species in Georgia. It is clear and well documented that the distributions of snails are heavily depended on the environmental factors whereas the role or even existence of competitive relationships as a factor affecting the snail species distribution is questionable (for reviews see Cameron, 2013)

One increasingly used approach for characterization of species distribution pattern is ecological niche modeling (ENM) approach (Guisan & Zimmermann 2000). In General, ENM is an approach which generates the probabilistic distribution of a given species by the constructing the distribution of the species specific suitable multidimensional niche space (defined by the input variable). ENM can be useful in delimiting the species specific ecological requirements and finding other potentially acting factors (such as interspecific interaction) shaping the species distribution (Soberon, 2005; Tarkhnishvili et. al., 2010; Lawing et al., 2012). Georgian *Heilx* species are almost equal in size (more than 40 mm in diameter) and there are no known differences in their ecological requirements (particularly food and space requirements, life history characteristics). All above mentioned leads to hypothesize that there may be a strong interspecific competition between this con-generics by which, they avoid co-existence in the same environmental patches. Alternatively the ecological requirements (or ecological niches) must be different enough to provide complete separation of the distributional ranges. If the former is true, than ENM must result in highly similar distribution patterns for both species and the opposite in later case (i.e. modeled potential distributions could be sufficient alone to explain the observed pattern without considering interspecific interactions). *C. calligera* is frequently co-occurring with both *Helix* species. Hence the prediction here is that competition between *C. calligera* and *Helix* spp. is not an important driver of their distribution and the ecological niche model should not be strongly differentiated. Here, I test these alternatives by constructing and comparing ecological niche distribution models susceptible for the two *Helix* species and *C. calligera* using ecological niche modeling approach.

MATERIALS AND METODS

Distributional data

In order to investigate the distribution pattern of the con-generic species of *Helix* in Georgia, I used the distributional data for both species recorded by myself during last 7 years (Fig 1; Appendix 1). In constructing ENMs, I used localities for which exact geographic coordinates are available; thus, in total I collected 49, 36 and 37 localities for *H. lucorum, H. buchii* and *C. callugera* respectively.

Envirnmental variables

The distribution of snail species is strongly affected by climate, vegetation and soil types (Dunk et al., 2004; Horsák, 2006). Hence it might be important to use the variables of each type in order to ensure the accuracy of ENM approach. Unfortunately, the information about soil variables important for snails (soil type, calcium content, PH and others) is either unavailable or in unacceptable resolution for Georgia. I used climate variables, vegetation data, land cover and geographic information, which are free to access. Specifically, I used 19 bioclimatic variables (with the resolution of 1 km^2) presenting biologically meaningful climatic information which is derived by the combinations of monthly temperature and rainfall (data and its detailed description are available at: http://www.worldclim.org/) (Hijmans et al., 2005). The composition of vegetation and its density are strongly depended on the climate (Woodward, 1987; Stephenson, 1990), however the distribution of vegetation is also affected by the temporal factors (such as harvesting, grazing and other anthropogenic and non-anthropogenic factors (Chuine & Beaubien, 2001; Palmer et al., 2005). By this reason I also include vegetation data with the climate variables in model building. SPOT Vegetation ten daily synthesis data (available at http://free.vgt.vito.be/) where used to extract monthly Normalized Difference Vegetation Index (NDVI) as a proxy of monthly vegetation cover. I used ten daily time series data from 2004 to 2010 to generate average monthly NDVI grids (12 variables in total) of 1 km resolution (using the free extraction software VGT Extract V2.0.1 available with the data). Together with the climate and vegetation data physical geographic variables such as elevation, aspect and slope (last two derived from the elevation data using Arc GIS 9.3) were also included in modeling. Besides these continuous variables, I also acquired land cover categories (includes 17 class) derived from MODIS land cover data (MCD12Q1 - Friedl et al., 2002; Friedl et al., 2010). This variable describes different types of land covers such is forest, grassland, cropland, settlements and others and can be useful in understanding of species distribution (more details about the land cover categories can be found in Appendix 2). In total 34 continuous and one categorical variable were acquired to build SDM (Table 1).

Distribution modeling

There are many algorithms available to model the potential distribution of species (Anderson et al., 2006). The choice of the modeling techniques depends on several factors. If true absence localities within the range of snail species are hard to define, the algorithms relied solely on presence data is the best choice (Pearson, 2007). Within the array of presence only modeling techniques Maximum Entropy (MAXENT) approach (Philips et al., 2004) seems to outperform significantly over the others (Gaston & Garcia-vinas 2011; Tognelli et al., 2009; Pearson et al., 2007; Hernandez et al., 2006, Elith et al., 2006). It uses information contained in presence localities to compare those from background data (randomly collected points sometimes named as pseudo absence localities) and calculates percent contributions of each input variables. There are several advantages by which MAXENT is frequently chosen. One of the most important of them is its powerful capability to analyze piecewise linear response of species on the explanatory variable ("hinge" feature) (Elith et al., 2011). In all modeling experiments I used MAXENT with the "hinge" function to calculate logistic model which returns a probabilities of occurrence for each grid cell ranging from 0 to 1. For each run 25 % of occurrences were randomly selected as test data and the remaining as training. I also calculate jackknife statistics for input variables to weight their significance in model building. Evaluation of model performance was assessed using the Areas Under the ROC (Receiver Operating Character) Curve (AUC) (Fielding and Bell, 1997). Models with AUC value more than 0.75 were considered as good.

In spite of the fact that MAXENT algorithm is one of the most robust method against multi co-linearity and high dimensionality in input data (Elith et al., 2011), prior to the final modeling I performed filtering of highly correlated variable as suggested by Wisz et al. (2013). For that I extracted values for all the localities using ArcGIS v9.3 (ESRI, Redlands, CA) and then subjected them to the pair-wise linear correlation (SPSS Inc., Chicago, IL, USA) to identify highly correlated pairs (R^2>0.75). One of the partner variables of highly correlated pair was removed by judging to which variable can be more important over its pair based on practical knowledge. In order to make two niche models comparable it is essential to generate models based on same input data. For this reason I removed only variables that are unimportant for both species. In this manner, I reduced variables to the 15, which were then subjected to model in MAXENT (Table 1).

The computation of the overlap between the two distribution models based on MAXENT output can be done either by direct calculation of probability values containing ASCII grids or by applying threshold to derive presence-absence potential distribution maps. In the first case I used ENMTools v3.1 (Warren et al., 2010) which calculates niche overlap using Hellinger's metric - *I* (Warren et al., 2010). This measure is simply similarity measure which is calculated after normalizing each model so that the sum of all the grid cell values in each model is 1. After calculating niche (model) overlap, I performed niche identity test (using ENMTools). That is, the occurrence data of both species is merged and then randomly divided into two new subsets (same number occurrence points for each species) for 100 times. For each replicates MAXENT runs are performed and overlap values are calculated. As the MAXENT model produces none zero probabilities (but close to zero if suitability is very low) for each grid cell, *I* index may be somewhat over estimation. To avoid this difficulty, I applied Maximum training sensitivity plus specificity threshold rule (Jiménez-Valverde & Lobo, 2007) to produce presence – absence suitability models and then simply calculated overlap percentage using ArcGIS (i.e. overlap = a/(b+c-a) where a is a number of overlapped pixels, b – number of presence pixels of first species and c - number of presence pixels of second species).

RESULTS

For all species MAXENT distribution models had very good performance measured by AUC value (training = 0.9, test = 0.82 for *H. buchii,* training = 0.96, test = 0.94 for *H. lucorum* and training = 0.91, test = 0.9 for *C. calligera*). Overall, models correctly predicted all known territories for both *Helix* species. Particularly, western part of the Gaucasus where *H. buchii* is absent was also excluded by MAXENT as well as Colchis lowland and dry eastern Georgian belt. For *H. lucorum*, west Georgian humid lowlands and most of the high mountainous forests were also correctly excluded by the model (Fig. 2). Highly susceptible area for *C. calligera* is intuitively somewhat smaller than expected. Specifically, all the high mountainous regions where excluded from the model. *C. clligera* is more widespread than any *Helix* species; however it is not known if this species finds high mountain forests optimal. Colchis lowland where *C. calligera* does occur (but with very low densities) is predicted as low susceptible.

The percent contribution of some input variables is very different between models. For *H. buchii* elevation, forest (Land cover – category 5 and 8) and vegetation density in August are most important variables that determine 60% of its distribution. Same factors are also most informative for the distribution of *H. lucorum* (68 %contribution in total) but in contrast to *H. buchii* categories 8 and 13 (savannas and urban areas respectively) have higher loadings (Table 1). For both species having the highest contribution of single variable is an elevation; however both have similar response along that variable. Altitude and slope were most important determinants for the distribution of *C. calliger* (89 % contribution). With increasing altitude and slope probability of occurrence (and model performance) of this species decreases (Appendix 3).

The distinctness of Ecological niches between all the pairs are significant (*P*< 0.01 after 300 randomized replication – Fig. 3) however the overlap between models of *Helix* species calculated using row output (i.e. each cell containing probability values) showed that Hellinger's similarity measure *I* = 55 % whereas the overlap between presence - absence models is much low (15 %). The overlap between *C.* calligera and *Helix* species is higher (*C. calligera* and *H.* lucorum (62%); *C. calligera* and *H. buchii* (69%)). Overlap calculated by presence absence maps were 36% between *H. buchii* and *C. calligera*, and 21% - between *H. lucorum* and *C. calligera* (Fig. 2). These statistics indicate that the suitable niche of all the pairs significantly differs as from each other but there are no absolute differences and the sympatric co-occurrence is expected in the contact zones.

DISCUSSION

The concept of species' niche is more complex by its original definition (Hutchinson, 1957, 1978) than it is used frequently in modern ecology. I.e. species distribution modeling which is one of the hot topics in ecology is entirely based on simplified niche concept determined by environmental factors alone. However, species actual distribution (realized niche) is proved to be strongly affected by biotic interactions (Chase & Leibold, 2003; Bascompte, 2009; van Dam, 2009) and dispersal limitations (Allouche et al., 2008; Tarkhnishvili et al., 2012). Hence, modeling the distribution of realized niche requires incorporation of this factors as well (Wisz et al., 2013; Kissling et al., 2012; Araújo & Luoto, 2007). In contrast to this, distribution pattern generated based only on environmental variable refers to the potentially susceptible areas were particular complex of environmental conditions are met (Pearson, 2007; Miller, 2010). If two closely related species have similar ecological requirements and are in sympatry, then there is expected a competitive relationships and vice versa – if the ecological niches are distinct, no competition is expected. However this pattern is something like an egg and chicken dilemma. The distinctness of ecological niches can probably be a function of competitive relationships as well (Whittaker et al., 1973). Since the modeled distributions represents the potentially susceptible areas of environmental requirements, this kind of analysis can be considered as a useful way to test whether species have similar environmental requirements. The distribution modeling results of *H. lucorum* and *H.buchii* showed that the ecological niches they occupy are significantly different than expected from the null distribution. There are significant differences in ecological niches of the remaining pairs - *H. lucorum* vs. *C. calligera* and *C. calligera* vs. *H.*

buchii as well. Apart of these significant differences, there is also some overlap between all three pairs meaning that theoretically they are able to live in sympatry in some areas. *C. calligera* co-exists with both species in many areas and hence the modeled overlap is in accordance with the actual situation, but this is not the case for *H. buchii* and *H. lucorum*. Why they do not co-occur? In order to pull out from that vague situation some additional information should be considered. First, the pattern described above can be assumed as an evidence of existence of some other limiting factors (e.g competition) in distribution of *H. lucorum* and *H. buchii* rather than simple difference in ecological niches. Indeed, if no such kind of limiting factors exist than all three species are expected to co-exist in contact zones. This is true in case of *C. calligera*. However this species is more distinct species phylogeneticaly than con-generic *Helix* and there might be ecologically well differentiated life strategies or other means of limiting similarity by which they avoid competitive relationship in the same habitat patch (Abrams, 1983). In spite of the fact that occupied ecological niches of *H. buchii* and *H. lucorum* are significantly different, the distinctness of ecological requirements is not gross enough to provide such a pattern. Specifically in two localities populations of both *Helix* species are so close to each other (several meter between the population edges) that there is no distinctness in environmental conditions. First locality is situated near Tsodoreti Lake (8 km west of Tbilisi). There is the road and the small hill above the lake; South exposition of that hill is occupied by both species of *Helix*. However *H. lucorum* is occupying areas along the road and *H. buchii* is found just above the population of *H. lucorum*. Another locality is around the Ananuri village where both *Helix* have mosaic spatial distribution (Fig. 1). Hence closeness of the populations is in accordance with the predictions of the modeling results and it is clear that something other than ecological niche differentiation is limiting these two species to mix up. Clearly it is not possible to talk about the strong interspecific competition confidently; however it seems that the competition is driving the distribution of these two *Helix* species at least partly. In Georgia *H. lucorum* is distributed almost everywhere around the anthropogenic landscapes (Mumladze, 2013). Until now, there is no any recorded occurrence in truly natural forest or grasslands (the distribution of that species is one of the best studied in Georgia (Lezhava, 1973; Mumladze, 2013)). Such a close relationship with anthropogenic habitats may be the result of predators such as large Carabid beetles (e.g. *Carabus caucasicus*) which are widespread in natural areas in the Caucasus and normally are scarce in anthropogenic areas (Niemelä et al., 2002). This idea is interesting in the view of historical distribution of *H. lucorum* which may be arrived in Georgia together with the human footprints during last several thousands of years (Lubel, 2004a,b). However dispersal control by predators alone is not enough to explain the local distributional patterns in above considered cases.

In conclusion, the analysis provided here shows that the distinctness of ecological niches cannot be considered as the main reason in shaping local spatial pattern for *H. lucorum* and *H. buchii*. Instead, other kind of factors like competition, predation, anthropogenic disturbance and etc. seem to play the important role in the limiting the dispersal of both species. In spite of the widespread consideration that the competition is unimportant or very week force in structuring terrestrial snail communities (Huntley et al., 2009; Schamp et al., 2010), particular cases can be showed opposite picture (Baur & Baur, 1990). In order to fully understand the mechanisms underlying the local pattern of spatial distribution of *Helix* species in Georgia one must test the importance of some potential limiting factors rather than ecological niche differentiation.

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REFERENCE

Abrams, P. (1983). The theory of limiting similarity. Annual review of ecology and systematics, 14, 359-376.

Allouche, O., Steinitz, O., Rotem, D., Rosenfeld, A., & Kadmon, R. (2008). Incorporating distance constraints into species distribution models. Journal of Applied Ecology, 45(2), 599-609.

Anderson, R.p., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., ... & Zimmermann, N.E. (2006). Novel methods improve prediction of species' distributions from occurrence data. Ecography, 29(2), 129-151.

Araújo, M.B., & Luoto, M. (2007). The importance of biotic interactions for modelling species distributions under climate change. Global Ecology and Biogeography, 16(6), 743-753.

Bascompte, J. (2009). Mutualistic networks. Frontiers in Ecology and the Environment 7, 429–436.

Baur, B., & Baur, A. (1990). Experimental evidence for intra-and interspecific competition in two species of rock-dwelling land snails. The Journal of Animal Ecology, 301-315.

Cameron, R.A. (2013). The Diversity of Land Molluscs-Questions Unanswered and Questions Unasked. American Malacological Bulletin, 31(1), 169-180.

Chase, J.M. & Leibold, M.A. (2003) Ecological niches: linking classical and contemporary approaches. University of Chicago Press, Chicago, IL.

Chuine, I., & Beaubien, E. G. (2001). Phenology is a major determinant of tree species range. Ecology Letters, 4(5), 500-510.

Dunk, J. R., Zielinski, W. J., & Preisler, H. K. (2004). Predicting the occurrence of rare mollusks in northern California forests. Ecological Applications, 14(3), 713-729.

Elith, J. Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Phillips, S.J., Richardson, K.S., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S., Wisz, M.S., Zimmermann, N.E. Novel methods improve prediction of species' distributions from occurrence data. Ecography 2006, 29, 129–151.

Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., & Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. Diversity and Distributions, 17(1), 43-57.

Fielding, A. H. and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24: 38-49.

Friedl, M. A., McIver, D. K., Hodges, J. C. F., Zhang, X. Y., Muchoney, D., Strahler, A. H., ... & Schaaf, C. (2002). Global land cover mapping from MODIS: algorithms and early results. Remote Sensing of Environment, 83(1), 287-302.

Friedl, M.A., Sulla-Menashe, D., Tan, B., Schneider, A., Ramankutty, N., Sibley, A., Huang, X.M. (2010) MODIS Collection 5 global land cover: algorithm refinements and characterization of new datasets. Remote Sensing of Environment, 114, 168–182.

Gastón, A., & García-Viñas, J. I. (2011). Modelling species distributions with penalised logistic regressions: A comparison with maximum entropy models. Ecological Modelling, 222(13), 2037-2041.

Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. Ecological modelling, 135(2), 147-186.

Hernandez, P.A.; Graham, C.H.; Master, L.L.; Albert, D.L. The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography 2006, 29, 773–785.

Henk, K. M., & Rittner, O. (2010). On the presence of Helix lucorum Linnaeus, 1758 (Mollusca, Gastropoda, Helicidae) in Le Vesinet, a western suburb of Paris.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas.International journal of climatology, 25(15), 1965-1978.

Horsák, M. (2006). Mollusc community patterns and species response curves along a mineral richness gradient: a case study in fens. Journal of Biogeography, 33(1), 98-107.

Huntley, J. W., Yanes, Y., Kowalewski, M., Castillo, C., Delgado-Huertas, A., Ibáñez, M., ... & de Torres, T. (2009). Testing limiting similarity in Quaternary terrestrial gastropods.

Jiménez-Valverde, A., & Lobo, J. M. (2007). Threshold criteria for conversion of probability of species presence to either–or presence–absence. Acta Oecologica, 31(3), 361-369.

Kissling, W. D., Dormann, C. F., Groeneveld, J., Hickler, T., Kühn, I., McInerny, G. J., ... & O’Hara, R. B. (2012). Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. Journal of Biogeography, 39(12), 2163-2178.

Koralewska-Batura, E. (1999). Helix lutescens Rossmässler, 1837 (Gastropoda: Pulmonata: Helicidae)–its structure, biology and ecology. Folia Malacologica, 7, 197-240.

Lawing, A. M., Meik, J. M., & Polly, P. D. (2012). Climate and Competition Shape Species' Borders: A Study of the Panamint (Crotalus stephensi) and Speckled (Crotalus mitchellii) Rattlesnakes. ISRN Zoology, 2012.

Lezhava, G. 1973. Terrestrial and freshwater molluscs. Georgian Academy of Science, Tbilisi. (In Georgian).

Lubell, D. 2004(a). Prehistoric edible land snails in the circum-Mediterranean: the archaeological evidence. In: Petits animaux et sociétés humaines du complément alimentaire aux resources utilitaires (Eds. J.P. Brugal and J. Desse). Éditions APDCA, Antibes.

Lubell, D. 2004(b). Are land snails a signature for the Mesolithic-Neolithic transition?. Documenta Praehistorica, 31, 1-24.

Miller, J. (2010). Species distribution modeling. Geography Compass, 4(6), 490-509.

Mumladze, L., Tarkhnishvili, D., Murtskhvaladze, M. (2013) Systematics and evolutionary history of large endemic snails from the Caucasus (Helix buchi, H. goderdziana). American Malacological Bulletin (In press)

Niemelä, J., Kotze, D. J., Venn, S., Penev, L., Stoyanov, I., Spence, J., ... & De Oca, E. M. (2002). Carabid beetle assemblages (Coleoptera, Carabidae) across urban-rural gradients: an international comparison. Landscape Ecology,17(5), 387-401.

Palmer, S. C. F., Gordon, I. J., Hester, A. J., & Pakeman, R. J. (2005). Introducing spatial grazing impacts into the prediction of moorland vegetation dynamics. Landscape ecology, 19(8), 817-827.

Pearson, R. G. (2007). Species' distribution modeling for conservation educators and practitioners. Lessons in Conservation (LinC) Developing the capacity to sustain the earth‘s diversity, 54.

Peltanová, A., Petrusek, A., Kment, P., & Juřičková, L. (2012). A fast snail's pace: colonization of Central Europe by Mediterranean gastropods. Biological Invasions, 14(4), 759-764.

Phillips, S. J., Dudík, M., & Schapire, R. E. (2004, July). A maximum entropy approach to species distribution modeling. In Proceedings of the twenty-first international conference on Machine learning (p. 83). ACM.

Schamp, B., Horsák, M., & Hájek, M. (2010). Deterministic assembly of land snail communities according to species size and diet. Journal of Animal Ecology, 79(4), 803-810.

Soberon, J. (2005). Interpretation of models of fundamental ecological niches and species' distributional areas.

Salgado, S.Q., alabau, A.L., & Meseguer, A.J.G. Nuevas localidades de Helix lucorum (Linnaeus, 1758) para la península Ibérica. SPIRA, 3: 193-195

Stephenson, N. L. (1990). Climatic control of vegetation distribution: the role of the water balance. American Naturalist, 649-670.

Tarkhnishvili, D., Gavashelishvili, A., Avaliani, A., Murtskhvaladze, M., & Mumladze, L. (2010). Unisexual rock lizard might be outcompeting its bisexual progenitors in the Caucasus. Biological Journal of the Linnean Society, 101(2), 447-460.

Tarkhnishvili, D., Gavashelishvili, A., & Mumladze, L. (2012). Palaeoclimatic models help to understand current distribution of Caucasian forest species. Biological Journal of the Linnean Society, 105(1), 231-248.

Tognelli, M. F., Roig-Junent, S. A., Marvaldi, A. E., Flores, G. E., & Lobo, J. M. (2009). An evaluation of methods for modelling distribution of Patagonian insects. Revista chilena de historia natural, 82(3), 347-360.

van Dam, N. M. (2009). How plants cope with biotic interactions. Plant Biology 11, 1–5.

Warren, D. L., R. E. Glor, and M. Turelli. 2010. ENMTools: a toolbox for comparative studies of environmental niche models. Ecography 33:607-611.

Wisz, M. S., Pottier, J., Kissling, W. D., Pellissier, L., Lenoir, J., Damgaard, C. F., ... & Svenning, J. C. (2013). The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. Biological Reviews, 88(1), 15-30.

Whittaker, R. H., Levin, S. A., & Root, R. B. (1973). Niche, habitat, and ecotope. American Naturalist, 321-338.

Woodward, F. I. (1987). Climate and plant distribution. Cambridge University Press.

Yildirim, M. Z., Kebapci, O., & Gumus, A. (2004). Edible snails (terrestrial) of Turkey. Turkish Journal of Zoology, 28, 329-336.

Variable	**Description**	**Percent contribution**		
		H. buchii	*H. lucorum*	*C. aclligera*
bio1	Annual mean temperature	3.4	3.6	4.6
bio2	Mean diurnal range (monthly mean, T° max -T° min)	5.4	4.6	0
bio3	Isothermality (bio2/bio7) x 100	-	-	-
bio4	Temperature seasonality (standard deviation X 100)	19.4	4	2.9
bio5	Maximum temperature of warmest month	-	-	-
bio6	Minimum temperature of coldest month	0	0	0
bio7	Temperature annual range (bio5-bio6)	-	-	-
bio8	Mean temperature of wettest quarter	-	-	-
bio9	Mean temperature of driest quarter	0	9.8	2.7
bio10	Mean temperature of the warmest quarter	2.4	16.8	0
bio11	Mean temperature of coldest quarter	0	0	0
bio12	Annual precipitation	-	-	-
bio13	Precipitation of wettest month	-	-	-
bio14	Precipitation of driest month	-	-	-
bio15	Precipitation seasonality (coefficient of variation)	-	-	-
bio16	Precipitation of wettest quarter	-	-	-
bio17	Precipitation of driest quarter	-	-	-
bio18	Precipitation of the warmest quarter	4.1	2.5	1.5
bio19	Precipitation of the coldest quarter	-	-	-
ndvi1	Normalized Difference Vegetation Index for January	-	-	-
ndvi2	- for February	-	-	-
ndvi3	- for March	-	-	-
ndvi4	- for April	-	-	-
ndvi5	- for May	20	0.5	46.5
ndvi6	- for June	20.9	0	1.6
ndvi7	- for July	3.9	0.9	0.1
ndvi8	- for August	0	27.8	2.1
ndvi9	- for September	-	-	-
ndvi10	- for October	-	-	-
ndvi11	- for November	-	-	-
ndvi12	- for December	-	-	-
landcover	Land cover categories	19	12.2	3.2
alt	Altitude	0	14.2	22.2
Slope	Slope	1.5	2.9	12.6
Aspect	Aspect	-	-	-

Table 1. Environmental variables used in the MAXENT modeling and the their percent contributions for building final models. Bold and underlined variables (left column) were used in final modeling as most informative and uncorrelated variables.

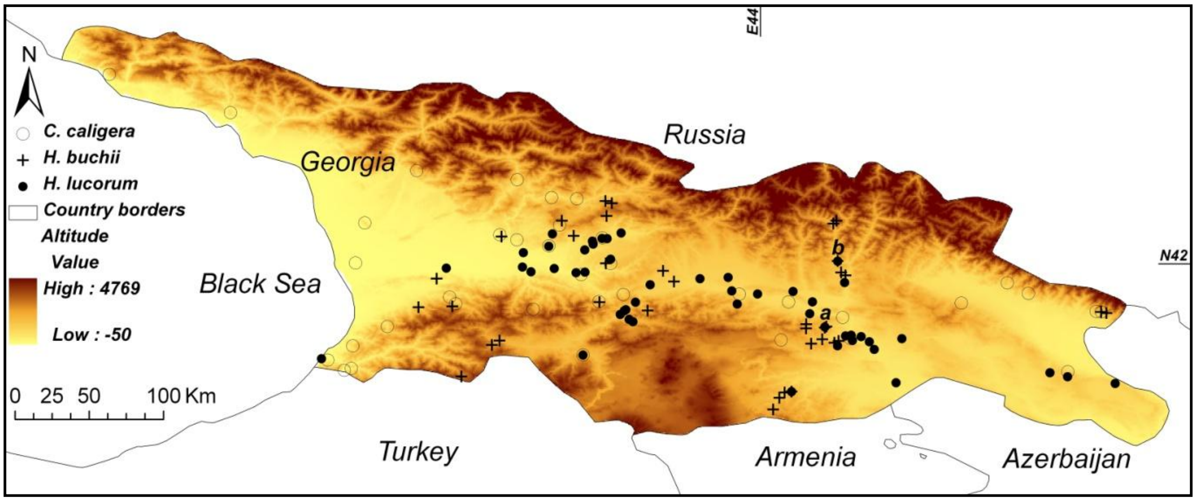

Figure 1. The map showing the study are with the sampling points for the analyzed species. Letters on the map stands for: *a* – Tsodoreti Lake; *b* – Ananuri (see the discussion section for details).

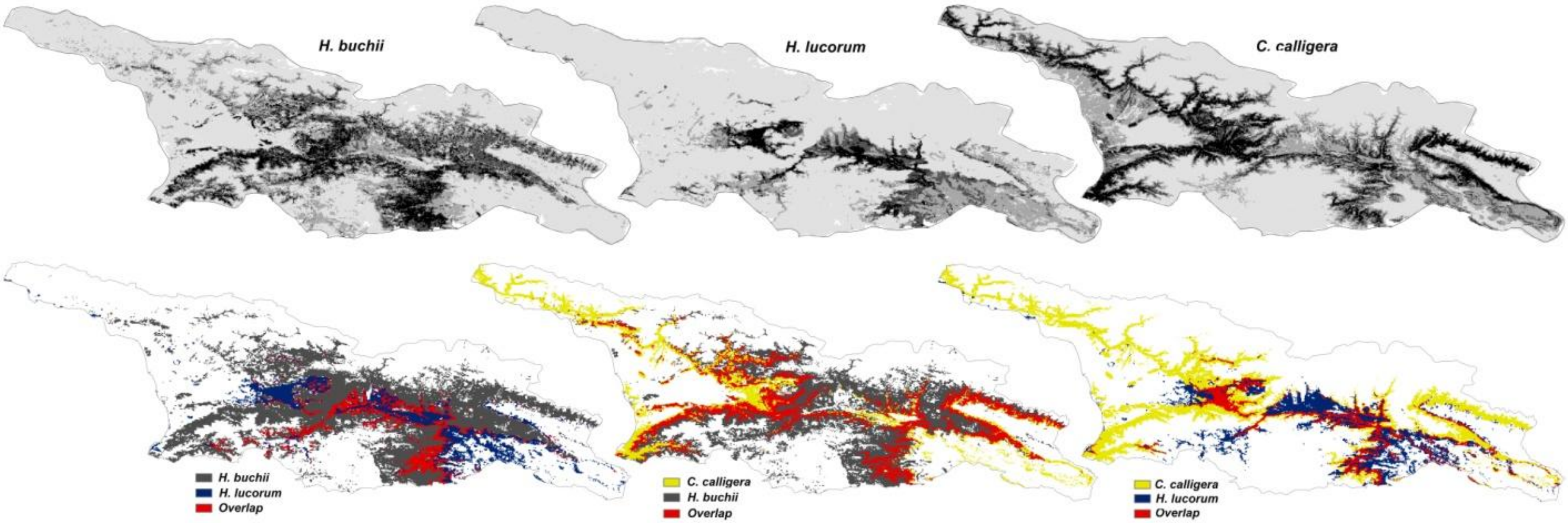

Figure 2. ENMs generated by MAXENT algorithm. Top maps represents logistic distribution for each species and bottom maps represents overlapped areas for all three pairs.

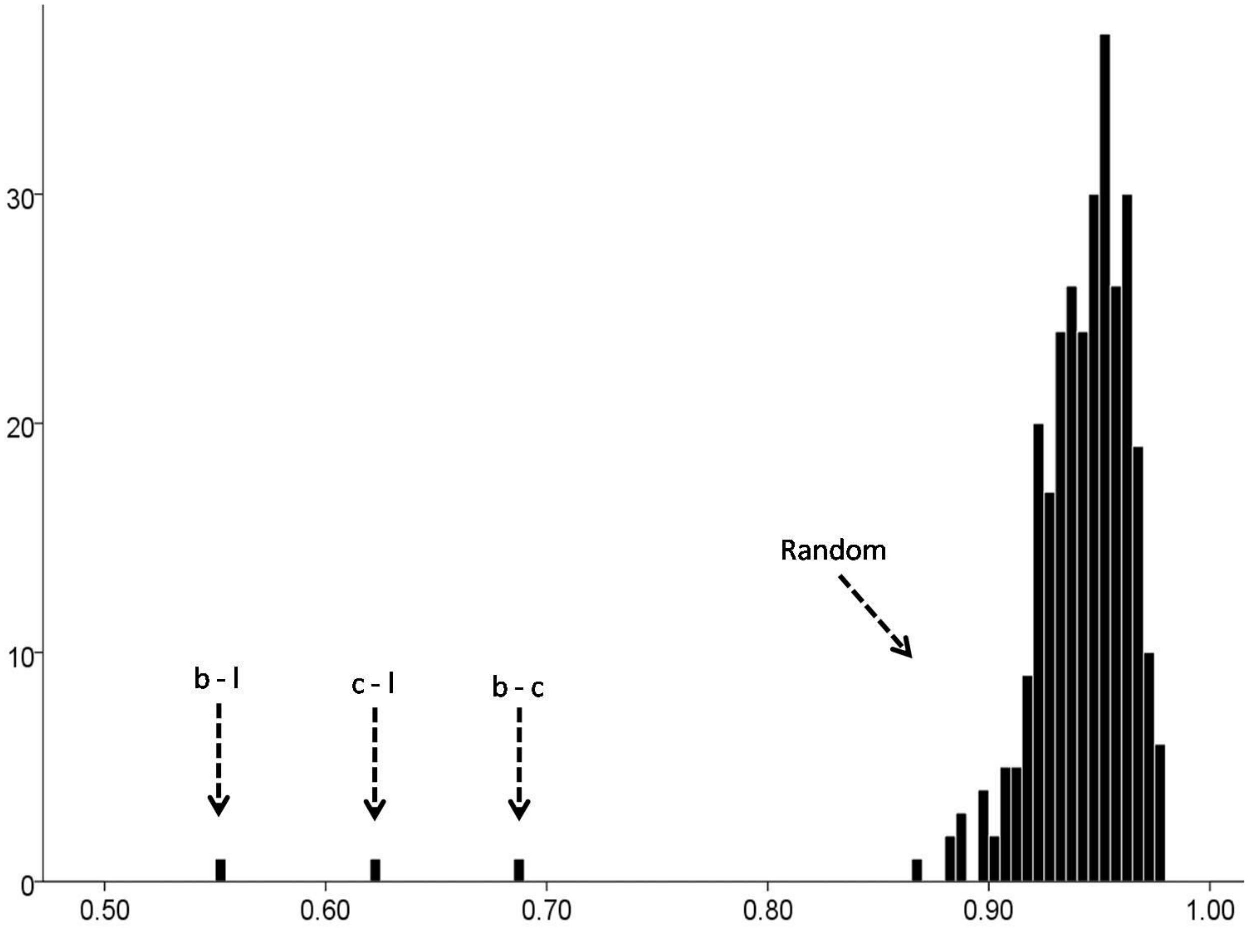

Figure 3. Histogram is showing the distribution of the overlap amounts between the predicted ecological niche ranges. b-l stands denotes the overlap between *H. buchii* and *H. lucorum*, c-l – between *C. calligera* and *H. lucorum*, b-c – between *H. buchii* and *C. calligera*. The right panel of the graph represents the distribution of range overlaps generated after 300 times randomisation

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Appendix 1. In the table there are showed GPS coordinates for all the localities used in ENM for all three species

H. lucorum		*C. calligera*		*H. buchii*	
N	E	N	E	N	E
41.4243	46.3833	41.5961	43.1598	41.8563	46.2996
41.4651	46.0950	42.3941	41.8376	41.6814	44.7083
41.4896	45.9886	42.7103	42.1522	41.6706	44.6833
41.6952	45.0912	42.1489	43.3273	42.0776	44.7507
41.6306	44.9245	42.3038	43.2767	42.0948	44.7242
41.6764	44.8940	42.2554	42.9526	42.1641	44.7028
41.7071	44.8447	42.1521	41.7814	42.4072	44.6949
41.6841	44.7922	41.5656	41.6131	42.3900	44.6770
41.7161	44.7846	41.5043	41.7136	41.7680	44.6342
41.7113	44.7498	41.5144	41.7558	41.7616	44.6245
41.6520	44.7014	41.6510	41.7645	41.6640	44.5424
42.0344	44.7449	41.7680	41.9739	41.7568	44.5112
41.7662	44.6243	41.9465	42.3517	41.7821	44.5120
42.1633	44.7033	41.9058	42.3877	41.3373	44.3500
41.9182	44.5499	41.9186	43.2553	41.2668	44.3118
41.8465	44.5334	41.9621	43.4043	42.1048	43.6454
41.3752	44.4233	42.5478	42.9687	41.9155	43.2598
41.9800	44.4321	42.5400	43.1219	42.1498	43.2986
41.9648	44.2176	42.3817	43.0178	42.5129	43.3349
41.9045	44.0944	41.8561	46.2998	42.4360	43.3031
41.9839	44.0609	41.8596	46.2683	42.3114	42.6666
42.0652	44.0387	41.4946	46.0960	42.4079	43.0315
42.0578	43.8686	41.8230	44.7332	41.6913	44.6091
42.0207	43.5666	41.6963	44.7794	41.8902	42.3683
41.9154	43.4780	42.0819	43.1489	41.4659	42.4236
41.7975	43.4624	42.2923	42.7588	42.3163	43.1036
41.8118	43.4389	42.3228	42.6554	41.8647	43.5511
41.8700	43.4192	41.8724	42.8584	42.5260	43.2962
41.8420	43.3853	41.6869	44.3594	41.8490	46.3313
42.1748	43.3275	41.9645	44.1067	41.6834	42.6539
42.3008	43.2754	41.9162	44.4052	41.3697	44.3819
42.2670	43.2217	42.6553	42.7609	42.0396	43.7112
42.2847	43.2171	43.0607	41.0246	41.6572	42.6083
42.0974	43.1723	43.2910	40.2898	41.3752	44.4233
41.5961	43.1598	41.9097	45.4511	42.0571	42.2737
42.3279	42.9749	41.9686	45.8576	41.8846	42.1629
42.2539	42.9524	42.0325	45.7301		

42.2151	42.7987
41.5740	41.5760
42.1209	42.3315
41.4286	45.0565
42.3336	43.3913
42.2996	43.3066
41.8637	43.4097
42.2313	43.1710
42.1281	42.7929
42.0998	42.8449
42.1192	42.9854
42.0944	43.1173

Appendix 2. Table represents Land Cover Categories used in MAXENT Modelling

Land Cover Class	Class Description
0	Water
1	Evergreen Needle-leaf forest
2	Evergreen Broad-leaf forest
3	Deciduous Needle-leaf forest
4	Deciduous Broad-leaf forest
5	Mixed forest
6	Closed shrublands
7	Open shrublands
8	Woody savannas
9	Savannas or very sparsely wooded area
10	Grasslands
11	Permanent wetlands
12	Grassland or Croplands
13	Urban and built-up
14	Cropland or Natural vegetation mosaic (e.g. Rhododendrin & Betula; subalpine forest)
15	Permanent snow and ice
16	Barren or sparsely vegetated
254	Unclassified

დანართები

დანართი 1

დანართში წარმოდგენილია ანბანურად დალაგებული ბიბლიოგრაფია საქართველოს მოლუსკების კვლევების შესახებ.

Clauss, E. (1990) Beitrag zur Landschneckenfauna des Schwarzmeer-Kustengebietes Adshariens (UdSSR) (Gastropoda). Malakologische Abhandlungen. 15: 63-71

Clauss, E. (1975) Zur Systematischen Stellung von Helicella tiflisiana (LINDHOLM, 1913). Malacologische Abhandlungen. 27: 1-4

Egorov, R.V. (2012) Conchological Review of the Land Snails of the Genus Caucasigena LINDHOLM, 1927 (Gastropoda: Pulmonata: Hygromiidae) with Some Notes on Other Caucasian Hygromiids. Conchylia. 42: 1-4

Egorov, R.V. (2002) Clausiliidae. Clausiliinae, Baleinae. Treasure of Russian Shells. 5: 2-77

Egorov, R.V. (2008) Illustrated catalogue of the recent terrestrial mollusks of Russia and adjacent

regions. - Treasure of Russian Shells. Treasure of Russian Shells, Supplement 5. : 1-179

Egorov, R.V., Greke, K. (2005) Orculoidea. Orculidae, Strobilopsidae. Treasure of Russian Shells. 7: 2-61

Ehrmann, P. (1931) Zur Kenntnis von Chondrina avenacea (Brug.) und ihren nächsten Verwandten. Archiv für Molluskenkunde. 63: 1-28

Gamtsemlidze, S.I. (1955) Contribution to study of malacofauna of Abkhasia. Proceedings of Sokhumi State Pedagogical University. VIII: 261-268

Gamtsemlidze, S.I. (1955) Some pest slugs and their control. Proceedings of Sokhumi State Pedagogical University. XVI: 53-55

Hausdorf, B. (1996) Die Orculidae Asiens. Archiv für Molluskenkunde. 125: 1-86

Hausdorf, B. (1993) Beiträge zur Nomenklatur der europaeischen Binnenmollusken, II. Nomenklatorische Bemerkungen zu palaearktischen Landschnecken (Gastropoda: Stylommatophora). Heldia. 2: 43-46

Hausdorf, B. (2001) A systematic revision of Circassina from the Western Caucasus region (Gastropoda: Hygromiidae). Journal of Molluscan Studies. 67: 427-446

Hausdorf, B. (2003) Revision of the genus Caucasocressa from the eastern Pontic Region (Gastropoda: Hygromiidae). Journal of Natural History. 37: 2627-2646

Hausdorf, B. (2000) The genus Monacha in the Western Caucasus (Gastropoda: Hygromiidae). Journal of natural History. 34: 1575-1594

Hesse, P. (1921) Beiträge zur näheren Kenntnis der Subfamilie Fruticicolinae. Archiv für Molluskenkunde. 53: 55-83

Hesse, P. (1933) Zur Anatomie und Systematik der Familie Enidae. Archiv für Naturgeschichte, Neue Folge. 11: 145-224

Hesse, P. (1914) Helix frequens Mousson (Helicidae, Mollusca). Mitteilungen des Kaukasischen Museums. 6: 253-270

Hudec, V. (1966) Succinea (Oxyloma) lejavai n. sp. aus der Grusinischen SSR. Achiv für Molluskenkunde. 95: ??-??

Hudec, V., Lezhava, G. (1970) Bernerkungen zur Erforschung der Landmollusken der Grusinischen sozialistischen Sowjetrepublik (II) 25 B [969] (3): 93-155, Taf. l-15.. Acta Musei Nat. Pragae. : 1-15

Hudec, V., Lezhava, G.I. (1967) Kalitinaia n. subgen. of the Xerosecta Monterosato, 1892 (Helicidae, Heliccellinae). Achiv für Molluskenkunde. 96: 131-137

Hudec, V., Lezhava, G.I. (1969) Drei neue Heliciden aus der Grusinischen SSRArchiv für Molluskenkunde. pp. 41-48

Hudec, V., Lezhava, G.I. (1970) Über konchyologisch sehr ähnliche kaukasische Heliciden (Mollusca, Pulmonata)Malakologischen Abhandungen Staatliches Museum für Tierkunde Dresden. pp. 15-31

Hudec, V., Lezhawa, G.I. (1967) Bemerkungen zur Erforschung der Landmollusken der Grusinischen Sozialistischen SowjetrepublikAkta Musei Nationalis Pragae. pp. 69-100

Hudec, V., Lezhawa, G.I. (1969) Bemerkungen zur Erforschung der Landmollusken der Grusinischen Sozialistischen Sowjetrepublik (II). Sbornik naÂrodnõ Âho muzea Praze B. 15: 93-155

Javelidze, G.I. (1941) Contribution to the malacofauna of Georgia and the bio-ecological study of Helix lucorum var. taurica Kryn.Dissertation : 101

Javelidze, G.I. (1972) Identification keys of for Georgian Terrestrial MolluscsMonograph. pp. 142

Javelidze, G.I. (1973) Freshwater MolluscsMonograph (Animal world of Georgia). pp.

Javelidze, G.I. (1941) Vector mollsucs of fasciolosis in GeorgiaProceedings of Kutaisi State Pedagogical Univerity. pp. 53-64

Javelidze, G.I. (1941) Contribution to the faunal study of terrestrial snails of GeorgiaProceedings of Tbilisi State University. pp. 113-122

Javelidze, G.I. (1948) Contribution to the study of the ecology of Helicella Derbentina Kryn. Proceedings of Tbilisi State University. XXXI: 41-57

Javelidze, G.I. (1949) Contribution to the study of bio-ecology of Helix lucorum var. taurica around of Tbilisi. Proceedings of Tbilisi State University. XXXIII: 163-170

Javelidze, G.I. (1952) Results of the study of the hosts of domestic animal helminths. Proceedings of Tbilisi State University. 46: 75-84

Javelidze, G.I. (1953) Contribution to the study of freshwater molluscs of Mingrelia. Proceedings of Tbilisi State University. 48: 123-130

Javelidze, G.I. (1954) Malacofauna of Samgori. Proceedings of Tbilisi State University. 54: 123-135

Javelidze, G.I. (1959) Study of the freshwater molluscs diversity in the Batumi and Keda region. Proceedings of Tbilisi State University. 70: 118-130

Javelidze, G.I. (1961) Study of the freshwater molluscs diversity in the Batumi and Khulo region. Proceedings of Tbilisi State University. 82: 117-182

Javelidze, G.I. (1968) Study of the freshwater molluscs of the Samtredia region. Proceedings of Tbilisi State University. 123: 231-237

Kantor, Yu.I., Sysoev, A.V. (2005) Catalogue of mollusks of Russia and adjacentb countries. Book. : 627

Khojevanishvili, S.I. (1941) Comperative study of malacofauna of western Georgia and south Kazakhistan. Dissertation. : 119

Khojevanishvili, S.I. (1942) Variation study of some western Georgian snails with environmental gradients. Proceedings of Gori State Pedagogical University. 1: 1-5

Kokotschashvili, G.V. (1956) Field guide of snails of Kutaisi. Book. : 50

Kokotschashvili, G.V. (1961) Rapana. Book. : 30

Kokotschashvili, G.V. (1941) Molluscs of west Georgia and their distribution. Dissertation. : 395

Kokotschashvili, G.V. (1976) Glossary of Conchology. Monograph. 79:

Kokotschashvili, G.V. (1961) Molluscs patronymic names in Georgian. Nature of Georgia. 1: 36

Kokotschashvili, G.V. (1941) Gastropods collected in Nasakirali. Proceedings of Kutaisi State Pedagogical Univerity. 111: 32-40

Kokotschashvili, G.V. (1943) List of malacological collection of Kutaisi State Pedagogikal University. Proceedings of Kutaisi State Pedagogical Univerity. V: 197-188

Kokotschashvili, G.V. (1946) Contribution to the study of the distribution of Limnea truncatula Proceedings of Kutaisi State Pedagogical Univerity. pp. 205-211

Kokotschashvili, G.V. (1948) Natural habitats of freshwater mollusc Physa acuta Drap. In GeorgiaProceedings of Kutaisi State Pedagogical Univerity. pp. 349-361

Kokotschashvili, G.V. (1958) Ovoviviparity in Georgian ClausiliidaeProceedings of Kutaisi State Pedagogical Univerity XVIII: 187-194

Kokotschashvili, G.V. (1963) Terms of Conchology . Proceedings of Kutaisi State Pedagogical Univerity. XXV: 290-304

Kokotschashvili, G.V. (1966) Toponymy in names of Georgian molluscs. Proceedings of Kutaisi State Pedagogical Univerity. XXVIII: 290-304

Lejava, G.I. (1965) Наземные моллюски Картли-Кахети (фауна, экология и хазяйственное значение). :автореф. дисс. … канд. биол. наук. Dissertation. : 252

Lejava, G.I. (1984) Land molluscs of Colchis lowland. In: Animal diversity in typical biocenoses of Colchis lowland. Ed, Kurashvili B.. :

Lejava, G.I. (1968) Terrestrial molluscs of Georgia and their economic importance. Monograph. : 62

Lejava, G.I. (1973) Terrestrial Molluscs. Monograph (Animal world of Georgia). IV:

Lejava, G.I. (1962) Contribution to the study Terrestrial Molluscas of Tusheti. Proceedings of the Georgian Academy of Science. XXIX: 327-332

Lezhava, G. (2000) The land shelled mollusces of Georgia. Proceedings of the institute of Zoology of Georgian Academy of Science. 22: 85-94

Lezhava, G. (2002) Land snails and slugs as a pests. Proceedings of the institute of Zoology of Georgian Academy of Science. 21: 81-94

Lezhava, G. (2004) Checklis of Terrestrial Molluscs of Georgia. Proceedings of the institute of Zoology of Georgian Academy of Science. : 60-62

Likharev, I.M., Schileyko, A.A. (2007) A new species and a new subgenus of the genus Acrotoma O. Boettger, 1881 (Pulmonata, Clausiliidae). Ruthenica. 17: 65-67

Lindholm, W.A. (1927) Zur Systematik und Nomenklatur einiger Heliciden und ihrer Verwandten. Archiv für Molluskenkunde. 59: 116-138

Lindholm, W.A. (1922) Neue Heliciden aus dem Kaukasus-Gebiete. Nachrichtsblatt der deutschen malakozoologische Gesellschaft. 45: 137 - 144

Lindholm, W.A. (1912) Eine neue kaukasische Clausilie. Nachrichtsblatt der Deutschen Malakozoologischen. 44: 202-203

Lindholm, W.A. (1913) Beschreibung neuer Arten und Formen aus dem Kaukasus-Gebiete. Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft. 45: 17-23, 62-69

Lindholm, W.A. (1914) Beschreibung vier neuer Landschnecken und einer neuen Untergattung aus dem Sudwestlichen Transkaukasien. Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft. 46: 33-38

Mumladze, L. (2013) Shell size differences in Helix lucorum Linnaeus, 1758 (Mollusca: Gastropoda) between natural and urban environments. Turkish Journal of Zoology. 37: 1-6

Mumladze, L., Cameron, R.A.D., Pokryszko, B.M. (2013) Endemic Land Molluscs in Georgia (Caucasus): how well are they protected by existing reserves and National Parks?. Journal of Molluscan Studies. ??: ??-??

Mumladze, L., Tarkhnishvili, D., Murtskhvaladze, M. (2013) Systematics and evolutionary history of large endemic snails from the Caucasus (Helix buchii, H. goderdziana). American Malacological Bulletin. 31: 1-10

Mumladze, L., Tarkhnishvili, D., Pokryszko, B.M. (2008) A new species of the genus helix from the lesser Caucasus (sw Georgia). Journal of Conchology. 39: 483-485

Neubert, E., Bank, R.A. (2006) Notes on the species of Caucasotachea 344 C. Boettger, 1909 345 and Lindholmia P. Hesse, 1919, with annotations to the Helicidae (Gastropoda: Stylommatophora: Helicidae). Archive Fur Molluskenkunde. 135: 101-132

Nordsieck, H. (1977) Zur Anatomie und Systematik der Clausilien, XVIII. Neuer Taxa rezenter Clausilien. Archiv für Molluskenkunde. 108: 73-107

Nordsieck, H. (1978) Zur Anatomie und Systematik der Clausilien, XX. Die rezenten Arten der Serrulininae und der Gattung Caspiophaedusa. Archiv für Molluskenkunde. 109: 91-101

Nordsieck, H. (1983) Neue Taxa rezenter europaischer Clausilien, mit Bemerkungen zur Bastardierung bei Clausilien (Gastropoda, Clausiliidae). Archiv für Molluskenkunde. 114: 189-211

Pokryszko, B.M., Cameron, R.A.D., Mumladze, L., Tarkhnishvili, D. (2011) Forest snail faunas from Georgian Transcaucasia: patterns of diversity in a Pleistocene refugium. Biological Journal of the Linnean Society. 102: 239-250

Retowski, O. (1914) Materialien zur Kenntnis der Molluskenfauna des Kaukasus. Mitteilungen des kaukasischen Museums. 6: 271-334

Riedel, A. (1958) Materialen zur Kenntnis der Zonitiden (Gastropoda) des Kaukasus und der Krim. Annales Zoologici. 17: 383-428

Riedel, A. (1966) Zonitidae (excl. Daudebardiinae) der Kaukasusländer (Gastropoda). Annales Zoologici. 24: 1-303

Riedel, A. (1988) Eine neue Vitrea-Art aus Transkaukasien (Gastropoda, Zonitidae). Folia Malacologica. 2: 73-76

Riedel, A. (1959) Further materials to the knowledge of Zonitidae (Gastropoda) of Soviet Armenia and neighboring countries. Zoologicheskij Sbornik. 11: 191-206

Rosen, O. (1914) Katalog der schalentragenden Mollusken des Kaukasus. Mitteilungen des Kaukasischen Museums. 6: 141-252.

Schileyko, A.A. (1978) On the systematics of Trichia s. lat. (Pulmonata: Helicoidea: Hygromiidae). Malacologia. 17: 1-56

Shyleiko, A.A. (1998) Treatise on Recent terrestrial pulmonate molluscs. Part 2. Gastrocoptidae, Hypselostomatidae, Vertiginidae, runcatellinidae, Pachnodidae, Enidae, Sagdidae. Ruthenica. 2: 127-261

Shyleiko, A.A. (1998) Treatise on Recent terrestrial pulmonate molluscs. Part 1. Achatinellidae, Amastridae, Orculidae, Strobilopsidae, Spelaeodiscidae, Valloniidae, Cochlicopidae, Pupillidae, Chondrinidae, Pyramidulidae. Ruthenica. 2: 1-127

Shyleiko, A.A. (2003) Treatise on Recent Terrestrial Pulmonate Molluscs Part 11 Trigonochlamydidae, Papillodermidae, Vitrinidae, Limacidae, Bielziidae, Agriolimacidae, Boettgerillidae, Camaenidae. Ruthenica. 2(11): 1467-1626

Simroth, H. (1901) Die Nacktschnecken des Russischen Reiches. Commissionäre der Kaiserlichen Akademie der Wissenschaften. :

Simroth, H. (1910) Kaukasische und asiatische Limaciden und Raublungenschnecken.. Ezhegodnik Zoologicheskogo Muzeya Imperatorskoi Akademii Nauk (Annuaire du Musée Zoologique. 15: 499-560

Simroth, H. (1912) Neue Beiträge zur Kennthis der kaukasischen Nacktschnecken.. Izvestiya Kavkazskago Muzeya. 6: 1-140

Starobogatov, Ya.I. (1996) Eurasiatic species of the genus Cochlicopa (Gastropoda, Pulmonata, Cochlicopidae) Cochlicopidae). Ruthenica. 5(2): 105-129

Suvorov, A.N. (2002) A new subgenus and three new species of the genus Acrotoma O. Boettger, 1881 (Pulmonata Clausiliidae) from western Transcaucasia. Ruthenica. 1: 67-80

Suvorov, A.N. (2003) A new species and genus of carnivorous slugs (Pulmonata Trigonochlamydidae) from West Transcaucasia. Ruthenica. 13: 149-152

Sysoev, A., Schileyko, A.A. (2009) Land Snails and Slugs of Russia and Adjacent Countries. Series Faunistica. Pensoft Publishers, Sofia-Moscow.. : 454

von Rosen, O. (1903) Neue Arten aus der Kaukasus und Zentralasien. Nachrichtsblatt der Deutschen Malakozoologischen. 35: 178-182

Wiktor, A. (2000) Agriolimacidae (Gastropoda: Pulmonata) – a systematic monograph. Annales Zoologici. 49: 347-590

Zilich, A. (1985) Die Typen und Typoide des Natur-Museums Senckenberg. 75: Mollusca: Pupillacea (5): Lauriinae, Argninae. Archiv für Molluskenkunde. 116: 119-136

Акрамовский, Н.Н., Алиев, А.Д. (1961) Расширение Ареала Моллюска Physa acuta Draparnaud в Закавказе (Gastr. Pulmonata, Physidae). Известиа Академии Наук Армианской СССР. 14: 1-3

Бирштейн, Я.А. (1940) Пещерная фауна западного Закавказья. Зоологический журнал. 29: 354-366

Калитина, З.И. (1954) К изучению наземных моллюсков Центрального Кавказа и Восточного Предкавказья. Автореферат диссертации ... кандидата биологических наук. :

Лежава, Г.И. (1962) Явление живорожаемости Laciniaria strauchi Bttg. (Gastropoda, Clausiliidae) и основные сведения о гео морфологии. Доклады АН СССР. 5: 231-232

Лежава, Г.И. (1967) Материалы к изучению наземных моллюсков Ширак-Эльдарской степи. Сб.: Материалы к фауне Грузии. : 5-10

Лежава, Г.И. (1966) Наземные моллюски. Сб.: Фауна б\п животных Триалетского хребта. : 9-20

Лежава, Г.И. (1983) Наземные моллюски Лагодехского заповедника. Сб.: Фауна и экология б\п животных Грузии. : 147-152

Лежава, Г.И. (1964) К фауне наземных моллюсков Восточной Грузии. Сообщения АН ГССР. XXXIV: 665-669

Лежава, Г.И., Нацвлишвили МГ (1965) Материалы к изучению моллюсков лесной зоны кахетинского участка Большого Кавказа. Сообщения АН ГССР. XXXIII: 661-667

Лихарев, И.М. (1958) Наземные моллюски (Кавказа). В кн.: Животный мир СССР. 5: 464-476

Лихарев, И.М. (1962) Клаузилииды (Clausiliidae). Фауна СССР, Моллюски. 3: 317

Лихарев, И.М, Виктор АЙ (1980) Слизни фауны СССР и сопредельных стран (Gastropoda terrestria nuda). Фауна СССР. Моллюски. 3: 437

Лихарев, И.М., Лежава ГИ (1961) Новый наземный моллюск их горной Тушетии Gastropoda, Clausilidae. Сообщения АН ГССР. : 473-477

Лихарев, И.М., Рамельмейер, Е.С. (1952) Наземные Моллюски Фауны СССР. М.; Л.: Изд-во АН СССР. : 512

Лихарев, И.М., Ридель, А. (1962) Новый закавказский наземный моллюск рода Oxychilus Fitz. (Gastropoda, Zonitidae). ТрудыЗоологического института Академии наук СССР. 30: 14-16

Нацвлишвили, М.Г. (1970) К изучению наземных моллюсков Рача-Лечхуми. Вестник Гос. музея Грузии. : 169-189

Нацвлишвили, М.Г. (1971) Моллюски и паразитирующие в них личинки трематод в окрестностях г.Тбилиси (внутренней и южной Картли) : автореф. дисс. ... канд. биол. наук. Ин-т зоологии АН АзССР. : 1-34

Нацвлишвили, М.Г. (1965) Некоторые сведения о наземных моллюсках Гегечкорского района. Сообщения АН ГССР. : 435-441

Нацвлишвили, М.Г. (1967) К изучению наземных моллюсков в окрестностях Тбилиси. Сообщения АН ГССР. : 191-194

Нацвлишвили, М.Г. (1968) К изучению личинок трематод наземных моллюсков окрестностей Тбилиси. Сообщения АН ГССР. : 445-448

Нацвлишвили, М.Г. (1972) Зараженность моллюсков дикроцелозом и фасциолозом. Сообщения АН ГССР. 68: 453-455

Нацвлишвили, М.Г. (1973) Сезонная динамика инвазии моллюсков личинками трематод в условиях окрестностей Тбилиси. Сообщения АН ГССР. : 725-727

Рамельмейер, Е.С. (1938) Наземные моллюски Лагодехского заповедника. Рукопись. :

Розен, О. (1901) Материалы к познанию фауны слизняков Кавказа и Средней Азии. Дневник Зоологического отделения Общества любителей естествознания, антропологии и этнографии. 3: 41467

Суворов, А.Н., Шилейко, А.А. (1991) Функциональная морфология устьевой арматуры в подсемействе Lauriinae (Gastropoda, Orculidae) и вопросы систематики группы. Ruthenica. 1: 67-80

Цветков, Б.Н. (1940) Заметка о пещерных моллюсках Закавказья. Бюллетень Московского общества испытателей природы, отдел биологический. 49: 57-59

Шелковников, А.Б. (1913) Поездла в Сванетию летом. Izvestiya Kavkazskago Muzeya. VII: 3-4

Шилейко, А.А. (1986) Contribution to the study of anatomy and systematics of Материали к изучений для анатомии и систематики Daudebardiidae (Gastropoda, Pulmonata). Proceedings of USSR Academy of Science. 148: 97-123

Шилейко, А.А. (1972) Таксономическая и географическая структура трибы Hygromiini Schileyko (Pulmonata, Helicidae). Зоологичес кий журнал. 51: 1129-1141

Шилейко, А.А. (1975) Моллюски подсемейства Lauriinae фауны СССР (Pulmonata, Pupillidae). Зоологический журнал. 54: 1767-1782

Шилейко, А.А. (1988) Новые и малоизвестные виды наземных моллюсков (Pulmonata) фауны СССР по материалам Зоологического музея Московского университета. Зоологический журнал. 67: 1303-1313

Шилейко, А.А. (1988) Два новых троглобион тных вида наземных легочных моллюсков (Daudebardiidae и Trigonochlamydidae) Гру зии. Зоологический журнал. 67: 1730-1735

Шилейко, А.А. (1986) Наземные моллюски семейства янтарок (Succineidae) фауны СССР. Сборник трудов Зоологичес кого музея МГУ. 24: 197-239

Шилейко, А.А. (1984) Наземные моллюски подо тряда Pupillina фауны СССР (Gastropoda, Pulmonata, Geophila). Фауна СССР, новая серия, № 130. МоллюскиЗ. 3: 399

Шилейко, А.А. (1978) Наземные моллюски надсемейства Helicoidea. Фауна СССР. Моллюски. 3: 384

Шилейко, А.А., Иззатуллаев, З. (1980) Таксоно мическая структура наземных моллюсков семейства Pupillidae фауны СССР и описание нового вида из Средней Азии. ДокладыАка демии наук Таджикской ССР. 23: 282-285

დანართი 2

ცხრილში მოცემულია საქართველოში გავრცელებული ხმელეთის მოლუსკების სია შესაბამისი ოჯახების მითითებით. მეხუთე სვეტი (გავრცელება) აღნიშნავს ცალკეული სახეობის გავრცელების საზღვრებს, კერძო: GE - საქართველოს ენდემი; CE - კავკასიის ენდემი; WS - ფართო გავრცელება.

ოჯახი	გვარი	სახეობა	ავტორი	გავრცელება
Aciculidae	Acicula	Acicula limbata	Reuss, 1860	WS
Aciculidae	Acicula	Acicula moussoni	O. Boettger, 1879	GE
Agriolimacidae	Deroceras	Deroceras agreste	(Linnaeus, 1758)	WS
Agriolimacidae	Deroceras	Deroceras bacurianum	(Simroth, 1912)	WS
Agriolimacidae	Deroceras	Deroceras caucasicum	(Simroth, 1901)	WS
Agriolimacidae	Deroceras	Deroceras osseticum	(Simroth, 1901)	CE
Agriolimacidae	Deroceras	Deroceras reticulatum	(Muller, 1774)	WS
Agriolimacidae	Deroceras	Deroceras subagreste	(Smiroth, 1892)	WS
Agriolimacidae	Krynickillus	Krynickillus melanocephalus	Kaleniczenko, 1851	WS
Agriolimacidae	Megalopelte	Megalopelte simrothi	Lindholm, 1914	WS
Boettgerillidae	Boettgerilla	Boettgerilla compressa	Simroth, 1910	GE
Boettgerillidae	Boettgerilla	Boettgerilla pallens	Simroth, 1912	WS
Bradybaenidae	Fruticicola	Fruticicola fruticum	(Muller, 1774)	WS
Carychiidae	Carychium	Carychium minimum	Muller, 1774	WS
Carychiidae	Carychium	Carychium tridentatum	(Risso, 1826)	WS
Carychiidae	Carychium	Carychium lederi	(O. Boettger, 1880)	WS
Carychiidae	Carychium	Carychium schlickumi	Strauch, 1977	WS
Chondrinidae	Chondrina	Chondrina clienta	Ehrmann, 1933	WS
Chondrinidae	Chondrina	Chondrina granum	(draparnaud, 1801)	WS
Chondrinidae	Chondrina	Chondrina avenacea	(Bruguiere, 1792)	WS
Clausiliidae	Acrotoma	Acrotoma baryshnikovi	Likharev and Schileyko, 2007	GE
Clausiliidae	Acrotoma	Acrotoma claussi	Nordsieck, 1977	GE
Clausiliidae	Acrotoma	Acrotoma gegica	Suvorov, 2002	GE
Clausiliidae	Acrotoma	Acrotoma juliae	Suvorov, 2002	GE
Clausiliidae	Acrotoma	Acrotoma komarowi	(O. Boettger, 1881)	GE
Clausiliidae	Acrotoma	Acrotoma laccata	(O. Boettger, 1881)	GE
Clausiliidae	Armenica	Armenica gracillima	(Retowski, 1889)	CE
Clausiliidae	Armenica	Armenica griseofusca	(Mousson, 1876)	GE
Clausiliidae	Armenica	Armenica unicristata	(O. Boettger, 1877)	CE
Clausiliidae	Caspiophaedusa	Caspiophaedusa perlucens	(O. Boettger, 1877)	CE
Clausiliidae	Elia	Elia derasa	(Mousson, 1863)	CE
Clausiliidae	Elia	Elia ossetica	(Mousson, 1863)	CE
Clausiliidae	Elia	Elia somchetica somchetica	(L. Pfeiffer, 1846)	CE
Clausiliidae	Elia	Elia tuschetica	Likharev et Lezhawa, 1961	GE
Clausiliidae	Euxinastra	Euxinastra hamata	(O. Boettger, 1888)	CE
Clausiliidae	Filosa	Filosa filosa	(Mousson, 1863)	CE
Clausiliidae	Kazancia	Kazancia lindholm	(Kobelt in Lindholm, 1912)	CE
Clausiliidae	Mentissoidea	Mentissoidea rupicola	(Mortillet, 1854)	CE
Clausiliidae	Micropontica	Micropontica closta	(O. Boettger, 1881)	GE
Clausiliidae	Mucronaria	Mucronaria acuminata	(Mousson, 1876)	GE
Clausiliidae	Mucronaria	Mucronaria duboisi	(Chrapentier, 1852)	CE
Clausiliidae	Mucronaria	Mucronaria index	(Mousson, 1863)	GE
Clausiliidae	Mucronaria	Mucronaria pleuroptychia	(O. Boettger, 1878)	CE
Clausiliidae	Mucronaria	Mucronaria strauchi	(O. Boettger, 1878)	GE
Clausiliidae	Pontophaedusa	Pontophaedusa funiculum	(Mousson, 1863)	CE
Clausiliidae	Pravispira	Pravispira semilamellata	(Mousson, 1863)	CE

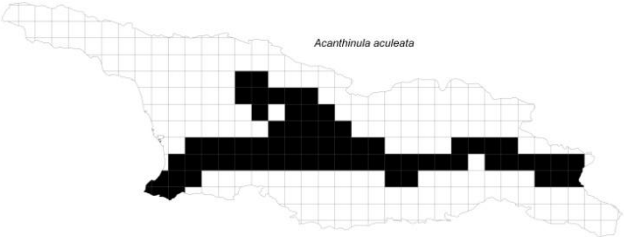
Clausiliidae	Quadriplicata	Quadriplicata aggesta	(O. Boettger, 1879)	CE
Clausiliidae	Quadriplicata	Quadriplicata dipolauchen	(O. Boettger, 1881)	GE
Clausiliidae	Quadriplicata	Quadriplicata lederi	(O. Boettger, 1879)	GE
Clausiliidae	Quadriplicata	Quadriplicata pumiliformis	(O. Boettger, 1881)	CE
Clausiliidae	Quadriplicata	Quadriplicata quadriplicata	(A. Schmidt, 1868)	CE
Clausiliidae	Quadriplicata	Quadriplicata subaggesta	(Retowski, 1887)	CE
Clausiliidae	Scrobifera	Scrobifera taurica	(L. Pfeiffer, 1848)	CE
Clausiliidae	Serrulina	Serrulina serrulata	(L. Pfeiffer, 1847)	WS
Clausiliidae	Serrulina	Serrulina sieversi	Likharev, 1962	CE
Clausiliidae	Serrulinella	Serrulinella senghanensis	(de Morgan in Germain, 1933)	WS
Clausiliidae	Strigileuxina	Strigileuxina reuleauxi	(O. Boettger, 1887)	CE
Clausiliidae	Strigileuxina	Strigileuxina lindholmi	(Lindholm, 1912)	CE
Cochlicopidae	Cochlicopa	Cochlicopa curta	Clessin, 1908	WS
Cochlicopidae	Cochlicopa	Cochlicopa nitens	(Gallenstein, 1852)	WS
Cochlicopidae	Cochlicopa	Cochlicopa lubrica	(Muller, 1774)	WS
Cochlicopidae	Cochlicopa	Cochlicopa lubricella	(Ziegler in Porro, 1838)	WS
Cochlicopidae	Cochlicopa	Cochlicopa lubricoides	(Potez et Michaud, 1838)	WS
Cochlostomatidae	Toffoletia	Toffoletia lederi	(O. Boettger, 1881)	CE
Cyclophoridae	Caspicyclotus	Caspicyclotus sieversi	(L. pfeiffer, 1871)	WS
Daudebardiidae	Daudebardia	Daudebardia nivea	Schileyko, 1988	GE
Daudebardiidae	Inguria	Inguria wagneri	(Rosen, 1911)	CE
Daudebardiidae	Sieversia	Sieversia heydeni	(O. Boettger, 1879)	CE
Daudebardiidae	Sieversia	Sieversia lederi	(O. Boettger, 1881)	WS
Daudebardiidae	Szuchumiella	Szuchumiella jetschini	(A. Wagner, 1895)	GE
Discidae	Discus	Discus ruderatus	(Ferussac, 1821)	WS
Enidae	Adzharia	Adzharia renschi	Hesse, 1933	GE
Enidae	Akramowskiella	Akramowskiella andronakii	(Lindholm, 1913)	CE
Enidae	Akramowskiella	Akramowskiella umbrosa	(Mousson, 1873)	CE
Enidae	Brephulopsis	Brephulopsis cylindrica	(Menke, 1828)	WS
Enidae	Caucasicola	Caucasicola raddei	(Kobelt, 1880)	CE
Enidae	Chondrula	Chondrula caucasica	(L. Pfeiffer, 1852)	WS
Enidae	Chondrula	Chondrula microtraga	(Parreyss in Rossmassler, 1839)	WS
Enidae	Chondrula	Chondrula sunzhica	Steklov, 1962	GE
Enidae	Chondrula	Chondrula tridens	(Muller, 1774)	WS
Enidae	Chondrus	Chondrus zebrula	(Ferussac, 1821)	WS
Enidae	Clausilioides	Clausilioides filifer	(Lindholm, 1913)	GE
Enidae	Euchondrus	Euchondrus acutior	(Lindholm, 1922)	WS
Enidae	Euchondrus	Euchondrus lamelliferus	(Rossmassler, 1859)	WS
Enidae	Georginapaeus	Georginapaeus hohenackeri	(L. Pfeiffer, 1848)	CE
Enidae	Imparietula	Imparietula Brevior	(Mousson, 1876)	CE
Enidae	Improvisa	Improvisa pupoides	(Krynicki, 1833)	WS
Enidae	Ljudmilena	Ljudmilena sieversi	(Mousson, 1873)	CE
Enidae	Ljudmilena	Ljudmilena tricolis	(Mousson, 1876)	GE
Enidae	Merdigera	Merdigera obscura	(Muller, 1774)	WS
Enidae	Peristoma	Peristoma boettgeri	(Clessin, 1883)	GE
Enidae	Peristoma	Peristoma lanceum	Schileyko, 1984	GE
Enidae	Pseudochondrula	Pseudochondrula lederi	(O. Boettger, 1883)	CE
Enidae	Pseudochondrula	Pseudochondrula seductilis	(Rossmassler, 1837)	WS
Enidae	Pseudochondrula	Pseudochondrula sinistrorosa	Kokotschashvili et Schileyko, 1984	GE
Enidae	Pseudochondrula	Pseudochondrula tetrodon	(Mortillet, 1854)	CE
Enidae	Pseudochondrula	Pseudochondrula tuberifera	(O. Boettger, 1879)	CE
Enidae	Retowskia	Retowskia schlaeflii	(Mousson, 1863)	CE
Enidae	Andronakia	Andronakia catenulata	(Lindholm, 1914)	CE
Euconulidae	Euconulus	Euconulus fulvus	(Muller, 1774)	WS

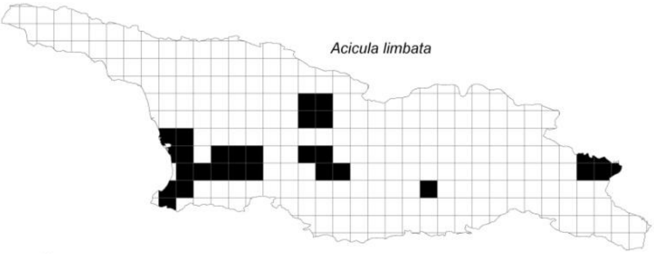
Ferussaciidae	Cecilioides	Cecilioides acicula	(Muller, 1774)	WS
Ferussaciidae	Cecilioides	Cecilioides raddei	(O. Boettger, 1879)	WS
Gastrocoptidae	Gastrocopta	Gastrocopta theeli	(Westerlund, 1876)	WS
Gastrodontidae	Zonitoides	Zonitoides nitidus	(Muller, 1774)	WS
Helicidae	Caucasotachea	Caucasotachea atrolabiata	(Krynicki, 1833)	CE
Helicidae	Caucasotachea	Caucasotachea calligera	(Dubois de Montpereux, 1840)	CE
Helicidae	Helix	Helix goderdziana	Mumladze et al., 2008	CE
Helicidae	Helix	Helix albescens	Rossmassler, 1839	WS
Helicidae	Helix	Helix buchii	(Dubios de Montpereux, 1839)	CE
Helicidae	Helix	Helix lucorum	Linnaeus, 1758	WS
Helicidae	Lindholmia	Lindholmia christophi	(O. Boettger, 1881)	CE
Helicidae	Lindholmia	Lindholmia nordmanni	(Mousson, 1854)	CE
Hygromiidae	Caucasigena	Caucasigena abchasica	(Lindholm, 1927)	CE
Hygromiidae	Caucasigena	Caucasigena armeniaca	(L. Pfeiffer, 1846)	CE
Hygromiidae	Caucasigena	Caucasigena eichwaldi	(L. Pfeiffer, 1846)	CE
Hygromiidae	Caucasigena	Caucasigena rengarteni	(Lindholm, 1913)	WS
Hygromiidae	Caucasigena	Caucasigena schaposchnikovi	(Rosen, 1911)	WS
Hygromiidae	Caucasigena	Caucasigena thalestris	(Lindholm, 1927)	CE
Hygromiidae	Caucasocressa	Caucasocressa ibera	Hausdorf, 2003	GE
Hygromiidae	Caucasocressa	Caucasocressa joannis	(Mortillet, 1854)	CE
Hygromiidae	Caucasocressa	Caucasocressa dasilepida	(Mabille, 1881)	CE
Hygromiidae	Circassina	Circassina frutis	(L. pfeiffer, 1859)	CE
Hygromiidae	Circassina	Circassina pachnodes	(O. Boettger, 1884)	CE
Hygromiidae	Circassina	Circassina pergranulata	Hausdorf, 2001	GE
Hygromiidae	Circassina	Circassina stephaniae	(Hudec et Lezhawa, 1970)	GE
Hygromiidae	Euomphalia	Euomphalia aristata	(Krynicki, 1836)	CE
Hygromiidae	Euomphalia	Euomphalia appeliana	(Mousson, 1876)	CE
Hygromiidae	Fruticocampylaea	Fruticocampylaea kobiensis	(O. Boettger, 1883)	GE
Hygromiidae	Fruticocampylaea	Fruticocampylaea narzanensis	(Krynicki, 1836)	CE
Hygromiidae	Hesseola	Hesseola solidior	(Mousson, 1873)	WS
Hygromiidae	Kalitinaia	Kalitinaia crenimargo	(L. Pfeiffer, 1848)	CE
Hygromiidae	Kalitinaia	Kalitinaia perspectiva	Hausdorf, 1993	CE
Hygromiidae	Kalitinaia	Kalitinaia tiflisiana	(Lindholm, 1913)	CE
Hygromiidae	Kokotschashvilia	Kokotschashvilia eberhardi	Schileyko, 1978	CE
Hygromiidae	Kokotschashvilia	Kokotschashvilia holotricha	(O. Boettger, 1884)	CE
Hygromiidae	Kokotschashvilia	Kokotschashvilia makvalae	(Hudec et Lezhawa, 1969)	GE
Hygromiidae	Kokotschashvilia	Kokotschashvilia tanta	Schileyko, 1978	GE
Hygromiidae	Monacha	Monacha cartusiana	(Muller, 1774)	WS
Hygromiidae	Monacha	Monacha perfrequens	(Hesse, 1914)	CE
Hygromiidae	Monacha	Monacha roseni	(Hesse, 1914)	CE
Hygromiidae	Monacha	Monacha samsunensis	(L. Pfeiffer, 1868)	WS
Hygromiidae	Monacha	Monacha subcarthusiana	(Lindholm, 1913)	CE
Hygromiidae	Oscarboettgeria	Oscarboettgeria euages	(O. Boettger, 1883)	CE
Hygromiidae	Platytheba	Platytheba mingrelica	(Hesse, 1921)	GE
Hygromiidae	Platytheba	Platytheba prometheus	(O. Boettger, 1883)	GE
Hygromiidae	Shileykoia	Shileykoia daghestana	(Kobelt, 1877)	CE
Hygromiidae	Stenomphalia	Stenomphalia maiae	(Hudec et Lezhava, 1969)	CE
Hygromiidae	Stenomphalia	Stenomphalia pisiformis	(L. Pfeiffer, 1846)	WS
Hygromiidae	Stenomphalia	Stenomphalia ravergiensis	(Ferussac, 1835)	WS
Hygromiidae	Stenomphalia	Stenomphalia selecta	(Klika, 1894)	CE
Hygromiidae	Stenomphalia	Stenomphalia septemgyrata	(Mousson, 1876)	WS
Hygromiidae	Teberdina	Teberdina flavolimbata	(O. Boettger, 1883)	CE
Hygromiidae	Xeropicta	Xeropicta derbentina	(Krynicki, 1836)	WS
Limacidae	Caucasolimax	Caucasolimax caucasicus	(Simroth, 1898)	GE

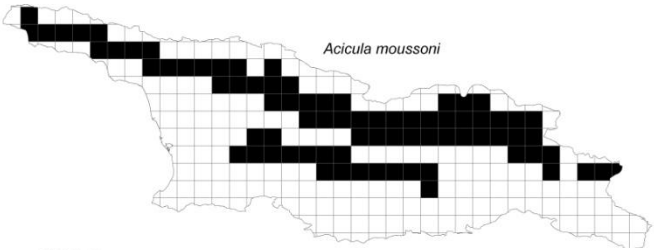
Limacidae	Eumilax	Eumilax brandti	(Martens, 1880)	CE
Limacidae	Eumilax	Eumilax intermittens	(O. Boettger, 1883)	CE
Limacidae	Gigantomilax	Gigantomilax koenigi	(Simroth, 1912)	CE
Limacidae	Gigantomilax	Gigantomilax lederi	(O. Boettger, 1883)	CE
Limacidae	Gigantomilax	Gigantomilax monticola	(O. Boettger, 1881)	CE
Limacidae	Limax	Limax maculatus	(Kaleniczenko, 1851)	WS
Limacidae	Metalimax	Metalimax elegans	Simroth, 1901	GE
Limacidae	Metalimax	Metalimax varius	(O. Boettger, 1884)	CE
Milacidae	Milax	Milax caucasicus	Simroth, 1912	CE
Oleacinidae	Poiretia	Poiretia mingrelica	(O. Boettger, 1881)	GE
Orculidae	Euxinolauria	Euxinolauria caucasica	(L. pfeiffer, 1857)	GE
Orculidae	Euxinolauria	Euxinolauria glomerosa	Suvorov et Schileyko, 1991	GE
Orculidae	Euxinolauria	Euxinolauria honesta	Suvorov et Schileyko, 1991	GE
Orculidae	Euxinolauria	Euxinolauria nemethi	(Hausdorf, 1996)	CE
Orculidae	Euxinolauria	Euxinolauria paulinae	(Lindholm, 1913)	CE
Orculidae	Euxinolauria	Euxinolauria pulchra	(Retowski, 1883)	GE
Orculidae	Euxinolauria	Euxinolauria rectidentata	Schileyko, 1975	GE
Orculidae	Euxinolauria	Euxinolauria silicea	Schileyko, 1975	GE
Orculidae	Euxinolauria	Euxinolauria sinangula	Schileyko, 1975	CE
Orculidae	Euxinolauria	Euxinolauria superstructa	(Mousson, 1876)	CE
Orculidae	Euxinolauria	Euxinolauria tenuimarginata	(Pilsbry, 1922)	CE
Orculidae	Euxinolauria	Euxinolauria zonifera	(Pilsbry, 1934)	CE
Orculidae	Lauria	Lauria cylindracea	(Da Costa, 1778)	WS
Orculidae	Pilorcula	Pilorcula aspinosa	Hausdorf, 1996	GE
Orculidae	Pilorcula	Pilorcula pusilla	Hausdorf, 1996	GE
Orculidae	Pilorcula	Pilorcula trifilaris trifilaris	(Mousson, 1863)	WS
Orculidae	Pilorcula	Pilorcula trifilaris longior	Hausdorf, 1996	WS
Orculidae	Pilorcula	Pilorcula trifilaris quadrifilaris	(Rosen, 1905)	CE
Orculidae	Schileykula	Schileykula batumensis	(Retowski, 1889)	GE
Orculidae	Sphyradium	Sphyradium doliolum	(Bruguiere, 1792)	WS
Parmacellidae	Parmacella	Parmacella ibera	Eichwald, 1841	GE
Punctidae	Punctum	Punctum pygmaeum	(Draparnaud, 1801)	WS
Pupillidae	Gibbulinopsis	Gibbulinopsis interrupta	(Reinhardt in Martens, 1876)	CE
Pupillidae	Gibbulinopsis	Gibbulinopsis signata	(Mousson, 1873)	WS
Pupillidae	Pupilla	Pupilla inops	(Reinhardt, 1877)	CE
Pupillidae	Pupilla	Pupilla muscorum	(Linnaeus, 1758)	WS
Pupillidae	Pupilla	Pupilla sterri	(Voith in Furnrohr, 1840)	WS
Pupillidae	Pupilla	Pupilla triplicata	(Studer, 1820)	WS
Pyramidulidae	Pyramidula	Pyramidula rupestris	(Draparnaud, 1801)	WS
Succineidae	Oxyloma	Oxyloma elegans	(Risso, 1826)	WS
Succineidae	Oxyloma	Oxyloma sarsi	(Esmark in Esmark et Hoyer, 1886)	WS
Succineidae	Succinea	Succinea putris	(Linnaeus, 1758)	WS
Succineidae	Succinella	Succinella oblonga	(Draparnaud, 1801)	WS
Trigonochlamydidae	Drilolestes	Drilolestes retowskii	(O. Boettger, 1884)	CE
Trigonochlamydidae	Hyrcanolestes	Hyrcanolestes velitaris	(Martens, 1880)	CE
Trigonochlamydidae	Lesticulus	Lesticulus nocturnus	Schileyko, 1988	GE
Trigonochlamydidae	Selenochlamys	Selenochlamys pallida	O. Boettger, 1883	CE
Trigonochlamydidae	Trigonochlamys	Trigonochlamys imitatrix	O. Boettger, 1881	CE
Truncatellinidae	Columella	Columella edentula	(draparnaud, 1805)	WS
Truncatellinidae	Truncatellina	Truncatellina claustralis	(Gredler, 1856)	WS
Truncatellinidae	Truncatellina	Truncatellina costulata	(Nilsson, 1822)	WS
Truncatellinidae	Truncatellina	Truncatellina cylindrica	(Ferussac, 1807)	WS
Truncatellinidae	Truncatellina	Truncatellina callicratis	(Gredler, 1853)	WS
Valloniidae	Acanthinula	Acanthinula aculeata	(Muller, 1774)	WS

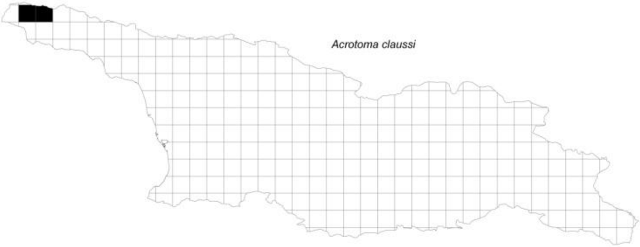
Valloniidae	Vallonia	Vallonia costata	(Muller, 1774)	WS
Valloniidae	Vallonia	Vallonia pilchella	(Muller, 1774)	WS
Vertiginidae	Vertigo	Vertigo antivertigo	(Draparnaud, 1801)	WS
Vertiginidae	Vertigo	Vertigo moulinsiana	(Dupuy, 1849)	WS
Vertiginidae	Vertigo	Vertigo pusilla	Muller, 1774	WS
Vertiginidae	Vertigo	Vertigo pygmaea	(Draparnaud, 1801)	WS
Vertiginidae	Vertigo	Vertigo sieversi	(o. Boettger, 1879)	CE
Vertiginidae	Vertigo	Vertigo substriata	(Jeffreys, 1830)	WS
Vertiginidae	Vertilla	Vertilla angustior	(Jeffreys, 1830)	WS
Vitrinidae	Phenacolimax	Phenacolimax annularis`	(Studer, 1820)	WS
Vitrinidae	Trochovitrina	Trochovitrina lederi	(O. Boettger, 1879)	GE
Vitrinidae	Vitrina	Vitrina Pellucida	(Muller, 1774)	WS
Zonitidae	Aegopinella	Aegopinella pura	(Alder, 1830)	WS
Zonitidae	Conulopolita	Conulopolita cavatica	(Riedel, 1966)	CE
Zonitidae	Conulopolita	Conulopolita raddei	(O. Boettger, 1879)	GE
Zonitidae	Conulopolita	Conulopolita sieversi	(O. Boettgeri, 1879)	CE
Zonitidae	Discoxychilus	Discoxychilus lindholmi	Reidel, 1966	CE
Zonitidae	Eopolita	Eopolita derbentina	(O. Boettger, 1886)	WS
Zonitidae	Oxychilus	Oxychilus crenimargo	(Retowskii, 1889)	CE
Zonitidae	Oxychilus	Oxychilus decipiens	(O. Boettger, 1886)	CE
Zonitidae	Oxychilus	Oxychilus deilus deilus	(Bourguignat, 1857)	WS
Zonitidae	Oxychilus	Oxychilus difficilis	(O. Boettger, 1888)	CE
Zonitidae	Oxychilus	Oxychilus discrepans	(Retowski, 1889)	CE
Zonitidae	Oxychilus	Oxychilus duboisi	(Charpentier in Mousson, 1863)	GE
Zonitidae	Oxychilus	Oxychilus imperator	Reidel, 1966	GE
Zonitidae	Oxychilus	Oxychilus Koutaisanus	(Mousson, 1863)	CE
Zonitidae	Oxychilus	Oxychilus oschtenicus	(O. Boettger, 1888)	CE
Zonitidae	Oxychilus	Oxychilus suaneticus	(O. Boettgeri, 1883)	CE
Zonitidae	Oxychilus	Oxychilus subeffuscus	(O. Boettger, 1879)	WS
Zonitidae	Oxychilus	Oxychilus sucinaceus	(O. Boettger, 1883)	CE
Zonitidae	Oxychilus	Oxychilus translucidus	(Mortillet, 1854)	WS
Zonitidae	Oxychilus	Oxychilus andronakii	(Lindholm, 1914)	CE
Zonitidae	Oxychilus	Oxychilus birsteini	Tzvetkov, 1940	GE
Zonitidae	Oxychilus	Oxychilus lederi	(O. Boettger, 1880)	GE
Zonitidae	Oxychilus	Oxychilus retowskii	(Lindholm, 1914)	CE
Zonitidae	Perpolita	Perpolita hammonis	(Strom, 1765)	WS
Zonitidae	Perpolita	Perpolita petronella	(L. Pfeiffer, 1853)	WS
Zonitidae	Vitrea	Vitrea angystropha	(O. Boettger, 1880)	CE
Zonitidae	Vitrea	Vitrea contortula	(Krynicki, 1837)	CE
Zonitidae	Vitrea	Vitrea contracta`	(Westerlund, 1871)	WS
Zonitidae	Vitrea	Vitrea praetermissa	Reidel, 1988	GE
Zonitidae	Vitrea	Vitrea pygmaea	(O. Boettger, 1880)	WS
Zonitidae	Vitrea	Vitrea rhododendronis	Reidel, 1966	GE
Zonitidae	Vitrea	Vitrea sorella	(Mousson, 1863)	GE
Zonitidae	Vitrinoxychilus	Vitrinoxychilus subsuturalis	(O. Boettger, 1888)	CE
Zonitidae	Vitrinoxychilus	Vitrinoxychilus suturalis	(O. Boettger, 1881)	CE

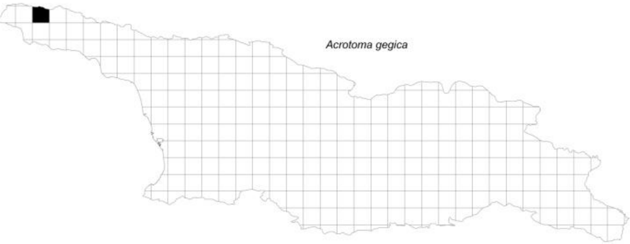
დანართი 3. საქართველოს ხმელეთი მოლუსკების გავრცელების რუკები. ინფორმაცია მოცემულია 20 კმ. კვ. ბადის მიხედვით. ნაჩვენებია მხოლოდ 234 სახეობის მოლუსკის გავრცელების შესახებ ინფორმაცია რომლებიც დალაგებულია ანბანის მიხედვით. სხვა სახეობების შესახებ (20-მდე) შესახებ გავრცელებისინფორმაცია არასაკმარისია შესაბამისი გარჩევადობის რუკის დასამზადებლად

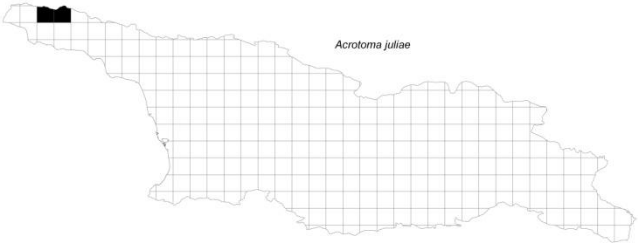


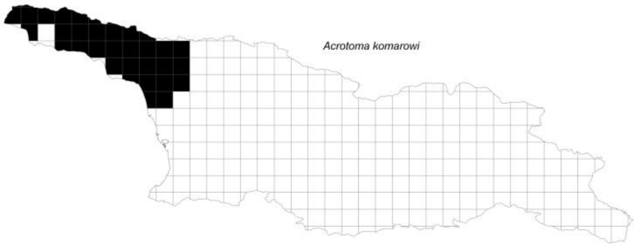


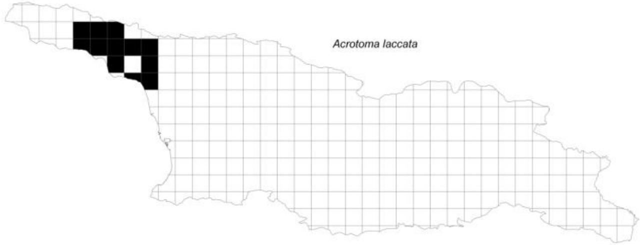


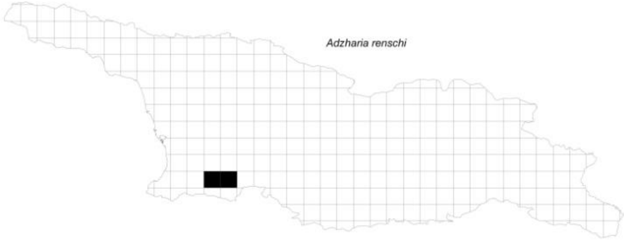


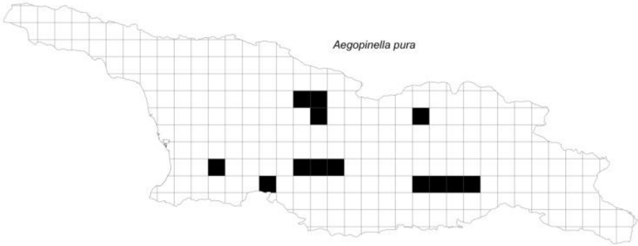


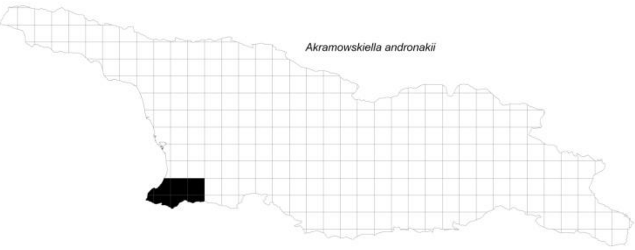


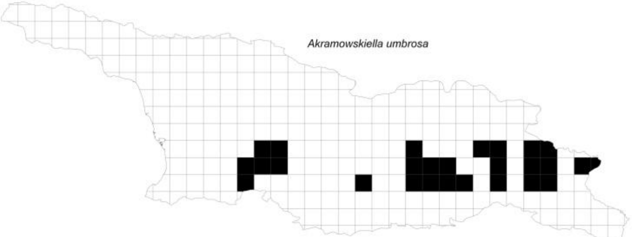


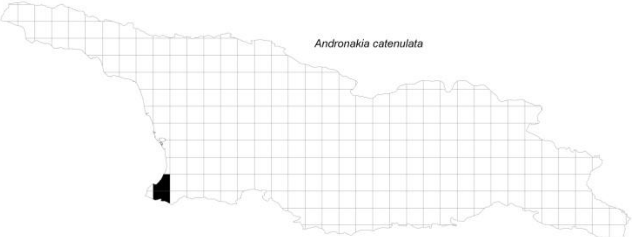


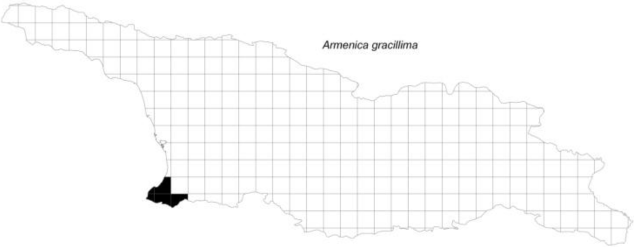


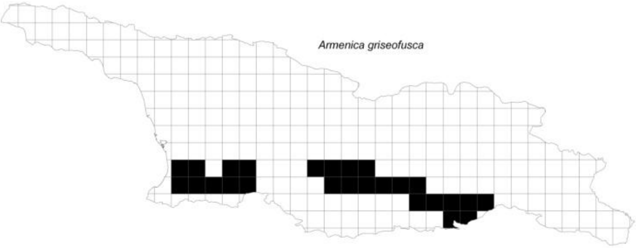


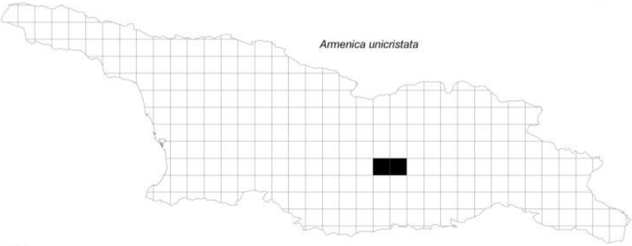


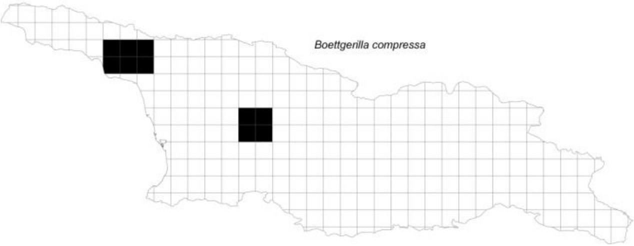

Akramowskiella umbrosa

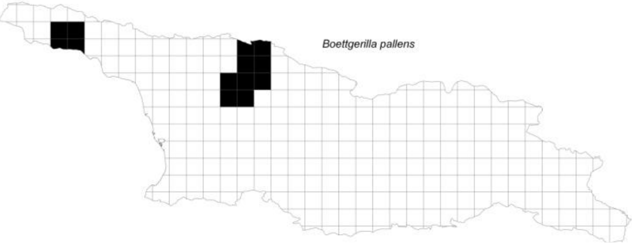

Andronakia catenulata

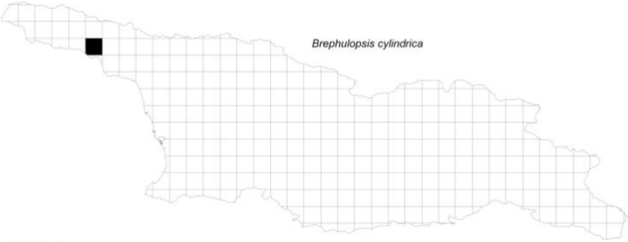

Armenica gracillima

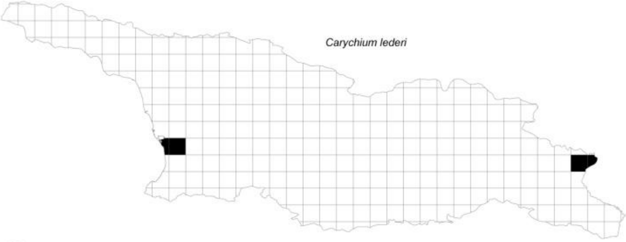

Armenica griseofusca

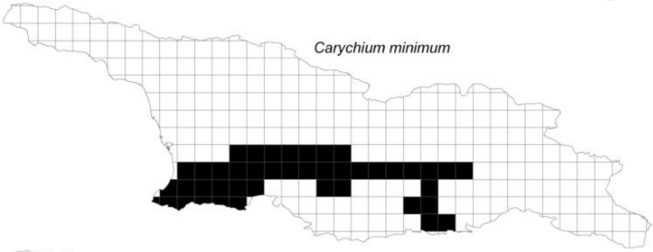

Armenica unicristata

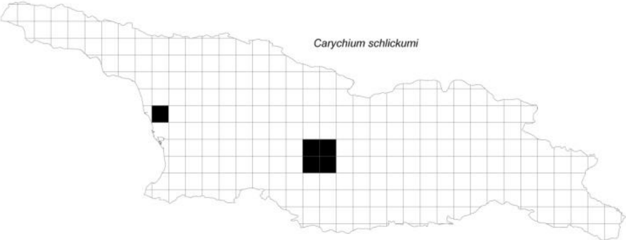

Boettgerilla compressa

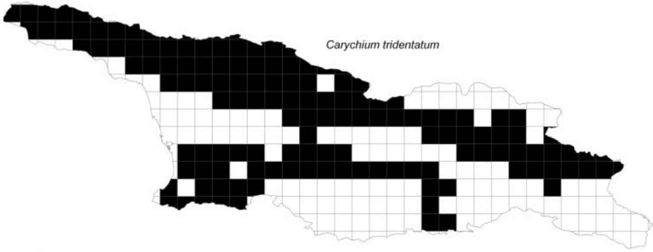

Boettgerilla pallens

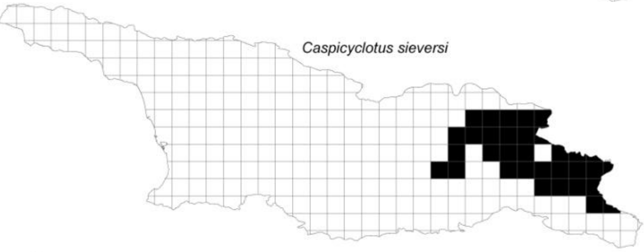

Brephulopsis cylindrica

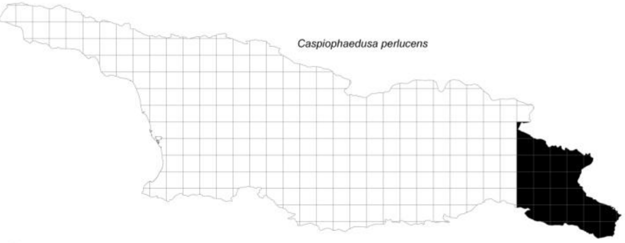

Carychium lederi

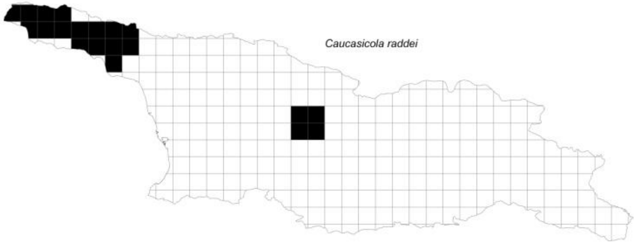

Carychium minimum

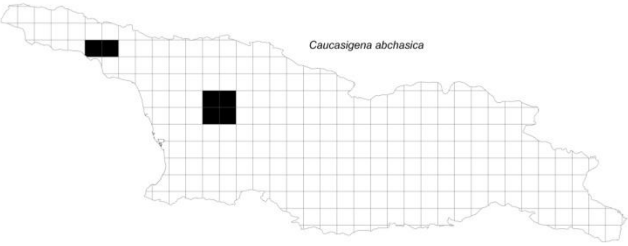

Carychium schlickumi


Carychium tridentatum

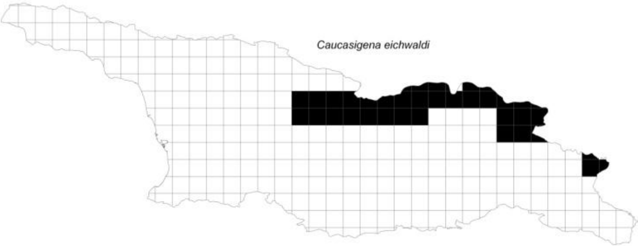

Caspicyclotus sieversi


Caspiophaedusa perlucens

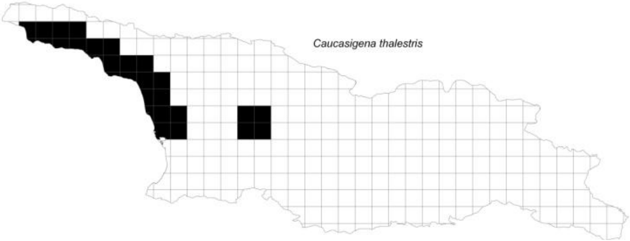

Caucasicola raddei


Caucasigena abchasica

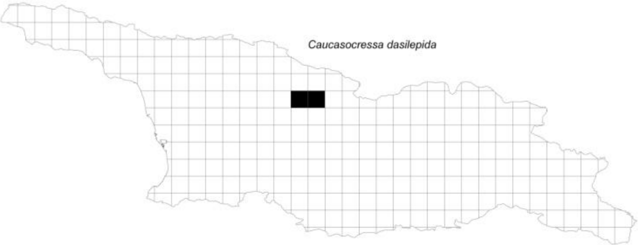
Caucasigena armeniaca



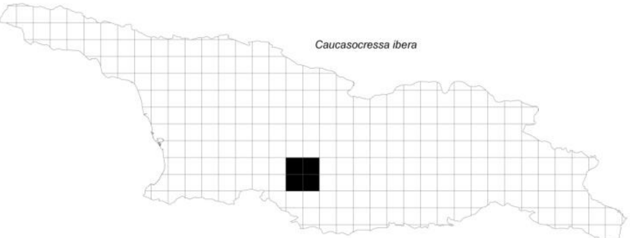
Caucasigena eichwaldi



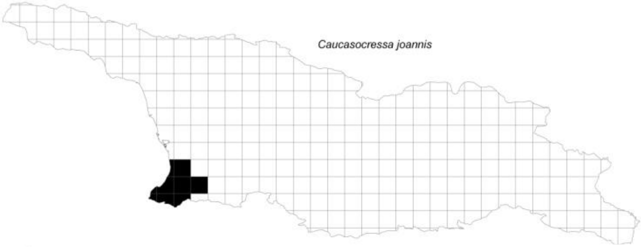
Caucasigena thalestris



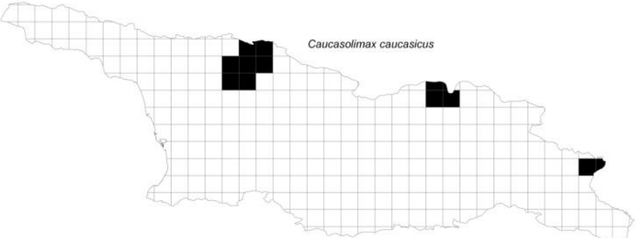
Caucasocressa dasilepida



Caucasocressa ibera



Caucasocressa joannis



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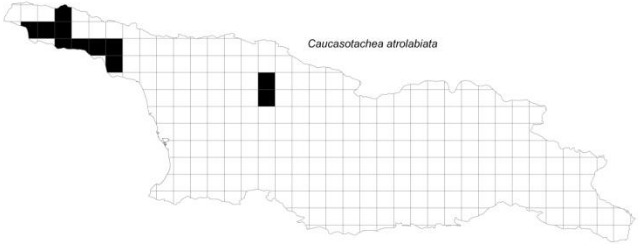

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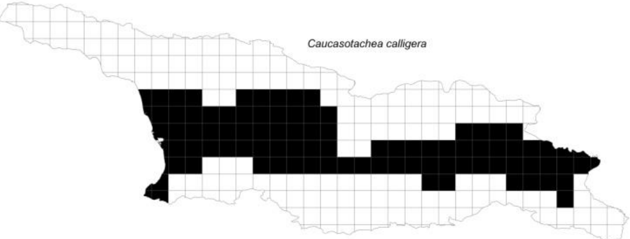

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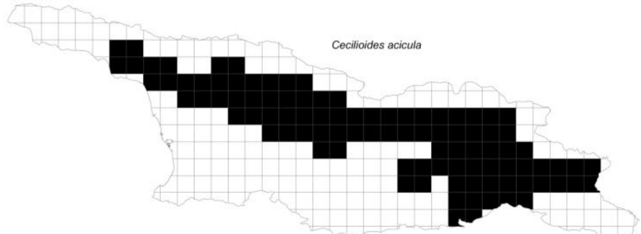

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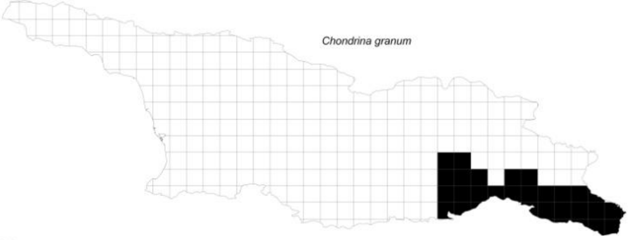

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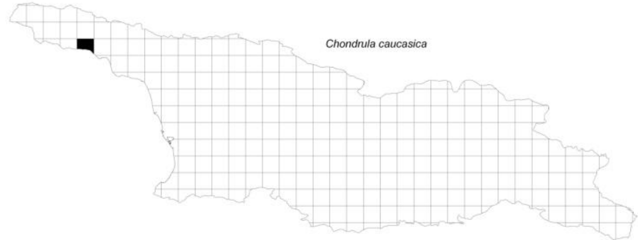

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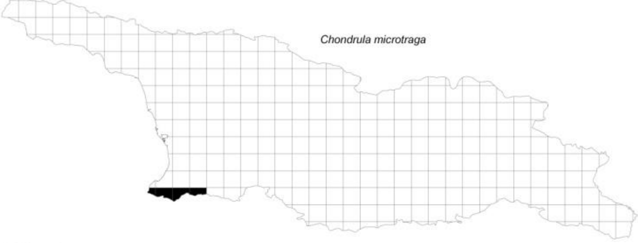

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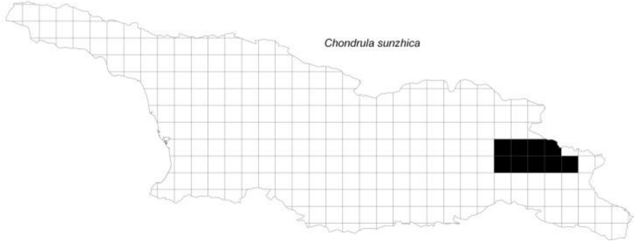

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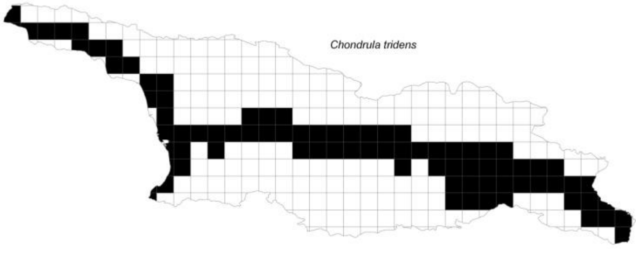
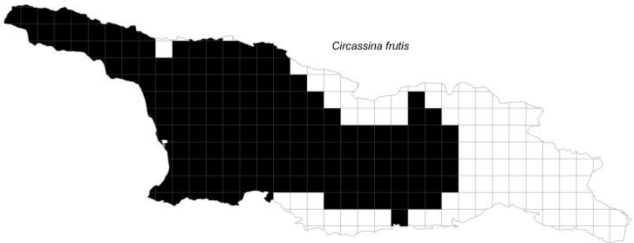


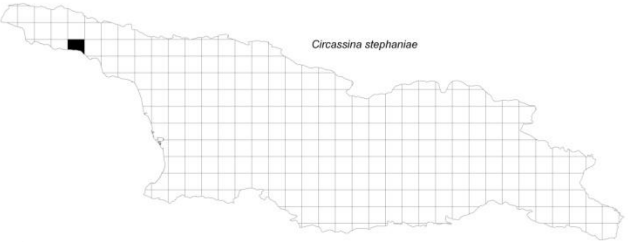
Chondrula tridens

Chondrus zebrula


Circassina frutis


Circassina pachnodes


Circassina pergranulata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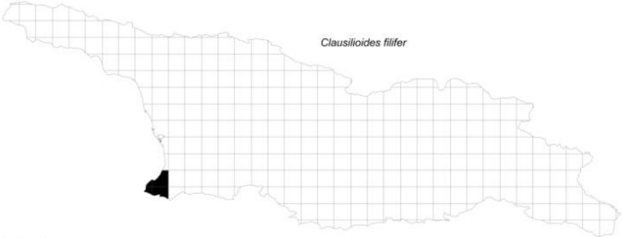
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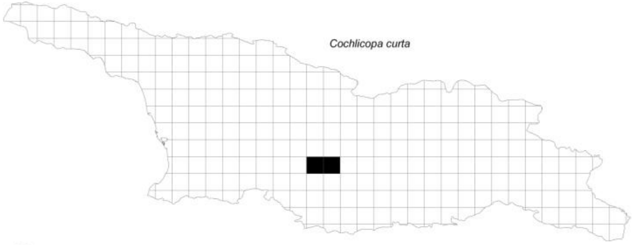
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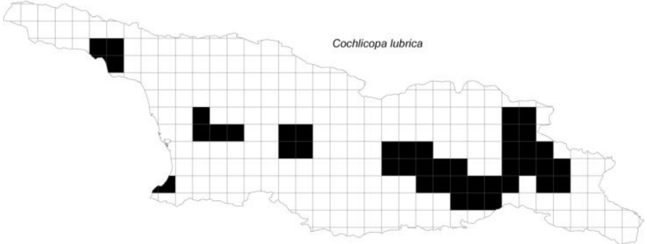
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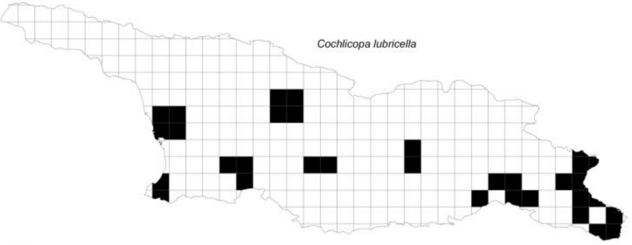
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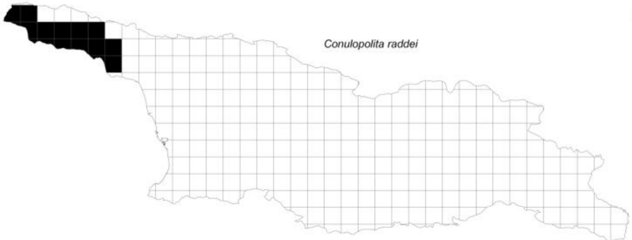
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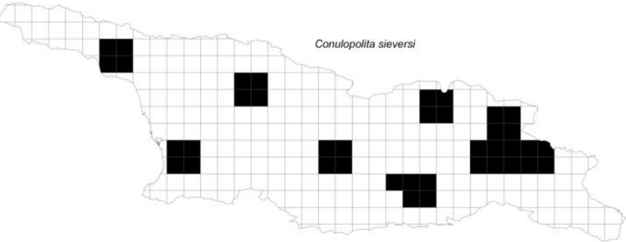
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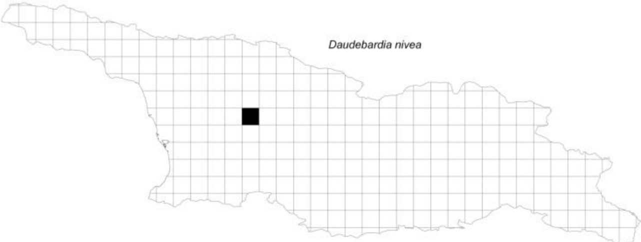
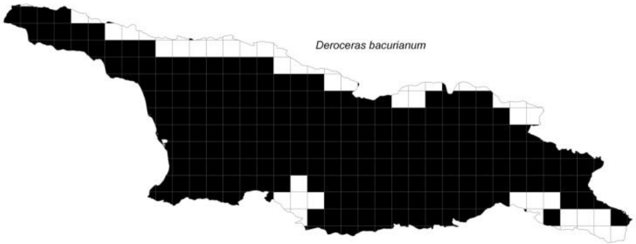

Daudebardia nivea


Deroceras agreste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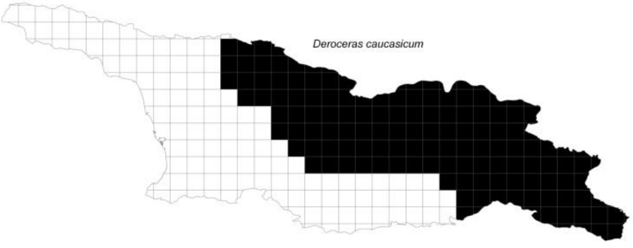
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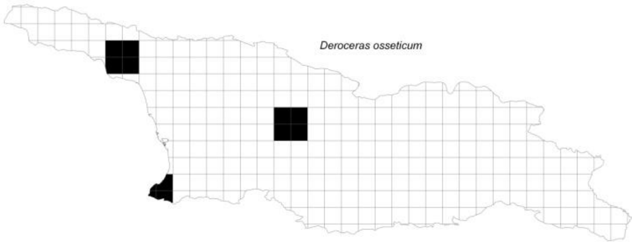
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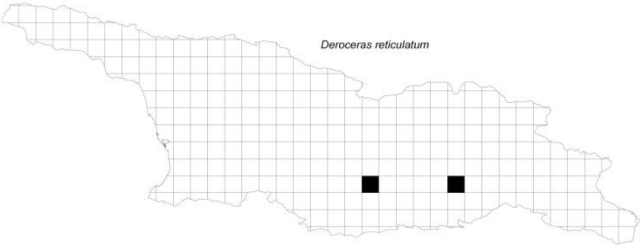
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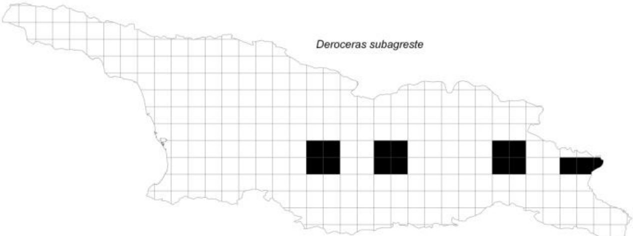
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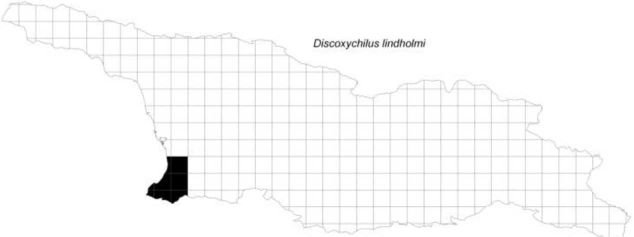
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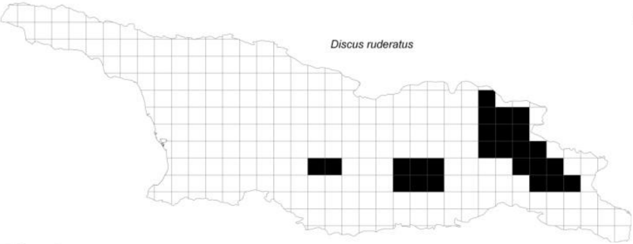
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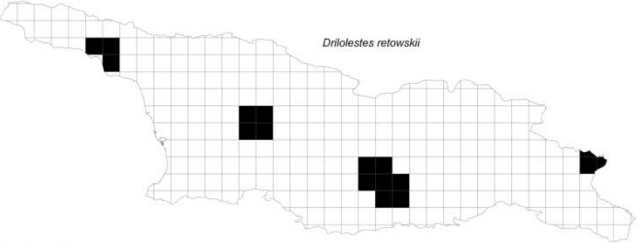
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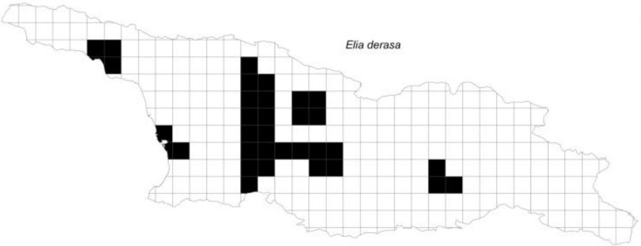
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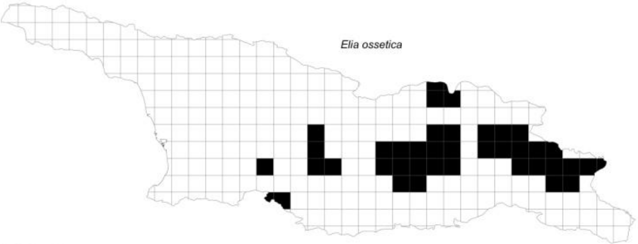
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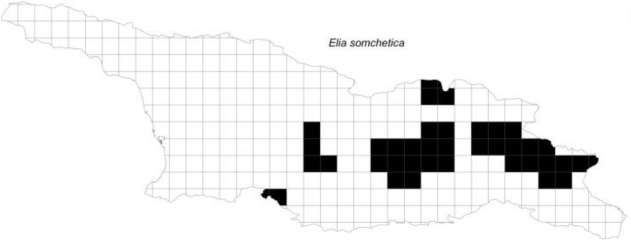
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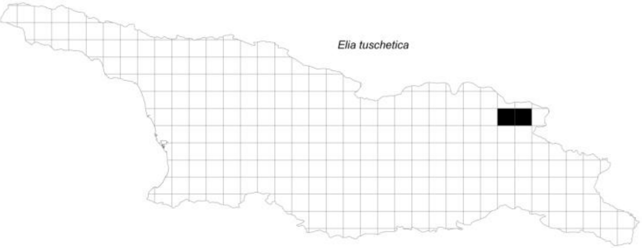
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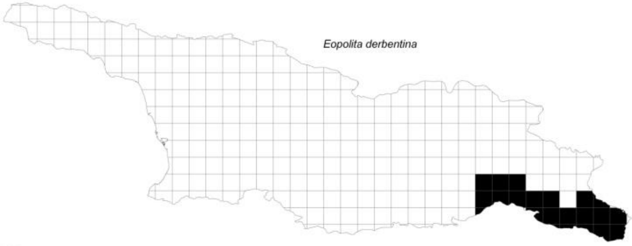
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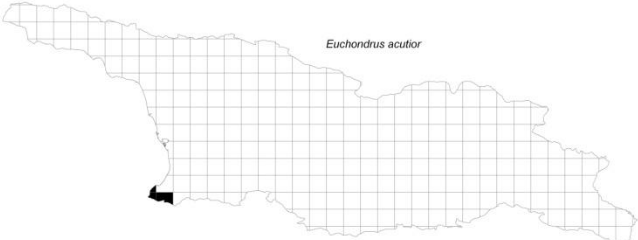
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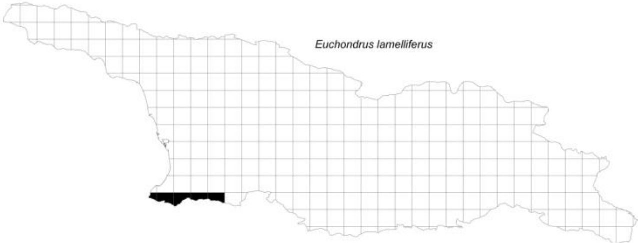
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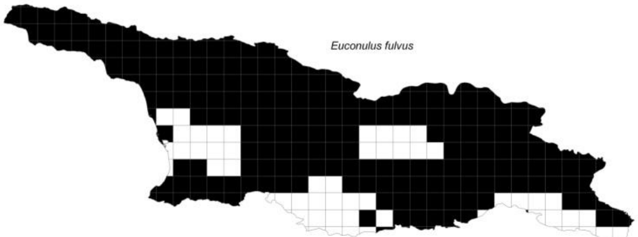
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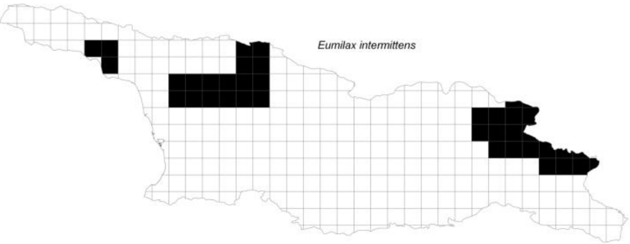
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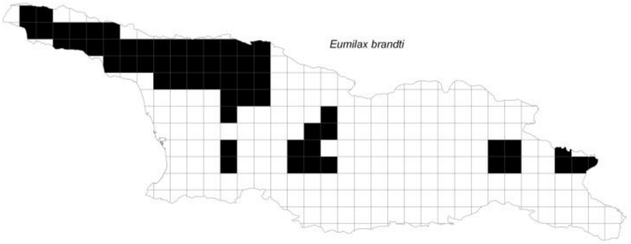
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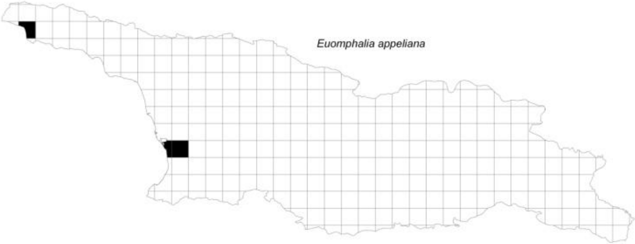

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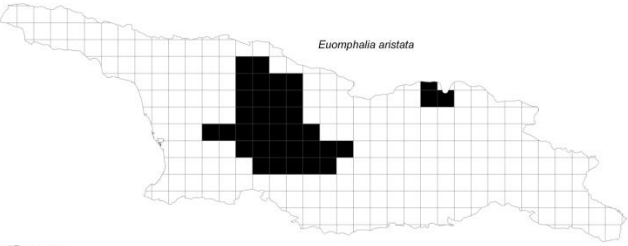

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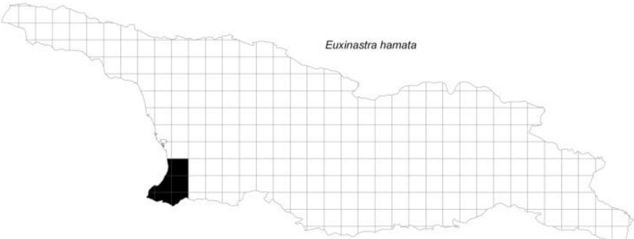
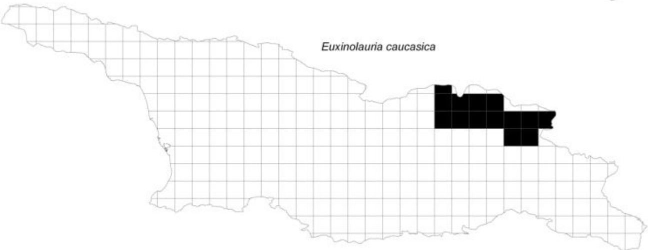
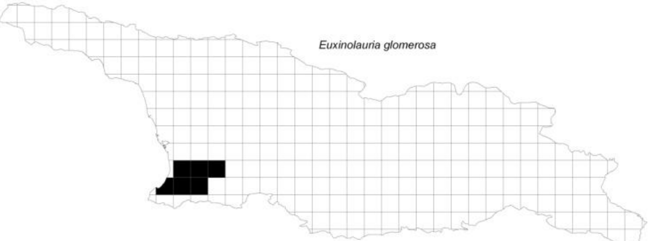


Euxinastra hamata



Euxinolauria caucasica



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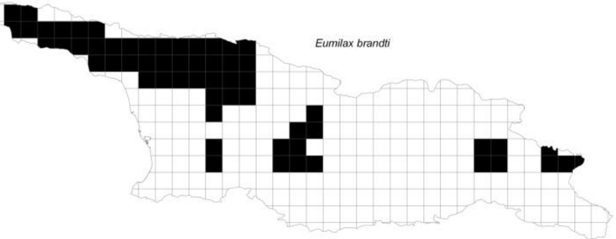

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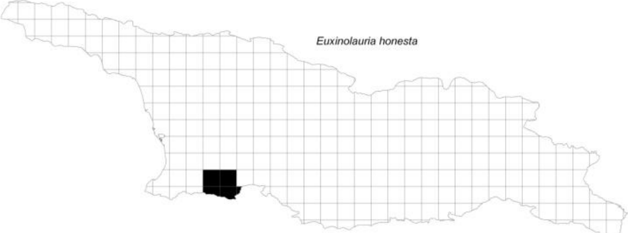

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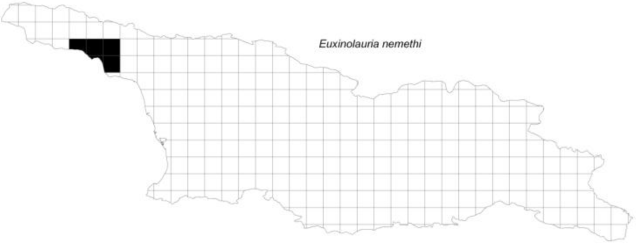

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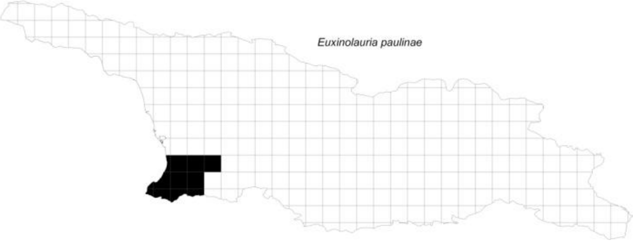

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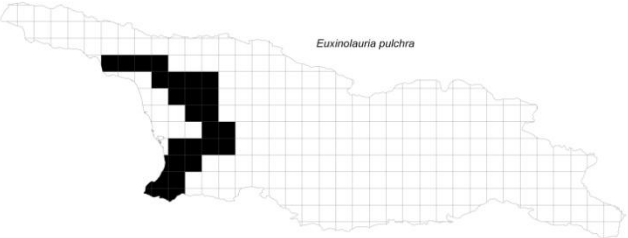
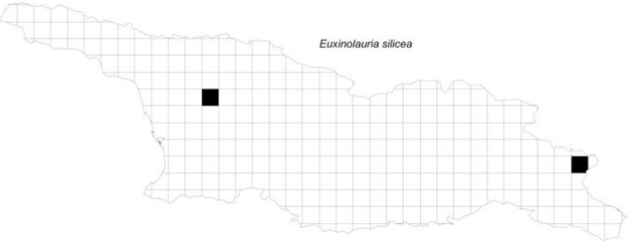


Euxinolauria pulchra

Euxinolauria rectidentata



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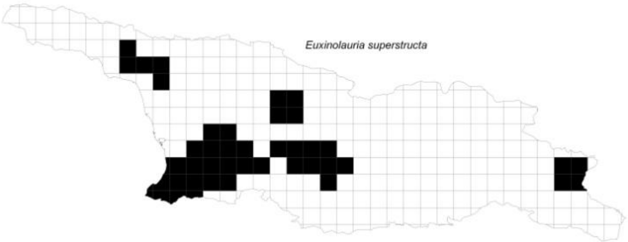
Euxinolauria sinangula



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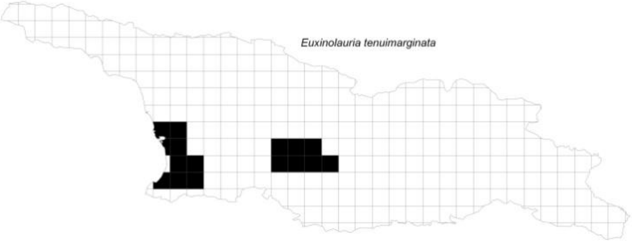

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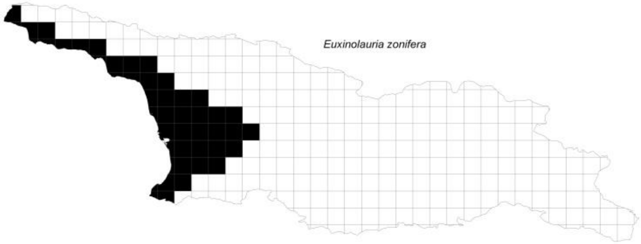

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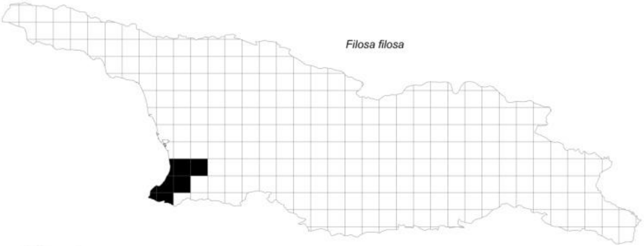
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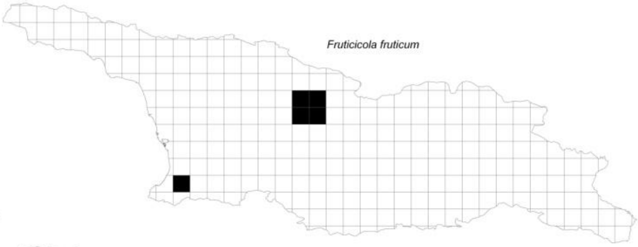
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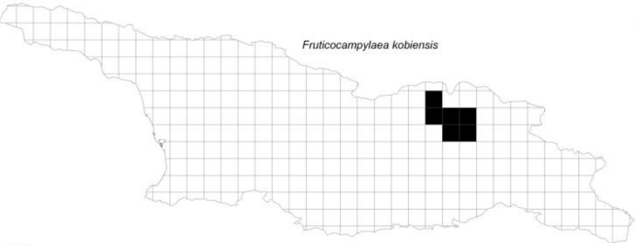
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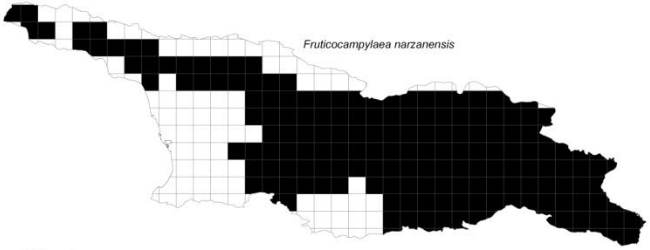
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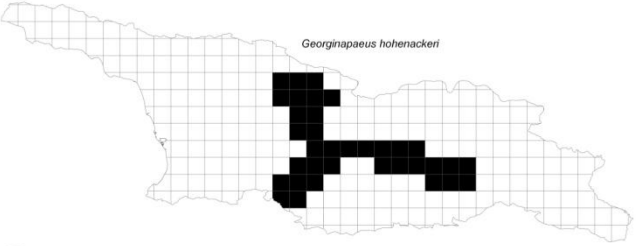
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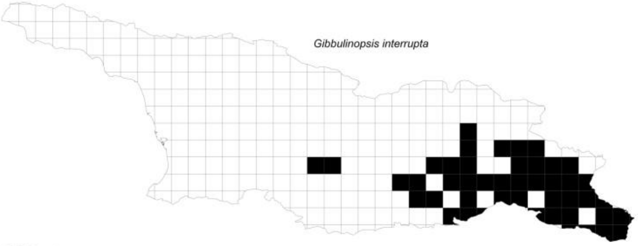
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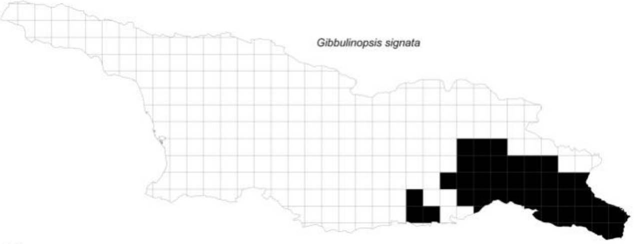
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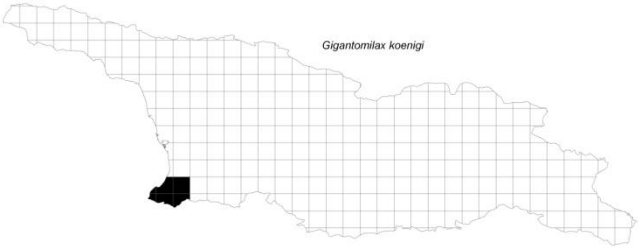
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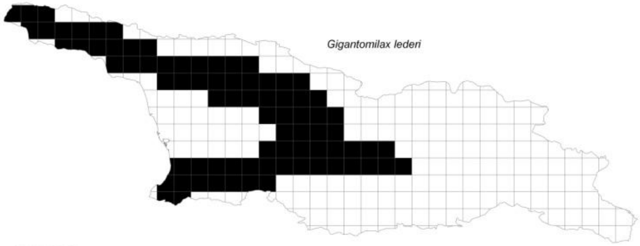
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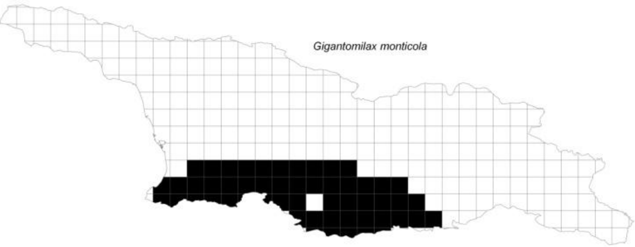
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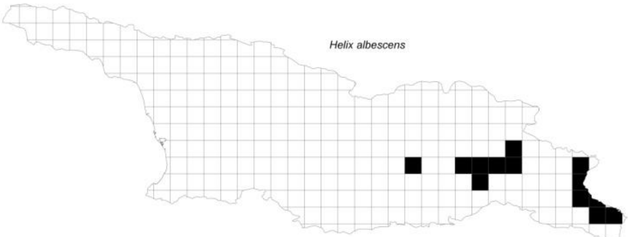
Helix goderdziana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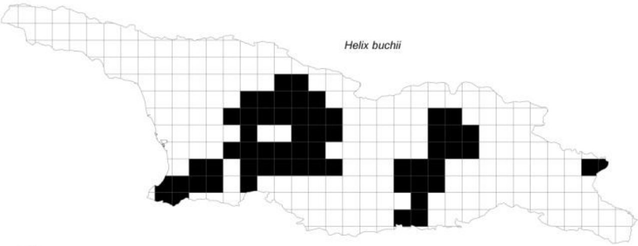
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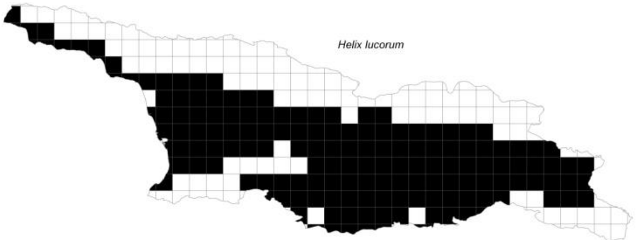
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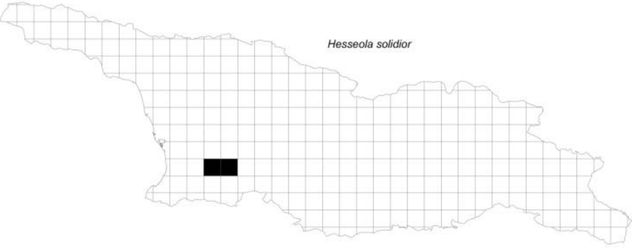
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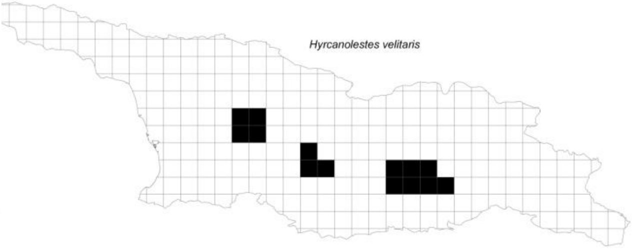
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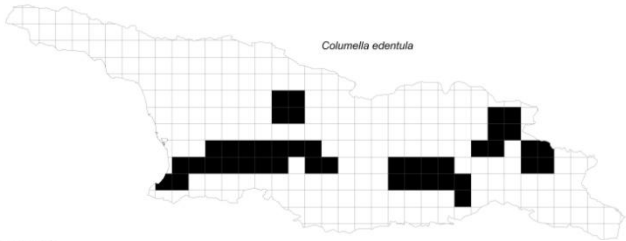
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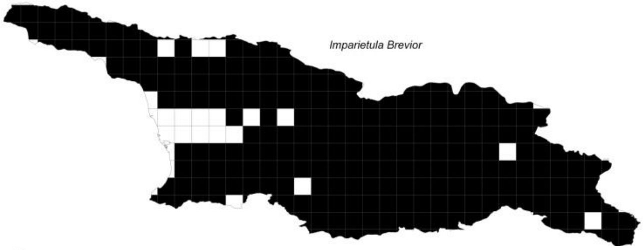
Conulopolita cavatica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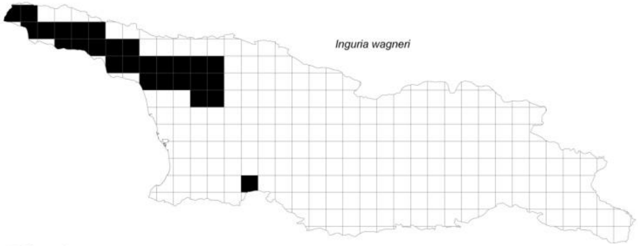
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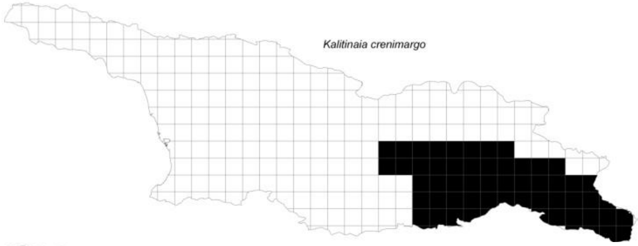
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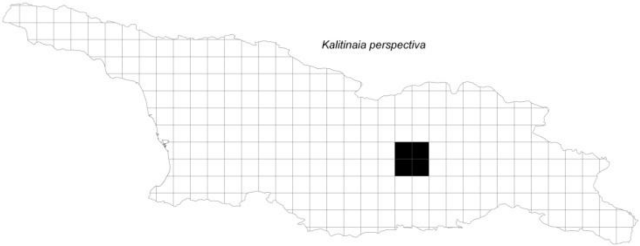
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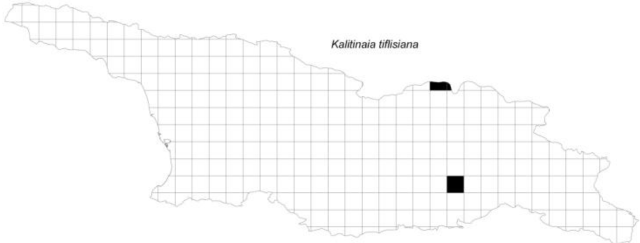
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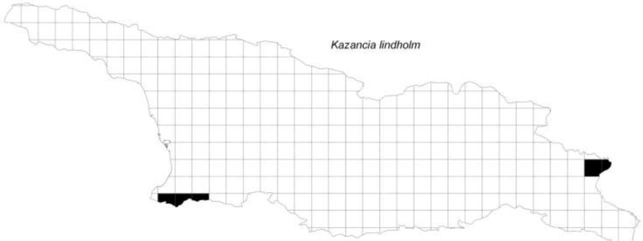
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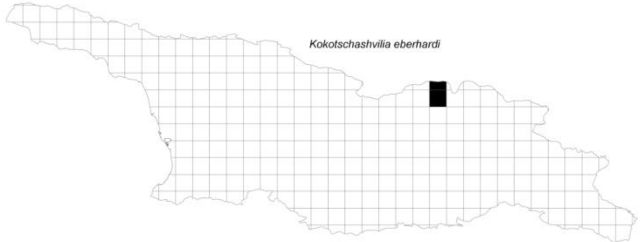
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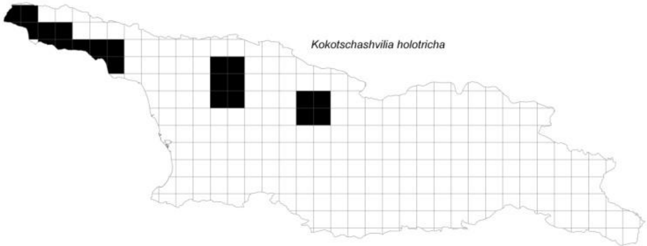
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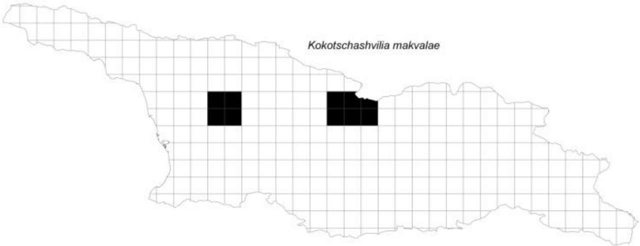
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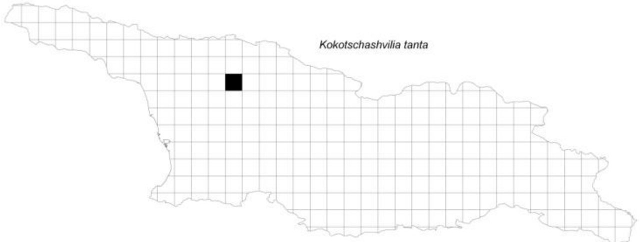
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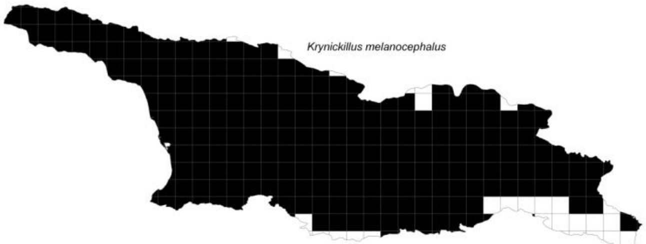
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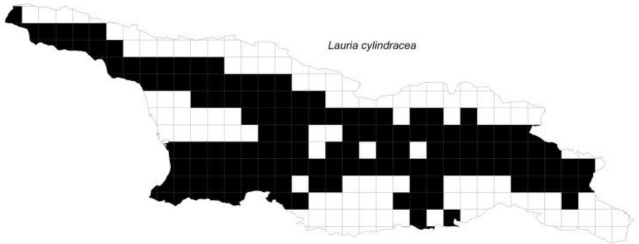
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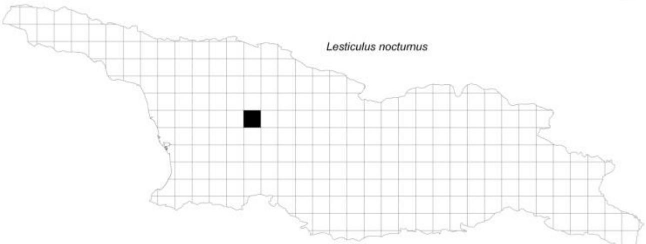
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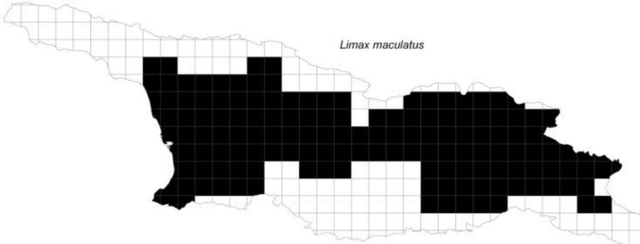
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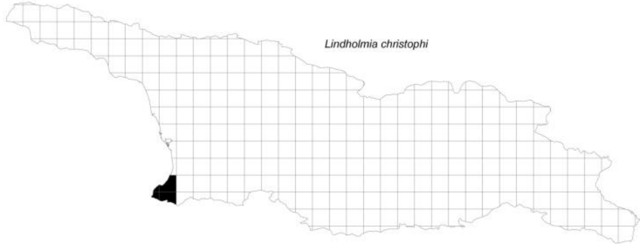
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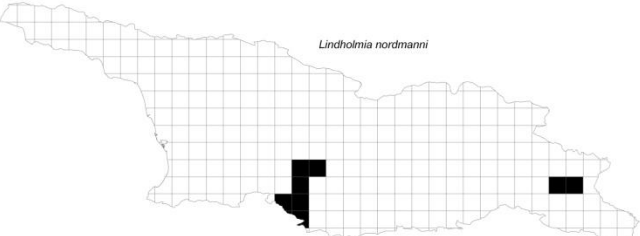
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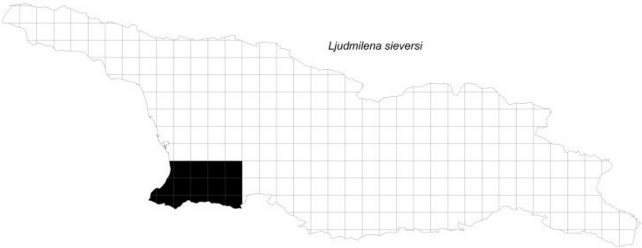
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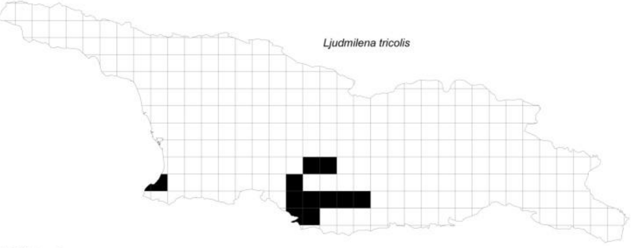
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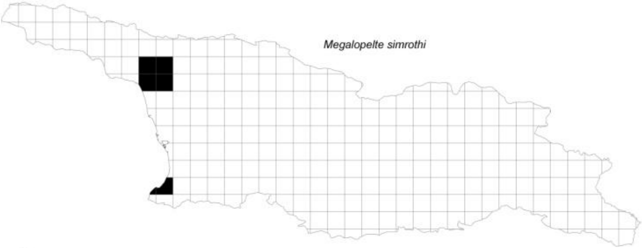
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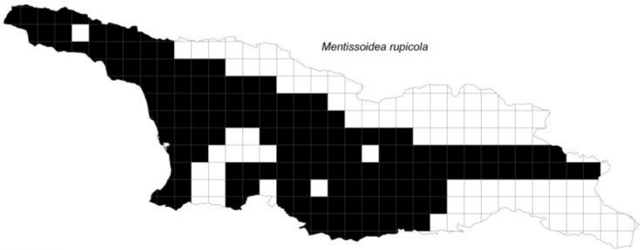
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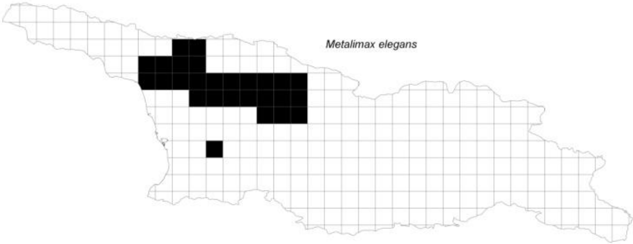
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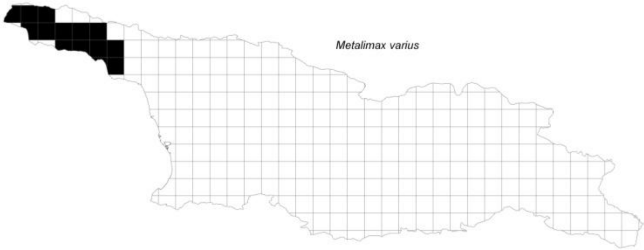
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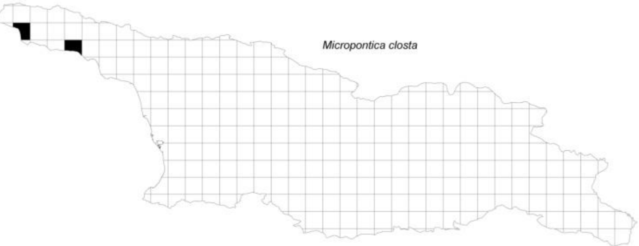
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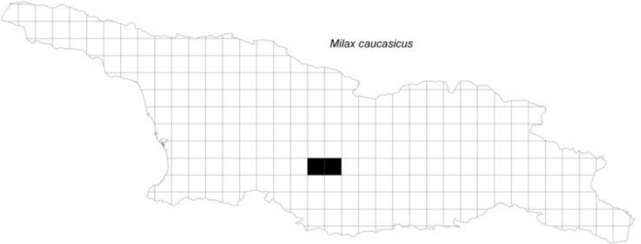
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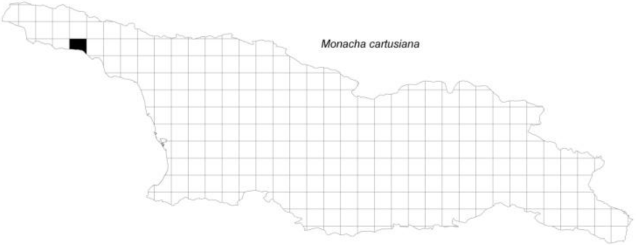
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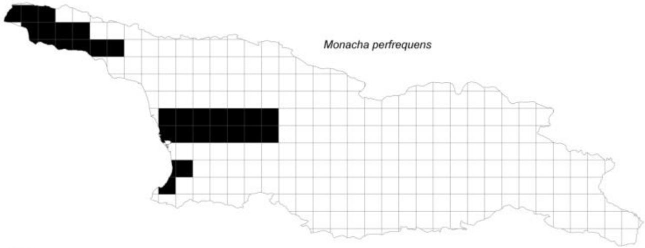
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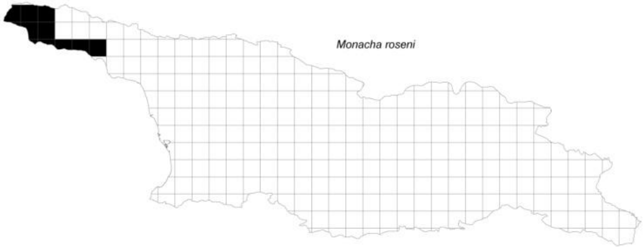
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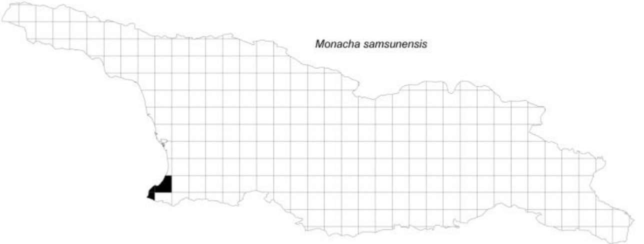
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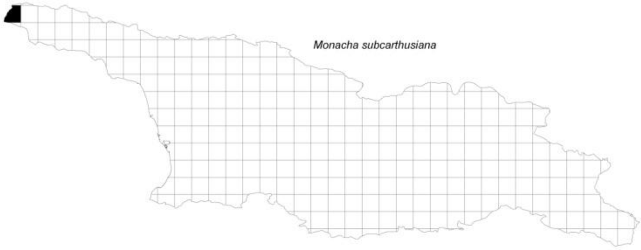
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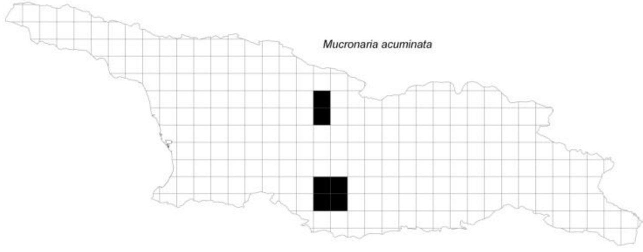
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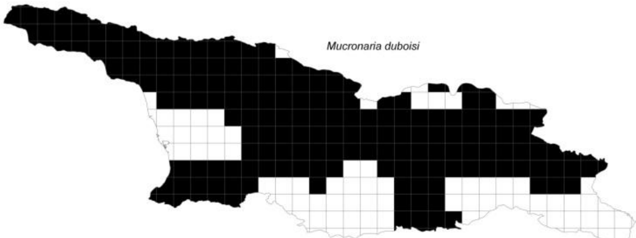

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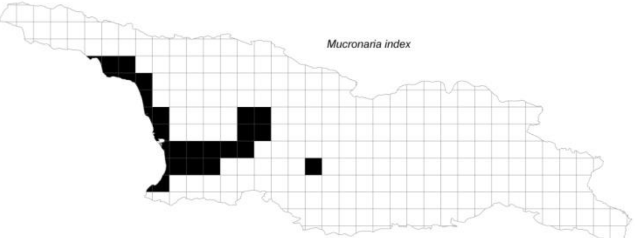
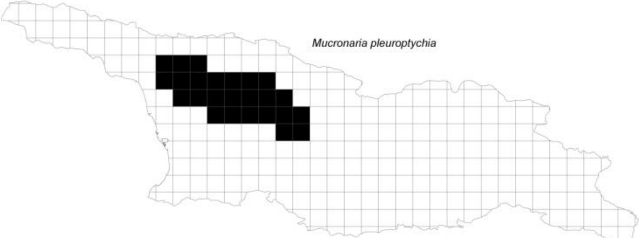


Mucronaria index



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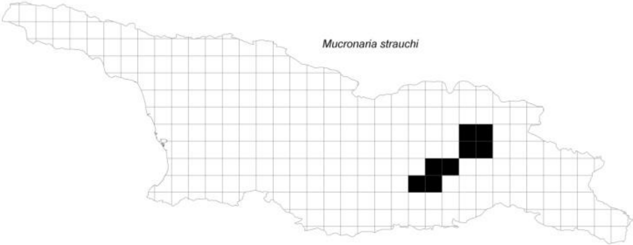

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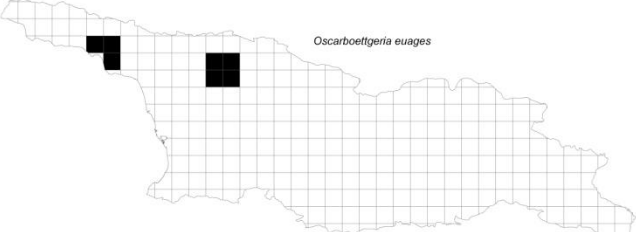

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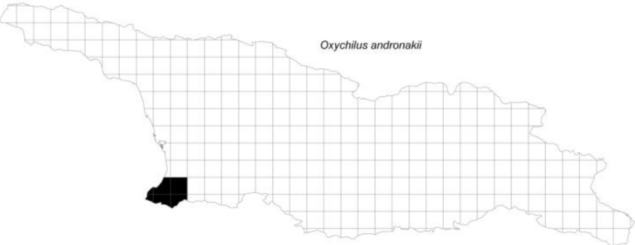

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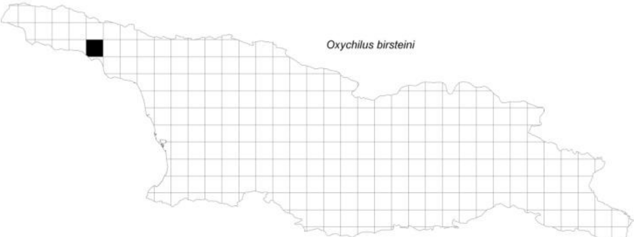

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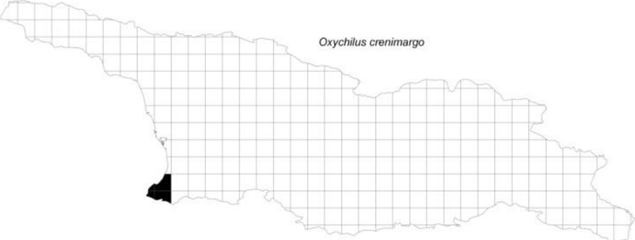

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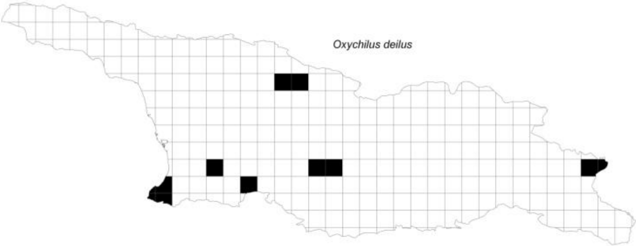

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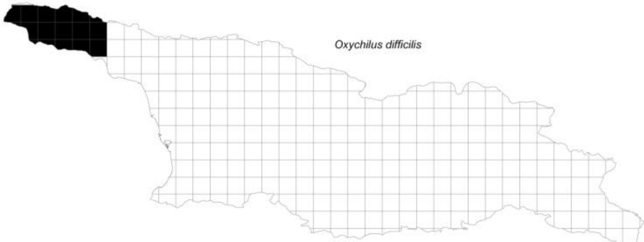

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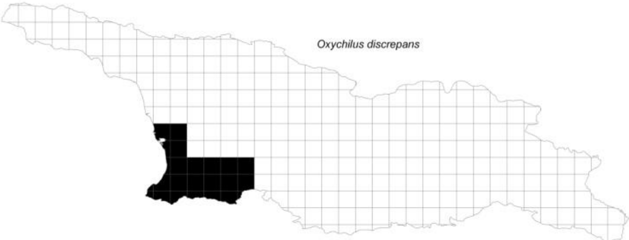

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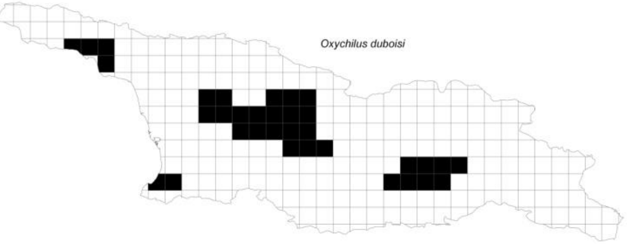

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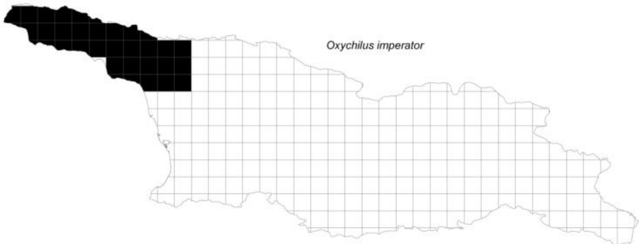

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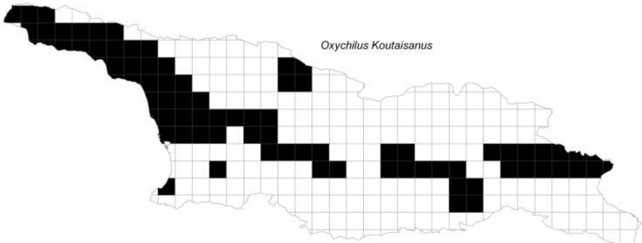

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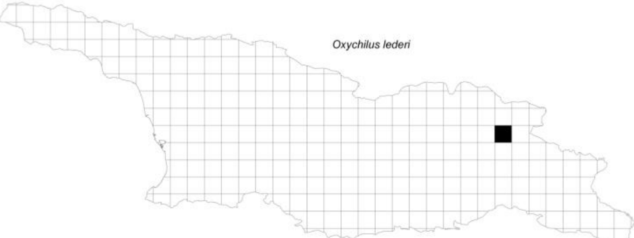

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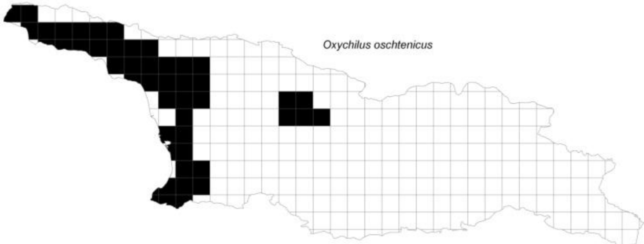

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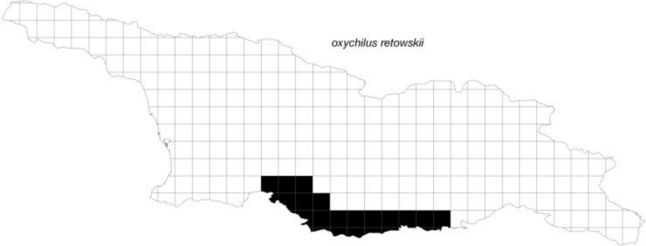
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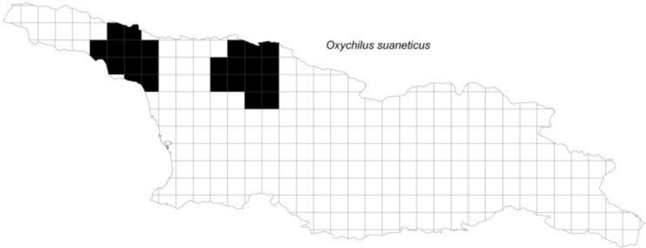
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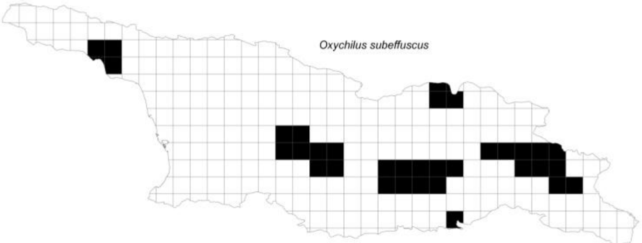
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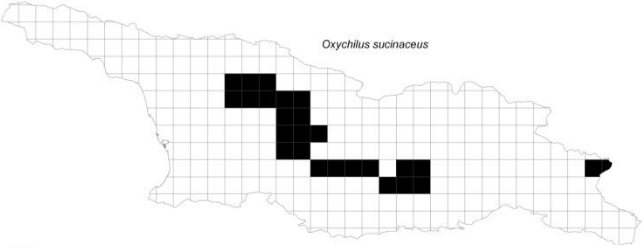
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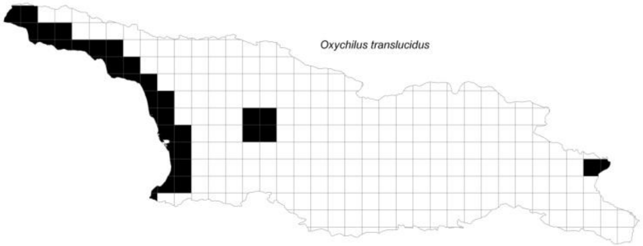
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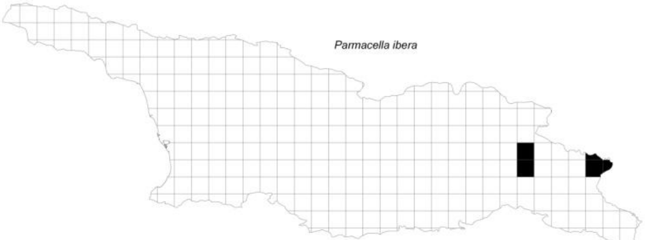
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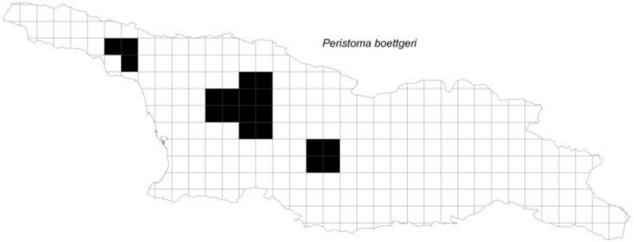
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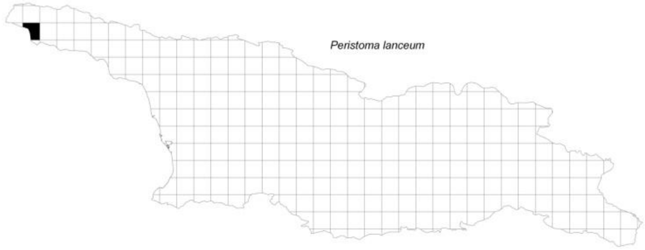
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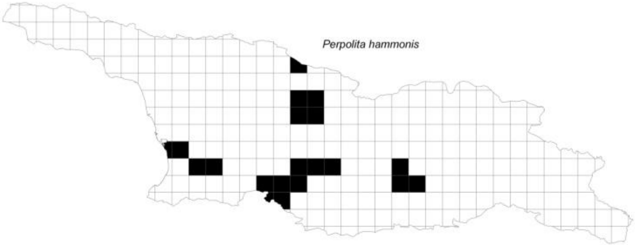
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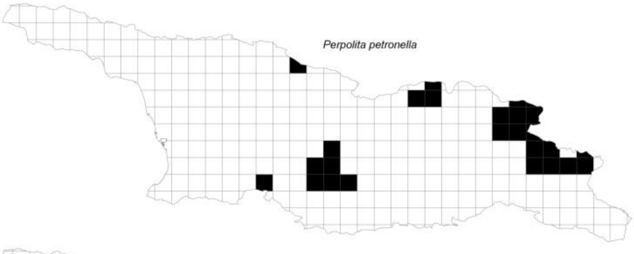
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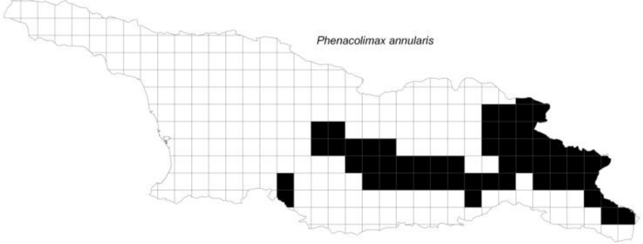
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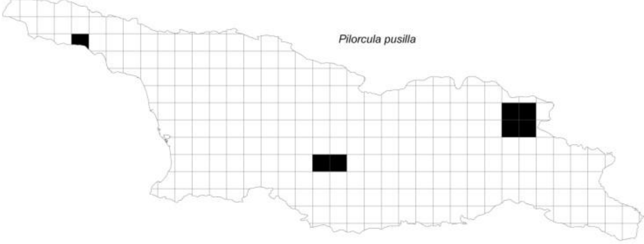
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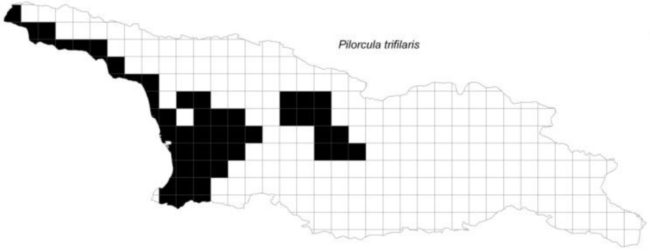
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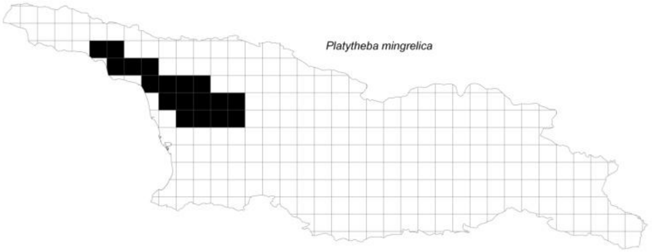
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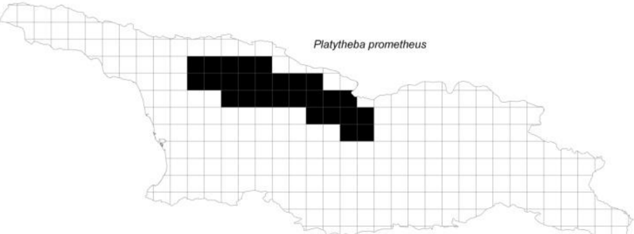
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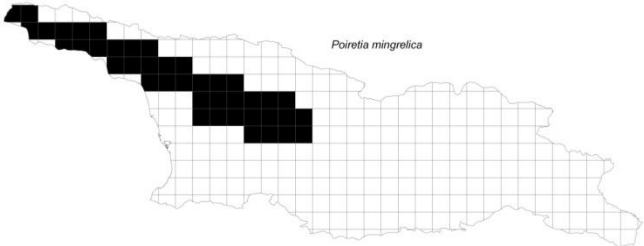
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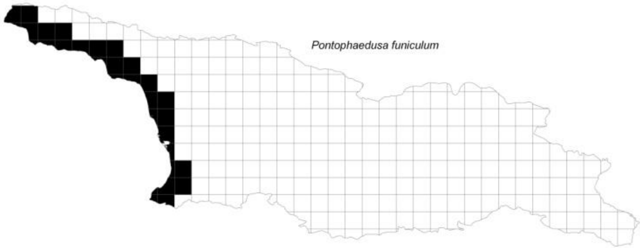
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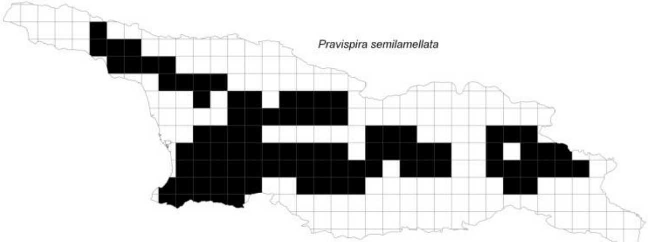
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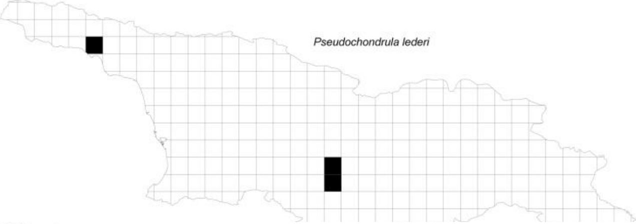
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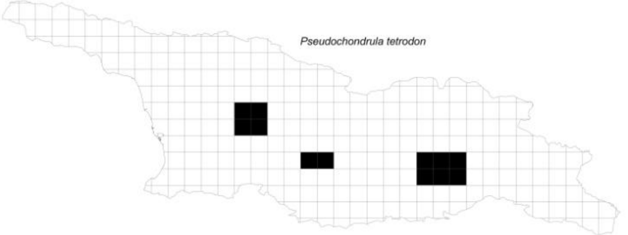
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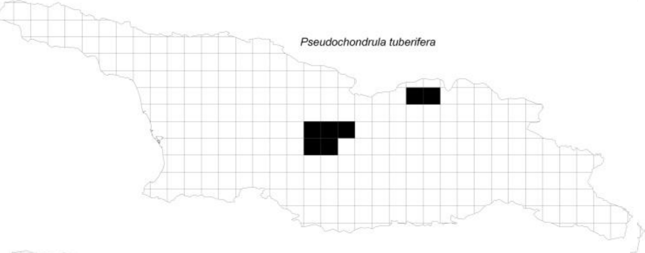
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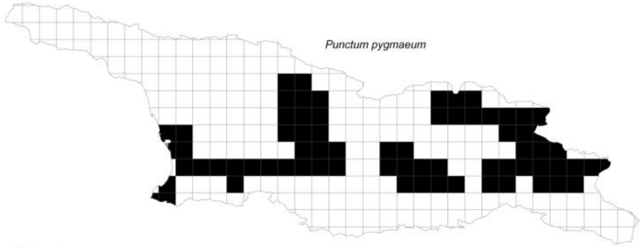
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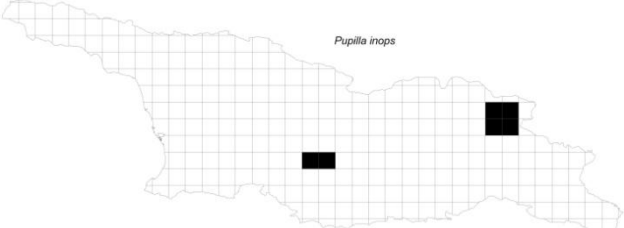
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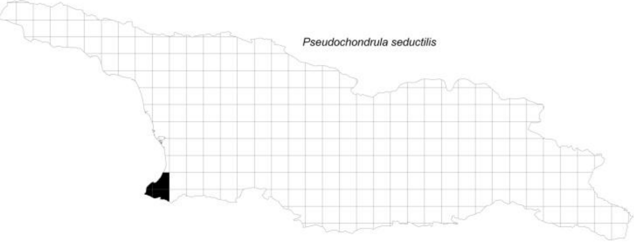
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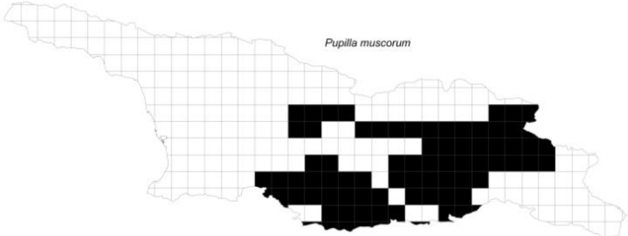
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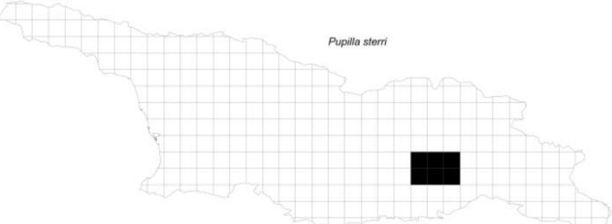
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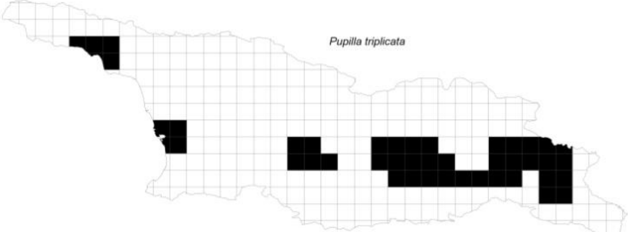
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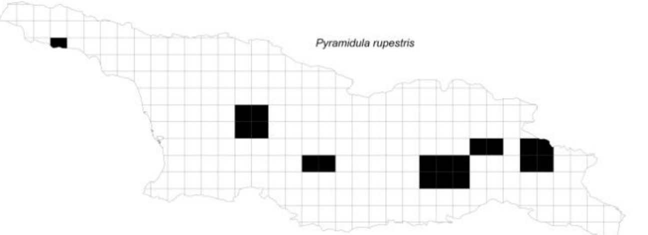
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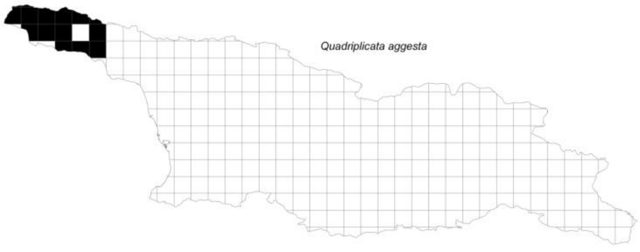
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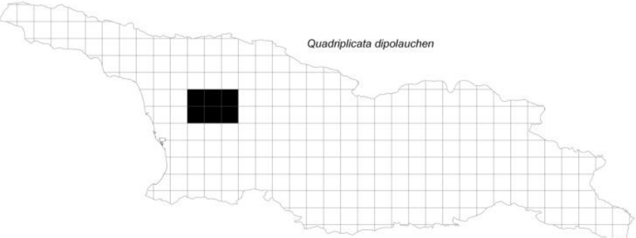
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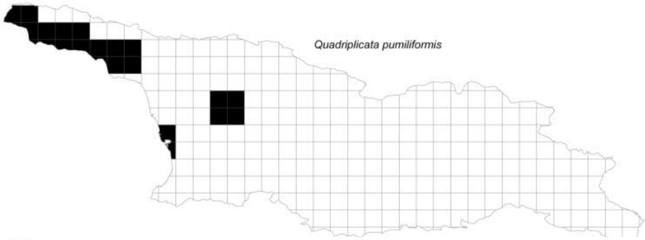
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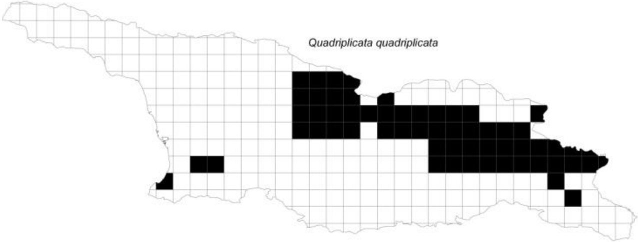
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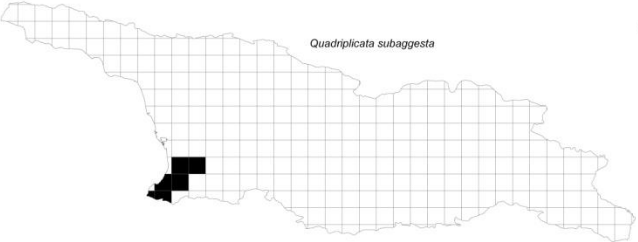
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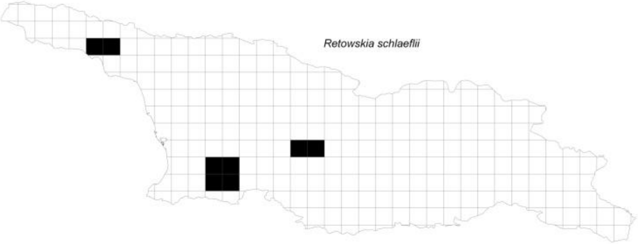
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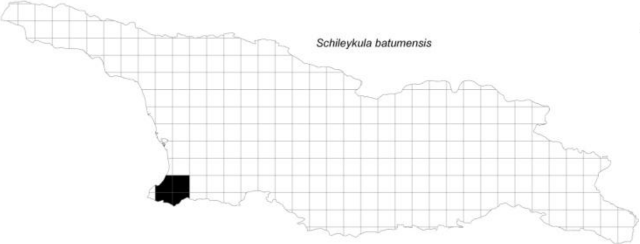
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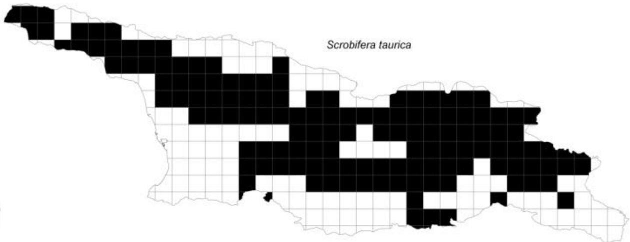
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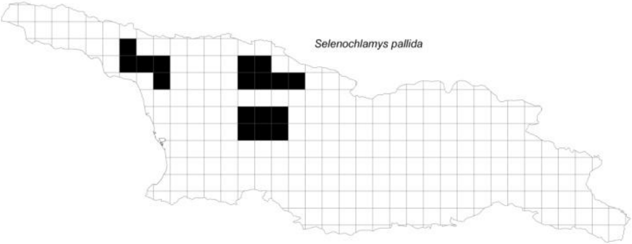
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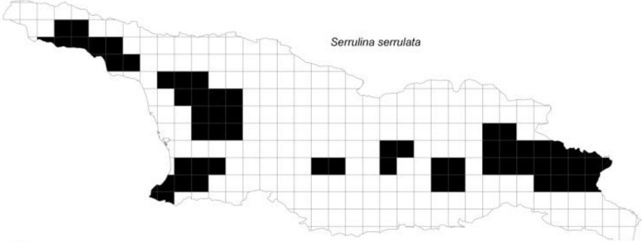
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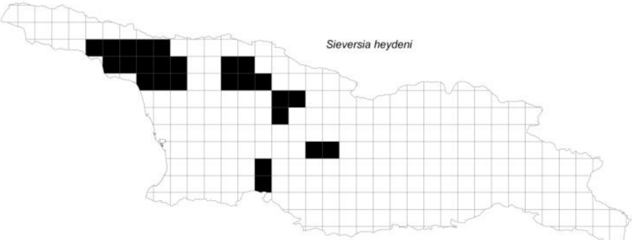
Serrulina sieversi


Shileykoia daghestana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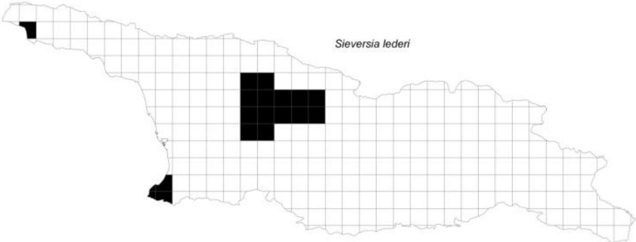
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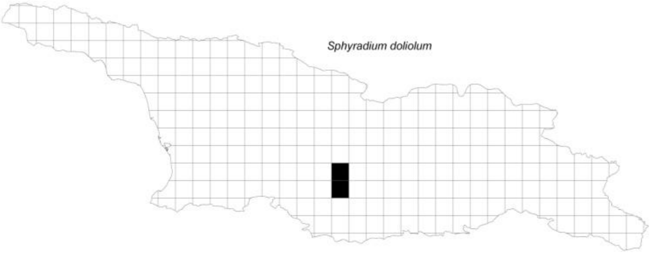
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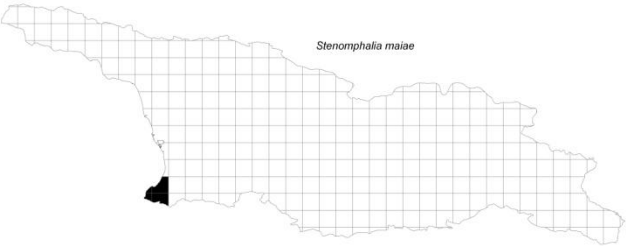
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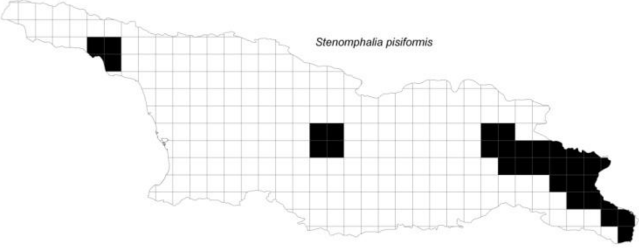
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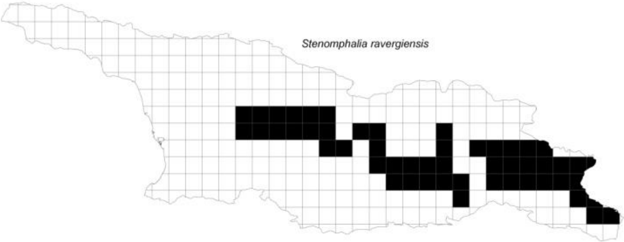
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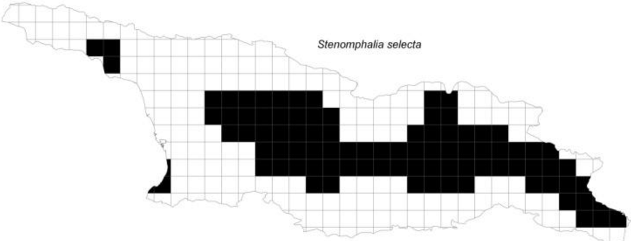
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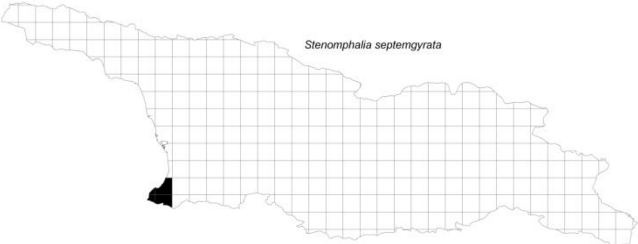
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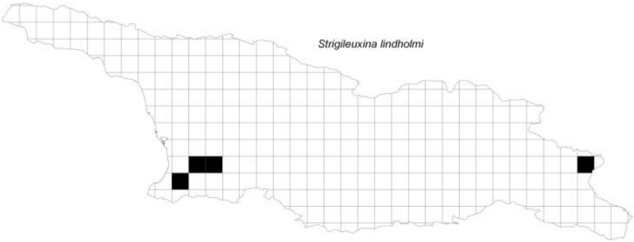
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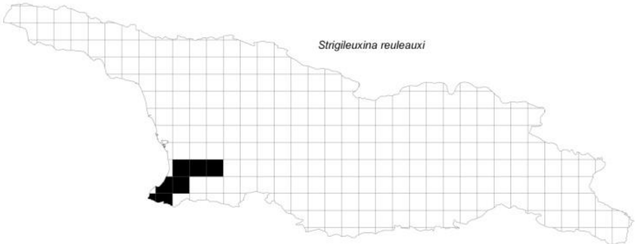
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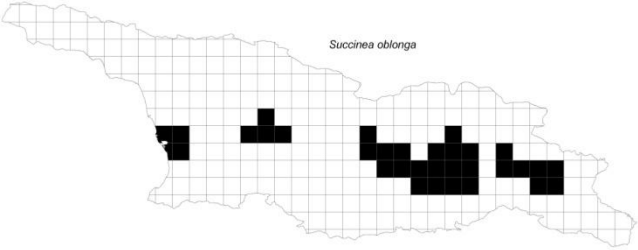
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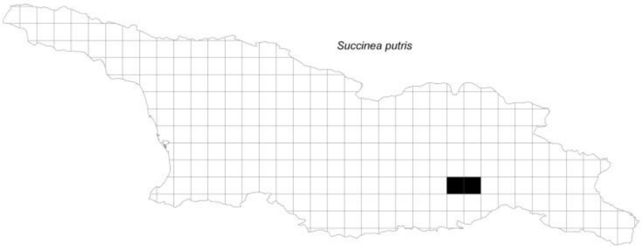
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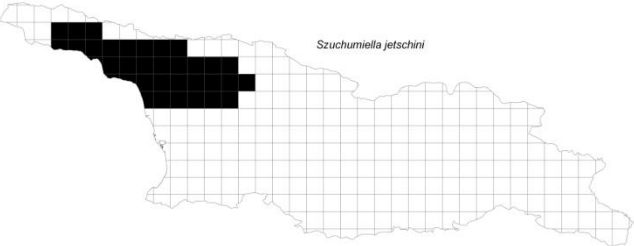
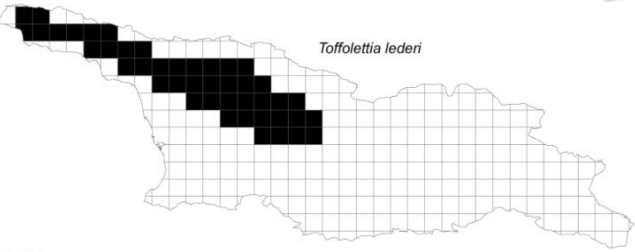

Szuchumiella jetschini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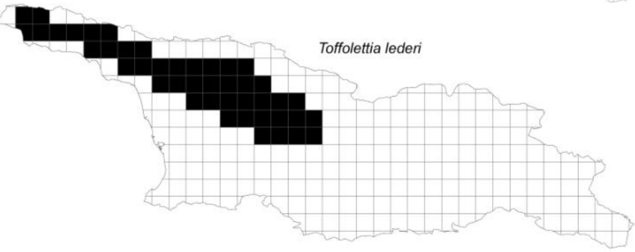
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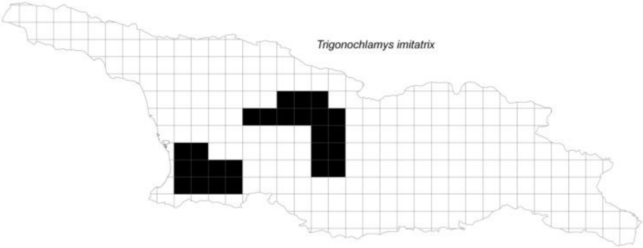
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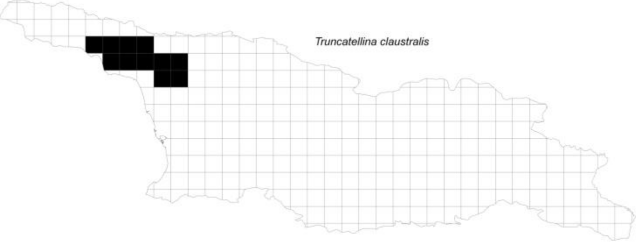
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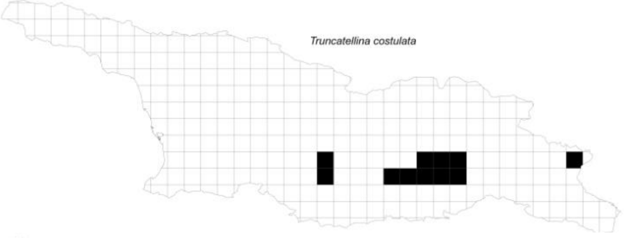
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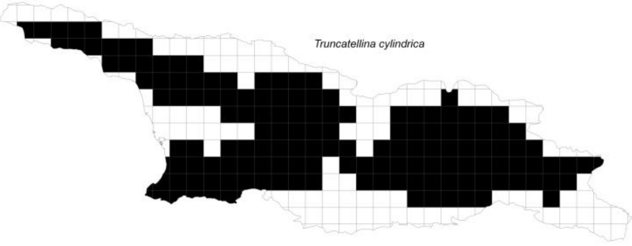
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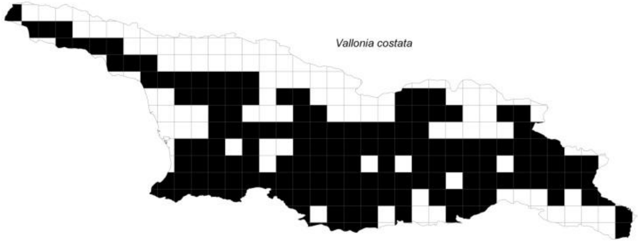
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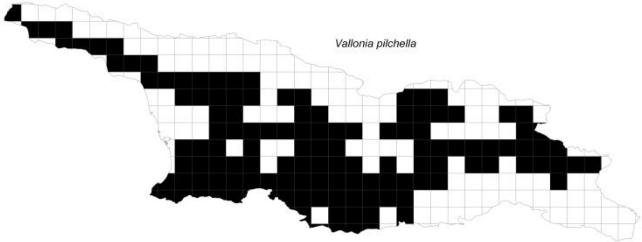
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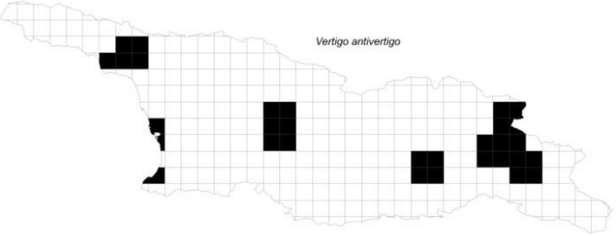
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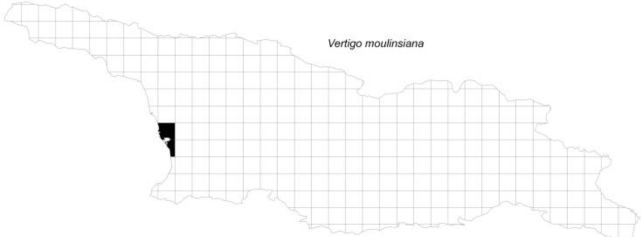
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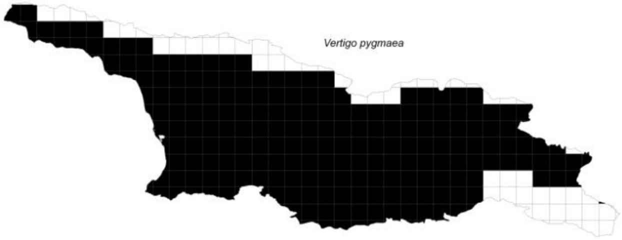
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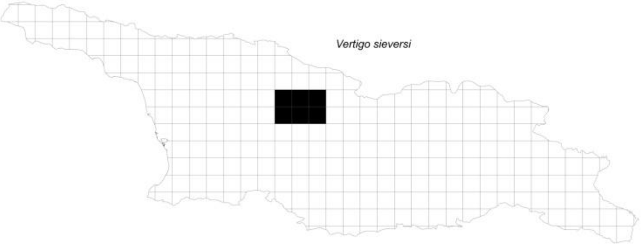
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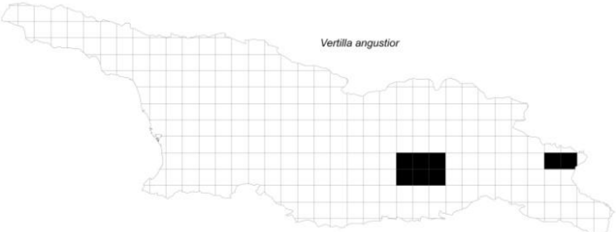
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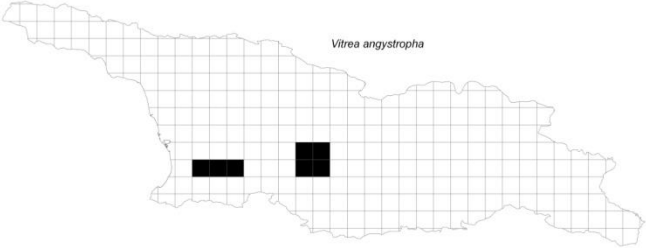
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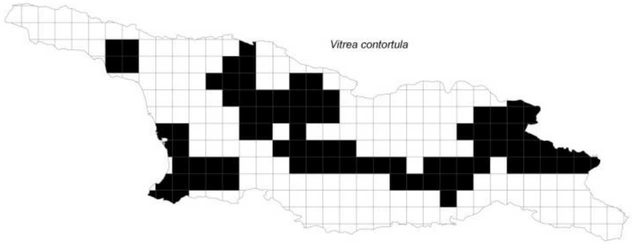
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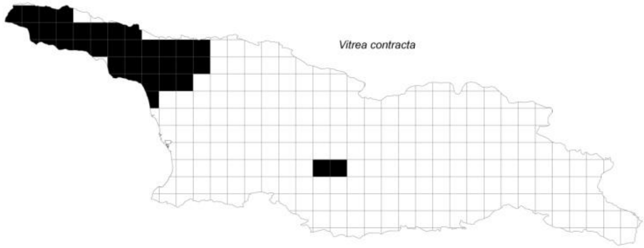
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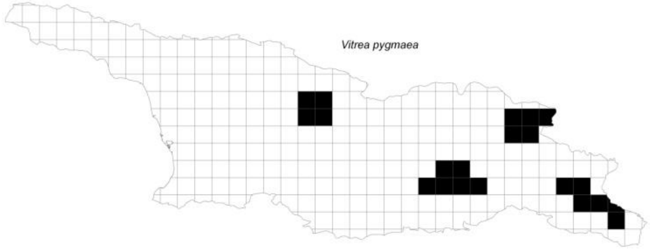
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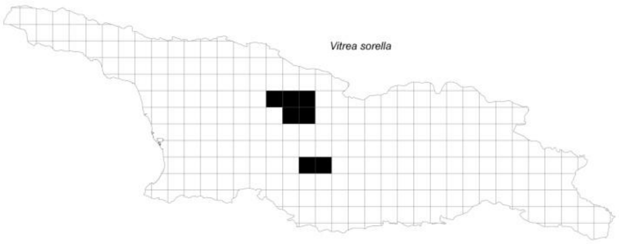
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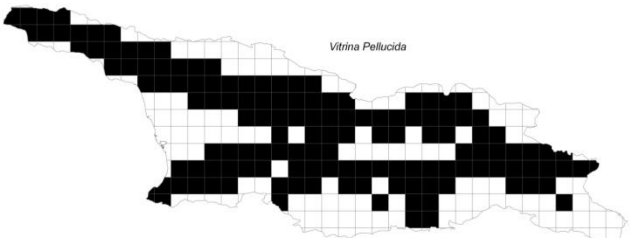
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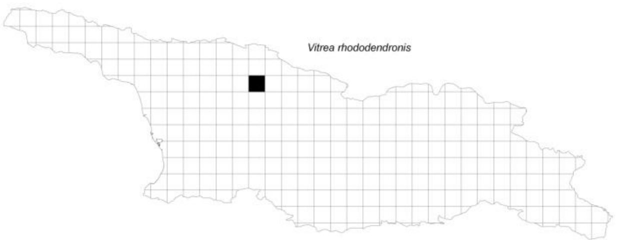
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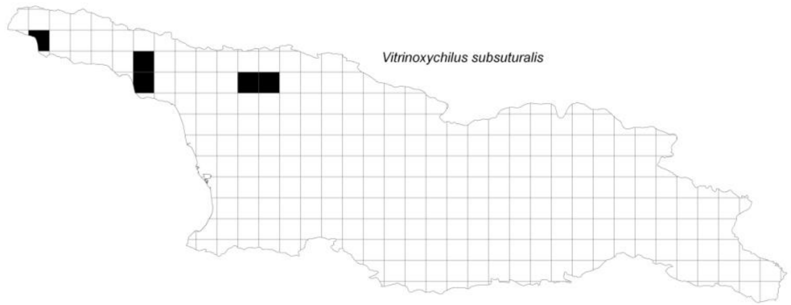

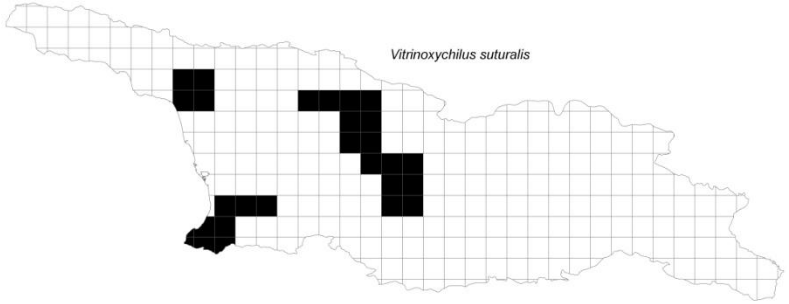

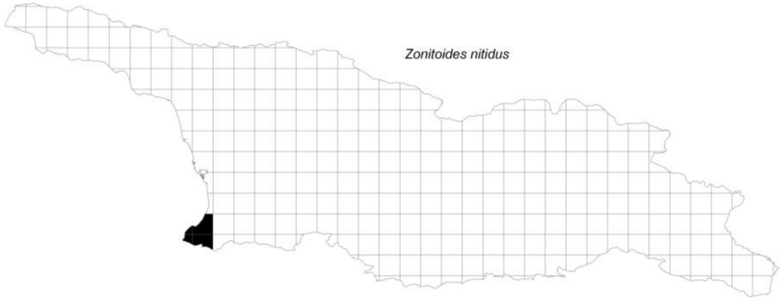

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