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

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

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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

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_j) 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).

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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).