

Biodiversity, productivity and stability in real food webs

Boris Worm¹ and J. Emmett Duffy²

¹Institute for Marine Science, Düsternbrooker Weg 20, 24105 Kiel, Germany

The global biodiversity crisis has motivated new theory and experiments that explore relationships between biodiversity (species richness and composition in particular), productivity and stability. Here we emphasize that these relationships are often bi-directional, such that changes in biodiversity can be both a cause and a consequence of changes in productivity and stability. We hypothesize that this bi-directionality creates feedback loops, as well as indirect effects, that influence the complex responses of communities to biodiversity losses. Important, but often neglected, mediators of this complexity are trophic interactions. Recent work shows that consumers can modify, dampen or even reverse the directionality of biodiversity-productivitystability linkages inferred from the plant level alone. Such consumer mediation is likely to be common in many ecosystems. We suggest that merging biodiversity research and food-web theory is an exciting and pressing frontier for ecology, with implications for biodiversity conservation.

Complex systems such as ecosystems, societies or markets can be simplified conceptually into three basic aspects: quality, quantity and temporal stability. Accordingly, ecologists have concentrated on three fundamental aspects of ecosystems: (1) species composition and richness, which describe qualitative variation of life; (2) biomass and productivity, which refer to the quantity and rate of production of living matter; and (3) stability, which can refer to the temporal constancy of a community, resistance to environmental change, or resilience after a disturbance. Although theory indicates that species composition and richness, productivity and stability can influence one another [1-3], these properties have been studied often in isolation or in pairwise fashion. Here we integrate theory and empirical results to suggest that linkages among biodiversity, productivity and stability are likely to be bi-directional. Thus, these properties will be studied most meaningfully together to characterize the feedback loops and indirect effects that might join them. We emphasize that trophic interactions influence strongly the magnitude and direction of these linkages. Integration of biodiversityecosystem functioning with food-web research poses an exciting challenge for ecology, and might be of growing importance for the conservation and management of globally changing ecosystems.

Biodiversity and productivity: give and take

Biodiversity has two main components at the species level: 'richness', or number of species; and 'composition', or identity of those species. Among the most stimulating themes developing in ecology over the past decade is the idea that the number of species, irrespective of their identities, can significantly influence ecosystem functioning (i.e. the cycling of energy, nutrients and organic matter that keeps ecosystems working). The societal implication of this concept is that species losses could generally harm ecosystems, and ultimately the human enterprise. Yet, since the earliest experiments testing such biodiversityfunctioning linkages, debate has focused on whether the effects of biodiversity on ecosystem functioning reflect primarily the influence of species richness or of composition [4-6]. Studies that attempted to separate the effects of composition and richness in terrestrial, freshwater and marine habitats usually found that both were important [7–13]. Some studies, however, could detect only compositional effects on productivity, but no richness effect [14–15]. Compositional effects trace back typically to a few functionally dominant species. Richness effects that are independent of species composition probably result from increased facilitation and niche complementarity at high species richness [11–12,16].

These results provide a change in perspective from the historical belief that species richness and composition are consequences, rather than a cause, of changes in productivity. For example, much previous experimental, descriptive and theoretical work showed that local richness was often related unimodally to productivity [2,17–19], whereas regional richness was often a linear function of productivity [19]. Because productivity in such studies reflected experimental or environmental gradients in resource supply, the emphasis was on the productivity potential of the environment controlling species richness. Indeed the direction of causality between richness and productivity has been a major source of contention [4,12]. This is due in part to the apparent conflict between the positive richness-productivity relationship in many experimental assemblages, and the declining richness often observed in transitions from mesotrophic to eutrophic systems [2,20–21]. This seeming contradiction appears in part because experiments simulate how changing species

²School of Marine Science, The College of William and Mary, Gloucester Point, VA 23062–1346, USA

pool size affects local productivity, whereas cross-site comparisons address how the productivity potential of the environment adjusts local richness given a particular species pool [12]. These points underscore that causality between biodiversity and productivity goes both ways: increasing potential diversity (species pool size) can enhance production, whereas increasing potential productivity (resource flux) adjusts local diversity (Figure 1). Reconciliation of the seemingly conflicting patterns requires (1) accounting for processes acting in both directions, and (2) distinguishing biological productivity *per se*, which is a function of the organisms, from productivity potential, which is a function of the organism-environment interaction.

Direct and indirect effects on stability

The linkage between biodiversity and stability depends on the scale of inquiry: compared with species-poor communities, species-rich communities often show greater fluctuations within individual populations [1], increased stability at the community level [22-23]. Community stability is defined here as the inverse of the temporal variability of an assemblage, such as measured by the coefficient of variation in aggregate biomass. Experimental evidence for a positive effect of species richness on community stability comes from kelp beds [24], aquatic microbial microcosms [25-26], grasslands [22], mycorhizal fungi [27], and marine invertebrate communities [28]. The general result was that species-rich communities showed reduced variation in aggregate biomass (higher community stability) under a range of environmental conditions, including stress and disturbance. However, methodology can influence results strongly, and multiple interpretations still exist for the available data (reviewed in [23]).

Again, some of these studies have been controversial because species composition often co-varies with richness, making these effects difficult to separate. Two studies have

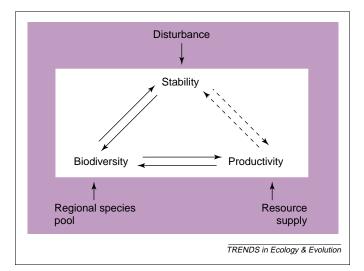


Figure 1. Reciprocal relationships among biodiversity (species composition and richness), productivity (the rate of production of organic matter) and stability (temporal constancy) within a local community (white area). Dotted arrows indicate hypothetical relationships. The effects of regional processes such as disturbance rate, resource supply and propagule supply from the regional species pool are also shown (purple area).

separated clearly compositional and richness effects on productivity and stability. One microcosm study of a simple plant-based food web documented strong effects of composition, but weak effects of diversity on community stability [29]. Plant biomass and productivity were affected strongly by both composition and diversity. Although more diverse communities tended to be more productive, stability sometimes declined with increased diversity. These results were corroborated by a grassland study, which showed that increased production in highdiversity assemblages might render them more vulnerable to drought, thereby reducing their resistance and resilience [30]. Although these two studies do not support the above-cited results that more diverse communities are more stable, they show how changes in diversity, productivity and stability are interdependent. They also suggest an indirect negative effect of a positive diversityproductivity linkage on stability. Such indirect effects could be common, but might be detectable only when diversity, productivity and stability are studied in combination.

Community stability, as defined above, is considered most meaningfully with reference to disturbances or other external events that induce destabilizing fluctuations in community biomass (Figure 1). Disturbance has welldocumented effects on local diversity. A high-disturbance environment is extremely unstable and can be tolerated usually only by few specially adapted species. Lowdisturbance environments are highly stable, but often support low species richness because competitive exclusion has time to run its course [31]. Accordingly, empirical studies in a range of ecosystems showed that highest richness often occurs at intermediate disturbance intensity or frequency, and, by inference, at intermediate community stability [2,31-33]. This illustrates again the bi-directionality of linkages between diversity and ecosystem properties. Biodiversity can influence community stability, but stability (driven by disturbance regime) can also influence diversity. As for the biodiversity-productivity linkage, the mechanisms differ in the two directions. First, diversity can increase community stability because a larger species pool provides a greater range of adaptive traits, which can keep performance stable under varying conditions. By contrast, the stability of the environment adjusts local richness within a given species pool. An intriguing question is whether a diverse community might stabilize the abiotic environment sufficiently (e.g. by ameliorating fluctuations in water availability or temperature) to influence disturbance regime and, in turn, diversity.

In conclusion, we suggest that changes in biodiversity can affect community stability, and changes in community stability can affect biodiversity (Figure 1). Finally, similar linkages might also exist between productivity and community stability. For example, one might suspect that enhanced community stability favours local productivity (Figure 1), but we know of no study that addresses these linkages explicitly.

Possible consequences

If our synthetic scheme (Figure 1) were realistic, it would have important consequences for the theory of biodiversity and for conservation because of potential feedbacks among

structural and functional, as well as biotic and abiotic, properties of ecosystems. Moreover, impacts could be mediated through both direct and indirect effects. First, it is well documented that species loss from established communities could directly change patterns of productivity and stability [34]. Such changes are mediated by compositional or richness effects, or both [12]. However, it seems highly unlikely that species losses do produce static changes in ecosystems. Instead, changes in productivity and stability might feed back dynamically on diversity, with further repercussions for ecosystem functioning. For example, a loss of structural species (trees, seagrasses, corals, or the like) could change not only mean productivity and habitat structure, but also render a community more susceptible to subsequent disturbances, leading to further destabilization and possibly the loss of other species. Indeed, simple models show that declining diversity increases the risk of further such 'cascading extinctions' [35]. Similarly, loss of functionally dominant species, such as keystone species [36], ecosystem engineers [37] or species with many trophic connections [38], would have particularly strong effects and could induce rapid and violent changes in local biodiversity.

Likewise, the loss of species can change productivity not only directly, but also indirectly through changes in the light, water and nutrient regimes. Such changes will impact often the productivity of remaining species because the local abiotic environment has changed. These changes could then feed back to adjust local diversity via the productivity-diversity link. Furthermore, these changes in productivity could affect community stability [30]. In short, we suggest that feedbacks and indirect effects among diversity, ecosystem structure and ecosystem functional processes could be important in real ecosystems.

Caught in the food web

No discussion of ecological feedbacks would be complete without considering trophic interactions, which represent perhaps the most important class of feedback phenomena in ecosystems. Yet, current understanding of linkages between biodiversity and ecosystem functioning is based largely on research in ungrazed grasslands and aquatic microcosms [39]. The majority of these studies have focused on ecosystem effects of plant species richness or composition. We know, however, that consumers influence structure and function of many ecosystems profoundly [21,40-42], and that they outnumber plant species greatly. Moreover, species at higher trophic levels generally face stronger average extinction threats than plant species, with important implications for ecosystem functioning [43]. Even in simple two-level food chains, addition of grazers can change the relationships between diversity, productivity and stability substantially from those derived from experiments that focused on plants alone. First, both theory [2,44] and field experiments [21,45] have shown that the effects of productivity and disturbance on diversity and ecosystem processes can reverse in direction depending on the presence or absence of herbivores. Second, simple grazer competition models suggest that plant community biomass generally will decline with increasing grazer diversity as the most effective grazer comes to dominate [46]. Species-rich consumer assemblages can also reduce aggregate resource abundance through complementary feeding preferences and facilitation [47,48]. The implication is that changing plant and grazer diversity might have opposite impacts on plant biomass, potentially canceling one another out (Figure 2). Experiments in microbial microcosms [49] and seagrass mesocosms [13] support these predictions and show that plant biomass declines with increasing grazer species richness. Perhaps most interestingly, positive effects of plant species richness on productivity were erased when consumers were introduced in grassland plots [50] and aquatic microcosms [51]. Invertebrate grazers also controlled algal biomass accumulation strongly in a rocky intertidal community, overriding potential effects of algal biodiversity [42]. Thus, consumers appear to change, dampen or reverse relationships between plant diversity and productivity (Figure 2). However, because so few studies have manipulated consumer diversity, the generality of these effects is uncertain.

Evaluating relationships between diversity, trophic processes and productivity might also depend on whether productivity is measured directly or estimated as plant biomass accumulation (as in most studies cited above). Perhaps the most general and ecologically significant effects of grazers are reduction of plant standing biomass and enhancement of nutrient regeneration, which together can reduce plant competition and stimulate primary productivity [52]. An important implication is that primary production and standing plant biomass might often be decoupled in grazed ecosystems [53]. Therefore, addition of consumers can decrease plant biomass, but actually increase primary production. Furthermore, there is evidence that increased grazer species richness enhances secondary production [13]. These complications have important implications for biodiversity-functioning relationships in real food webs and warrant further study.

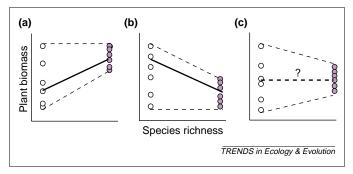


Figure 2. Potentially opposing influences of diversity on primary productivity at adjacent trophic levels as predicted from theory and recent experiments. Productivity (here measured as plant biomass accumulation) increases with plant species richness (plant diversity effect) (a), decreases with herbivore richness (grazer diversity effect) (b), but expectations are less clear with two (or more) trophic levels (net diversity effect) (c). Open and filled symbols represent low-and high-diversity assemblages, respectively. Solid lines indicate the mean, and dotted lines bound the range of hypothesized responses with changing species richness.

Emerging complexity

Although simple models and experiments suggest countervailing impacts of plants and grazers on ecosystem properties, a common theme of nearly all studies to date is the pervasiveness of complex interactions in food webs. In multilevel food webs, emergent effects of biodiversity could arise from complex trophic interactions between plants, grazers and predators, which often influence ecosystem properties through indirect effects that cannot be predicted by simply adding up their individual impacts [10,13,40,51]. Such complexity can arise from a host of indirect interactions [40] as well as interference competition among consumers or intraguild predation. Is there any hope of extracting generalizations from such complexity?

Cause for optimism comes from the vigorous research in food-web ecology, which has developed parallel themes to diversity research. Again, the core question is whether the identities of a few dominant species (called strong interactors or keystone species) or the total number of species and trophic links (including many weak interactors) determines community structure, function and stability. Interaction strength is defined as the mean per capita effect of a predator on its prey [54]. Strong interactors have disproportionate effects on community structure; for example, by keeping competitively dominant prey species in check [36]. However, real food webs appear to be characterized by many weak and only few strong interactions [54,55]. Are most species simply passengers in ecosystems that are run basically by a few dominants? Models that account for differences in interaction strength indicate that weak interactors play a crucial role by dampening oscillations between consumers and resources. and decreasing the statistical chance of extinction [55]. An analysis of 104 real food webs confirmed that many weak interactors enhance community stability and might be important in maintaining food web complexity and species diversity [56]. Likewise, recent experiments in marine food webs revealed, on average, variable and often strong effects of weak interactors [57,58].

Concluding from these studies, species composition (with respect to few strong interactors) and species richness (with respect to many weak interactors) determine jointly the structure, function and stability of communities. Therefore, biodiversity loss will transform and destabilize complex food webs, irrespective of which species are affected. Such results from food-web ecology parallel those from experimental diversity research and highlight the promise of integrating these thriving but largely separate fields.

Conclusions

We conclude that the effects of biodiversity loss on communities and ecosystems are complex owing to indirect effects and feedbacks mediated by changes in community stability, productivity and food-web interactions. Although many of these effects are poorly explored and some are entirely hypothetical, there is much empirical evidence that the loss of species can bring about complex and dramatic reorganizations of ecosystems, including trophic cascades [41], cascading extinctions [35] and rapid shifts to undesirable

stable states [59]. Trophic interactions play important roles in most of these processes. Thus, to better understand these important issues, it is crucial that biodiversity, stability and productivity are studied together in the context of real food webs. We suggest three specific topics for further research: First, the possible existence of feedback loops and indirect effects between diversity, productivity and stability calls for rigorous theoretical and empirical exploration (Figure 1). Second, we require systematic experimental and observational studies of how diversity losses at higher trophic levels influence lower trophic level diversity, productivity and stability. Of particular interest is how changes in diversity interact at different trophic levels (Figure 2). This could be addressed, for example, via factorial manipulations of plant, herbivore and predator diversity. Third, to place experimental studies in a realistic context, we need a reinvigorated search for 'community disassembly rules'; that is, general patterns in the sequence of species and functional group losses from real food webs. Uncovering such rules, if they exist, will help make diversity experiments even more relevant to addressing the ongoing crisis of eroding global biodiversity.

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