

# Importance versus intensity of ecological effects: why context matters

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**In any ecological study, target organisms are usually impacted by multiple environmental drivers. In plant interaction research, recent debate has focussed on the importance of competition; that is, its role in regulating plant success relative to other environmental drivers. Despite being clearly and specifically defined, the apparently simple concept of the importance of competition has been commonly overlooked, and its recognition has helped reconcile long-running debates about the dependence of competition on environmental severity. In this review, we argue that extending this formalised concept of importance to other aspects of ecology would be beneficial. We discuss approaches for measuring importance, and provide examples where explicit acknowledgement of this simple concept might promote understanding and resolve debate.**

## Two different uses of 'importance'

Ecologists often consider a statistically detectable effect of an ecological driver as indicating that this driver is 'important'. In some instances, a more refined approach is adopted, based on whether a detectable driver has consequences for a metric of interest. For example, if competition (see [Glossary](#)) produces exclusion of species, it is judged important to species coexistence in a community [1,2]. However, both cases represent a conventional, binary judgement on the importance of an effect based on the detectability of its consequences. However, in plant interaction research in particular, a more formalised definition of 'importance' has been proposed, this being the effect of competition in regulating plant success as a proportion of the impact of the environment overall [3]. This formalised concept allows one to move from binary answers concerning the role of competition (is it important or not?) to a more quantitative approach (how important is competition relative to other environmental drivers?). After its initial formalisation, and although having some occasional usage (e.g. [4,5]), the formalised concept of competition importance was largely overlooked for a considerable period. More recently, however, it has received increased interest, especially with respect to its potential for resolving long-running debates in plant interaction research ([6,7]; also see below).

The simplicity of the formalised concept of importance, when combined with its potential for resolving one of the major debates of plant ecology, motivated us to consider whether the concept could be extended to other aspects of ecology, such as understanding the structuring of communities, organismal territoriality and the biodiversity consequences of climate change. Here, we argue that such extensions are not only possible, but will also generate new knowledge and advance these ecological fields. Below we: (i) more fully explain the formalised concept of importance using its application to the study of plant competition as an illustrative example; (ii) show how this concept can be extended to most types of environmental effect on an organism; and (iii) provide examples of other areas of

## Glossary

**Assembly rules:** the processes determining the composition of communities such that they are non-random assemblages of species; includes the effects of biotic interactions.

**Canonical correspondence analysis (CCA):** a type of multivariate analysis that examines the links between environmental conditions and changes in the abundance and composition of species along ecological gradients.

**Competition index (interaction index):** a tool to quantify the effects of competing (interacting) organisms on each other based on experimental data; usually compares growth (or another measure of success) of individuals with and without neighbours and quantifies the effect as a ratio.

**Ecological communities and metacommunities:** community refers to groups of organisms in a specific place and/or time. The metacommunity concept extends the spatial and temporal scales of a community and considers patterns and mechanism of the distribution of species across local communities that are potentially interconnected through migrations and dispersal, and thus share a common regional species pool.

**Ecological gradient:** a gradual change in environmental conditions through space (or time) across local ecological communities related to variations in climate, soil type, and so on.

**Facilitation and competition:** facilitation is a type of interaction between organisms that is beneficial to at least one of the participants; by contrast, competition refers to detrimental effects between interacting organisms.

**Multivariate analysis:** statistical methods to observe and analyse more than one variable at a time.

**Plant strategy:** the combination of traits found within a given plant species or ecotype that is expected to provide it with increased fitness in a particular environment. A major plant strategy theory is the C-S-R theory of Grime [15], which states that plants cannot be good simultaneously at competing for resources and tolerating stress or disturbance, but that instead there is a trade-off between the adaptations associated with three main strategies: competitor (C), stress tolerator (S), and ruderal (R).

**Rarefaction:** a statistical process enabling the prediction of absolute species richness for a given community based on multiple random resampling of community composition (e.g. species count) data. Rarefaction enables calculation of the species richness for a given abundance of organisms and the construction of a so-called 'rarefaction curve': a plot of the number of species as a function of the number of individuals sampled.

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ecology (including, but not limited to, the study of organismal interactions) where we believe use of the importance concept might be beneficial.

### Plant competition: its importance versus its intensity

The formalised concept of the importance of plant competition is simple. First, we consider the fitness of a plant (or, more often, a surrogate of fitness; e.g. seed production) under optimal conditions at the most benign extreme of an environmental gradient, and without competition. We then examine its realised fitness at any given point on the gradient under both the full suite of impacts from its environment, as well as in the absence of competition. From this, we can see the total impact of the environment on our target organism, and can assess the importance of competition as the proportional impact of competition relative to the overall impact of the environment [3,6–8]. This concept can be applied irrespective of the scale of measurement, from individual organisms to populations, and from short-term (hours to days) to long-term (growing season or successional) observations [7,9–13]. In contrast to the formalised importance, the intensity of competition is formalised as its absolute effect; that is, the difference in success (however measured) of our target plant in the presence and absence of competition. Competition intensity is an absolute measure in that it is not placed within the context of the full suite of environmental impacts on the organism. More information on approaches to measuring competition importance is provided in Box 1.

These simple definitions have straightforward consequences. Other conditions being equal (i.e. when other impacts of the environment are held constant), reducing or increasing the intensity of competition will proportionately reduce or increase its importance. However, other conditions are rarely equal in the natural world, and this correlation is disrupted when other environmental factors (almost inevitably) change: the importance of competition (and its consequences) will change even if its intensity remains constant, because other impacts of the environment will increase or decrease relative to the impacts of competition; hence, the intensity and importance of competition need not be correlated [3].

Surprisingly, the concept of the importance of competition has long been overlooked, despite its simplicity and its utility in resolving controversies concerning the changing role of competition along productivity gradients, and attempts to draw attention to it [4,5]. Specifically, reanalysis of extensive data sets shows that the importance of competition can increase with productivity, whereas the intensity of competition changes relatively little [6,8]. Thus, the concept of competition importance enables one to understand apparent variation in the role of competition as a community-structuring and evolutionary force in the natural world. For example, one can understand why competition in unproductive environments, despite being measurable (and often intense), is a relatively weaker force, and also why competitive exclusion occurs in relatively productive and stable environments [6–8,14]. One can also then understand the evolution of a competitive (C) plant strategy [15] in productive environments, as it is in these systems that competition is the main regulator of

success; in more stressful or disturbed environments, competition is relatively less important and, hence, plants evolve stress-tolerant (S) or ruderal (R) strategies, respectively; that is, evolutionary responses that are more suited to the prevailing environmental conditions.

### Extending the concept of importance

Our argument in favour of extending the concept of importance beyond the study of plant–plant interactions is two-fold. First, because an organism experiences multiple environmental impacts, it is always legitimate to ask the following: what is the relative share of the effect of interest in determining overall performance of the target organism or population? It is straightforward to envisage the concept of importance when applied to other aspects of ecology, including other impacts and other types of organism. For example, grazing can be intensive, but its effect relatively unimportant because other environmental factors (e.g. shade, soil type, etc.) affect the fitness of a given target organism more strongly. The importance of any effect, biotic (e.g. predation, parasitism or allelopathy) or abiotic (e.g. soil pH or aridity) can be considered in this manner. In short, although there might be some need for discussion as to the most appropriate analytical technique for assessing importance, there is no theoretical reason to refrain from the extension of the formalised concept of importance to any ecological effect exerted on any organism by its (biotic or abiotic) environment. At a practical level, quantifying the importance of plant interactions often requires the same data as quantifying their intensity [3,6–9,11,12,16] (also see Box 1). At this stage, it is unclear whether this will, in general, be true for other ecological effects, although the work by Dhondt [10] on animal interactions (as discussed in detail below) indicates that this might be the case for interactions between other organismal groups. Initially, however, extension of the formalised concept of importance depends more on its conceptual acceptance by researchers.

Our second argument for extending the concept of importance beyond the sphere of plant–plant interactions is that it will be useful in other areas of ecology. We illustrate this point by providing some examples of where explicit acknowledgement of this simple concept might promote understanding and resolve debate. These examples include other types of interaction, move beyond the study of individuals to explore the structuring of communities and consider the role of processes other than biotic interactions.

### Animal interactions

Tit (Paridae) species are classic targets when studying both territoriality and density dependence of clutch size in birds. However, not all studies show the same ecological processes to be operating: in a review of 57 long-term population studies, only around half detected density dependence [17]. Dhondt [10] in his own study of territoriality in birds (great and blue tits – *Parus major* and *Cyanistes coeruleus*, respectively) along a gradient of habitat quality (food supply), demonstrated how application of the formalised concepts of importance and intensity could explain some of the apparently contradictory results in previous work. Distinguishing the importance from the intensity of

### Box 1. Measuring the importance of competition

The formalised importance of competition (the proportional impact of competition relative to the overall impact of the environment) has been quantified in various ways. Here, we consider a few of the possible alternative approaches to measuring the importance of competition.

Originally, Welden and Slauson suggested using the determination coefficient ( $R^2$ ) [3]: a demographic parameter (e.g. population or individual growth rate, fecundity, size, or fitness) is regressed against organismal density. Intensity can be measured as the slope of the regression equation, whereas importance is calculated as the proportion of the variation explained by the regression equation, or as  $R^2$  (see also [10,11]).

Currently, the most widely used measure of importance, the index  $C_{imp}$ , uses maximum performance of a phytometer, experimentally isolated from neighbour competition, as a reference for assessing changes in the relative impacts of competition and the overall environment along a productivity gradient [6–8]. As previously outlined [7],  $C_{imp}$  can be expressed as a product of two ratios (Equation 1):

$$C_{imp} = \{[w_m - w(N)]/w_m\} * \{w_m/[W_{MAX} - w(N)]\} \quad (1)$$

where  $w_m$  is plant performance (e.g. size at the point of measurement) without competition owing to the removal of neighbours,  $w(N)$  is plant performance with competition from intact neighbours at the

same point on an environmental gradient, and  $W_{MAX}$  is maximum performance of an isolated plant along the productivity gradient. The first ratio represents a popular index of competition intensity (e.g.  $C_I$  in [5]), and the second ratio is a function scaling the impact of competition relative to the overall negative impact of the environment. Such representation is important because it shows that the intensity of competition is a component of its importance, and that one is in fact quantifying the importance of a particular intensity of competition under given environmental conditions.  $C_{imp}$  has been successfully used not only with phytometers, but also with density-dependent growth data [11]. There are also modifications suggested for quantifying the importance to accommodate a competition–facilitation continuum [13,16]. Interestingly,  $C_{imp}$  can also be derived from population dynamics models [7,9,49]; therefore, these two approaches are related.

Finally, population-modelling approaches could provide a tool for assessing competition importance. For example, Chesson and colleagues analysed the relative roles of harsh and fluctuating environmental conditions [1] and spatial heterogeneity [2] in the dynamics of competing populations. Their models were designed to understand the mechanisms of competition by distinguishing intra- versus interspecific competition and analysing how they are related to the coexistence of (two) populations in the presence of environmental variability.

competition for food across a gradient of habitat productivity enabled him to demonstrate that territoriality reduced the intensity of competition among birds in productive habitats. Competition intensity was greater in low-quality habitats, probably because birds violated territoriality owing to the need to find enough food. At the same time, the importance of competition was higher in homogeneous and productive habitats as the relative impact of other biotic and abiotic factors were less pronounced. Consequently, Dhondt predicted that, in studies of territorial animals, density-dependent effects on reproduction are more likely to be detected in low-quality, unproductive sites, where competition is more intense. This demonstrates that competition can act in different ways depending on whether it is important or intense (using our formalised definitions): in the environments where it is important, competition leads to territoriality, whereas in the environments where it is less important but still intense, it leads to density-dependent effects. However, why does territoriality not develop in systems where competition is intense? Is it because of the greater impact of inhibitory factors other than competition, factors which are themselves relatively more important in these systems? This example also demonstrates the difference between the formalised and more casual use of ‘importance’ in the ecological literature. The formalised importance of competition is lower in the unproductive environment (because of the greater impact of other regulatory factors). Nevertheless, competition is still playing a statistically detectable role in determining bird ecology, and so competition is not (in the casual sense) unimportant.

#### *The existence and structuring of communities*

The existence of communities is hotly debated, with some theorists calling for ‘disintegration’ of the ecological community and others defending the usefulness of the community concept (see most recently [18–21]). One of the possible sources of this debate is continuing disagreement

and apparent contradictions concerning the processes that structure communities (linked to criticism of community ecology overall, particularly its inability to come up with general rules and principles [22]). For example, metacommunity theory considers four mechanisms (patch dynamics, species sorting, mass effects and the neutral model) as determining species composition of local communities from a regional species pool [23]. Although the theory allows for simultaneous operation of these mechanisms, at least two of them are conflicting, namely species sorting through competition and niche separation, and the neutral model, which assumes that species are essentially equivalent in their competitive and dispersal abilities such that the primary determinants of local species composition and abundance are stochastic demographic processes and dispersal limitation [1,2,23,24].

Models that explicitly predict the changing role of competition (and facilitation) along productivity (or, reciprocally, environmental severity) gradients can provide a starting point for understanding these apparent contradictions. One such model is the stress-gradient hypothesis (SGH), which predicts that the role of competitive effects is higher under productive environmental conditions, whereas the role of facilitative effects increases as environmental severity (either biotic or abiotic) increases [25–28]. Notably, however, experimental tests of the SGH have generally not included consideration of the importance of biotic interactions (although see e.g. [6,29]); they have tended to focus instead on measures of competition intensity (e.g. the index of relative neighbour effect (RNE) or derivatives of it, such as relative interaction intensity (RII), which compares plant performance in the presence and in the absence of neighbours [30]).

Better integration of the concept of importance into models such as the SGH would enable one to understand not only how the dominant types of interaction change with variation in environmental conditions, but also how their relative role changes. Along a gradient, there will be

conditions when biotic interactions (positive or negative) become important, and then determine local species composition to a considerable extent (as envisaged by interac-

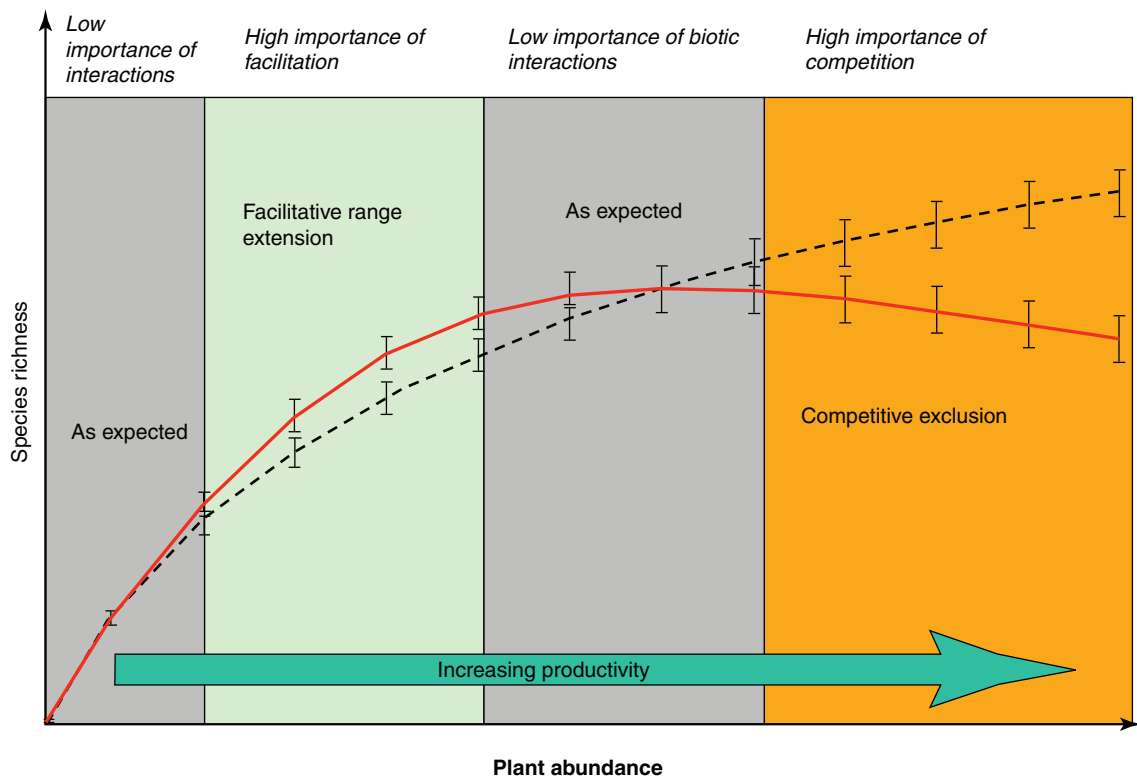
apparently mutually exclusive mechanisms might be integrated in metacommunity theory, and is perhaps an important step in developing a predictive integrated

### Box 2. Changes in the importance of competition and facilitation for community structure

Conceptually, expected changes along a productivity gradient in the importance of competition and facilitation, and subsequent variation in their impacts on the structure (species richness) of a plant community, can be visualised by comparing two hypothetical relationships. In Figure 1, the red, solid line shows the observed relationship between local species richness and productivity, and might be constructed based on community sampling data. The black, dashed line shows species richness across the gradient of productivity predicted from a rarefaction null-model that ignores plant–plant interactions; this model predicts species richness from the regional species pool and local plant abundance, which in turn is determined by productivity. In unproductive sites with few plants, the probability of finding many species is low, and vice versa; in productive habitats with abundant plants, the null-model predicts high species richness. The illustrative error bars around both the observed and predicted lines show the statistical uncertainty that is generally associated with such observations and predictions. They also indicate confidence intervals: when these overlap, observed and null-model predicted species richness do not differ significantly (see [50] for real-world examples and applications).

When the hypothetical null-model curve is compared with the hypothetical observed curve, it is expected that, under extremely

stressful conditions, as well as at moderate productivity (grey zones), the differences between the observed and expected values are statistically insignificant (i.e. the confidence intervals of the observed and predicted lines overlap). This is because biotic interactions have a negligible effect under overwhelmingly strong environmental severity (when productivity is very low), and because facilitative and competitive effects counterbalance each other at moderate productivity [28,44], leaving the regional species pool to determine species richness proportional to plant abundance. Under moderate stress, however, facilitation becomes important and helps many species to extend their range and penetrate abiotic filters (light-green zone), thus increasing species richness significantly as compared with the values expected from productivity alone [28]; this is shown by the observed richness being significantly greater than the expected richness in this zone. At high productivity (light-red zone), competition becomes important, and reduces species richness significantly (shown by the observed richness being significantly lower than predicted richness) owing to the exclusion of competitively inferior species. Figure 1 thus shows how one can integrate knowledge of when interactions are important into a broader understanding of how productivity drives species richness across large-scale gradients.



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Figure 1. Diversity–productivity relationships.

tion-based community assembly rules), whereas under other conditions, abiotic environmental filters will be more important and, thus, local species composition will simply correlate with the regional species pool (as predicted by neutral migration- and dispersal-based models: Box 2). This then provides an explanation as to how, for example,

framework for community ecology.

#### The intermediate disturbance hypothesis

One widely used model in current ecological theory is the intermediate disturbance hypothesis (IDH), which states that local species diversity is maximised when ecological



disturbance is neither too rare nor too frequent [14,31–35]. Notably, however, this model remains popular in spite of equivocal empirical evidence that questions its generality [36]. Researchers now try to refine the IDH by attempting to identify those contexts under which diversity does and does not peak at intermediate levels of disturbance [37–39]. This is effectively an attempt to understand when disturbance is important. Recognising this distinction, rather than simply measuring the impact of disturbance (its intensity), and quantifying the importance of disturbance using approaches such as the determination coefficient (Box 1) can directly address this problem of generality (or a perceived lack of it) for the IDH.

For example, Suzuki *et al.* [40] found that species richness of ground vegetation in temperate forests peaked at moderate deer density, as predicted by the IDH. Multivariate analysis showed that grazing was the most important factor explaining species distributions, followed by forest type, topographical wetness index and canopy openness (Suzuki *et al.*, unpublished data). In particular, deer grazing explained the distribution of palatable and unpalatable species: at intermediate deer density, both grazing-tolerant and intolerant species mixed and generated a peak of species richness. By contrast, Sasaki *et al.* [41] in Mongolian steppe found that soil type was a more important determinant of species distributions than was grazing, which explained the absence of the predicted unimodal shape of species richness along the grazing disturbance gradient. Although one might initially conclude that, in the former study, the IDH was supported because grazing was important, whereas in the latter it was unimportant, such analyses are not a true test of the formalised importance of grazing disturbance. The canonical correspondence analysis (CCA) used in both of these studies only assesses the percentage of variation explained in the data set relative to the tested environmental drivers and, thus, does not address the problem of quantifying the (formalised) importance of disturbance (i.e. the role of disturbance relative to the total impact of the environment). Genuine quantification of the importance of disturbance from such data is possible, as has been shown, for example, by Bongers *et al.* [42] using  $R^2$  (see also Box 1). These authors found that disturbance explains more diversity variation and, hence, is more important, in dry than in wet tropical forests, possibly because understorey plants in wet forests have lower desiccation risk following canopy loss because of higher soil water availability. Such an approach can be applied to species groups: Bongers *et al.* also found that disturbance explained the increase in pioneer species and decrease in shade-tolerant species along a disturbance gradient. However, for other species, the strength of the relationships between their abundance and disturbance (as expressed by  $R^2$  values) was rather low. Hence, disturbance is a relatively less important regulator of abundance for those species that do not specialise in disturbance or shade tolerance.

#### *Predicting and understanding biotic impacts of climate change*

Climate effects on biotic processes and the distribution of species are clearly not straightforward. For example, a

meta-analysis of detected tree-line shifts in response to climate warming showed variable levels of temperature response [43]. Notably, the tree-lines that were more strongly growth limited by temperature were more likely to have advanced than were those under milder conditions (where climate had a proportionately smaller regulatory role). This suggests that the most immediate and clear responses to climate change will be seen where climate has greater importance in directly regulating biological processes. Indeed, the link between the importance of climate and the response of communities to climate change has been demonstrated experimentally. For example, in a study of alpine snowbed communities, Schöb *et al.* [44] showed that, in general, biotic interactions in snowbeds are intense but relatively unimportant, not least because of the simultaneous operation of positive and negative plant–plant interactions that counterbalance each other (see ‘moderate productivity’ conditions, Box 2). They have further shown that, under such circumstances, climatic drivers become proportionally more important, and lead to the invasion of snowbeds by other plant species.

Such an understanding of the importance of climate drivers is not simply of interest to local-scale studies of particular communities or species. Climate envelope models (CEMs) are popular tools for assessing large-scale changes in species distributions under global warming. CEMs are based on the axiomatic assumption that climate controls species distributions. Yet the usefulness of CEMs is subject to debate [45–47]. To help resolve this debate, Beale *et al.* [48] used robust null models to test CEMs for the distributions of 100 European bird species. They found that CEMs produced valid range predictions for species in more northern latitudes, but that predictions were powerless (no better than a climate-free null) for southern species. This result is not surprising: because CEMs focus mainly on climate as a major regulator of species distributions in milder habitats, where other processes (such as biotic interactions, and intense land use and habitat fragmentation) are more important in determining species success and distributions, one would expect CEMs to lose power. Thus, the concept of importance helps us to understand why variation is seen in biotic responses to climate drivers and also in our ability to predict biotic responses based on climatic variables alone.

#### **Concluding remarks**

To date, discussion of the formalised concept of importance only in the context of plant competition might have generated a false impression that this is the only area of ecological research where it is applicable. The concept of importance, the relative role of a process or driver, can be applied to many processes and with respect to many outcomes, including (as we have shown above) individual and population success, community structure and the ecological impacts of climate change. What is perhaps off-putting about the formalised concept of importance is its simplicity: how can anything so simple be useful? However, when we start to explore how often this simple concept is not acknowledged, with resultant confusion in our attempts to develop broadly applicable synthetic ecological models, then we start to realise that ‘simple’ does

not equate to 'obvious', and that explicit recognition of the formalised concept of importance might be widely beneficial in ecology.

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