Ecology, 93(6), 2012, pp. 1482–1487

Niche and fitness differences relate the maintenance of diversity to ecosystem function: comment

Michel Loreau,[1,2,6] Jurgis Sapijanskas,[1,3]
Forest Isbell,[1,4] and Andy Hector[5]

The relationship between biodiversity and ecosystem functioning (BEF) has been one of the most vibrant research fields in ecology and environmental sciences over the past two decades. Hundreds of experiments have now manipulated species diversity to test its effects on a wide range of ecosystem properties. Methods that partition the effect of functional complementarity between species from that of selection for species with particular traits have been instrumental in clarifying the results of these experiments and in resolving debates about potential underlying mechanisms (Loreau and Hector 2001, Cardinale et al. 2007). Relatively few studies, however, have sought to disentangle the actual biological mechanisms at work in the effects of biodiversity on ecosystem functioning. Yet theory shows that different coexistence mechanisms can lead to different BEF relationships (Mouquet et al. 2002). Understanding the mechanisms that drive the functional consequences of biodiversity and their connections with those that determine the maintenance of biodiversity is key to making BEF research more predictive and more relevant to natural, non-experimentally manipulated ecosystems (Loreau 2010).

The recent theoretical study by Carroll, Cardinale, and Nisbet (2011; hereafter CCN) makes a valuable contribution toward the goal of linking the maintenance of diversity and its functional consequences. CCN use MacArthur's (1972) classical consumer–resource model to develop new measures of niche difference (ND) and relative fitness difference (RFD) between consumers. They then explore the relationships between these new measures and the widely used additive partition (AP) of the net biodiversity effect into a complementarity effect (CE) and a selection effect (SE), as well as the relative yield total (RYT), a measure closely related to CE (Loreau and Hector 2001). Their analysis leads them to conclude that "post hoc statistical methods currently used to discern the mechanisms that drive effects of diversity on biomass do not necessarily reflect real biological processes that relate to mechanisms of species coexistence." This conclusion serves as a reminder that, however useful, no post hoc analysis will ever be able to replace detailed knowledge of the biological mechanisms at work.

But CCN also suggest that the ND and RFD metrics they devise are more appropriate than AP for identifying mechanisms that drive BEF relationships; accordingly, they propose that future theoretical and empirical work should focus on "predicting community biomass from three independent variables: ND, RFD, and species richness." As we explain here, we feel that these additional conclusions are unwarranted; they are based on the implicit assumption that CCN's new approach is intrinsically better than AP without any independent demonstration that it does in fact do a better job. On the other hand, CCN's study raises valid questions about the scope and limitations of AP, which has been sometimes liberally interpreted in the recent literature. In this comment, therefore, we would like to (1) revisit the scope and limitations of the AP approach, (2) discuss some of the limitations of CCN's new proposed approach, and (3) briefly suggest some directions that could be taken to move BEF research forward.

When two of us proposed AP 10 years ago (Loreau and Hector 2001), it was in the context of a raging debate about the interpretation of BEF experiments (Loreau et al. 2001). The main interest of this approach was to allow testing of hypotheses that assume changes in numerical dominance among species but no functional complementarity, such as the much-debated "sampling effect" and "mass ratio" hypotheses. Essentially, these hypotheses propose that changes in community production or biomass can be explained simply by zero-sum changes in the relative abundances of species in mixture. The alternative, that communities are more (or less) than the sum of their parts, has for a long time been termed overyielding (or underyielding). AP has played a

Manuscript received 13 May 2011; revised 5 October 2011; accepted 7 October 2011. Corresponding Editor: S. J. Schreiber.

[1] Department of Biology, McGill University, 1205 avenue Docteur Penfield, Montreal, Quebec H3A 1B1 Canada.
[2] Centre for Biodiversity Theory and Modelling, Experimental Ecology Station, Centre National de la Recherche Scientifique, 09200 Moulis, France.
[3] AgroParisTech ENGREF, 19 avenue du Maine, 75015 Paris, France.
[4] Department of Ecology, Evolution and Behavior, University of Minnesota, 1987 Upper Buford Circle, Saint Paul, Minnesota 55108 USA.
[5] Institute of Evolutionary Biology and Environmental Studies, University of Zürich, Winterthurerstrasse 190, 8057 Zürich, Switzerland.
[6] E-mail: michel.loreau@ecoex-moulis.cnrs.fr

valuable role for testing these types of null hypothesis via its two components, SE and CE.

SE is a straightforward application of a basic statistical approach: it is a covariance term that relates the performance of a species in mixture (whether its relative yield increases or decreases relative to expectations) to its monoculture biomass. It is positive when species with large monoculture biomasses on average perform better in mixtures, and negative when the reverse is true. When changes in relative abundances follow a zero-sum game, then SE (whatever its sign) will explain the effects of diversity on mixture yield. Ecologists are familiar with covariances and correlations; thus SE is relatively simple and easy to understand.

CE quantifies overyielding, i.e., an increase in mixture yield above the zero-sum expectation (or underyielding when mixtures produce less than expected), which provides a simple, operational way to define functional complementarity by its net effect at the community level. Although technically CE has the dimension of absolute yield, one advantage is that it is closely related to the relative yield and RYT concepts used in plant ecology and intercropping since the 1950s and they are therefore once again familiar to ecologists and relatively well understood. In addition, CE and RYT have the nice property of being directly connected to the conditions for stable coexistence in the classical Lotka-Volterra competition model (Vandermeer 1981, Loreau 2004).

In total, the AP and RYT frameworks are relatively simple and based on long-established methodologies that are familiar to many ecologists. We therefore feel that, despite their limitations, they will continue to have great value for performing tests of null hypotheses such as the sampling effect and mass ratio hypotheses, and for generating alternative hypotheses about possible mechanisms underlying BEF relationships detected in experiments.

It is important to note, however, that CE and RYT do not provide quantitative measures of resource partitioning because they potentially combine the effects of a wide range of species interactions, as one of us established clearly (Loreau 1998). A positive CE (or, equivalently, $RYT > 1$) means that niche differentiation (partitioning of either resources or natural enemies), positive interactions, or some combination thereof, are strong enough to outweigh interference competition or other negative species interactions that might decrease relative yields in mixture. Conversely, a negative CE (or $RYT < 1$) indicates that negative species interactions are strong enough to outweigh the positive effects of niche differentiation and positive interactions on relative yields in mixture. Thus, AP was devised as a tool to test hypotheses, not as a tool to identify the type and strength of species interactions. It is the sign and relative magnitude of CE and SE that matter in hypothesis testing, while their absolute magnitudes should be interpreted more cautiously because of the range of biological processes that can affect them.

Liberal interpretations of AP as a means to identify and quantify species interactions may have resulted from ambiguous usage of the term "mechanism" in the BEF literature as well as in other areas of ecology. A "mechanism" denotes any lower-level process that contributes to generating a higher-level "phenomenon" of interest. In this sense, although CE and SE, the two components of AP, provide information about which mechanisms are compatible with the observed effects of biodiversity on ecosystem functioning, they do not themselves correspond to particular biological mechanisms because they combine the effects of a potentially wide range of individual-level processes on the community-level phenomenon of yield, hence their appropriate designation as "effects." The literature, however (including Loreau and Hector 2001), has often used the terms "mechanisms," "classes of mechanisms," or "types of mechanisms" to describe CE and SE, leading sometimes to the improper interpretation that they quantify individual-level biological processes. Just as with any other approach, greater terminological and conceptual clarity is likely to help better appreciate the scope and limitations of AP.

The new approach proposed by CCN relies on an attempt to formalize Chesson's (2000) conceptual distinction between stabilizing and equalizing coexistence "mechanisms." They build measures of ND and RFD that capture these two "mechanisms" based on the sensitivities of species' invasion rates to interspecific competition. Specifically, ND is measured as one minus the geometric mean of these sensitivities, while RFD is measured as their geometric standard deviation. CCN then show that both increasing ND and decreasing RFD increases RYT and CE, in contrast to their intuitive expectations that only ND should affect RYT and CE based on the assumption that the latter measure resource partitioning between species. This particular result leads them to conclude that current measures of functional complementarity "give a largely skewed estimate of resource partitioning." There are, however, several fundamental problems with this interpretation.

The first problem follows directly from the above discussion of the concept of "mechanism." While Chesson's distinction is useful to identify two types of constraints that affect coexistence, we know of no evidence that these constraints reflect independent biological processes, and hence that they correspond to distinct biological mechanisms. Just as with CE and SE, the so-called stabilizing and equalizing "mechanisms" define effects at the community level (specifically, on coexistence); these effects also summarize a wide range of species interactions, including resource partitioning, natural enemy partitioning, facilitation, and interference. Even in the specific context of consumer-resource interactions considered by CCN, deterministic niche differences between species include differences in niche height (absolute level of resource consumption), niche breadth, and niche overlap. Differences in niche height and niche breadth are usually implicitly related to RFD, while low niche overlap is usually associated with ND (despite the fact that niche overlap is only one component of niche differences) because it is a necessary condition for stable coexistence. Differences in niche height and niche breadth, however, also affect quantitative measures of niche overlap and the amount of niche overlap that is necessary to allow coexistence. Therefore, except in special cases, ND and RFD should be expected to reflect the operation of a number of overlapping lower-level processes. Thus, our first conclusion is that AP and the distinction between stabilizing and equalizing "mechanisms," or, more appropriately, effects, are two alternative ways to sort the community-level effects of individual-level mechanisms.

A second conclusion follows immediately from the first. Since the two alternative frameworks provide different ways to define and aggregate the community-level consequences of individual-level processes and since they work with different quantities (sensitivity of invasion rates to interspecific competition vs. yield), it is hardly surprising that they produce different results. The fact that both ND and RFD affect CE and SE can be no more an argument for rejecting the latter than the reciprocal fact that both CE and SE affect ND and RFD would be an argument for rejecting ND and RFD. Therefore, without some independent confirmation, CCN's results neither justify their suggestion that ND and RFD are more appropriate than AP for identifying mechanisms that drive the BEF relationships, nor do they support their claim that CE gives a skewed estimate of resource partitioning.

This brings us to a third issue: the specific limitations of the ND and RFD metrics within the context of BEF research. In contrast to AP, which was tailored to test hypotheses about the effects of biodiversity on yield, ND and RFD bear no necessary relation to yield and other ecosystem properties that are measured in biodiversity experiments. The simple relationships that are often assumed between community-level resource depletion, production, and biomass at equilibrium hold only under restricted conditions that may apply to annual plants but not necessarily to other organisms (Loreau 2010). The connections between these equilibrium properties and the sensitivity of species' invasion rates to interspecific competition are bound to be even weaker because the traits that govern a species' ability to invade a subset of a community are not necessarily the same as those that govern its yield once established in the full community. There is mounting evidence that the strength of trophic interactions depends on the presence and density of other species and that these trophic interaction modifications themselves interact (Golubski and Abrams 2011), generating a plethora of higher-order density-dependent effects in communities. For instance, Bogran et al. (2002) demonstrated phenotypic plasticity in host use by parasitoids along two niche axes, such that parasitoid species that appear redundant when studied independently may become complementary when they coexist. In such cases, niche differences measured using invasion rates have little to do with overyielding detected in biodiversity experiments. Experimental evidence also suggests that both the magnitude and the nature of biodiversity effects may change over time (Cardinale et al. 2007). Thus, while sensitivities of invasion rates are useful within the context of coexistence theory, it is doubtful that they will generally provide robust predictors of equilibrium ecosystem properties. It is also unclear how ND and RFD can be used to test some of the basic hypotheses of interest in BEF research. For instance, the sampling effect hypothesis assumes specifically that the species with the highest monoculture yield or carrying capacity outcompetes the others in mixtures. ND and RFD are unable to test this hypothesis because, contrary to SE, they are insensitive to the ranking of species' carrying capacities (Appendix A). For all these reasons, it seems to us that the AP approach has a distinct practical advantage for hypothesis testing in biodiversity experiments.

Last, the results reported by CCN are largely restricted to two-species systems, with some additional simulations for three and four species. Although the general trends they reveal seem to be robust, they should not mask some significant deviations from these trends, which confirm that ND and RFD bear no simple relations to overyielding, and hence that their use as tools to interpret biodiversity experiments would require more careful examination. In particular, CCN's central result that RYT (and hence CE) increases as ND increases and as RFD decreases does not always hold, even within the restricted scope of MacArthur's model. For some scenarios and parameter values, opposite patterns can be found.

To illustrate and understand this possibility, we use the continuous formulation of MacArthur's model because it provides an explicit measure of niche differences (sensu niche overlap) between species along a resource gradient (Sapijanskas and Loreau 2010), and we focus on the specific example of four consumer species distributed in two functional groups. For simplicity, we assume that the two species in each functional group i have the same niche width, σ_i, and that the two functional groups are different enough (i.e., are spread out enough along the resource gradient) that competitive interactions between groups is negligible. In this case, ND, RFD, and RYT can be obtained analytically (Appendix B):

$$\mathrm{ND} = 1 - \exp\left[-\frac{1}{8}\left(\frac{\Delta_1^2}{\sigma_1^2} + \frac{\Delta_2^2}{\sigma_2^2}\right)\right] \tag{1}$$

$$\mathrm{RFD} = \exp\left\{\frac{1}{8}\sqrt{\left(\frac{\Delta_1^2}{\sigma_1^2} - \frac{\Delta_2^2}{\sigma_2^2}\right)^2 + 32\left[\left(\log\frac{K_{1a}}{K_{1b}}\right)^2 + \left(\log\frac{K_{2a}}{K_{2b}}\right)^2\right]}\right\} \tag{2}$$

$$\mathrm{RYT} = \frac{2 - \exp\left(-\frac{\Delta_1^2}{4\sigma_1^2}\right)\left(\frac{K_{1a}}{K_{1b}} + \frac{K_{1b}}{K_{1a}}\right)}{1 - \exp\left(-\frac{\Delta_1^2}{2\sigma_1^2}\right)} + \frac{2 - \exp\left(-\frac{\Delta_2^2}{4\sigma_2^2}\right)\left(\frac{K_{2a}}{K_{2b}} + \frac{K_{2b}}{K_{2a}}\right)}{1 - \exp\left(-\frac{\Delta_2^2}{2\sigma_2^2}\right)} \tag{3}$$

where K_{ia} and K_{ib} are the carrying capacities of the two species in functional group i, and Δ_i is the distance between their niche centers along the resource gradient.

As expected, ND decreases exponentially as niche overlap within functional groups increases (remember that niche overlap between functional groups is assumed to be negligible). RFD has two components: the first term under the square root in Eq. 2 is a measure of the difference between the two functional groups in the amount of niche overlap within the group, while the second is a measure of competitive dominance within the groups. Note that niche overlap affects both ND and RFD, such that the two measures are not independent from each other, as we suggested above based on intuitive arguments. But niche overlap and competitive dominance interact more strongly in RYT since the relative yield total of each functional group weighs the effect of niche overlap by competitive imbalance such that decreased niche overlap has a disproportionately larger positive effect when species are competitively dissimilar (i.e., when $K_{ia}/K_{ib} + K_{ia}/K_{ib}$ is larger). Since RYT incorporates the effects of niche overlap and competitive imbalance in different ways than do ND and RFD, all sorts of relationships between these measures are possible, including relationships that are opposite to those found by CCN, i.e., RYT can decrease, rather than increase, as ND increases and as RFD decreases (Fig. 1). Note that these findings do not prove that there is anything intrinsically wrong with the approach based on ND and RFD. But they do challenge the use of these metrics as some sort of self-evident reference against which RYT and AP should be assessed. We see no justification for assuming the superiority of the first approach over the second.

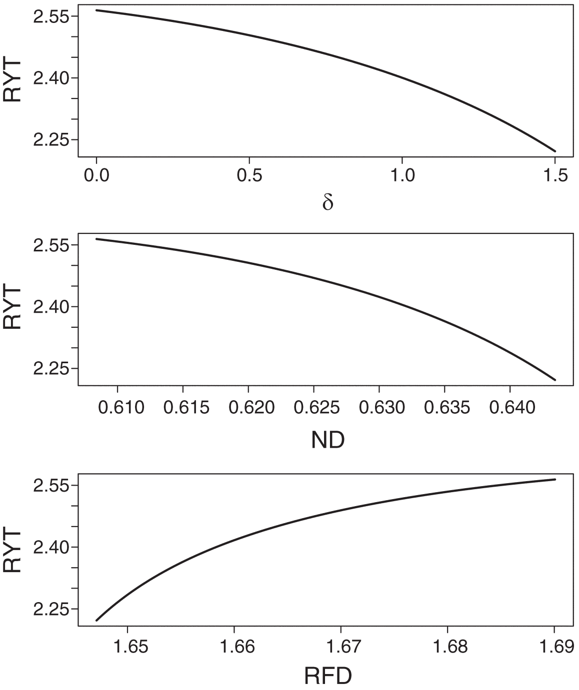

FIG. 1. Changes in the relative yield total, RYT, and the resulting relationships between RYT and niche difference (ND) or relative fitness difference (RFD) when niche overlap varies in a community of four species distributed in two functional groups (Eqs. 1–3). Niche overlap is here varied in opposite directions in the two functional groups using the following transformation:

$$\left\{\frac{\Delta_1^2}{\sigma_1^2}, \frac{\Delta_2^2}{\sigma_2^2}\right\} \to \left\{\frac{\Delta_1^2}{\sigma_1^2} - \delta, \frac{\Delta_2^2}{\sigma_2^2} + 1.5\delta\right\}$$

where δ is a nonnegative parameter that allows niche overlap to vary from the reference situation (in which $\delta = 0$). K_{ia} and K_{ib} are the carrying capacities of the two species in functional group i, Δ_i is the distance between their niche centers along the resource gradient, and σ_i is the niche width of group i. Parameters were chosen such that there is both greater niche overlap ($\Delta_1/\sigma_1 < \Delta_2/\sigma_2$) and greater competitive imbalance ($K_{1a}/K_{1b} + K_{1b}/K_{1a} > K_{2a}/K_{2b} + K_{2b}/K_{2a}$) in the first functional group. ND and RFD are increasing and decreasing functions, respectively, of δ. Yet, RYT decreases with δ because the competitive imbalance between the two groups is sufficiently large for the positive effect of reduced niche overlap in the second group ($\Delta_2^2/\sigma_2^2 + 1.5\delta$) to overwhelm the negative effect of increased overlap in the first ($\Delta_1^2/\sigma_1^2 - \delta$) (Appendix C). In this example, $\Delta_1^2/\sigma_1^2 = 3$, $\Delta_2^2/\sigma_2^2 = 4.5$, $K_{2a} = K_{2b}$, and $K_{1a} = 2K_{1b}$. Stable coexistence of the four species requires $\delta < 1.4$.

Where does all this leave the BEF research field? Methods based on relative yield, in particular AP, have been the primary tool used in identifying biodiversity effects over the last 10–15 years. CCN's study reiterates that CE cannot be directly equated to resource partitioning, and shows that CE and SE do not correspond to stabilizing and equalizing coexistence effects. This is not surprising because CE and SE were not developed to quantify resource partitioning or coexistence mechanisms. Instead, CE and SE are useful tools to test hypotheses. For example, Cardinale (2011) used AP in the analysis of a recent experiment where SE and CE appear to do a good job in identifying the signatures of species dominance and complementarity, respectively. Unfortunately, the ND and RFD measures proposed by CCN are also unable to quantify biological processes such as resource partitioning because, like CE and SE, they are net measures of multiple biological processes. Thus, it is unclear how they can contribute to enhance our ability to detect biological mechanisms.

Given the limitations inherent in all preexisting post hoc statistical methods (reviewed in Hector et al. 2009) and CCN's new approach, how can we make further progress in understanding the mechanisms that explain the maintenance of biodiversity and its functional consequences? We believe that such progress requires at least two key ingredients. The first is expanding theory that connects the microscopic mechanics of species interactions and the macroscopic properties of whole ecosystems. There have been recent developments in this area (Loreau 2010), and we welcome CCN's work as a new contribution toward this shared goal. The main challenge for theory development will be to keep a unifying perspective while examining the mechanistic details of species interactions. The distinction between stabilizing and equalizing coexistence effects provides one possible unifying framework, but others are conceivable. One of the important roles of ecological theory should be to build and explore alternative unifying frameworks that link the microscopic and macroscopic properties of ecosystems. Second, we need a new generation of experiments that analyze the individual- and population-level processes that generate the effects of biodiversity on ecosystem functioning. When two of us proposed the AP methodology (Loreau and Hector 2001), we concluded that this methodology "cannot replace direct experimental investigations into the mechanisms at work in responses to biodiversity changes at the ecosystem level, which are now critical to further progress in this area." This conclusion is still topical today. A few pioneering studies have experimentally manipulated available niche space (Dimitrakopoulos and Schmid 2004, Cardinale 2011) or species' niches through evolution (Gravel et al. 2011) to test for the role of resource partitioning in shaping BEF relationships. Others have manipulated intra- and interspecific population densities simultaneously to disentangle the roles of niche differences and facilitation in overyielding (Gross et al. 2007, Northfield et al. 2010). Still others have manipulated the presence of mutualists (van der Heijden et al. 1998) or pathogens (Maron et al. 2011, Schnitzer et al. 2011) to test for their role in driving BEF relationships. But overall the number of studies that have tested underlying mechanisms explicitly is still too limited to draw general conclusions on the lower-level processes that drive BEF relationships and the way these processes interact. Combining innovative theory and experiments that allow us to disentangle these processes and bring them together in a coherent unifying framework should now be a major research focus in community and ecosystem ecology.

Acknowledgments

M. Loreau was supported by the Natural Sciences and Engineering Research Council of Canada and the Canada Research Chair program. J. Sapijanskas was funded by the French Ministry of Agriculture. A. Hector was supported by Microsoft Research as a visiting researcher in computational ecology and environmental sciences.

Literature cited

Bogran, C. E., K. M. Heinz, and M. A. Ciomperlik. 2002. Interspecific competition among insect parasitoids: field experiments with whiteflies as hosts in cotton. Ecology 83:653–668.

Cardinale, B. J. 2011. Biodiversity improves water quality through niche partitioning. Nature 472:86–89.

Cardinale, B. J., J. P. Wright, M. W. Cadotte, I. T. Carroll, A. Hector, D. S. Srivastava, M. Loreau, and J. J. Weis. 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. Proceedings of the National Academy of Sciences USA 104:18123–18128.

Carroll, I. T., B. J. Cardinale, and R. M. Nisbet. 2011. Niche and fitness differences relate the maintenance of diversity to ecosystem function. Ecology 92:1157–1165.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31:343–366.

Dimitrakopoulos, P. G., and B. Schmid. 2004. Biodiversity effects increase linearly with biotope space. Ecology Letters 7:574–583.

Golubski, A. J., and P. A. Abrams. 2011. Modifying modifiers: what happens when interspecific interactions interact? Journal of Animal Ecology 80:1097–1108.

Gravel, D., T. Bell, C. Barbera, T. Bouvier, T. Pommier, P. Venail, and N. Mouquet. 2011. Experimental niche evolution alters the strength of the diversity–productivity relationship. Nature 469:89–92.

Gross, N., K. N. Suding, S. Lavorel, and C. Roumet. 2007. Complementarity as a mechanism of coexistence between functional groups of grasses. Journal of Ecology 95:1296–1305.

Hector, A., T. Bell, J. Connolly, J. Finn, J. W. Fox, L. Kirwan, M. Loreau, J. McLaren, B. Schmid, and A. Weigelt. 2009. The analysis of biodiversity experiments: from pattern toward mechanism. Pages 94–104 *in* S. Naeem, D. E. Bunker, A. Hector, M. Loreau, and C. Perrings, editors. Biodiversity, ecosystem functioning, and human wellbeing: an ecological and economic perspective. Oxford University Press, Oxford, UK.

Loreau, M. 1998. Separating sampling and other effects in biodiversity experiments. Oikos 82:600–602.

Loreau, M. 2004. Does functional redundancy exist? Oikos 104:606–611.

Loreau, M. 2010. From populations to ecosystems: theoretical foundations for a new ecological synthesis. Princeton University Press, Princeton, New Jersey, USA.

Loreau, M., and A. Hector. 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412:72–76.

Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294:804–808.

MacArthur, R. H. 1972. Geographical ecology: patterns in the distribution of species. Princeton University Press, Princeton, New Jersey, USA.

Maron, J. L., M. Marler, J. N. Klironomos, and C. C. Cleveland. 2011. Soil fungal pathogens and the relationship between plant diversity and productivity. Ecology Letters 14:36–41.

Mouquet, N., J. L. Moore, and M. Loreau. 2002. Plant species richness and community productivity: why the mechanism that promotes coexistence matters. Ecology Letters 5:56–65.

Northfield, T. D., G. B. Snyder, A. R. Ives, and W. E. Snyder. 2010. Niche saturation reveals resource partitioning among consumers. Ecology Letters 13:338–348.

Sapijanskas, J., and M. Loreau. 2010. Cascading extinctions, functional complementarity, and selection in two-trophic-level model communities: a trait-based mechanistic approach. Journal of Theoretical Biology 267:375–387.

Schnitzer, S. A., J. N. Klironomos, J. HilleRisLambers, L. L. Kinkel, P. B. Reich, K. Xiao, M. C. Rillig, B. A. Sikes, R. M. Callaway, S. A. Mangan, E. H. v. Nes, and M. Scheffer. 2011. Soil microbes drive the classic plant diversity–productivity pattern. Ecology 92:296–303.

van der Heijden, M. G. A., J. N. Klironomos, M. Ursic, P. Moutgolis, R. Streitwolf-Engel, T. Boller, A. Wiemken, and I. R. Sanders. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature 396:69–72.

Vandermeer, J. 1981. The interference production principle: an ecological theory for agriculture. BioScience 31:361–364.

Supplemental Material

Appendix A

Proof showing that, contrary to the selection effect (SE), niche difference (ND) and relative fitness difference (RFD) are insensitive to the ranking of carrying capacities in the classical two-species Lotka-Volterra model (*Ecological Archives* E093-130-A1).

Appendix B

MacArthur's model with four species and two functional groups distributed along a continuous resource gradient (*Ecological Archives* E093-130-A2).

Appendix C

Proof that reduced niche overlap has a stronger effect on the relative yield total of functional group *i* (RYT$_i$) when competitive imbalance is higher in MacArthur's model with four species and two functional groups (*Ecological Archives* E093-130-A3).

Ecology, 93(6), 2012, pp. 1487–1491
© 2012 by the Ecological Society of America

Niche and fitness differences relate the maintenance of diversity to ecosystem function: reply

Ian T. Carroll,[1,3] Bradley J. Cardinale,[2] and Roger M. Nisbet[1]

In Carroll et al. (2011), we used a novel interpretation of Chesson's (2000) stabilizing and equalizing mechanisms of biodiversity to link the causes of diversity to its consequences for biomass yield. We defined two quantities, niche difference (ND) and relative fitness difference (RFD), and showed how these jointly control the relative yield total (RYT) in a simple version of MacArthur's consumer–resource model. Our work exemplified how theory can link the maintenance of biodiversity to its impacts on ecosystem functioning and revealed that mechanisms that reduce fitness inequality can have the same effect on yield as mechanisms that increase a niche difference. We also demonstrated a systematic deviation between ND and the complementarity effect (CE), a component of the method of additive partitioning that has been widely calculated for biodiversity experiments (AP; Loreau and Hector 2001). MacArthur's model provides an explicit case in

Manuscript received 13 May 2011; revised 5 October 2011; accepted 7 October 2011. Corresponding Editor: S. J. Schreiber.

[1] Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, California 93106 USA.

[2] University of Michigan, School of Natural Resources and Environment, Ann Arbor, Michigan 48109 USA.

[3] E-mail: carroll@lifesci.ucsb.edu

which CE, contrary to its frequent interpretation, is not equivalent to niche partitioning.

In their comment, Loreau et al. (2012; hereafter Loreau et al.) question the value of our work on the ND and RFD concepts, stating that "[their] results neither justify their suggestion that ND and RFD are more appropriate than AP for identifying mechanisms that drive the BEF relationships, nor do they support their claim that CE gives a skewed estimate of resource partitioning." We did not suggest that ND and RFD should replace additive partitioning. As we discuss here, AP can provide useful information about biodiversity studies, so long as it is interpreted correctly. But we did show that ND/RFD does a better job of identifying the biological mechanisms that drive *coexistence* in MacArthur's model. ND unambiguously quantifies the strength of resource partitioning whereas CE clearly confounds effects of resource partitioning and fitness differences. We agree with Loreau et al. that, like AP, ND/RFD respond to multiple biological mechanisms. But we demonstrated that the biological mechanisms causing variation in ND/RFD can be possible to discern and always relate more directly to the means of coexistence than do the mechanisms causing variation in AP.

Loreau et al. also observe that ND/RFD "bear no *necessary* relation" to yield or other equilibrium properties (emphasis added), and use this to argue against any further study of associations between ND, RFD, and RYT. We agree that metrics like ND and RFD, which are based on invasion rates of small populations, do not *in general* determine the equilibrium properties of a dynamical system. To argue that invasibility never bears any relation to equilibrium properties like RYT, however, precludes exploring the possibility that some ecological processes may drive both BEF relationships and coexistence. Indeed, we reported that ND and RFD in MacArthur's model are very strongly associated with RYT, and proposed that this association is likely to occur in other models, and may also occur in natural communities. Even in the constrained model presented by Loreau et al., we will show below that 98% of ND and RFD adjustments that favor coexistence increase RYT, in agreement with the trend we previously reported. These successful applications of the ND/RFD metrics, along with their fundamental connection to a component of ecological dynamics that can maintain diversity, offer sufficient reason to promote, rather than discourage, further study of relationships between ND, RFD, and effects of biodiversity.

In what follows, we elaborate on the points made in the two preceding paragraphs: (1) the degree to which AP and ND/RFD can be related to biological mechanisms and (2) Loreau et al.'s concern about possible limitations to the generality of our results. The comment also advances some ideas about future research directions for BEF with which we agree, so we end our reply with additional recommendations for how to advance these goals.

Relating AP and ND/RFD to mechanisms

Loreau et al. begin by clarifying what the complementarity effect (CE) and selection effect (SE), the two metrics that together comprise their method of additive partitioning (AP), say about ecological mechanisms. At issue is whether CE can be interpreted as a measure of niche partitioning and/or facilitation. Earlier work by Loreau and Hector (2001) stated that "distinguishing the effects of niche differentiation and facilitation may often be difficult in practice; therefore, we refer to these mechanisms collectively as 'complementarity.'" In the current comment, Loreau et al. have modified their description of CE to include niche differentiation, facilitation, as well as negative interactions. Paraphrasing their comment, "complementarity" is a way of quantifying a community-level effect on overyielding that responds to the net balance of all biological interactions between species. We welcome this updated and expansive view of CE, which should bring to close any debate over whether CE quantifies niche partitioning.

But while we think that Loreau and Hector's (2001) method for partitioning yield data has been misinterpreted, we agree with Loreau et al.'s current point that ND and RFD are not synonymous with a specific biological mechanism. ND and RFD simply distinguish two categories of biological process that drive interspecific competition and thereby impact the possibility of competitive coexistence. Any researcher who directly measures ND in an experiment has simply quantified average interspecific competition, reductions of which are the dynamical result of niche differentiation. But obtaining this value empirically does not reveal the source of competition (e.g., nutrients, breeding sites, release from predators, etc.), nor does it say which species in the system exhibit niche partitioning. Thus, just as CE should not be interpreted as a particular biological mechanism, neither should ND or RFD be assumed to describe a particular mechanism. We differ with Loreau et al., however, on putting aside these metrics because of their generality. Rather than ignoring them, researchers should compliment measurement of these metrics with careful theoretical or empirical analysis, conducted in specific systems, that reveals precisely what mechanisms drive the effects measured by AP and ND/RFD.

Our original paper exemplifies how ND/RFD can be related to fundamental ecological mechanisms using MacArthur's consumer–resource model. We gave a detailed account of how biological processes in the model control ND and RFD, despite Loreau et al.'s claim that such an understanding is impossible to achieve. Moreover, by explicitly relating CE/SE to

ND/RFD, we also showed how the same biological processes drive the results of AP. Chesson (1990) revealed how a few key processes in MacArthur's model, including linear functional responses, constant per-capita mortality and logistically growing resources, drive what we later called ND and RFD. Chesson's (1990) insight was that resource partitioning can be measured by a correlation coefficient (Chesson's ρ), which he could write in terms of the (mechanistic) model parameters. Our paper showed that, by measuring consumer populations' growth rates and calculating ND you achieve the very same measure of resource partitioning. Within the constraints of MacArthur's model, ND precisely equates to resource partitioning.

Our mechanistic interpretation of ND in MacArthur's model undermines Loreau et al.'s statement that we failed to "support [our] claim that CE gives a skewed estimate of resource partitioning." Loreau et al. overlook the fact that ND, although multifaceted in general, is a precise measure for resource partitioning, and only resource partitioning, in MacArthur's model. Knowing this, we further showed that CE would only be fully determined by resource partitioning in the case of perfect symmetry between two consumers' sensitivity to competition (when $S_1 = S_2$ in our Eq. 5). When there is any asymmetry in the consumers' sensitivity to competition (as is probably always true), CE will return a value less than what occurs in a symmetric community with the same level of resource partitioning. Contrary to the claim of Loreau et al., this means CE does indeed give a biased estimate of resource partitioning in MacArthur's model. That conclusion could only be refuted by finding a correspondence between CE and some other precise measure of resource partitioning in a competition model that allowed asymmetric competition; for example, if Loreau et al. had found that only their niche overlap parameters (Δ_i and σ_i) controlled CE. For the purpose of measuring resource partitioning between two of MacArthur's consumers, ND in fact does better than CE, and no independent confirmation is necessary.

Real competitors are not bound by MacArthur's rules, so it is reasonable for Loreau et al. to raise the question of whether ND and RFD provide information about biological mechanisms independently of the system in which they are measured. In particular, their comment expresses skepticism about whether ND truly measures niche differences in the way it was once thought that CE measured niche partitioning. The logic of ND is derived from a way of describing the ecological niche recently advanced in coexistence theory (Adler et al. 2007). In this framework, the niche involves any property of an ecosystem that affects population regulation, and niche differences describe any cause for self-regulation to be greater than regulation by the populations of other species. Thus, while ND does not necessarily correspond to a particular biological process (e.g., differential use of nutrients), it does categorize ecological mechanisms according to important principles in coexistence theory. The level of abstraction needed to define ND and RFD also allows them to be compared across different ecosystems, a critical feature for understanding how the strength of coexistence varies across ecological communities.

Association between ND/RFD and RYT

Loreau et al.'s second major concern is with the generality of our conclusions. Their comment offers two lines of reasoning for why ND/RFD might be poor predictors of RYT. First, they point to recent experimental evidence that controls over RYT at equilibrium can be decoupled from the fate of invaders, the possibility of which was long ago recognized in theory (Maynard Smith 1974: chapter 5). Second, they examine a model with four consumers, and find that certain parameter choices can simultaneously increase ND, decrease RFD and decrease RYT. This response of RYT to changes in ND and RFD is opposite from what we report for just two consumers, so Loreau et al. suggest that their finding counters the generality of our results. We address each line of reasoning in turn.

Loreau et al. first point out the potential for decoupling between the growth rates of small populations invading established communities and the biomass yield of the system at equilibrium. It is certainly true that the dynamics of small populations do not dictate properties of the system near some other equilibrium. For example, well known mechanisms like Allee effects can cause small populations to go extinct while allowing larger ones to reach a stable, interior equilibrium. Loreau et al. cite recent studies confirming plasticity in trophic interactions that might also isolate invasion dynamics from equilibrium properties. But this is not as strong a limitation of the ND/RFD metrics as Loreau et al. suggest. Our original paper clearly rests on the premise (whose limitations are noted in Appendix A to the original) that coexistence is decided by long-run low-density growth rates, "for it is at the boundary that questions of coexistence have ultimately to be settled" (Law and Blackford 1992). When our premise holds, any theory that links coexistence mechanisms with biodiversity-function relationships will have to introduce metrics such as ND/RFD that characterize invasibility. The challenge is to determine how rapidly the demonstrated coupling between the growth rates of small populations and the long run effects of diversity on yield disappears with additional complexity.

In their comment, Loreau et al. present a specific theoretical result that runs counter to the trend reported in our paper, and they claim this as evidence for a lack of generality in our conclusions. Contrary to their claim, a complete analysis of Loreau et al.'s hypothetical community of four consumers in two guilds shows that the conclusions presented in our paper are robust. Their version of MacArthur's consumer–resource system is more complex than our two-consumer case, but still simple enough to allow an exhaustive exploration of the model parameters. Loreau et al. explored the parameters enough to show that ND and RFD can have an array of effects on RYT. We also investigated their model and found that, considering the entire parameter space, Loreau et al.'s characterization only holds for 2% of ND and RFD perturbations (our calculation is described fully in the Appendix). The other 98% of perturbations that increase ND or decrease RFD also *increase* RYT. The rare case that Loreau et al. interpret as a "counter-example" does not detract from the general trend reported in our paper.

We know that ND/RFD are not going to constrain RYT so tightly in every model or ecological community, but that is no reason to abandon them. The linear functional response in MacArthur's model, which strongly links the boundary and interior equilibria, is undoubtedly responsible for the tight relationships we report. A logical next step would be to examine nonlinear functional responses, and subsequently add even greater complexity. We did not, and do not, suggest that biodiversity effects can be *universally* partitioned by ND and RFD in the manner of AP. Had this been our intent, the inability to systematically decompose RYT into a contribution from ND and a contribution from RFD would be a problem. Instead, our paper set out to discover whether or not ND/RFD have any relationship to RYT. ND/RFD are not the final answer to the question of how mechanisms that control coexistence relate to BEF relationships. Absent a truly general theory of species coexistence it is premature to expect a complete answer, but ND/RFD appear to be powerful concepts that indisputably provide a conditional answer and a reasonable point of departure for new biodiversity theory.

Where to from here?

Loreau et al. conclude with their vision for how future research might proceed to elucidate the mechanisms that underlie biodiversity effects on ecosystem-level processes. They argue that we need "expanding theory that connects the microscopic mechanics of species interactions and the macroscopic properties of whole ecosystems," and "a new generation of experiments that analyze the individual- and population-level processes that generate the effects of biodiversity on ecosystem functioning." We certainly wouldn't argue against producing more theory and better experiments. But as we do so, we believe researchers are going to have to take a more hierarchical view in their exploration of mechanisms, and will need to embrace a far greater variety of experimental and analytical tools than random biodiversity manipulations analyzed by post-hoc tests of additive partitioning.

To illustrate ways we might improve our approach, consider how we might go about testing one of the seminal hypotheses of the field of biodiversity and ecosystem functioning. From the beginning, it was hypothesized that diverse communities would be more productive than less diverse communities because niche differences among species allow diverse communities to capture a greater fraction of biologically essential resources (Tilman et al. 1997). The first step toward testing this hypothesis was to perform experiments in which we manipulated the richness of species—mostly primary producers, and often in grasslands—in experimental units (plots, pots, etc.) and then examined how richness impacted the accrual of biomass (Loreau et al. 2001). As of 2009, we had amassed 295 of these experiments documenting 479 effects of producer diversity on biomass yield, of which 86% were positive (Cardinale et al. 2011).

Many of the experiments published through 2009 used Loreau and Hector's (2001) method of additive partitioning to ask whether the documented effects of species richness on biomass yield were the result of species-specific selection effects, or alternatively, were due to the influence of more than one species. Meta-analyses of the additive partitioning metrics have shown that selection effects explain roughly 50% of the net diversity effect in the typical experiment, and the remaining 50% is attributable to "complementarity" (Cardinale et al. 2011). Values of complementarity have proven to be negative in 20% of studies (Cardinale et al. 2011), emphasizing that this metric does not represent niche partitioning or facilitation as Loreau and Hector (2001) proposed. Thus, after completing this second step, we know that diversity tends to enhance yield in the vast majority of experiments, that we cannot explain this by selection effects alone, and that biological processes involving two or more species are important. We don't have rigorous confirmation of what those biological processes might be.

Therefore, we proposed that a third step toward testing the original hypothesis might be to design additional, supplementary experiments in which we introduce each focal species into established communities that are already at steady-state and measure rates of invasion. We showed in our original paper (Carroll et al. 2011) that the geometric mean of the invasion rates can be used as a direct measure of the strength of niche differences (ND) among species. Assuming we were successful at measuring ND experimentally and compared it to a measure of overyielding, we would then know whether niche differences do, in fact, promote positive effects of biodiversity on yield. But we would still not know what those niche differences represent biologically. To get at the precise cause of niche differences among species, we have to take a fourth step that involves additional experiments in which we (1) directly manipulate or remove the presumed resources for which species express differential utilization (Cardinale 2011), (2) document spatial or temporal differences in the use of limiting biological resources (McKane et al. 1990), or (3) track or manipulate the evolution of resource specialization that allows species to coexist (Gravel et al. 2011).

Note that with each additional step, we get increasingly detailed information about the biological mechanisms that underlie the impacts of species diversity on biomass production. But greater detail comes with increasing effort and difficulty, and the added information comes at the expense of generality since the processes are more likely to depend on the specific traits of the focal species or characteristics of the system. It is for this reason that we did not suggest abandoning Loreau and Hector's (2001) metrics of additive partitioning. Those metrics are easy to calculate, and are general, which makes them broadly useful. But they contain limited information, which is why we proposed that these general methods must now be complimented by increasingly detailed theory and experiments. The field of biodiversity and ecosystem functioning will advance most quickly if we can take our generalities and augment them with more detailed case studies that get us closer to the precise biological mechanisms that are operating in individual systems. That is our hope for the field, and the motivation behind Carroll et al. (2011).

Literature cited

Adler, P. B., J. Hille Ris Lambers, and J. M. Levine. 2007. A niche for neutrality. Ecology Letters 10:95–104.

Cardinale, B. J. 2011. Biodiversity improves water quality through niche partitioning. Nature 472:86–89.

Cardinale, B. J., K. L. Matulich, D. U. Hooper, J. E. Byrnes, E. Duffy, L. Gamfeldt, P. Balvanera, M. I. O'Connor, and A. Gonzalez. 2011. The functional role of producer diversity in ecosystems. American Journal of Botany 98:572–592.

Carroll, I. T., B. J. Cardinale, and R. M. Nisbet. 2011. Niche and fitness differences relate the maintenance of diversity to ecosystem function. Ecology 92:1157–1165.

Chesson, P. 1990. MacArthur's consumer–resource model. Theoretical Population Biology 37:26–38.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31:343–366.

Gravel, D., T. Bell, C. Barbera, T. Bouvier, T. Pommier, P. Venail, and N. Mouquet. 2011. Experimental niche evolution alters the strength of the diversity–productivity relationship. Nature 469:89–92.

Law, R., and J. C. Blackford. 1992. Self-assembling food webs: a global viewpoint of coexistence of species in Lotka-Volterra communities. Ecology 73:567–578.

Loreau, M., and A. Hector. 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412:72–76.

Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294:804–808.

Loreau, M., J. Sapijanskas, F. Isbell, and A. Hector. 2012. Niche and fitness differences relate the maintenance of diversity to ecosystem function: comment. Ecology 93:1482–1487.

Maynard Smith, J. 1974. Models in ecology. Cambridge University Press, Cambridge, UK.

McKane, R. B., D. F. Grigal, and M. P. Russelle. 1990. Spatiotemporal differences in N-15 uptake and the organization of an old-field plant community. Ecology 71:1126–1132.

Tilman, D., D. Lehman, and K. Thompson. 1997. Plant diversity and ecosystem productivity: theoretical considerations. Proceedings of the National Academy of Sciences USA 94:1857–1861.

SUPPLEMENTAL MATERIAL

Appendix

Calculating the frequency of effects on relative yield total (RYT) counter to the trend reported in Carroll et al. (2011) (*Ecological Archives* E093-131-A1).