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CONSEQUENCES OF DOMINANCE: A REVIEW OF EVENNESS EFFECTS ON LOCAL AND REGIONAL ECOSYSTEM PROCESSES

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Abstract. The composition of communities is strongly altered by anthropogenic manipulations of biogeochemical cycles, abiotic conditions, and trophic structure in all major ecosystems. Whereas the effects of species loss on ecosystem processes have received broad attention, the consequences of altered species dominance for emergent properties of communities and ecosystems are poorly investigated. Here we propose a framework guiding our understanding of how dominance affects species interactions within communities, processes within ecosystems, and dynamics on regional scales. Dominance (or the complementary term, evenness) reflects the distribution of traits in a community, which in turn affects the strength and sign of both intraspecific and interspecific interactions. Consequently, dominance also mediates the effect of such interactions on species coexistence. We review the evidence for the fact that dominance directly affects ecosystem functions such as process rates via species identity (the dominant trait) and evenness (the frequency distribution of traits), and indirectly alters the relationship between process rates and species richness. Dominance also influences the temporal and spatial variability of aggregate community properties and compositional stability (invasibility). Finally, we propose that dominance affects regional species coexistence by altering metacommunity dynamics. Local dominance leads to high beta diversity, and rare species can persist because of source–sink dynamics, but anthropogenically induced environmental changes result in regional dominance and low beta diversity, reducing regional coexistence. Given the rapid anthropogenic alterations of dominance in many ecosystems and the strong implications of these changes, dominance should be considered explicitly in the analysis of consequences of altered biodiversity.

Key words: *ecosystem function; evenness; invasion; metacommunity; productivity; species coexistence; species identity; stability; trait variance.*

INTRODUCTION

Human domination of ecosystems (Vitousek et al. 1997b) has lead to dramatic changes in the composition of ecological communities, with respect to the number of coexisting species (species richness) and the dominance structure (evenness) in the community. Ecologists are challenged to understand and predict the consequences of these changes in the biota. Therefore, recent years have seen an increasing number of studies dealing with the consequences of species richness for ecosystem functioning. While the results of these studies are far from unanimous, important central tendencies for

effects of species loss emerged. Recent reviews (Hooper et al. 2005, Balvanera et al. 2006, Cardinale et al. 2006) suggested that reductions in the numbers of species affect important ecosystem processes such as the production of new biomass and the efficiency of resource use. Other properties of ecosystems have also been aligned to species richness, e.g., invasibility (Levine and D'Antonio 1999), temporal stability (Loreau et al. 2002), and resilience (Reusch et al. 2005).

The alteration of biotic communities by major anthropogenic stressors not only alters the number of species in most ecosystems, but also their relative abundance and thereby dominance or evenness. (The Appendix provides a glossary of terms.) More importantly, evenness often responds more rapidly to human activities or altered environmental constraints than species richness, and might also lead to rapid responses

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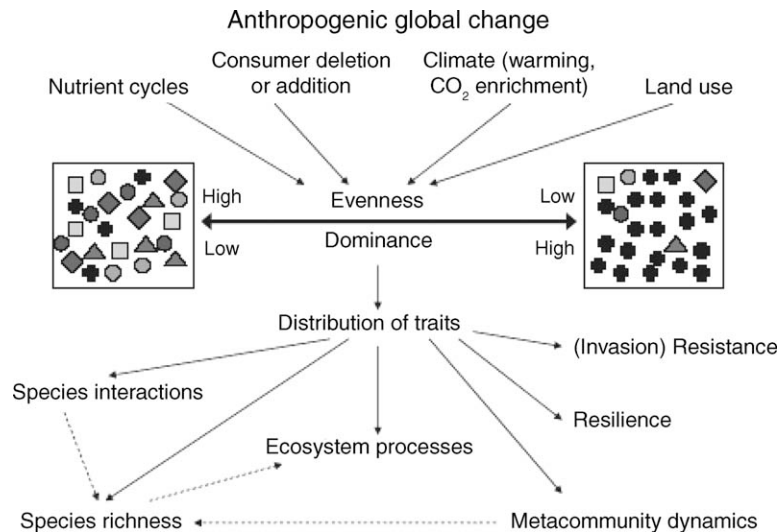


FIG. 1. Anthropogenic alterations of nutrient cycles, consumer presence, climate, and land use alter the dominance or evenness of ecological communities. This results in an altered distribution of traits in the community, with direct (solid arrows) and indirect (dotted arrows) consequences for species interactions, coexistence, ecosystem function, and stability on the local scale, and metacommunity dynamics on the regional scale. In the left box, the different symbols represent a variety of species; in the right box, a single species is dominant.

in ecosystem functions before species actually are driven to extinction (Chapin et al. 2000). Given these scenarios, the distribution and variance of traits within a community may be more important for aggregate performance of communities than the number of traits (i.e., species richness) (Norberg 2004).

Comparably few studies have analyzed the consequences of altered dominance structure, although dominance (or evenness) has repeatedly been shown to be a unique measure of biodiversity, which complements information from richness estimates (Stirling and Wilsey 2001, Wilsey et al. 2005). Some studies that have tested the correlation between diversity components suggest that richness and evenness may not be correlated positively (Buzas and Hayek 1996, Stirling and Wilsey 2001). Stirling and Wilsey (2001) combined published data from a variety of studies and found that correlations between species richness and evenness were strongly positive for invertebrate animals and weakly positive for vertebrates, but negative for plants. Those findings suggest that measures of evenness can provide a significant amount of information on variance in diversity that will be independent of variance in species richness alone (Wilsey et al. 2005).

Major human alterations of life on earth, such as climate change, modifications of global biogeochemical cycles, and deletion or addition of species in food webs, strongly affect evenness (Fig. 1). Anticipated global changes in temperature and carbon dioxide availability are predicted to alter dominance structure. A recent meta-analysis showed that experimental warming increased dominance (and decreased evenness) in plant communities across the tundra biome (Walker et al. 2006). Experimental warming also affected dominance in other

terrestrial (Klanderud and Totland 2005) and aquatic (Stachowicz et al. 2002) communities. Increasing CO₂ availability altered dominance in grasslands (Niklaus et al. 2001). Recent paleoecological evidence indicates that fossil abundance data reflect real abundance distributions (Kidwell 2001, 2002); thus, we might expect to learn more about the climate-related shifts in evenness over long time scales (Powell and Kowalewski 2002).

In addition to climatic forcing, dominance is strongly determined by alterations of biogeochemical cycles and by introductions or deletions of consumer species. It has been suggested that while abiotic factors (e.g., physical conditions) tend to predict species richness patterns, biotic factors (e.g., grazing) at population or community levels are more likely to be responsible for controlling species densities (Therriault and Kolasa 1999). Consequently, alteration of competition and consumption will play a major role in structuring ecosystems. Humans have increased the global availability of resource nutrients (Vitousek et al. 1997a, Tilman 1999, Bergström and Jansson 2006, Bragazza et al. 2006), and such fertilization, by homogenizing available resources, strongly decreases evenness and increases dominance in almost all ecosystems (Harpole and Tilman 2007, Hillebrand et al. 2007). In a large-scale meta-analysis across ecosystems (Hillebrand et al. 2007), fertilization significantly decreased and herbivores significantly increased evenness in plant and algal communities. As consumer species are under high anthropogenic pressure in many ecosystems (Duffy 2002, Myers and Worm 2003, Lotze et al. 2006), additional effects on evenness can be expected, especially as consumption strongly counteracts enhanced dominance in fertilized environments.

Species introductions and invasion by exotic species also alter dominance structure of the natural assemblage, as exotic species often show an initial dominance (Seabloom et al. 2003, Guo et al. 2006). While the results of observational studies of evenness–invasibility relationships have not been consistent, demonstrating both positive (Robinson et al. 1995) and negative (Mattingly et al. 2007) responses, there is agreement that species invasions are an important factor driving changes in dominance patterns (Woitke and Dietz 2002). Furthermore, successful invasions resulting from exotic species with functional traits that are different from those of the dominant native species (Vitousek and Walker 1989, Symstad 2000, Fargione et al. 2003) will have potentially different effects on ecosystems (e.g., utilization of formerly underutilized resources), in contrast to the situation when the invader is functionally similar to dominant native species (Bock and Bock 1992, Reed et al. 2005).

Given these dramatic changes in the dominance structure of communities worldwide, it is astonishing how little we know about the consequences of dominance for aggregate community properties or ecosystem processes. In the following review, we will present the state of understanding of how altered dominance affects species interactions, species coexistence, and important ecosystem processes, and present a concept of potential pathways for these dominance effects. We start with processes within communities and ecosystems, but also deal with larger temporal and spatial scales including metacommunities and regional dynamics.

DOMINANCE EFFECTS WITHIN COMMUNITIES

The dominance distribution of species primarily determines the distribution of traits within a community or a functional group (e.g., primary producers). As species differ in important traits (resource uptake efficiency, vulnerability to consumers, thermal tolerance, etc.), the traits of the dominant species contribute more to aggregate processes in communities and ecosystems than the traits of rare species (Norberg 2004). Thus, the effect of dominance comprises both an effect of the degree of dominance and the identity of the dominant species, i.e., the trait variance and the average trait value. We next identify how dominance affects species interactions and species coexistence, and then we ask how these consequences in dominance alter emergent ecosystem processes and properties.

Species interactions

The presence of a dominant species often alters interspecific interactions in a community (Fig. 1). Classical ecological concepts of keystone species (Menge et al. 1994), foundation species (Dayton 1975), and ecosystem engineers (Lawton and Jones 1995) reflect the importance of the presence of certain species for ecosystem functioning (although these species do not necessarily have to be dominant in terms of biomass or abundance). The presence of such a species alters the

architectural structure of the habitat as well as the flow of energy and matter, thereby affecting species composition and biomass of the surrounding community (Dayton 1975, Lawton and Jones 1995, Ervin and Wetzel 2002, Eriksson et al. 2006).

In addition to such obvious cases, where the entire function relies on the presence of a dominant species, increasing inequality in the distribution of traits alters the relative importance of intraspecific vs. interspecific interactions, suggesting that competition can be a potential explanation for effects of evenness. Differences in the relative strength of intra- vs. interspecific interactions can significantly alter population dynamics (Chesson 2000, Adler et al. 2007). Compared to a more even community, dominance leads to higher importance of intraspecific interactions for the dominant species, and greater importance of interspecific ones for rare species. Assuming species compete for a single resource, populations largely regulated by intraspecific interactions will exhibit dynamics predicted by basic logistic growth models and grow to some carrying capacity. Those experiencing stronger interspecific interactions, if they persist in a stable way, will maintain lower abundances. Thus, anthropogenic forcing, which alters community evenness, will affect the magnitude and importance of intra- vs. interspecific interactions. Our ability to predict the competition consequences of altered evenness patterns depends on our ability to estimate the relative strengths of these interactions.

Beyond simple competitive interactions, altered dominance can have other, community-wide effects. If a certain type of interaction or trait (e.g., nitrogen fixer, intermediate host, etc.) is associated with a single dominant species, increased evenness, where noninteracting species are increasing in abundance, will reduce certain community processes (dilution effect). However, if a certain type of interaction or process involves all the members of a community, increasing dominance could have one of two potential consequences. The first consequence involves how the dominant species affects mean community performance. If the dominant performs better than the mean of the community, this process or interaction (e.g., disease transmission) will increase, and vice versa if the dominant performs below average. Secondly, when synergistic interactions are important for the community, reduced evenness may have negative consequences, because synergistic interactions fail if one species completely dominates the assemblage.

The latter case has been shown for pollination mutualism and for the associational resistance against grazing. Ghazoul (2006) manipulated the evenness of plant community composition and found significant effects on pollination rates. The target plant species showed higher pollination rate and seed production when co-occurring with other species because such an assemblage of species attracted more pollinators through a greater variance in floral displays. However, when the other species became dominant, pollination

rates of the target species declined. In a meta-analysis of grazing experiments on periphyton, the grazer effect on algal biomass declined with increasing algal diversity, which in the most parsimonious model comprised both species richness and a measure of evenness (Hillebrand and Cardinale 2004). Whereas higher algal richness can be aligned to higher resistance to consumption by the higher probability of encompassing grazing-resistant species in more species-rich communities, the effects of higher evenness are most probably based on a synergistic property such as associational resistance (Wahl and Hay 1995).

As an example for the dilution effect described above, dominance has also been suggested to play an important role in the transfer of pathogens or parasites (Ostfeld and Keesing 2000). In a simulation model, Schmid and Ostfeld (2001) found high disease risk if competent hosts were dominant, but low risk if incompetent hosts were dominant. Thus, depending on the identity of the dominant species, pathogen transfer was increased or decreased. Evenness per se had no effect for disease risk in contrast to richness, which reduced disease risk by introducing a dilution effect between host and nonhost species.

As a final example, cascading trophic interactions may have a strong indirect component via the alteration of plant evenness. In a terrestrial field experiment, Schmitz (2006) observed weak direct predator effects on the aggregate community biomass, but strong indirect effects on element cycling and light availability mediated by plant evenness and species dominance. Such cryptic cascades, which have weak effects on biomass but strong effects on composition and process rates, have been observed for aquatic systems as well (Tessier and Woodruff 2002).

Thus, factors increasing or decreasing the dominance in a community alter the distribution of traits in a community (Fig. 1), which in turn has direct consequences for the magnitude of intra- and interspecific interactions as well as community dynamics or processes that depend upon the trait distribution of the community. At present, generalizations across interaction types and ecosystems are inhibited by the small number of studies looking at consequences of dominance for a certain interaction (competition, consumption, or mutualism). However, we propose that the specificity of the interaction and the degree of synergism are important constraints for the effect of dominance on species interactions. Species-specific interactions may increase or decrease with dominance, depending on whether the dominant species is involved (pathogen transfer), whereas synergistic effects within trophic levels (associational resistance) or across trophic levels (pollination) may be fostered by evenness.

Species coexistence

Dominance affects the number of coexisting species in two different ways (Fig. 1). First of all, evenness alters the number of species per unit area (or volume) by

altering the shape of species–area relationships (SARs) (He and Legendre 2002, Green and Ostling 2003). More species are found in a defined area if the assemblage has higher evenness. This pattern has important consequences for species coexistence under habitat fragmentation (see also *Dominance effects in metacommunities*), as SARs predict that reductions in habitable areas have more dramatic consequences at high dominance (He and Legendre 2002, Green and Ostling 2003). Experimental evidence corroborates that extinction risk increases with dominance, as plant extinctions were higher in plots sown with low compared to high evenness (Wilsey and Polley 2004).

Second, evenness predetermines the effect of abiotic and biotic factors on species richness. In a meta-analysis of fertilization and herbivory experiments across aquatic and terrestrial ecosystems (Hillebrand et al. 2007), plant community evenness stood out as the single most important variable mediating the response of species richness. At high dominance, fertilization decreased and consumption increased species richness, as fertilization obviously enhanced the success of an already dominant competitor and led to species extinction, whereas consumption prevented extinction by reducing dominance. By contrast, in plant communities with low dominance, fertilization increased and consumption decreased species richness.

Ecosystem processes

Research on biodiversity effects on ecosystem function began more than a decade ago by testing the importance of species richness for primary productivity (Naeem et al. 1994, 1996, Tilman et al. 1996). Meanwhile, the array of processes investigated as important ecosystem processes has been increased (Giller et al. 2004), and a number of reviews summarizing the effect of richness on ecosystem functions have been published (Hooper et al. 2005, Balvanera et al. 2006, Cardinale et al. 2006). The consequences of evenness for aggregate process rates in ecosystems have largely been overlooked, but there are a handful of studies that provide some theoretical and empirical insight into evenness–function relationships.

An early model by Nijs and Roy (2000) suggested that primary productivity increases in a community with all aspects of diversity, comprising richness, evenness (trait variance), and degree of difference (difference between trait values). However, Norberg et al. (2001) showed that this conclusion strongly depends on environmental variability and the time scale considered. In a stable environment, a certain optimal trait allows the highest process rates, and any deviance from this trait (by increasing evenness) will reduce process rates. Thus, the highest production will occur in a system highly dominated by the most productive species, whereas all resources diverged into less productive species will reduce total production. On a longer time scale, however, when environmental fluctuations play a significant role, productivity is enhanced by higher trait

variance (Norberg et al. 2001), suggesting that high evenness allows communities to quickly adapt to new environmental constraints and to sustain high productivity over time.

Given these contrasting predictions, it is not surprising that the empirical evidence for evenness–productivity relationships is divergent as well. Some studies have found increasing productivity with increasing evenness, others increasing productivity with increasing dominance. As an example, Wilsey and Potvin (2000) analyzed the effects of evenness on plant productivity in an old field in Quebec and found a positive evenness–productivity relationship irrespective of the identity of the dominant species. Plant productivity in experimental grassland communities also increased with increasing evenness, resulting in decreased light availability (i.e., increased resource use efficiency) (Mattingly et al. 2007). Total annual cover in an old field slightly increased with increasing evenness (Stevens and Carson 2001). By contrast, Mulder et al. (2004) examined the Biodepth grassland experiments and found increased biomass production with lower evenness, when comparing plots with similar initial richness. In addition, evenness and biomass production across all plots were also negatively correlated.

In addition to direct links between evenness and ecosystem functions, other studies have focused on how evenness affects the relationship between richness and function. Again, the outcome is very inconclusive. Dominance led to more pronounced overyielding of biomass production in some grassland mixtures (Roscher et al. 2005), while in contrast two recent studies found higher overyielding with increased evenness (Kirwan et al. 2007, Polley et al. 2007). Kirwan et al. (2007) analyzed a multisite experiment across Europe and found that across all studied sites, richness effects in polycultures increased with increasing evenness. Finally, a third set of studies found no alteration of richness effects by dominance (Polley et al. 2003, Wilsey and Polley 2004).

In the face of obviously contrasting findings, it appears necessary to define what kind of processes influence the relationship between evenness and productivity. Polley et al. (2003) suggested that this relationship may depend on the relative importance of the two most commonly reported mechanisms for biodiversity effects: selection (or sampling effect, when species with particular traits are favored) and complementarity (based on niche differentiation or facilitation between species). Selection effects may be insensitive to species evenness or even enhanced by strong dominance, while complementarity processes and facilitation are promoted by evenness. Cardinale and Palmer (2002) found that in the absence of disturbance, the dominance of the superior competitor among three caddisfly species led to selected ecosystem processes being largely controlled by a single species. Similarly, other studies suggested that increased total biomass, even with increasing number of species, was mostly caused by the dominant species (Engelhardt

and Ritchie 2001). However, if instead of selection effects, species interactions drive biodiversity effects, increasing evenness enhances complementarity and thus primary production (Kirwan et al. 2007). This is in line with what we predicted for species interactions. If synergistic interactions such as complementary resource or facilitation drive an ecosystem process, increased dominance will lead to a reduction of this function. If, however, the identity of the dominant species (selection effect) predetermines a process rate, dominance may have positive or negative interactions based on the average performance of the dominant species. However, whether the prevailing mechanism of biodiversity effects can properly predict the consequence of dominance for ecosystem processes has yet to be fully explored. Models suggest that a more even distribution of traits (i.e., higher trait variance) can also enhance productivity via sampling effects if the environment shows strong fluctuations (Norberg et al. 2001).

Empirical results on dominance effects on ecosystem processes other than productivity are rare. Negative effects of evenness were observed for decomposition rates by benthic invertebrates in streams. Here, for a given species richness, the decomposition rate in streams was much higher when the shredder community was highly dominated by a single species (Dangles and Malmqvist 2004). Likewise, the number of species needed to maintain decomposition increased with increasing evenness (Dangles and Malmqvist 2004). The above-mentioned study by Ghazoul (2006), which investigated pollination rates as an ecosystem process, found intensified pollination on the target species if other species became more abundant; however, if the other species became dominant, their effect on pollination became negative.

The importance of dominance for ecosystem functions has also triggered interest in the concept of functional dominance or functional evenness, i.e., the evenness of species contribution to certain ecosystem functions within ecosystems (Mason et al. 2005, Mouillot et al. 2005). As example, Mouillot et al. (2005) suggested that functional richness and functional evenness may vary independently of one another. Balvanera et al. (2005) analyzed functional evenness for pollination and carbon storage and found that most functions are highly dominated by few species. Likewise, Larsen et al. (2005) found high functional dominance for pollination by bees and dung burial by beetles. Moreover, they found that the most functionally efficient species were also most extinction prone, which highlights the importance of evenness for maintaining ecosystem functions in a variable environment.

Stability

The debate about how diversity affects community stability has a long history (Elton 1958) and a high complexity, additionally complicated by the different definitions of stability (Grimm and Wissel 1997). For our review, we resolve the broad spectrum of definitions

into two components: on one hand the stability of measurable functional properties of the ecosystem (e.g., biomass, productivity) (Mulder et al. 2004) and on the other hand the stability of community composition (e.g., species diversity) (Grimm and Wissel 1997). Diversifying between functional and structural aspects of stability seems to be necessary, as functional stability does not necessarily imply community stability (Tilman 1996). For example, an extremely dynamic community can develop in a simple ecosystem and still maintain a stable ecosystem function (Fernandez et al. 1999). Even if we are able to observe changes in biotic compositions, this need not lead to changes in process rates.

Most (but not all) empirical studies conclude that richness decreases the temporal variability of aggregate (community) biomass and abundance as well as species composition (Tilman 1996, McGrady-Steed and Morin 2000, Cottingham et al. 2001, Morin and McGrady-Steed 2004, Shurin et al. 2007). However, the variability in abundance of individual populations can be unrelated to species richness and overall community stability (Lehman and Tilman 2000, Romanuk and Kolasa 2002). Theoretical evidence suggests that the stabilizing effect of richness on temporal fluctuations can only be observed at low dominance (Doak et al. 1998). At high dominance, one or few species make such large contributions to the aggregate biomass that there is no averaging effect reducing variability across the community (Cottingham et al. 2001). Thus, dominance reduces the stabilizing effect of richness.

Stability can also be understood as the response of a community to external forcing, which is usually measured as community resistance or community resilience. Resistance is the ability to withstand an external event, whereas resilience refers to the ability to recover from such an event. With the exception of invasion resistance (see *Invasibility*), the effect of dominance on resilience or resistance has rarely been analyzed directly. Conceptually, we propose that both of these components can be affected by species richness and dominance in different ways (Fig. 2). Resilience often depends on the presence of a certain trait, which allows recovery from external disturbance. Resilience thus correlates with the response diversity of an assemblage (Elmqvist et al. 2003), which is best aligned to the richness in traits (e.g., species richness). An assemblage with more species will thus more likely comprise the species that are able to recover rapidly (Fig. 2B, D) compared to a species-poor assemblage (Fig. 2A, C). Effects of species richness on community resistance, however, are less predictable, because higher species richness enhances the probability that an assemblage will contain highly resistant as well as highly susceptible species. Thus, resistance may be more connected to dominance instead of richness (Fig. 2), with the outcome depending on the identity of the dominant species and the importance of synergistic interspecific interactions. If the dominant species is susceptible to the disturbance, its community will have lower resistance (Fig. 2C, D) than communities with

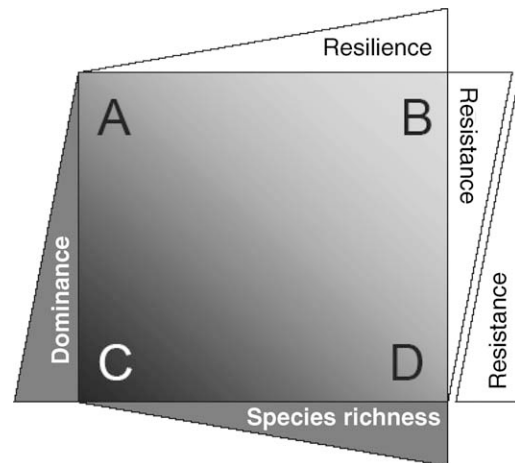


FIG. 2. Resistance and resilience are defined as two components of relative stability. While resilience increases with increasing species richness, resistance increases with increasing dominance. We define four scenarios: (A) communities with low stability (low species richness and low dominance); (B) communities with high stability (high richness and low dominance); (C) communities with very low stability (low species richness and high dominance); (D) communities with high stability, depending on the dominance of disturbance-tolerant or disturbance-susceptible species.

more even trait distribution (Fig. 2A, B). But such communities will also gain evenness following disturbance, due to the subtraction of highly dominant species that did not survive the disturbance. Communities with more even distribution of traits will also be more resistant if resistance is mainly expressed by positive interactions between species, e.g., by associational resistance (Wahl and Hay 1995) or by facilitation from neighboring species (Bertness and Ewanchuk 2002, Pennings et al. 2003). By contrast, in communities where dominance is due to species highly resistant to disturbance, an increase in evenness will reduce community resistance. Such communities will also be highly resilient, because in this case, species susceptible to disturbance are rare in a community, and their contribution to the ecosystem processes (e.g., productivity) is not significant and the recovery to the stage prior to disturbance will be faster.

The few empirical findings are in agreement with these conceptual relationships between evenness and resistance on one hand and species richness and resilience on the other hand (Fig. 2). An early study assessing plant communities during old-field succession in xeric habitats found that the younger field, with a lower species diversity (including richness and evenness), seemed to be more resilient but less resistant. By comparison, the older field, with higher species diversity, exhibited higher resistance but lower resilience (Leps et al. 1982). In aquatic laboratory microcosms, the resilience of entire algal communities following a perturbation (density-independent mortality) increased with increasing domi-

nance of a few species, especially unicellular green algae (Steiner et al. 2006). Thus, communities showing high community-wide resilience also showed strong decreases in evenness, whereas those communities gaining evenness through perturbation had low resilience. Engelhardt and Kadlec (2001), in their study on submersed aquatic macrophytes in wetlands, concluded that resilience was not mediated by diversity, but they suggested that the presence of the best competitor and most productive species that also has low resistance to disturbance overall decreases system resilience. In contrast, contribution of a disturbance-tolerant species may increase resilience (Engelhardt and Kadlec 2001). Likewise, interspecific interactions may increase community resistance under harsh climatic conditions, but may result in competitive interactions under benign conditions (Bertness and Ewanchuk 2002). It is important to note that because experimental studies have yet to independently manipulate dominance and species richness, it is difficult to truly assess our conceptual model. We hope that future experiments will test the role of dominance on stability and offer insights into the stability consequences of changes in biodiversity.

Invasibility

A great deal of attention has been directed to studies that investigated the relationship between species richness and invasibility at single points in time, but very little has been done to examine the role of evenness, or the dynamics of these relationships across time (Emery and Gross 2006). Observational and experimental studies both acknowledge that the effect of species diversity on vulnerability to invasion depends not only on species richness but also on many other components, such as composition and species interactions, and thus likely evenness. Conceptually, increasing evenness should reduce invasibility due to more niches being filled in the native community, resulting in increased invasibility in strongly dominated communities. However, dominance may decrease invasibility if the dominant species can prevent further colonization, e.g., by monopolizing space or allelopathic interactions, that is, when the dominant species can create a more competitive or more stressful environment.

Most empirical studies testing for effects of dominance or evenness on invasion resistance concluded that invasibility decreased with increasing evenness because communities are more invasion resistant when local niches are filled by representatives from available functional groups (Mwangi et al. 2007, Zavaleta and Hulvey 2007), but others found no effect of dominance per se (Emery and Gross 2006). Extreme dominance means that sites are likely lacking in critical functional groups and are thus more susceptible to invaders (Dunstan and Johnson 2006). Smith et al. (2004) suggested that invasion seems to be actually facilitated by dominant species because reduced dominance increased environmental stress. They experimentally lessened the dominance of C_4 grasses in native grassland,

which also in return moderated invasibility, i.e., higher evenness led to higher invasion resistance. Smith et al. (2004) concluded that when richness and dominance were separately manipulated, richness had no effect on invasion, and dominance was the most important factor determining invasiveness.

Similar effects were also observed in other studies. Invasibility of planted grasslands decreased with increasing evenness, i.e., enhanced dominance led to stronger invasibility of dicot invaders but had no effect on monocot invaders (Wilsey and Polley 2002). Losure et al. (2007) found in their grassland study that increased dominance significantly enhanced invader biomass, but only when the size structure was similar: dominance had no effect when tall and small species were combined. Thus, evenness effects depended on the size structure of the plant community.

These findings imply that dominance is a very important factor in community characteristics influencing invasibility. Despite this overall agreement, the results are not entirely unanimous. Two other studies showed no significant effect of evenness on invasibility. In one study, the Shannon index composed of richness and evenness was positively correlated to invasibility of grasslands, but eliminated from the model when other factors were taken into account (Foster et al. 2002). In another study, invasibility was not affected by evenness although evenness altered primary productivity and light availability in the native community (Mattingly et al. 2007).

DOMINANCE EFFECTS IN METACOMMUNITIES

While changes in species dominance have important consequences on local-level processes, dominance can also have consequences for spatial processes and mechanisms of coexistence. Species abundances at any given locale are the product of numerous ecological processes operating across a number of spatial scales (Leibold et al. 2004, Holyoak et al. 2005, Freestone and Inouye 2006). Taking a metacommunity approach, there are two types of dominance possible: (1) local dominance/regional evenness (DE) and (2) local dominance/regional dominance (DD) (Fig. 3). Depending on the scale at which species dominate, we should expect different effects on species richness.

When species dominate locally but not regionally (DE), this likely reflects historical or abiotic heterogeneity among locales, and is apparent in high beta diversity. Species achieve dominance in locales for which they are the best competitor for local niche conditions (Fig. 3A). In the absence of dispersal, competitive inferiors would be expected to eventually go extinct, enhancing local dominance. However, with among-patch dispersal, rare species persist because population birth rates are supplemented by immigrants from high-abundance patches (source-sink dynamics), thus increasing the likelihood of maintaining a balance between the number of births and deaths (Horn and MacArthur 1972, Chesson 2000, Hoopes et al. 2005, Mouquet et al.

2006). Therefore, greater heterogeneity among patches results in a higher probability that different species will dominate locales, and in turn enhances local species richness through source–sink dynamics.

However, large-scale, anthropogenically induced environmental changes, such as changes in disturbance regimes or nutrient eutrophication, can alter not only what species dominates locally, but also reduce among-patch heterogeneity (Mouquet et al. 2006, Urban et al. 2006, Harpole and Tilman 2007), resulting in large-scale dominance and low beta diversity. Large-scale dominance has immediate implications on species coexistence through statistical sampling based on species–area relationships. Green and Ostling (2003) illustrated that an increase of dominance and conspecific aggregations at the regional scale leads to an increase in subregional endemic species diversity, but at the same time, decreases total species diversity in that subregion.

Beyond species–area relationships, in a region where a single species dominates all locales (Fig. 3B) there will be very few immigrants representing locally rare species. Therefore, source–sink dynamics will not be a major diversity-enhancing process, and further declines in local richness should be observed as rare populations move toward extinction. In a rare test of the effects of reduced regional evenness, Urban et al. (2006) showed that large-scale anthropogenic pressures caused local richness declines as well as decreases in beta diversity in stream invertebrate communities, and that this diversity loss was reinforced by lack of sufficient immigrating species to recolonize extirpated populations.

While among-site evenness is easily understood in the context of abiotic heterogeneity, large-scale evenness can also be an emergent outcome of historical processes and stochastic community assembly, even when locales have identical abiotic characteristics (Fukami 2004, Cadotte 2007). Few studies have explicitly tested the role of history and local vs. regional dominance. However, Cadotte (2006) manipulated initial beta diversity in aquatic laboratory microcosms, including a treatment where all species were allowed to colonize all patches in a metacommunity (DD scenario above), and a treatment where no species was allowed to colonize every patch (DE). He showed that even though superior competitors dominated individual patches in the DE scenario, these patches exhibited invasion resistance and resulted in enhanced regional-scale coexistence and species richness compared to the DD scenario.

CONCLUSIONS AND OUTLOOK

Changes in species dominance have attracted increased attention because species distribution responds more rapidly to human activities than changes in species richness. This relationship has important consequences to ecosystems long before any of the species are driven to extinction. While species extinction removes species and their interactions from a community, changes in species evenness may quantitatively and qualitatively alter interaction effects not inferable from studies on

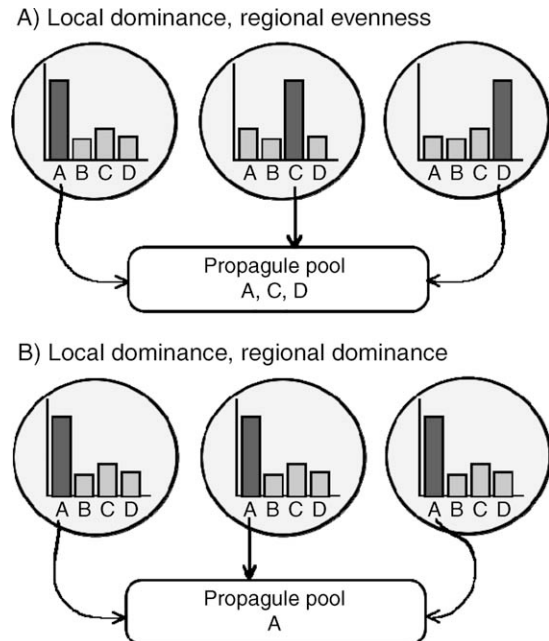


FIG. 3. Community dominance can be observed at two spatial scales, with differing consequences on ecological processes. In this cartoon, all patches contain four species (A–D), but their relative abundances vary among patches, and local dominance results in a high output of propagules. (A) Dominance at small scales can reflect superior competition for limiting resources, but heterogeneity in the dominant species at larger scales supports increased local richness through source–sink dynamics, since the propagule pool is represented by locally dominant species. (B) Regional dominance likely results from large-scale environmental changes that homogenize local conditions, and here source–sink dynamics no longer enhance local richness.

extinctions. We hope that by highlighting the importance and underrepresentation of evenness studies, ecologists will develop research programs around the effects of changes in evenness.

It is widely accepted that previous thinking about diversity–stability hypotheses strongly relied on species richness, due to concerns about loss of individual species, particularly in terms of conservation. However, concentrating exclusively on the number of species alone may limit our understanding of structure and function in ecosystems. From a conservation perspective, it is important to acknowledge that both species richness and evenness will respond in different ways to human impact (i.e., habitat fragmentations or resource homogenization). To be able to predict the consequences of human impact, it is imperative to consider the inclusion of all diversity elements in forecasting future changes.

Shifting our interest toward better understanding of species dominance and community structure does not necessarily mean that we are less concerned about species extinctions. Those two elements are very strongly related, and it makes more sense to acknowledge the role of evenness in processes such as species diversification.

Finally, both richness and evenness are rather coarse descriptors of communities, and future studies on consequences of altered community structure for ecosystem functions and regional processes will profit from a trait-based perspective, including both the mean trait values and the trait variance around this mean. Most evenness indices provide a single-value descriptor of the ratio of dominant to rare species. There is little consensus on which of the many available indices to prefer (Smith and Wilson 1996). Evenness is supposed to be a component of species diversity that should be mathematically independent from species richness. However, this is not true for many of the indices, especially at low richness (Smith and Wilson 1996). Moreover, evenness indices do not reflect whether the dominant species differs in important traits compared to the rare species. As outlined above, the consequences of dominance for ecosystem processes or species interactions may strongly differ, depending on whether the dominant species reflects average trait values or has traits dissimilar to the rest of the community. Thus, it seems necessary to define dominance not only by the frequency distribution of traits, but also by average trait values. Taxonomic distinctness measures try to integrate such information in diversity indices.

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APPENDIX

A glossary of terms related to ecosystem function is available in ESA's Electronic Data Archive (*Ecological Archives* E089-092-A1).