

Don't Diss Integration: A Comment on Ricklefs's Disintegrating Communities

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Introduction

Ricklefs (2008) proposes “disintegration” of the local-community concept. To truly understand species coexistence and diversity, we are told to restrict our focus to processes that occur spatially at regional scales and temporally at geological scales, primarily speciation and extinction. Furthermore, populations should be the exclusive subject of study. In his words, “I argue here that local coexistence can be understood only in terms of the distributions of species within entire regions, which are determined by diversification and adaptation within the regional ecological space in combination with the interactions of species over entire regions” (p. 742). While unraveling processes at large scales has obvious merit, studies at the scale of interacting individuals—the scale of communities—are vital for developing a mechanistic understanding of key processes regulating biodiversity or coexistence across a range of spatial and temporal scales.

Arguments against Community Ecology

Ricklefs makes two arguments concerning community ecology in his article that are not relevant to his proposal to “disintegrate” local communities. First, he argues that community ecology has been developing slowly and in isolation from other fields. However, community ecology is not isolated; interactions among species have been studied with modern techniques from a wide range of fields, including molecular genetics, physiology, geology, information theory, phylogenetics, and sociology, making community ecology highly synthetic. Nonetheless, criticism of the progress of community ecology as a discipline is not an argument for the nonexistence of communities, and on this basis it is not possible to logically conclude, as Ricklefs does, that “disintegrating ‘community’ might be justified” (p. 742).

Second, and in a similar vein, Ricklefs uses criticism of particular research topics in community ecology as an argument against the concept of communities per se. He cites Lawton's (1999, p. 183) concern that “the major weakness of traditional community ecology ... is its overwhelming emphasis on localness” (Ricklefs 2008, p. 742). Certainly, if we wish to identify general patterns or rules, studies across a broad range of scales are needed. This is why the message to regionalize and generalize is widely emphasized by community ecologists. Numerous reviews, meta-analyses, and multisite comparative studies, many by community ecologists, have provided important information about the generalities or changing nature of eco-

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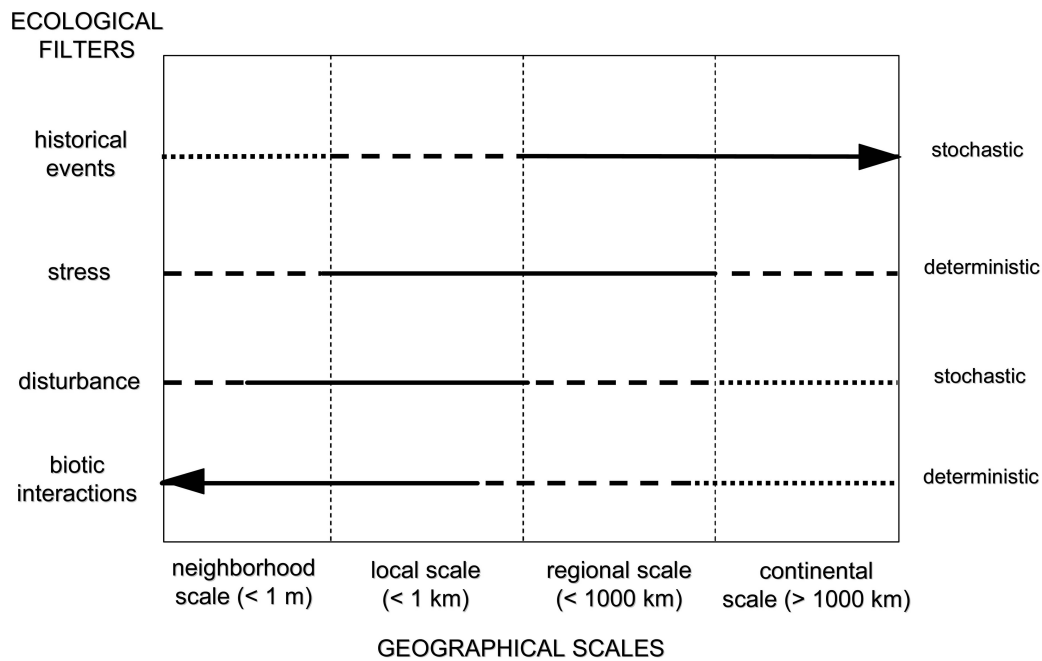


Figure 1: Diagrammatic representation of how key ecological filters regulating the composition of plant communities operate over a range of scales. For example, biotic interactions tend to regulate plant community composition at the neighborhood to local scale (*solid lines*) but become decreasingly influential at the regional scale (*dashed lines*) and continental scale (*dotted lines*). However, these general trends should not be taken as indicating that, for example, biotic interactions cannot influence community composition over large parts of a species' range or drive significant large-scale changes in that range. Taken from Michalet and Touzard (2010) and developed from Lortie et al. (2004).

logical processes across large-scale environmental gradients (e.g., Bertness and Ewanchuk 2002; Callaway et al. 2002; Maron et al. 2004; Bangert et al. 2008). The development of new paradigms, such as the metapopulation (Levins 1969; Hanski 1999), as discussed by Ricklefs, has helped to integrate local effects into a broader consideration of processes occurring in local communities. Community ecologists have been active in taking forward such developments, and hence the claim by Lawton (with which Ricklefs concurs)—that current community ecology is overwhelmingly local in its focus—is outmoded. Irrespective of its accuracy, however, the claim of excessive localness of focus by community ecologists is not a logical argument against the concept of communities per se.

A Straw Man for Local Communities

In addition to his criticism of community ecology, Ricklefs directly criticizes the local-community concept itself. First, a lack of neatness is something that, according to Ricklefs, counts against it. Ricklefs argues that communities do not fit readily into the environmental hierarchy of organism-population-community-ecosystem-biosphere in the way that “species fit into genera and genera make up families” (p. 742). However, the concepts of populations, ecosys-

tems, and even species have fuzzy borders and definitional problems. Should we also, as a consequence, abandon the species concept? This lack of neatness is not, therefore, a strong argument against the community concept, whereas including communities in the standard environmental hierarchy is heuristically useful in that it recognizes important processes that occur over a range of scales (fig. 1).

Although Ricklefs acknowledges that local-scale processes may influence assemblage structure, the arguments frequently seem ambiguous: he also argues that the community concept is a distraction, as studies of coexistence at the local scale cannot act as a basis for formulating general theories of species diversity. However, as we discuss below, local- (community-)scale processes, although tending to regulate diversity at the local scale (fig. 1), can have clear regional-scale effects.

Ricklefs's second main argument hinges on what he considers to be the constrictive nature of the community concept. For example, he states that “from the distribution of species along environmental or geographic gradients, the local community can be reduced to a single point shared by many species. Lacking spatial extent, this ‘point community’ ceases to be an entity” (p. 744). He proposes that community disintegration is “made necessary by the spatial extent of their component populations” (p. 742)

and that there is a need to replace these “artificial local-community boundaries with a time-space continuum of process and pattern in population and community ecology” (p. 744). This can be true only if we accept Ricklefs’s rather restricted depiction of communities. Most, if not all, ecologists would argue that communities are not unchanging lists of species present at all points in what might be called a community’s range; rather they are assemblages of species that are relatively consistent across significant (ecologically meaningful) areas of space and periods of time (Callaway 1997). Communities may be defined by the species that are consistently excluded from them, as well as those that are consistently included (Paine 1966; Connell 1972, 1975; Grime 1973). In summary, communities are where organisms interact, resulting in unique sets of selection pressures and placing species in different communities on particular evolutionary trajectories. Analyses at larger scales may actually mask these patterns within the geographic mosaic of coevolution (Thompson 2005).

Ricklefs also states that “ecologists, for the most part, continue to regard local communities as ecological units with individual integrity” (p. 741) and that “ecologists consistently define communities as units: generally, populations of different species living within a specified location in space and time” (p. 742). Again, such a definition of the community fails to accurately represent current understanding. The entire population of a species need not occur within a community for community-specific interactions and properties to arise and have regional-scale consequences (Turkington and Mehrhoff 1990; Callaway 1997; Whitham et al. 2003; Callaway and Ridenour 2004; Ehlers and Thompson 2004; Thompson 2005; Bangert et al. 2008; Grøndahl and Ehlers 2008). For example, the modeling studies of Gomulkiewicz et al. (2000) demonstrate the evolutionary effects of local hotspots of reciprocal fitness effects between interacting species, and their potential regional-scale consequences, despite the embedding of these hotspots within surrounding communities without this reciprocal fitness interaction. Community ecologists understand that population processes occurring outside of a local community have effects on local composition, function, and evolutionary dynamics: the interplay between evolution in spatially structured populations and ecological dynamics in spatially structured communities (i.e., metacommunities) has been argued by Urban et al. (2008). This approach emphasizes the role of spatial variation and coupling (through both gene flow within species and dispersal among local communities), which together determine the potential for local adaptation and species sorting, and the spatial and temporal patterns of interspecific interactions (and hence local selection of species). In contrast, Ricklefs uses relatively old work to support his depiction of communities as constraining entities and hence

his call for disintegration. Whittaker (1967) is cited to support the “open-community concept” of Gleason (1926), but a later study by Shmida and Whittaker (1981) that demonstrated nodes of species clustering across large scales (chaparral and desert) is not discussed. In the latter, species-specific, local, interdependent interactions appear to be determining the composition of plant communities, that is, species coexistence, and many studies have demonstrated similar processes (Callaway 2007). To give just a handful of examples from this extensive literature, Cavieres et al. (2002, 2005) demonstrate how direct, facilitative interactions increase species richness in Andean cushion plant communities, while the work of both Levine (1999) and Callaway and Pennings (2000) demonstrates the important role of both direct and indirect positive and negative interactions in regulating plant community composition. Furthermore, the recent work of Rajaniemi et al. (2006) on the relative roles of various filtering processes (dispersal, local climatic conditions, species interactions) in determining the composition of nested species pools supports the proposition that interaction processes have a greater influence on community composition (specifically, species richness) at smaller, as opposed to larger, spatial scales (although, as mentioned above, they can in some instances scale up to have regional-level effects).

The common denominator here is Ricklefs’s omission of important recent developments in community ecology that have moved us beyond useful but inevitably oversimplistic starting points and have broken down the barriers between ecological disciplines to provide a genuinely productive synthesis. We propose that a better representation of our current understanding of the community is given, for example, by the integrated-community (IC) concept of Lortie et al. (2004). Those authors argue that “real communities are likely never functioning fully as either groups of individual species (present only due to individual tolerances) or as assemblages of perfectly integrated species (facilitating one another or directly interacting)” (p. 435). The IC concept is only one example of a general trend in community ecology toward a much more integrative understanding of community-structuring processes that explicitly acknowledges the importance of processes at a range of scales for the delimitation, structuring, and functioning of communities. Community ecologists are capable, with the help of such concepts, of approaching the processes that regulate communities through a consideration of multiple scales simultaneously. Thus, it is incorrect to state, as Ricklefs does, that the “occurrence of species elsewhere within a region is of no consequence” (Ricklefs 2008, p. 744), and it is irrelevant to point out that “a local community cannot be inclusive of the populations of its component species” (p. 742).

The Role of Local-Scale Processes in Regulating Large-Scale Patterns

The heart of Ricklefs's specific proposal for disintegrating the community concept appears to be that studying local-scale processes does not help us to understand the regulation of species assemblages or diversity on anything other than a very restricted spatial or temporal scale: only by moving away from such work (which at the same time, he argues, necessitates abandoning the local community concept) can we understand the processes that regulate large-scale patterns of diversity and coexistence. But would disintegrating the concept of the community and focusing on understanding processes operating only at the scale of the biogeographic region really be an important step forward for understanding biodiversity and species coexistence? We do not think so. We have already described a number of studies that illustrate that local-scale processes can regulate diversity and coexistence across a range of scales. We now wish to explore in more detail some examples of the role of local-scale processes in regulating both local and regional species diversity and coexistence.

Ricklefs focuses particularly on the relationships between local and regional diversity, arguing that if they are strongly correlated, then local-scale processes have relatively little regulatory role. Importantly, some studies specifically demonstrate how biotic interactions can disrupt correlation between regional and local diversity. For example, McLaughlin and Bowers (2006) found no evidence of a species pool effect on richness at the community scale in southeastern Arizona grasslands. In comparison to other grassland types in North America, these mixed-grass prairies are landscapes with high species richness, providing a large pool of potential colonizing species at the community scale. Yet alpha diversity was low and beta diversity was high within these landscapes, despite a relative lack of habitat diversity, most probably because of negative plant-plant interactions resulting in species exclusion. Bossuyt et al. (2005) obtained very similar results for another type of vegetation: dune slack plant communities. Here, a populous regional species pool of more than 80 species was associated with local species densities of 10 species m^{-2} or less; again, local richness was more heavily regulated by competitive exclusion. Given such evidence, it is not surprising that a study conducted in two regions of Europe (Siena, Italy, and Bremen, Germany; Chiarucci et al. 2006) found poor correlation between regional species pool size and local species richness.

Further evidence that local-scale processes might generate a mismatch between regional- and local-scale diversity comes from studies of the difference in species diversity and composition between European alpine plant communities from calcareous and siliceous rocks. Con-

sistent with Ricklefs's stance, high species richness of plant communities from calcareous mountains has been attributed to the influence of regional species pools. Grime (1979) argued that European calcareous areas are more widespread in southern latitudes and that acidic (siliceous) northern areas—under higher abiotic constraint—might have relatively depauperate species pools after Quaternary species migrations. However, the lower species richness of subalpine communities on mesic siliceous soils of the French Alps is demonstrably the result of competitive exclusion of stress-tolerant “calcareous species” by competitive “siliceous species” (Choler et al. 2001; Michalet et al. 2002). Conversely, the more stressful environment on dry calcareous outcrops reduces competition and enables the occurrence of a high number of stress-tolerant species (Grime 1973). Furthermore, it has been argued by Michalet et al. (2006) and shown by Liancourt et al. (2005) that facilitation of stress-intolerant species by stress-tolerants further contributes to the species richness of communities on calcareous substrates. These drivers of local species richness may in turn influence large-scale species richness patterns, depending on the regional occurrence of rock types.

Clearly, abandoning the study of interactions at the community level would significantly limit our ability to explain species coexistence and biodiversity in many environments. Furthermore, it is only by working at these scales that we are starting to understand, as discussed above, the intricacy of indirect interactions and their effects on coexistence (e.g., Levine 1999; Callaway and Pennings 2000; Pugnaire and Lázaro 2000; Pagès and Michalet 2006), including the genetic basis of these interactions across a diverse community of organisms from microbes to vertebrates (e.g., Bailey et al. 2006; Crutsinger et al. 2006; Shuster et al. 2006; Whitham et al. 2006; Schweitzer et al. 2008). Scaling this knowledge up only adds to our understanding (Bangert et al. 2008).

To further illustrate these points, we describe below some specific examples that clearly demonstrate how a proper understanding of large-scale diversity patterns can develop only by consideration of processes occurring at the small-to-local—that is, the community—spatial and temporal scale.

Evolution and Species Pools

Ricklefs describes the way in which large-scale evolutionary and extinction processes can influence regional species pools, along with the types of species anomalies that these processes can create. However, there are two interesting problems with the presentation of these topics, both of which derive from the exclusivity of the role given to large-scale processes. First, regional species pool processes are

not the only ones that affect the distribution and abundance of species at any scale. Second, it is unlikely that these species pools emerged *ex nihilo* and that contemporary evolution is “waiting” for continental drift to occur before affecting changes in pool composition. It is much more likely that the spectacular melange of interactions uncovered by community ecologists during the past few decades currently shapes and alters these species pools, which in turn respond to long-term and regional-scale processes, much as they probably did 60 million years ago.

Evidence for the evolutionary importance of interactions identified from the study of local processes is common. For example, studies of local interactions between *Artemisia tridentata* and *Pinus ponderosa* shed light on competition as a process contributing to post-Pleistocene replacement of conifer forests in the Great Basin with desert shrubs (Callaway et al. 1996). Studies of local interactions among invasive and native species point to evolutionary trajectories occurring at regional scales, trajectories that could not be perceived without insight at the local scale (Callaway and Ridenour 2004). Recent studies also demonstrate that in different areas along environmental gradients, interactions among the species that constitute local communities can affect their evolutionary trajectories, that selection acts on genetic differences at the community level (Whitham et al. 2006), and that the genetic characteristics of a resource can affect community structure at both local and regional scales (Bangert and Whitham 2007). Similar broad conclusions by colleagues working specifically in the field of large-scale drivers of species richness are not discussed by Ricklefs. For example, Harrison and Cornell—cited by Ricklefs—state that “it is inescapably true that regions are made up of localities, and that local ecological processes and dispersal among localities must reciprocally contribute to regional patterns” (Harrison and Cornell 2008, p. 974).

Ricklefs criticizes community ecology for exclusivity, citing MacArthur’s (1965) 40-year-old argument that understanding large-scale historical and geographic processes is unnecessary because only local processes influence species coexistence. But recent work on the evolutionary effects of interactions demonstrates how community ecology has moved on from such early conclusions toward an ecological-historical (phylogeny-based) approach. For example, Valiente-Banuet et al. (2006) found that species that currently exist in Mediterranean climates around the world but evolved in the Quaternary facilitate species that evolved much earlier, in the climate of the Tertiary. It is likely that regeneration niches provided by the “Quaternary species”—their local-scale interactions—are the primary reason for the continued existence of many “Tertiary species” in the current regional species pool. In other words, facilitative ecological relationships among species

appear to have been particularly important in limiting the extinction of lineages during the shift from the mesic Tertiary period to the unusually dry Quaternary, when global deserts developed. Moreover, by building on the concepts of phylogenetic community ecology (Webb et al. 2002) and analyzing a large worldwide database, Valiente-Banuet and Verdú (2007) found that Tertiary species’ regeneration niches were strongly conserved across evolutionary history. Likewise, by using a phylogenetic supertree, they challenged the traditional community assembly rules (habitat filtering and competitive exclusion) by showing that facilitative relationships of recent lineages conserved the regeneration niches of older, distant lineages. In so doing, these relationships have increased the phylogenetic diversity of communities. These are excellent examples of how, in current community ecology, regional (historical) and local processes have been combined to provide complete “interdependent” perspectives as never before. Other examples of ecologists integrating regional- and local-scale spatial processes and geological-scale temporal processes include synthesis of phylogenies and contemporary evolution by exotic invaders (e.g., Maron et al. 2004), the linking of evolutionary phylogenies of insect speciation and specialization to hosts (e.g., Farrell and Mitter 1990; Farrell 1998), exploration of latitudinal gradients in plant-insect and plant-plant interactions (e.g., Bertness and Ewanchuk 2002; Siska et al. 2002), integration of geomorphology with long-term community development (e.g., McAuliffe 1994), biogeographic comparisons of plant-plant interactions (e.g., Reader et al. 1994; Callaway et al. 2002; Brooker et al. 2005; Kikvidze et al. 2005; Tirado and Pugnaire 2005), and biogeographic studies of invasions (e.g., Reinhart et al. 2003; Callaway et al. 2004). Furthermore, recent empirical studies show that the local patterns of genetics-based community structure can scale up to the regional level. In a study of cottonwood (*Populus* spp.) in western North America (Bangert et al. 2008), differences in composition of leaf-modifying arthropod communities were found to be similarly influenced by host tree genetics across scales from the individual tree to the region (720,000 km²). Recent meta-analyses have demonstrated the generality of these genetics-based approaches (Bailey et al. 2009). Jablonski (2008), in a far-reaching commentary on the links between biotic interactions and macroevolution, argues that “despite the enormous literature on biotic interactions in modern and ancient systems, biotic factors are poorly understood as macroevolutionary agents” (p. 716) and that this is in part a failure of integration across fields and scales. However, and in contrast to Ricklefs’s argument in favor of focusing only on large-scale processes, Jablonski (2008, p. 716) recommends that “an integrated approach will be more profitable

than the predominant thinking of either camp” sitting at the extremes of scales.

*The Response of Natural Systems to
Environmental Change*

Although Ricklefs’s call conflicts with many recent articles that demonstrate the benefits of cross-scale integration, he specifically mentions the review by Agrawal et al. (2007), which “emphasized the central role of species interactions on local scales in limiting coexistence” (Ricklefs 2008, p. 741). His concern with this review appears to be, in part, that it was “commissioned by the National Science Foundation to recommend research priority areas in population and community ecology” (p. 741). Importantly, though, Agrawal et al.’s review is not alone in coming to such conclusions. Tylianakis et al. (2008, p. 1351) conclude that “in order to reliably predict the effects of GEC [global environmental change] on community and ecosystem processes, the greatest single challenge will be to determine how biotic and abiotic context alters the direction and magnitude of GEC effects of biotic interactions,” or, to put it another way, the big challenge is to work out the role of local-scale processes in regulating large-scale responses.

The necessity of understanding this role in the context of GEC is demonstrated by a recent study of climate envelope modeling. This modeling technique has been a source of considerable debate because of its approach to the relative roles of large-scale versus local processes in regulating distributions and because of its neglect of biology and genetics in determining species’ responses to climate change (and ultimately determining diversity; Hampe 2004; Pearson and Dawson 2004; Guisan and Thuiller 2005; Brooker et al. 2007; O’Neill et al. 2008). Beale et al. (2008) assessed the ability of climate envelope models to predict the ranges of European bird species. They showed that, when an appropriate null model was applied, climate envelope models were significantly better than the null at modeling species distributions for only 32 out of the 100 species examined. However, they also found that these 32 species showed comparatively northerly distributions. Previous studies had suggested that climate is likely to have a stronger influence in extreme environments because of a reduced role of local-scale processes, specifically biotic interactions (Brown et al. 1996; Brooker 2006). Although land use change and habitat fragmentation are also likely to have influenced the distribution of the more southerly bird species examined (and hence to have reduced the strength of the link between large-scale drivers such as climate and species distributions), Beale et al. also noted, on the basis of the work of Suttle et al. (2007), that local-scale processes such as biotic interactions “can over-

whelm the direct impacts of climate” (Beale et al. 2008, p. 14910). Consequently, ignoring local-scale processes might give highly misleading predictions concerning species’ responses. Critically, this example demonstrates the potential inaccuracies that could occur if developments in ecology exclusively considered processes at the large environmental scales.

Conclusions

Perhaps what all of these examples emphasize is the need for a balanced approach to this issue. At root, our concern is about Ricklefs’s proposition that large-scale processes, as stated at the beginning of this comment, “can be understood *only* in terms of the distributions of species within entire regions” (p. 742, emphasis added). In response, we are not similarly proposing that our way is the only way or that there is one optimum and primary scale of study; instead, we accept that processes over a range of scales influence the composition of species pools and coexistence, as set out in up-to-date overviews of the subject such as the IC concept of Lortie et al. (2004), the recent review by Harrison and Cornell (2008), and figure 1. Mechanistically, a community is linked by the interactions among its members, many of which are genetically based (interspecific indirect genetic effects; Shuster et al. 2006) and encompassed within a community genetics framework (Whitham et al. 2006; Wade 2007). This, we believe, is an accurate reflection of our current understanding in community ecology. From this, we would propose that cross-scale studies, in which developing an understanding of local-scale processes is as strong an element as understanding regional- or global-scale processes, and which also consider the interdependence between regional and local scales, seem to be one of the most productive avenues for future research. We must also understand the genetics-based interactions among species in a community on which natural selection may act to produce different evolutionary trajectories in different environments (Thompson 2005; Whitham et al. 2006). It is not necessary, however, to disintegrate the community concept in order to achieve these goals; that can be argued for only on the basis of outmoded concepts.

Ricklefs (2008, p. 742) correctly states that “it has been eight decades since Gleason (1926) challenged Clements’s (1916) perception of the community as an integral unit in ecology.” However, it has long been accepted that the Clementsian position, in which the community is the expression of some general organizing principle, is unrealistic and idealistic holism (Atsatt and O’Dowd 1976; Callaway 1997, 2007; Lortie et al. 2004). But after decades of studying local community processes, we must also accept that strict Gleasonian individualistic perspectives are equally

unrealistic (Callaway 2007). The Clements-Gleason dichotomy has heuristic value, but it is essential that we move beyond it by exploring the new, emergent properties and processes that arise when species live together in an integrative manner—where the issue of the boundaries of communities is really secondary—especially at a time when integration among fields is essential for dealing with current environmental challenges.

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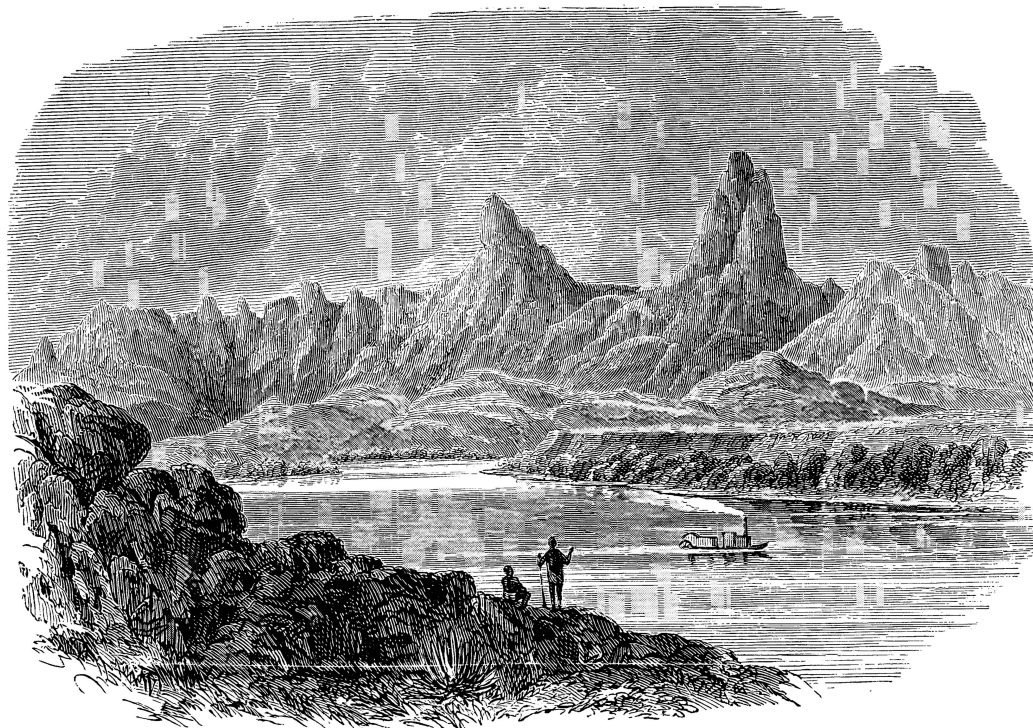
Literature Cited

- Agrawal, A. A., D. D. Ackerly, F. Adler, A. E. Arnold, C. Caceres, D. F. Doak, E. Post, et al. 2007. Filling key gaps in population and community ecology. *Frontiers in Ecology and the Environment* 5: 145–152.
- Atsatt, P. R., and D. O'Dowd. 1976. Plant defense guilds. *Science* 193:24–29.
- Bailey, J. K., S. C. Wooley, R. L. Lindroth, and T. G. Whitham. 2006. Importance of species interactions to community heritability: a genetic basis to trophic-level interactions. *Ecology Letters* 9:78–85.
- Bailey, J. K., J. A. Schweitzer, F. Úbeda, J. Koricheva, C. J. LeRoy, M. D. Madritch, B. J. Rehill, et al. 2009. From genes to ecosystems: a synthesis of the effects of plant genetic factors across levels of organization. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364:1607–1616.
- Bangert, R. K., and T. G. Whitham. 2007. Genetic assembly rules and community phenotypes. *Evolutionary Ecology* 21:549–560.
- Bangert, R. K., E. V. Lonsdorf, G. M. Wimp, S. M. Shuster, D. Fischer, J. A. Schweitzer, G. J. Allan, J. K. Bailey, and T. G. Whitham. 2008. Genetic structure of a foundation species: scaling community phenotypes from the individual to the region. *Heredity* 100:121–131.
- Beale, C. M., J. J. Lennon, and A. Gimona. 2008. Opening the climate envelope reveals no macroscale associations with climate in European birds. *Proceedings of the National Academy of Sciences of the USA* 105:14908–14912.
- Bertness, M. D., and P. J. Ewanchuk. 2002. Latitudinal and climate-driven variation in the strength and nature of biological interactions in New England salt marshes. *Oecologia (Berlin)* 132:392–401.
- Bossuyt, B., O. Honnay, and M. Hermy. 2005. Evidence for community assembly constraints during succession in dune slack plant communities. *Plant Ecology* 178:201–209.
- Brooker, R., Z. Kikvidze, F. I. Pugnaire, R. M. Callaway, P. Choler, C. J. Lortie, and R. Michalet. 2005. The importance of importance. *Oikos* 109:63–70.
- Brooker, R. W. 2006. Plant-plant interactions and environmental change. *New Phytologist* 171:271–284.
- Brooker, R. W., J. M. J. Travis, E. J. Clark, and C. Dytham. 2007. Modelling species' range shifts in a changing climate: the impacts of biotic interactions, dispersal distance and the rate of climate change. *Journal of Theoretical Biology* 245:59–65.
- Brown, J. H., G. C. Stevens, and D. M. Kaufmann. 1996. The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics* 27:597–623.
- Callaway, R. M. 1997. Positive interactions in plant communities and the individualistic-continuum concept. *Oecologia (Berlin)* 112: 143–149.
- . 2007. Positive interactions and interdependence in plant communities. Springer, Dordrecht.
- Callaway, R. M., and S. C. Pennings. 2000. Facilitation may buffer competitive effects: indirect and diffuse interactions among salt marsh plants. *American Naturalist* 156:416–424.
- Callaway, R. M., and W. M. Ridenour. 2004. Novel weapons: a biochemically based hypothesis for invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment* 2:436–443.
- Callaway, R. M., E. H. DeLucia, D. Moore, R. Nowack, and W. D. Schlesinger. 1996. Competition and facilitation: contrasting effects of *Artemisia tridentata* on *Pinus ponderosa* versus *P. monophylla*. *Ecology* 77:2130–2141.
- Callaway, R. M., R. W. Brooker, P. Choler, Z. Kikvidze, C. J. Lortie, R. Michalet, L. Paolini, et al. 2002. Positive interactions among alpine plants increase with stress. *Nature* 417:844–848.
- Callaway, R. M., G. C. Thelen, A. Rodriguez, and W. E. Holben. 2004. Soil biota and exotic plant invasion. *Nature* 427:731–733.
- Cavieres, L., M. T. K. Arroyo, A. Penalzoza, M. Molina-Montenegro, and C. Torres. 2002. Nurse effect of *Bolax gummifera* cushion plants in the alpine vegetation of the Chilean Patagonian Andes. *Journal of Vegetation Science* 13:547–554.
- Cavieres, L. A., C. L. Quiroz, M. A. Molina-Montenegro, A. A. Muñoz, and A. Pauchard. 2005. Nurse effect of the native cushion plant *Azorella monantha* on the invasive non-native *Taraxacum officinale* in the high-Andes of central Chile. *Perspectives in Plant Ecology, Evolution, and Systematics* 7:217–226.
- Chiarucci, A., D. Viciani, C. Winter, and M. Diekmann. 2006. Effects of productivity on species area curves in herbaceous vegetation: evidence from experimental and observational data. *Oikos* 115: 475–483.
- Choler, P., R. Michalet, and R. M. Callaway. 2001. Facilitation and competition on gradients in alpine plant communities. *Ecology* 82:3295–3308.
- Clements, F. E. 1916. *Plant succession: analysis of the development of vegetation*. Carnegie Institution of Washington Publications 242:1–512.
- Connell, J. H. 1972. The ecology of rocky shores. *Annual Review of Ecology and Systematics* 3:169–192.
- . 1975. Some mechanisms producing structure in natural

- communities: a model and evidence from field experiments. Pages 460–490 in M. L. Cody and J. M. Diamond, eds. *Ecology and evolution of communities*. Belknap, Cambridge, MA.
- Crutsinger, G. M., M. D. Collins, J. A. Fordyce, Z. Gompert, C. C. Nice, and N. J. Sanders. 2006. Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science* 313:966–968.
- Ehlers, B. K., and J. Thompson. 2004. Do co-occurring plant species adapt to one another? the response of *Bromus erectus* to the presence of different *Thymus vulgaris* chemotypes. *Oecologia* (Berlin) 141:511–518.
- Farrell, B. D. 1998. Inordinate fondness explained: why are there so many beetles? *Science* 281:555–559.
- Farrell, B. D., and C. Mitter. 1990. Phylogenesis of insect/plant interactions: have *Phyllbrotica* leaf beetles (Chrysomelidae) and the Lamiales diversified in parallel? *Evolution* 44:1389–1403.
- Gleason, H. A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53:7–26.
- Gomulkiewicz, R., J. N. Thompson, R. D. Holt, S. L. Nuismer, and M. E. Hochberg. 2000. Hot spots, cold spots, and the geographic mosaic theory of coevolution. *American Naturalist* 156:156–174.
- Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242:344–347.
- . 1979. *Plant strategies and vegetation processes*. Wiley, Chichester.
- Grøndahl, E., and B. K. Ehlers. 2008. Local adaptation to biotic factors: reciprocal transplants of four species associated with aromatic *Thymus pulegioides* and *T. serpyllum*. *Journal of Ecology* 96:981–992.
- Guisan, A., and W. Thuiller. 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 Letters* 13:469–470.
- Hanski, I. 1999. *Metapopulation ecology*. Oxford University Press, Oxford.
- Harrison, S., and H. Cornell. 2008. Toward a better understanding of the regional causes of local community richness. *Ecology Letters* 11:969–979.
- Jablonski, D. 2008. Biotic interactions and macroevolution: extensions and mismatches across scales and levels. *Evolution* 62:715–739.
- Kikvidze, Z., F. I. Pugnaire, R. W. Brooker, P. Choler, C. J. Lortie, R. Michalet, and R. M. Callaway. 2005. Linking patterns and processes in alpine plant communities: a global study. *Ecology* 86:1395–1400.
- Lawton, J. H. 1999. Are there general laws in ecology? *Oikos* 84:177–192.
- Levine, J. M. 1999. Indirect facilitation: evidence and predictions from a riparian community. *Ecology* 80:1762–1769.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15:237–240.
- Liancourt, P., R. M. Callaway, and R. Michalet. 2005. Stress tolerance and competitive-response ability determine the outcome of biotic interactions. *Ecology* 86:1611–1618.
- Lortie, C. J., R. W. Brooker, P. Choler, Z. Kikvidze, R. Michalet, F. I. Pugnaire, and R. M. Callaway. 2004. Rethinking plant community theory. *Oikos* 107:433–438.
- MacArthur, R. H. 1965. Patterns of species diversity. *Biological Reviews* 40:510–533.
- Maron, J. L., M. Vilá, R. Bommarco, S. Elmendorf, and P. Beardsley. 2004. Rapid evolution of an invasive plant. *Ecological Monographs* 74:261–280.
- McAuliffe, J. R. 1994. Landscape evolution, soil formation, and ecological patterns and processes in Sonoran Desert bajadas. *Ecological Monographs* 64:111–148.
- McLaughlin, S. P., and J. E. Bowers. 2006. Plant species richness at different scales in native and exotic grasslands in southeastern Arizona. *Western North American Naturalist* 66:209–221.
- Michalet, R., and B. Touzard. 2010. Biotic interactions, biodiversity and community productivity. In F. I. Pugnaire, ed. *Positive plant interactions and community dynamics*. CRC, Boca Raton, FL (forthcoming).
- Michalet, R., C. Gandoy, D. Joud, J.-P. Pagès, and P. Choler. 2002. Plant community composition and biomass on calcareous and siliceous substrates in the northern French Alps: comparative effects of soil chemistry and water status. *Arctic, Antarctic, and Alpine Research* 34:102–113.
- Michalet, R., R. W. Brooker, L. A. Cavieres, Z. Kikvidze, C. J. Lortie, F. I. Pugnaire, A. Valiente-Banuet, and R. M. Callaway. 2006. Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecology Letters* 9:767–773.
- O'Neill, G. A., A. Hamann, and T. Wang. 2008. Accounting for population variation improves estimates of the impact of climate change on species' growth and distribution. *Journal of Applied Ecology* 45:1040–1049.
- Pagès, J.-P., and R. Michalet. 2006. Contrasted responses of two understorey species to direct and indirect effects of a canopy gap. *Plant Ecology* 187:179–187.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100:65–75.
- Pearson, R. G., and T. P. Dawson. 2004. Bioclimate envelope models: what they detect and what they hide. *Global Ecology and Biogeography Letters* 13:471–473.
- Pugnaire, F. I., and R. Lázaro. 2000. Seed bank and understorey species composition in a semiarid environment: the effect of shrub age and rainfall. *Annals of Botany* 86:807–813.
- Rajaniemi, T. K., D. E. Goldberg, R. Turkington, and A. R. Dyer. 2006. Quantitative partitioning of regional and local processes shaping regional diversity patterns. *Ecology Letters* 9:121–128.
- Reader, R. J., S. D. Wilson, J. W. Belcher, I. Wisheu, P. A. Keddy, D. Tilman, E. C. Morris, et al. 1994. Plant competition in relation to neighbor biomass: an intercontinental study with *Poa pratensis*. *Ecology* 75:1753–1760.
- Reinhart, K. O., A. Packer, W. H. Van der Putten, and K. Clay. 2003. Plant–soil biota interactions and spatial distribution of black cherry in its native and invasive ranges. *Ecology Letters* 6:1046–1050.
- Ricklefs, R. E. 2008. Disintegration of the ecological community. *American Naturalist* 172:741–750.
- Schweitzer, J. A., J. K. Bailey, D. G. Fischer, C. J. LeRoy, E. V. Lonsdorf, T. G. Whitham, and S. C. Hart. 2008. Plant-soil microorganism interactions: a heritable relationship between plant genotype and associated soil microorganisms. *Ecology* 89:773–781.
- Shmida, A., and R. H. Whittaker. 1981. Pattern and biological microsite effects in two shrub communities, southern California. *Ecology* 62:234–251.
- Shuster, S. M., E. V. Lonsdorf, G. M. Wimp, J. K. Bailey, and T. G.

- Whitham. 2006. Community heritability measures the evolutionary consequences of indirect genetic effects on community structure. *Evolution* 60:991–1003.
- Siska, E. L., S. C. Pennings, T. L. Buck, and M. D. Hanisak. 2002. Latitudinal variation in palatability of salt-marsh plants: which traits are responsible? *Ecology* 83:3369–3381.
- Suttle, K. B., M. A. Thomsen, and M. E. Power. 2007. Species interactions reverse grassland responses to climate change. *Science* 315:640–642.
- Thompson, J. N. 2005. *The geographic mosaic of coevolution*. University of Chicago Press, Chicago.
- Tirado, R., and F. I. Pugnaire. 2005. Community structure and positive interactions in constraining environments. *Oikos* 111:437–444.
- Turkington, R., and L. A. Mehrhoff. 1990. The role of competition in structuring pasture communities. Pages 307–340 in J. B. Grace and D. Tilman, eds. *Perspectives on plant competition*. Academic Press, San Diego, CA.
- Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11:1351–1363.
- Urban, M. C., M. A. Leibold, P. Amarasekare, L. Meester, R. Gomulkiewicz, M. E. Hochberg, C. A. Klausmeier, et al. 2008. The evolutionary ecology of metacommunities. *Trends in Ecology & Evolution* 23:311–317.
- Valiente-Banuet, A., and M. Verdú. 2007. Facilitation can increase the phylogenetic diversity of plant communities. *Ecology Letters* 10:1029–1036.
- Valiente-Banuet, A., A. Vital, M. Verdú, and R. M. Callaway. 2006. Modern Quaternary plant lineages promote diversity through facilitation of ancient Tertiary lineages. *Proceedings of the National Academy of Sciences of the USA* 103:16812–16817.
- Wade, M. J. 2007. The co-evolutionary genetics of ecological communities. *Nature Reviews Genetics* 8:185–195.
- Webb, C. O., D. D. Ackerly, M. A. McPeck, and M. A. Donoghue. 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics* 33:475–505.
- Whitham, T. G., W. P. Young, G. D. Martinsen, C. A. Gehring, J. A. Schweitzer, S. M. Shuster, G. M. Wimp, et al. 2003. Community and ecosystem genetics: a consequence of the extended phenotype. *Ecology* 84:559–573.
- Whitham, T. G., J. K. Bailey, J. A. Schweitzer, S. M. Shuster, R. K. Bangert, C. J. LeRoy, E. V. Lonsdorf, et al. 2006. A framework for community and ecosystem genetics: from genes to ecosystems. *Nature Reviews Genetics* 7:510–523.
- Whittaker, R. H. 1967. Gradient analysis of vegetation. *Biological Reviews of the Cambridge Philosophical Society* 42:207–264.

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“The north-western prolongation of the Purple Hills, which form the first three cañons in the river. The two pinnacles of ‘Chimney Peak,’ looming up in the background, are composed of trap. This being much harder than the material of the neighboring rocks has yielded less to the action of the elements,” from “The Chasms of the Colorado,” by A. Hyatt (*American Naturalist*, 1868, 2:359–365).