

Biodiversity and Ecosystem Functioning: The Role of Trophic Interactions and the Importance of System Openness

Robert D. Holt and Michel Loreau

INTRODUCTION

A central theme in ecology is that population dynamics, species coexistence, and, ultimately, the entire organization of communities are all profoundly influenced by the complex web of trophic interactions that binds the lives of species together (Pimm 1982; Polis and Winemiller 1996). (The term "trophic interaction" here denotes feeding relationships between species, usually implying transfers of energy and nutrients.) A priori, given the growing evidence for trophic cascades (Pace et al. 1999) and other system-wide manifestations of trophic interactions (e.g., Elliott et al. 1983, Hairston and Hairston 1993; DeRuiter, Neutel, and Moore 1995; Grover and Loreau 1996), it would be shocking if trophic interactions did not significantly influence the impact of biodiversity on ecosystem processes. Indeed, there is suggestive evidence in the literature that the detailed character of trophic interactions has strong ecosystem impacts (Pastor and Cohen 1997; Naeem and Li 1998). The presence or absence of single consumer species or trophic guilds can have large ecosystem effects (Huntly 1991; Jones and Lawton 1995; see, e.g., McNaughton, Banyikwa, and McNaughton 1997; Mulder et al. 1999). For instance, at Cedar Creek, deer exclosures led to

substantial increases in both total plant biomass and soil nitrogen, concordant with changes in species composition (Ritchie, Tilman, and Krops 1998). Our purpose in this chapter is not to review such examples (which we find compelling) but to address conceptual issues on the interface of food web ecology and ecosystem ecology.

To extend the theory of plant diversity and ecosystem functioning (see chapters 2, 9, and 10) so as to encompass food web effects, we consider a two-trophic-level analogue of the basic one-level ecosystem model (see chapter 8), including explicit herbivore dynamics. Our basic approach will be to develop analogues of the "sampling effect" model (Tilman 1999b), where the sampling could occur either among producers facing herbivory, or instead among the herbivores themselves. Incorporating realistic food web dynamics greatly inflates the parameter set and analytical difficulty of the basic ecosystem model, and so as a "first pass" through the problem we sketch trends apparent from analyses of limiting cases of the basic model with herbivory. Because many consumers are highly mobile, relative to producers, it is natural to consider the consequences of different patterns of system "openness" when addressing the food web dimension of the diversity-ecosystem interface. After some general remarks on the relationship between the sampling model and community assembly, and the issues of trophic complexity and system openness, we describe how we incorporated herbivory into the basic model and present our findings. We then discuss important avenues for future work, and conclude by outlining a set of qualitative messages about the relationship of diversity and ecosystem functioning.

THE SAMPLING EFFECT MODEL AND COMMUNITY ASSEMBLY

The "sampling effect" model relates diversity to ecosystem functioning by fusing two insights (Aarssen 1997; Tilman et

al. 1997; Tilman 1999b; see also Huston 1997). The first is that the amount of interspecific phenotypic variation available that can impact ecosystem attributes should scale with the richness of the species pool from which local communities are assembled. The second is that local communities are restricted subsets of regional species pools (Roughgarden and Diamond 1986; Weiher and Keddy 1995), and that interspecific interactions restrict community membership. In some circumstances, simple rules determine which species drawn from the regional pool will dominate. For instance, the " R^* -rule" states that if a guild of competitors contends for a single resource in a stable environment, the species that persists at the lowest resource level displaces all others (Tilman 1982, 1990b).

We call such rules of local dominance and community membership "sorting rules." Tilman et al. (1997) use a sorting rule to show that total community biomass should increase monotonically with diversity, and that the pool of unconsumed resource should decline with diversity. Even complex systems at times match simple sorting rules (e.g., Tilman 1990b; Grover and Holt 1998). In this chapter we assume that species vary in such a way that a single species dominates in each trophic level. The basic question then is how rules of dominance (defining the outcome of species sorting at each level) map onto shifts in ecosystem processes, as subordinate species are replaced by dominant species during community assembly.

IMPORTANCE OF TROPHIC COMPLEXITY AND SYSTEM OPENNESS

The phenotypic diversity of primary producers pales when compared with the diversity of heterotrophic consumers (see Naeem, chapter 5 herein). A substantial fraction of the diversity of life revolves around the diversity of ways heterotrophic consumers find, capture, and utilize their resources. This diversity of trophic interactions is ex-

pressed in the reticulate patterns of food webs and in the complexity of routes for nutrient recycling. Given the great variety of food web structures that exist among communities, in the search for general principles relating trophic interactions to ecosystem functioning we expect a priori to find numerous exceptions to any suggested generalization, depending on the detailed interaction structure of multi-trophic communities. We suspect the great diversity of food web patterns may provide one class of explanations for variability among systems in ecosystem functioning.

For instance, consumers can profoundly change rules of coexistence and exclusion for producers, as well as alter the relative abundances of those producers that do coexist (Holt, Grover, and Tilman 1994; Grover and Holt 1998; Leibold 1996; Olff and Ritchie 1998). Take almost any model of competitive interactions among producers and add herbivory. If herbivores are tightly specialized to particular producer species, this facilitates coexistence. Generalist herbivores by contrast can either facilitate coexistence or make it more difficult (Grover and Holt 1998; Olff and Ritchie 1998). Moreover, herbivore effects on producer coexistence can be modulated by the action of higher trophic levels. Classic food chain models (Oksanen et al. 1981; Oksanen and Oksanen 2000) predict that the response of plant biomass to nutrient enrichment is profoundly impacted by interactions among higher trophic levels. But the precise relationship depends strongly on whether or not multiple species coexist in each trophic level, and the reticulate pattern of feeding links in the food web (Abrams 1993).

At times, single consumer species ("keystone" species) have disproportionately large effects on community structure. Theoretical and empirical studies of multispecies assemblages with strong interactions suggest that the impact of keystone species on ecosystem functioning depends on numerous details of both the biology of the keystone species and the interaction structure of the entire system. Counter-intuitive effects frequently emerge because of the simul-

taneous interaction of multiple feedback loops and frequency-dependence in trophic interactions (Roughgarden 1976; Holt 1997).

Food web dynamics can also alter the diversity–ecosystem relationship by changing patterns of spatial coupling. Experimental field studies are conducted at small spatial scales where spatial flows can have a significant impact on ecosystem dynamics. There is a growing recognition of the importance of spatial flows among habitats as modulators of local food web and ecosystem dynamics (DeAngelis 1992; Holt 1996, 1997; Nisbet et al. 1997; Polis, Anderson, and Holt 1997; Huxel and McCann 1998; Loreau 1998a). At the basal level of abiotic resources in the basic ecosystem model (Pacala and Kinzig, chapter 8), rainfall and deposition provide inputs of abiotic resources in terrestrial habitats, and drainage and leaching likewise describe outputs. Consumers are often highly mobile and readily couple the dynamics of spatially distant communities (Holt 1996). Heterotrophic consumers thus provide multiple conduits for spatial exchange among ecosystems. System openness in general clouds rules of community structure derived from local exclusion (Loreau and Mouquet 1999; Holt and Gonzalez, ms.). Recurrent immigration can permit species to persist as community members, even though they tend toward local exclusion.

Ecosystems are likely to differ greatly in the way they are coupled to the external world via spatial flows at different trophic levels. We show below that the pattern of openness strongly influences how community rules of organization map onto ecosystem functioning (see also Holt, in press, and Loreau and Holt, in prep.).

TOWARD AN ECOSYSTEM MODEL WITH TROPHIC INTERACTIONS

Modifying the basic ecosystem model of this book so as to capture the main chains of trophic interactions known to be

significant in ecosystems (see Naeem, chapter 5) leads to models of daunting dimensionality and complexity. It is useful to consider first simpler systems. In the next few paragraphs, we describe how we splice herbivory into the basic ecosystem model (Pacala and Kinzig, chapter 8). The expanded model has two new compartments, describing herbivore population dynamics, and a detrital pool generated by the herbivore. We assume that herbivory is "laissez-faire" (Caughley and Lawton 1981); that the rate of per capita herbivory is given by a type II functional response, parameterized by an attack rate a' , a saturation constant h , and an assimilation efficiency of c ; and that herbivore deaths are constant (at per capita rate μ'). In a spatially open system with a single herbivore species, we assume a constant rate of immigration, I , and a constant per capita rate of emigration, e ; in a spatially closed system, these parameters are set equal to zero. With these assumptions, the herbivore population has the following dynamics:

$$dH/dt = H[c a' B / (1 + a' h B) - \mu'] + I - eH. \quad (11.1)$$

The herbivore generates a detrital pool of abundance C_H , which has the following dynamics:

$$dC_H/dt = H\mu' + H(1 - c) (a' B / (1 + a' h B)) - \lambda_f C_H. \quad (11.2)$$

We assume that herbivores potentially contribute to detrital pools via direct deaths, or unassimilated consumption, and do not discriminate between these two detrital sources. We also assume that decomposition is fast, at the same rate as the fast pool of producer-generated detritus. To complete the model, we must add a second mortality term in the producer equation of the basic model, describing mortality due to consumption by herbivores as follows: $-H B a' / (1 + a' h B)$. To simplify the algebra, we assume below that nutrient and water uptake are described by Michaelis-Menten ki-

netics, with $\theta = 1$. There is also an added term in the nitrogen equation.

Now imagine that a species pool exists for both herbivores and producers. As in simple one-trophic-level models of the sampling mechanism, we assume that the phenotypic variation in this pool is along a single axis, expressed as variation in a single rate parameter at a time. This constrained variation precludes local coexistence. However, as in the "sampling effect" model, regional species diversity could still influence local processes by increasing the range of variation in key system parameters available via colonization. We will allow colonization in just one trophic level at a time.

Case I: Ecosystem Closed at Top, Open at Bottom

Assume that a single producer species is present, and consider first species sorting of herbivores. With a single herbivore species, equilibrium plant biomass is $B^* = \mu' / a' (c - \mu' h)$. When two herbivores are together in the same community, they will compete for resources (plant biomass). The winning species is the one that can persist at the lower B^* . The winning herbivore species will be the species with higher attack rate, a' , or assimilation efficiency, c , or lower handling time, h , or direct density-independent mortality, μ' . Each parameter defines a different "sorting rule," or mechanistic reason for local competitive dominance by herbivores.

Now assume that a single herbivore species is present, and consider species sorting among plants, which vary in just one parameter of the model. A variant of the argument in Holt, Grover, and Tilman (1994) reveals that producer coexistence is impossible; the winning producer species is the one that both reduces resources to the lowest level, and supports the greatest herbivore numbers. In the general ecosystem model augmented with herbivory, this leads to seven "sorting rules": the dominant producer species will be the one with lower K_L , K_N , or K_W (greater resource uptake

rates); or the one with higher r (greater maximal production); or the one with lower a' (lower vulnerability to herbivory); or with lower μ (losses other than to herbivory) or γ (respiratory costs).

Rather than lay out all the tedious algebraic details, table 11.1 describes the general direction of change in each of the ecosystem properties considered in this book, given sorting (one parameter at a time) in both the herbivore and producer communities. For simplicity, in generating the results summarized in this table, we assumed that water was not limiting (i.e., $W \gg K_W$). The table also describes the impact of species sorting in the producer community in the absence of herbivores. One reads the table as follows: If a fat arrow points up (or down), this implies that species diversity (scaling the phenotypic variation available for sorting) for most parameters in that trophic level has a monotonic effect on a given ecosystem attribute (the rows); parameters that deviate from these overall trends are listed in lines below the arrows. If arrows point in both directions, effects may go in either direction, depending on exact parameter values. If an entry says "no effect," that means that for most parameters, diversity did not influence that aspect of ecosystem functioning. The table indicates qualitatively the range of potential effects of diversity on ecosystem characteristics, given bilevel trophic interactions.

In the absence of herbivores, the ecosystem properties of autotroph biomass, NPP, carbon storage, nitrogen mineralization, and evapotranspiration all tend to increase with species sorting at the producer trophic level. There are exceptions to this rule of thumb, however, when species differ in their basic density-independent rates of mortality. For instance, a decrease in death rates can increase biomass sufficiently to reduce NPP because of increased light competition.

In the presence of a single species of herbivore, many ecosystem processes also increase due to sorting among pro-

TABLE 11.1. Summary of Changes in Ecosystem Processes Given Sorting in Herbivore and Producer Communities

	System Open at Bottom			System Open at Top
	Producer Sorting		Herbivore Sorting	Producer Sorting
	No Herbivore	With Herbivore		
B^*	↑	no effect	↓	no effect
NPP	↑	↑	↑ or ↓ ^d	no effect
CS	$\mu \pm^a$	$\mu \ 0$	↑ or ↓ ^e	$\mu \downarrow$
	↑	↑		no effect
N_{\min}	↑	$\mu \pm^b$	↑ or ↓ ^f	$\mu \downarrow$
		↑		no effect
ET	↑	$\mu \pm^c$	↓	$\mu \downarrow$
		↑		no effect
H^* or H prod.		$\mu, \gamma \ 0$	↑ or ↓ ^g	$\mu \downarrow, \gamma \downarrow$
		↑		no effect
		$\mu \downarrow$		

In this table, producer parameters are r , K_L , K_N , γ , and μ . Herbivore parameters are a' , h , m , and c . The attack rate a' and handling time h can also be considered producer parameters, and producer sorting by varying these parameters has the opposite effect on the ecosystem attributes as does herbivore sorting. Therefore, conditions d through g below also apply to producer sorting on a' or h (second column), but with the inequality in the opposite direction. Producer sorting by a' or h increases all the ecosystem attributes except herbivore density and herbivore productivity (for which they have no effect) for the system open at the top (last column).

^a↑ iff $r' < (\gamma + \mu)^2 K_L / \gamma$

^b↑ iff $\frac{c}{m} > (1 - f) \left(\frac{1}{\lambda_s} - \frac{1}{\lambda_f} \right)$

^c↑ with sorting by μ iff $v_h > v_p$

^d↑ iff $B^* > \sqrt{r' K_L / \gamma} - K_L$, $r' = rD / (D + K_N \zeta)$, $B^* = m / [a(c - mh)]$

^e↑ iff $B^* > \sqrt{\frac{r' K_L (1 + m / \lambda_f c)}{(1 + m / \lambda_f c)(\gamma + \mu) - m(1 + \mu f / \lambda_f + \mu(1 - f) / \lambda_s)}} - K_L$ (except for c, m)

^f↑ iff $B^* > \sqrt{\frac{r' K_L}{\gamma + \mu [1 - (v_p / v_h)]}} - K_L$

^gBoth ↑ with sorting by $a', c, h; H$ prod. ↑ with sorting by m iff $B^* >$

$\sqrt{\frac{r' K_L}{\gamma + \mu}} - K_L; H^* \uparrow$ with sorting by m iff $B^* > \sqrt{\frac{r'(K_L a h - 1)}{a h (\gamma + \mu)}} - K_L$

TROPHIC INTERACTIONS: THEORY

TABLE 11.1. *Continued*

If the limit on B^* in condition e or f is complex (a negative value under the square root), then the herbivore sorting always decreases the ecosystem attribute, while for condition g , a complex value indicates that H^* always increases with herbivore sorting by m .

For herbivore sorting by changing c or m , in the system open at the bottom, the condition for increase in Carbon Storage is:

$$\left[(\gamma + \mu) \left(h + \frac{1}{\lambda_f} \right) - \left(1 + \frac{\mu(1-f)}{\lambda_s} + \frac{\mu f}{\lambda_f} \right) \right] \\ (B^* + K_L)^2 > r \left[K_L \left(h + \frac{1}{\lambda_f} \right) - \frac{1}{a} \right]$$

ducers. However, producer biomass does not increase, unless species vary in a' (the per capita rate of consumption by herbivores), in which case B^* increases as more-resistant producers replace less-resistant producers. Variation in this parameter can also potentially lead to declines in ecosystem attributes. As before, countervailing trends can arise if species vary in their direct mortality rates. Overall, adding herbivory weakens the impact of sorting at the producer level on ecosystem functioning.

Given a species pool of herbivores, and a single resident producer species, sorting favors the herbivore that can persist at the lowest plant biomass. Herbivore sorting tends to reduce evapotranspiration. Herbivore sorting can either increase—or decrease—NPP, nitrogen mineralization, and carbon storage. Overall, sorting at the herbivore trophic level tends to depress ecosystem attributes, opposite to the trends expected given sorting at the producer level.

Case II: Ecosystem Closed at Bottom, Open at Top

Now consider the same system, but with herbivore immigration and emigration at the top, and nutrient closure at the bottom (which we ensure by setting deposition and leaching both to zero). We consider only species sorting at

the producer level, with a single herbivore species (but see Discussion). Table 11.1 describes the impact of such sorting on ecosystem attributes. Plant biomass is now unaffected by species sorting, unless species differ in their vulnerability to herbivory. A decrease in direct mortality implies a decline in NPP, carbon storage, nitrogen mineralization, and evapotranspiration. Decreases in herbivory increase all these ecosystem attributes. Interspecific variation in many of the other parameters describing resource uptake, respiration, and maximal growth has no effect on these ecosystem traits (sorting by γ does reduce evapotranspiration). The nature of coupling between the local system and the external environment thus qualitatively influences the mapping of species sorting at the community level on ecosystem functioning.

In short, the expanded basic ecosystem model reveals that the relationship of biodiversity to ecosystem functioning depends on (1) the presence or absence of trophic interactions; (2) the level at which biodiversity enters the system (viz., the contrasting effects of sorting at producer vs. herbivore levels), and (3) the precise nature of system openness.

DISCUSSION

We caution that these results all involve species sorting from regional pools where species differ along just a single dimension (represented by values of one parameter). More broadly, in natural systems one might expect coupling among parameters because of trade-offs (e.g., between resource assimilation and escape from herbivory). Incorporating trade-offs could well change the impact of sorting rules on ecosystem functioning. Moreover, and very importantly, trade-offs can permit local coexistence. For instance, if herbivores differentially attack a superior competitor among

the producers and ignore inferior competitors, inferior resource competitors can persist. In the limit of very effective herbivory, system properties should converge on those determined by the inferior competitor alone. We have also not considered sorting that occurs simultaneously at producer and consumer levels. Diversity at different trophic levels is expected to be mutually interdependent (Siemann et al. 1998, Knops et al. 2000), and a deeper understanding of ecosystem impacts of biodiversity surely requires an articulation of this interdependency.

The above protocol assumed that species sorting from competitive exclusion occurred on timescales that were short, relative to the rate of colonization from the regional species pool. A very simple way to permit local coexistence is for recurrent immigration from the species pool to occur at rates sufficient to offset local extinctions (Levin 1974, Holt 1993). Even if a single species is expected to dominate in a closed community, high species richness may be observed in an open community due to immigration of locally inferior species, comprising "sink" populations (Loreau and Mouquet 1999).

Permitting recurrent immigration (and emigration) has two distinct effects on ecosystem processes. First, it adds inputs and outputs to ecosystem compartments. We noted above that spatial linkages can qualitatively alter the expected relationship of biodiversity to ecosystem processes (see table 11.1). Second, immigration can counteract the directional effects of sorting via systematic changes in system parameters. Rather than discuss models with recurrent immigration in detail, we here summarize conclusions that will be presented more fully elsewhere (Loreau and Holt, in prep.).

Assume that there is no herbivory, with a local competitive dominance hierarchy in competition for a limiting resource, combined with immigration-extinction dynamics. The nutrient pool is closed, except via fluxes in the pro-

ducers. If the producer species differ only in resource uptake rates, then there is *no* effect of diversity on primary production. An increase in producer diversity lowers the average uptake rate, per producer (across individuals, in all species), but this is precisely compensated by an increase in resource availability. If instead, producer species differ only in their density-independent death rates, then production will be *higher* in more diverse systems. The reason is that if species with high death rates are maintained via immigration, then more diverse systems have higher individual turnover rates, therefore more rapid recycling of nutrients to the free resource pool. Finally, if species differ only in their rates of emigration, production is *lower* in more diverse systems. Emigration is akin to mortality in determining local dominance, but also permits additional channels of nutrient loss from the system. More diverse systems can thus have a higher rate of resource drain from the local nutrient pool, ultimately lowering production.

The models we have considered assume very simple type I and II functional responses. Future work should include more realistic renditions of herbivore feeding behavior (Farnsworth and Illius 1998; Ginnett and Demment 1995; Schmitz, Beckerman, and Litman 1997). Over evolutionary timescales, plant-herbivore interactions can also strongly influence detrital pathways for nutrients. For instance, Steinberg, Estes, and Winter (1995) argue that the presence of the sea otter in the north Pacific, but not in the south Pacific, has led to systematic differences in the fraction of production devoted by algae to defensive compounds. They suggest that because sea otters were very effective at limiting invertebrate herbivores such as sea urchins prior to human impacts (Estes and Duggins 1995), over evolutionary timescales there has been much more intense herbivory in the southern hemisphere than in the northern hemisphere. Detritus produced by algae in the southern hemisphere may thus be less readily decomposed and support more attenu-

ated detrital-based food chains. An evolutionary perspective may be necessary to explain some variation among studies on the observed impact of trophic interactions on ecosystem processes. For instance, Milchunas and Lauenroth (1993; see also Lennartson et al. 1997) suggestively found in a global survey of vertebrate herbivore enclosure experiments that the impact of grazers on primary production varied with the length of shared evolutionary history between producers and herbivores. Other topics needing examination in future work include impacts of higher trophic levels (e.g., trophic cascades) on ecosystem functioning, and detrital-based food webs.

CONCLUSIONS

As noted in the Introduction, systems vary tremendously in the detailed structure of food webs. Such variation is likely to be key to understanding the influence of biodiversity on ecosystem functioning. However, we suspect that the following insights we have drawn from the basic ecosystem model augmented with herbivory will apply much more broadly:

1. *Simple models may suffice to predict effects of species sorting on ecosystem functioning.* Many of the trends arising from species sorting in the "basic" but rather complex ecosystem model of the book also seem to appear in much simpler models (Holt in press). For instance, almost any model of competitive interactions among herbivores predicts that the dominant herbivore will be the one that can persist at the lowest abundance of producers. This will often imply overexploitation, and a lower abundance of the dominant herbivore. This in turn implies that species sorting at the herbivore level may initially increase total system biomass, but that eventually total biomass will surely decline as very effective consumers come to dominate the system. Detailed ecosystem models are undoubtedly needed to generate precise

predictions, but many key qualitative features may be captured and more clearly understood by analyzing related, simpler models.

2. *General trends in the effect of diversity on ecosystem functioning are present, but may differ among functional groups in the same ecosystem.* An important concern is the level at which sorting occurs versus the level at which the ecosystem effect is measured. For instance, in the system closed except for nutrient inputs, in most cases species sorting at the producer level increased ecosystem functioning. Species sorting at the herbivore level, by contrast, overall tended to reduce ecosystem functioning. There thus may be countervailing effects of diversity on ecosystem processes at different trophic levels.

3. *Effects of species sorting depend on the mechanistic parameter determining dominance.* Species sorting does not have an inevitable effect on ecosystem functioning. Different systems may show different relationships between diversity and ecosystem processes, if they differ in the axes along which competitive dominance is expressed. For example, table 11.1 shows that if a herbivore is present, and producers differ only in their basic mortality rate (with the producer with the lowest mortality rate being the best competitor), sorting toward lower mortality does not influence net primary production. However, if the producers instead differ in their basic assimilation rate of the resource, sorting toward more efficient producers increases net primary production.

4. *The presence of higher trophic levels influences the effect of species sorting on ecosystem functioning.* Given herbivory, the ability to withstand herbivory becomes an important component of plant competition. In some cases, sorting among producers toward lower herbivory rates can reduce ecosystem functioning.

5. *Spatial openness influences the mapping of species sorting onto ecosystem functioning.* The effects of diversity on system functioning (via species sorting) can be influenced by changing which compartment of the ecosystem is coupled

via flows to the external environment (see table 11.1). If species are maintained in local communities by immigration, then diversity in the regional species pool may have disparate effects on local ecosystem processes, depending on the parameter determining local competitive dominance.

6. *Species redundancy is a property not of species, but of species in particular systems.* Species are "redundant" with respect to certain system attributes, if their replacement does not change that attribute (Lawton and Brown 1993). In comparing the range of models we have considered, whether or not variation in a particular parameter of producer species leads to redundancy depends on the entire structure of the system (e.g., the presence or absence of herbivores, or the pattern of system openness). Two species may be functionally redundant in one setting, yet be nonredundant in another. As an example from table 11.1, if producer species in a system open at the bottom differ in basic mortality, and there is no herbivory, species sorting at the producer level increases biomass, nitrogen mineralization, and evapotranspiration. These species clearly are not redundant, because species substitution leads to a change in ecosystem functioning. However, if a herbivore is present, then species sorting for this same parameter has no effect on plant biomass or evapotranspiration. These species are thus redundant, given herbivory. More radically, if one compares systems open to spatial fluxes only at the bottom resource level with systems open only via herbivore fluxes, many species traits that are nonredundant in the former are redundant in the latter (in that species sorting does not alter ecosystem functioning).

Our most basic, qualitative conclusion is that in considering the impact of biodiversity on ecosystem functioning, a diversity of effects should be expected, depending on the presence and importance of trophic interactions, and the nature of system openness. This expectation of a diversity of outcomes is consistent with a recent review of empirical studies by Schläpfer and Schmid (1999), who reported con-

siderable diversity among studies in the ecosystem effects of biodiversity. We end by conjecturing that some of this manifest heterogeneity reflects the varying importance of trophic interactions and system openness among ecological systems.

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