CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

TROPHIC RANK AND THE SPECIES–AREA RELATIONSHIP

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Abstract. The species–area relationship may be the strongest empirical generalization in community ecology. We explore the effect of trophic rank upon the ''strength'' of the species–area relationship, as measured by z, the slope of a log(species) vs. log(area) plot. We present a simple model for communities closed to immigration, composed of ''stacked specialist'' food chains (where each plant species supports a specialist herbivore, which in turn sustains a specialist carnivore, etc.), that predicts z should increase with trophic rank; the model brings out some of the spatial implications of sequential dependencies among species. We discuss empirical examples in which the z values of taxa differing in trophic rank were reported and lament the shortage of well-documented examples in the ecological literature. Several examples fit the expected pattern, but others do not. We outline several additional reasons why z values might increase with trophic rank, even for generalists. If the qualitative assumptions of the model are relaxed, the predicted effect of trophic rank on z should weaken or even be reversed. Trophic rank may not have a systematic effect on the species–area relationship if (1) there are strong top-down interactions leading to prey extinctions; (2) communities are open, with recurrent immigration, particularly at higher trophic ranks; (3) consumers are facultative generalists, able to exist on a wide range of resource species; or (4) systems are far from equilibrium. Our aim in this thought piece is to stimulate community ecologists to link theoretical and empirical studies of food web structure with analyses of spatial dynamics and landscape ecology, and to encourage empirical studies of the species–area relationship focused on comparisons across taxa varying in trophic rank.

Key words: distribution; generalist; island; patch; specialist; specialist vs. generalist food webs; species–area; trophic rank and species–area relationship.

INTRODUCTION

The tendency for species richness to increase with area (the ''species–area relationship'') is one of the most robust empirical generalizations in ecology (May 1975, Rosenzweig 1995). Most studies of species–area patterns have focused on particular taxa, guilds, or functional groups, rather than broader comparisons within entire communities. Yet, comparisons of species–area relationships among taxa or functional groups can highlight essential differences in their spatial dynamics and responses to spatial heterogeneity (Kareiva 1994). For instance, biogeographic studies of West Indies vertebrates reveal stronger species–area relationships for nonflying mammals than for bats or birds, consistent with the likely greater importance of mobility for determining local community composition in the latter groups (Wright 1981).

A familiar way to characterize the structure of entire communities is to construct food webs, which are interlinked chains of trophic interactions that define energy and material flows among species (Pimm 1982, Cohen et al. 1990). An enormous amount of work has been devoted to empirical and theoretical food web analyses (e.g., Martinez 1991, Pimm et al. 1991, Havens 1993, Polis and Winemiller 1996), with a growing interest in spatial aspects of food web ecology (e.g., Briand and Cohen 1987, Schoener 1989, Warren 1989,

Winemiller 1990, Martinez and Lawton 1995, Holt 1996*a*, *b*, Polis et al. 1996, 1997, Harte and Kinzig 1997). A simple descriptor of a species position in a food web is its "trophic rank." Our specific purpose in this paper is to explore the proposition that trophic rank may systematically influence the strength of the species–area relationship. Our more general aim is to highlight the importance of linking studies of food web structure with spatial and landscape ecology.

There are various ways to define trophic rank (Yodzis 1989:209). For instance, if for each quantum of energy consumed by an individual in a focal species, one were to back-calculate the number of species through which that quantum had passed before being consumed, the "trophic rank" of the species might be the average length of all such energetic pathways. Ambiguities in assignment of species to trophic ranks arise principally because of trophic generalization (e.g., omnivores feed at multiple levels). If food webs were comprised entirely of specialists, with specialist carnivores consuming specialist herbivores feeding on single plant species, there would be no ambiguity in trophic rank assignment.

We first briefly review salient aspects of species–area theory. We then present a simple model that predicts that the species–area relationship should be stronger at higher trophic levels, when most consumers are trophic specialists. Next, we sketch empirical examples in which species–area relations were assessed for taxa differing in trophic rank. The theoretical predictions match some, but not all, patterns in these systems. In the *Discussion,* we examine alternative reasons why trophic rank might influence the species–area relation, as well as factors obscuring such an influence. In particular, we argue that the effect of trophic rank on the species–area relationship may often be weaker (or even reversed) in webs characterized by trophic generalists.

A PRÉCIS OF THE SPECIES–AREA RELATIONSHIP

There are three basic kinds of species–area relationships (Holt 1992, Rosenzweig 1995): (1) species richness vs. sample area in nested samples, within a defined habitat or region (a "type-1" species–area relationship); (2) total species richness vs. total area, among habitats or regions differing in area (e.g., islands in an archipelago; a "type-2" relationship); (3) local species richness in a sample of defined size, among habitats or regions differing in area (a "type-3" relationship). Types 1 and 2 have received the most attention in the literature (Rosenzweig 1995). Often, a power law $S = cA^z$, or, equivalently, $\log(S) = \log(c) + z \log(A)$, provides a reasonable statistical summary for the increase of species richness with area (Rosenzweig 1995), where S is the number of species and A is area. The quantity z describes the strength of the scaling of species richness with area; z is independent of the units used to measure area (Rosenzweig 1995:21).

There are three explanations for species–area rela-

tionships (Connor and McCoy 1979, Williamson 1981): sampling, habitat heterogeneity, and colonization–extinction dynamics.

Sampling.—Consider a type-1 species–area relationship, for instance nested quadrats used to sample a plant community. Very small quadrats necessarily contain few individuals; at small spatial scales, an increase in species richness with increasing quadrat size almost surely reflects merely an increase in sample size (Rosenzweig 1995). Sampling effects may also explain some type-2 relationships. Type-3 species–area relationships, however, automatically control for sample area, and so are less prone to sampling effects (Holt 1992).

Habitat heterogeneity.—For type-1 and type-2 species–area relationships, habitat heterogeneity is likely to increase with area (Williamson 1981, Rosenzweig 1995). This can influence species richness, because large areas are likely to include habitats needed by species with specialized habitat requirements.

Dynamics.—Island (type-2) species–area relationships (where each sample is a distinct island community) typically have higher z values than do type-1 relationships on nearby mainlands (e.g, MacArthur and Wilson, 1967:10). This systematic difference between island and mainland species–area relationships usually reflects spatially mediated processes (Holt 1993, Rosenzweig 1995). For instance, local mainland communities are likely to enjoy higher colonization and lower extinction rates than comparable communities on islands, and can be enriched via source–sink and metapopulation dynamics (Holt 1993).

The relative importance of sampling, heterogeneity, and colonization–extinction dynamics as explanations for species–area relationship on islands and island analogs (e.g., host plants) is still the subject of considerable debate (e.g., Nilsson et al. 1988, Hart and Horwitz 1991). For the most part, we focus here on how trophic rank might influence type-2 species–area relationships among isolated "island" communities, where one might expect to observe colonization–extinction dynamics for trophically linked species.

A LIMITING CASE: TIGHT TROPHIC SPECIALIZATION

For simplicity, consider an idealized community comprised of trophic specialists (in the *Discussion,* we examine a broader range of scenarios). We analyze how z should vary with trophic rank, using a generalization of the incidence function model of Holt (1993, 1996*a*). The "mainland" community contains m food chains of length $n,$ i.e., m plant species, each with its specialist herbivore, each in turn with *its* specialist carnivore, and so on. This trophic organization may describe some assemblages composed of insects that are plant specialists and parasitoids that are herbivore specialists. The mainland community of "stacked specialists" is assumed to be the source pool for a set of islands. Label each species in a food chain by trophic rank (i.e., spe-

cies 1 is the basal producer; species 2 is the herbivore, etc.). In a snapshot of the system, a fraction $p(i)$ of islands (of given area, distance from source pool, etc.) will contain species i. When plotted against variables such as area, $p(i)$ is the "incidence function" (Gilpin and Diamond 1981, Hanski 1992).

Now, assume species i is absent unless its required food resource, species $i - 1$, is present. This implies nested distributions; species $i - 1$ may be present without species i. Define the "conditional incidence function" $p(i|i - 1) = p(i)/p(i - 1)$ as the conditional probability that species i is present, given that its required food is present (Holt 1993). The basal species' incidence is $p(1)$, so the incidence of species i arises from compounding conditional incidence functions, as follows:

$$p(i) = p(1) \prod_{n=2}^{i} p(i|i - 1). \quad (1)$$

For simplicity, assume all rank i species have the same conditional incidence function; all species of a given rank thus have the same incidence function. $p(i)$ is the probability that a given species of rank i is present on an island, so the expected number of species of rank i on the island is $S_i = mp(i)$, thus $\log(S_i) = \log(m) + \log(p(i))$. The strength of the species–area relationship is

$$z_i = d \log(S_i)/d \log(A) = d \log(p(i))/d \log(A). \quad (2)$$

Now, further assume that basal incidence and the conditional incidence function for each higher rank increase with area (as often observed, Hanski, 1992). One general reason to expect this arises from basic properties of small populations (Pimm 1991, Lawton 1995). If the expected population density of species i is constant, total population size scales linearly with island area. Populations on small islands are likely to risk extinction due to demographic and environmental stochasticity, even if their required resources are present. Formally, we assume that

$$\frac{\partial p(1)}{\partial \log(A)} > 0, \quad \text{and} \quad \frac{\partial p(i|i - 1)}{\partial \log(A)} > 0 \quad (i > 1) \quad (3)$$

where variables other than $\log(A)$ (e.g., distance to a source) are assumed to be held constant. Taking the logarithm of $p(i)/p(i - 1)$, and differentiating with respect to $\log(A)$, leads to

$$z_i = \frac{\partial \log[p(i)]}{\partial \log(A)}$$

$$= \frac{1}{p(i|i - 1)} \frac{\partial p(i|i - 1)}{\partial \log(A)} + \frac{\partial \log[p(i - 1)]}{\partial \log(A)} \quad (4)$$

where the right-most term is z_{i-1}. If the conditional incidence function increases with $\log(A)$, $\log[p(i)]$ increases faster with $\log(A)$ than does $\log[p(i - 1)]$. Thus, *species–area relationships should be stronger (i.e. greater z) at higher trophic ranks.*

Predicting that z increases with increasing trophic rank emerges from the concatenation of three qualitative assumptions: (1) species at each level are trophic specialists on a single species in the level below (a "stacked specialist" community organization); (2) specialist consumer populations do not persist in the absence of the resource population they require; (3) species are not guaranteed to be present, even if their required resources are, and a species' presence becomes more likely on larger areas, given the presence of the needed resource population. These three qualitative assumptions are consistent with a wide range of dynamical possibilities (e.g., explicit colonization–extinction models for food chains with "bottom-up" control [Holt 1996*a, b*]). These assumptions do not require a dynamic equilibrium between colonization and extinction; the predicted patterns may emerge, for instance, in a community being assembled by colonization (Drake 1990, Luh and Pimm 1993). Nor do they require that consumer populations be less abundant than resource populations. In the *Discussion* we explore how violating these three assumptions alters the predicted effect of rank on the species–area relationship. In particular, for reasons given later, trophic generalists might often show different patterns than specialists. (Though our focus is on the species–area relationship, it should be noted that if conditional incidence declines with distance from source areas, effects of distance on species' richness should also be stronger at higher trophic rank in communities dominated by trophic specialists.)

EXAMPLES

One purpose we have in presenting this conceptual paper is to stimulate comparative empirical studies of species–area relationships across taxa varying in trophic rank. Though the ecological literature is replete with species–area datasets (Connor and McCoy 1979), few investigators have explicitly examined a range of taxa, differing in trophic rank, simultaneously in a given archipelago or array of habitat patches (Spencer 1995). In our judgement, there are *no* reasonably complete studies of the structure of whole food webs, resolved to the level of species, for islands varying in size or distance from defined source pools. However, there are tantalizing hints in the literature of systematic differences among systems in the influence of trophic rank upon *z*. In the following paragraphs, we draw together the salient conclusions of examples known to us, which mostly deal with subwebs or incompletely resolved webs. Rather than discuss any particular system in great detail, we simply ask whether the reported *z* values (or related attributes) match the qualitative pattern predicted by the above model. We should stress that we take reported results at face value. A task for future work will be to conduct more rigorous analyses (once a wider range of suitable datasets are available) with an eye towards the hypotheses presented here.

1) Itamies (1983) reported *z* values for plants and

Lepidoptera on Baltic islands. The values were reported to differ strongly; $z_{plants} = 0.362$, and $z_{leps} = 0.671$. Given that most of the Lepidoptera are specialists or oligophages (Itamies 1983), these data are consistent with our prediction that specialist consumers should exhibit stronger species–area relationships than do their resource populations.

2) Kruess and Tscharntke (1994) examined the distribution on experimental and natural red clover patches of insect herbivores and specialist herbivores. Both area (in natural meadows) and distance (in meadows and experimental patches) exerted more pronounced effects on species richness in parasitoids than on their hosts, and the effects were in the predicted direction. These patterns have persisted for the past four years (T. Tscharntke, *personal communication*).

3) Glasser (1982) reanalyzed data from four islands in the classic defaunation experiments of Simberloff and Wilson (1969) and demonstrated a broad pattern of sequential colonization in these arthropod communities, with herbivores colonizing prior to their predators and parasitoids. Though Glasser did not explicitly make this point, herbivore species richness averaged over the last three months of the experiment is relatively uniform across mangrove islet sizes, whereas there are markedly fewer total predator and parasitoid species on the smaller islands. These data match the prediction that species of higher rank have stronger species–area relationships.

4) Schoener and Spiller (1995) used sticky traps to examine insect communities of small Bahamian islands. The fraction of captured insects comprised of parasitoids declined with decreasing island area and increasing distance from neighboring large islands. This data set does not quite address species–area theory, as it reports the fraction of total individuals, not the fraction of the total species list comprised of parasitoids. Still, this finding is consistent with our theoretical expectations. Preliminary sorting by species supports the conclusion that small and distant islands are disproportionately poor in parasitoid species (T. Schoener, *personal communication*).

5) Nilsson et al. (1988) and J. Bengtsson (*personal communication*) report z values for a variety of taxa occupying islands in Lake Malaren, Sweden. The taxa and their respective z values are as follows: plants, 0.1; snails, 0.156; carabids, 0.361; spiders, 0.228; and birds, 0.616. The pattern here may not be entirely consistent with our theory (depending on the relative trophic rank assignments of carabids and spiders), but at least the basal trophic layers (plants and snails) have shallower species–area relationships than do higher ranked species (carabids, spiders, and birds).

6) Our prediction of an effect of trophic rank on the species–area relationship rests on a lower level prediction, namely that trophic rank, in part, predicts the spatial incidence of species, independent of abundance. Wright and Coleman (1993) provide supportive data.

These authors isolated nematode assemblages in soil cores over a 16-mo period and monitored changes in community composition and trophic structure. Many extinctions occurred. Those species that persisted tended to be abundant initially, and of lower trophic rank, than species going extinct. An analysis of covariance showed that both abundance and trophic rank significantly and independently contributed to survival; higher ranked species did not persist as long as lower ranked species, even controlling for abundance effects.

7) Havens (1992) (and see Martinez [1993]) described the pelagic food webs of 50 lakes in the Adirondacks with 10–74 taxonomic species (mean = 38 species). If lakes can be viewed as aquatic "islands," these webs allow us to assess effects of trophic rank on the species–area relationship. The webs are based on species lists obtained via consistent sampling procedures performed in 1984 (e.g., epilimnion phytoplankton tows, vertical zooplankton tows, and fish traps and nets). We assigned a rank to each consumer species in the webs by calculating the mean length of all food chains leading from basal resources to the consumer. Basal resource species have rank one, while consumers are given a rank equal to their mean chain length (rounded off to the nearest integer) plus one. The logarithm of species richness at each rank was regressed against the logarithm of surface area, leading to an estimate of the z value for species of each rank and an error term for the z value (the standard error of the regression slope). Although there is a positive slope of regression of z values vs. trophic rank, the slope is not significantly different from zero. (N. D. Martinez, *unpublished analyses*). At best, then, Havens' lake datasets provide weakly corroborative evidence in favor of the rank dependency theory. We suggest in the *Discussion* that the lack of fit to the theoretical prediction may be due to widespread trophic generalism in pelagic lake organisms.

8) Islands in the Gulf of California support plant communities typical of Sonoran desert associations, and, despite low and temporally variable productivity, are surprisingly rich in species (Case and Cody 1983). Ongoing studies by G. Polis and associates are documenting distributional patterns of species at several trophic levels (Due 1992, Polis and Hurd, 1995, 1996; G. A. Polis, *unpublished data*), building on published distributional data for reptiles (Case 1983), plants (Cody et al. 1983), and birds (Cody 1985). Preliminary analyses using data on islands ranging 0.001–1208 km^2 suggest a pattern contradicting the prediction of the "stacked specialist" model, with estimated z values as follows: vascular plants, 0.424; scorpions, 0.162; land mammals, 0.160; reptiles, 0.319; and land birds, 0.291 (G. Polis, *unpublished results*). The vertebrate taxa in this study are trophically heterogeneous (e.g., "reptiles" include a herbivore [chuckwalla] as well as carnivorous snakes and arthropodivorous lizards). Nonetheless, quite clearly, the lowest trophic level (plants)

has a higher z value than many higher ranked consumers.

9) A recent study by Spencer et al. (*in press*) of invertebrate communities in temporary ponds in Israel has shown that the proportion of predatory species increases with pool surface area, implying that predators in these communities have larger z values.

To summarize our impression of highlights of these empirical studies, study number six suggests trophic rank influences incidence, even independent of population size. Studies one through five and nine all match the qualitative predictions. Study number seven provides, at best, weak support for the theory, whereas study number eight reveals a pattern in z values opposite to that predicted. In the *Discussion,* we present some ideas as to the factors that may lead to such differences among systems.

DISCUSSION

The incidence function model formalizes the qualitative notion that trophic specialization entails a compounding of spatial effects: specialist taxa of high trophic rank are constrained in their distribution by processes that operate directly upon their own dynamics, as well as by spatial constraints impinging on those lower-ranking taxa upon which they depend. One consequence of sequential trophic dependencies among specialist species is that spatial effects compound in the assembly of food chains. This implies that the species–area relationship should become stronger (viz., higher z) at higher trophic levels.

However, other factors can lead to the same predicted effect of trophic rank on z; hence, observing the pattern need not support the above theory. Moreover, in many reasonable circumstances the predicted effect should not occur at all. Here, we first discuss alternative factors that can lead to positive trophic effects on $z,$ and then examine the consequences of weakening the three qualitative assumptions of our model.

Alternative explanations for greater z at higher trophic ranks

Energetics, trophic rank, and population size.—The usual dynamical explanation for the species–area relation goes as follows: small area $\Rightarrow$ low abundance $\Rightarrow$ high extinction rates $\Rightarrow$ low incidence on small areas. If population size systematically declines with increasing trophic rank (say, for energetic reasons), higher ranked species should be more prone to extinction on small islands (Schoener 1989), leading to stronger species–area relationships at higher levels. This prediction arises from the effect of trophic position on population size and, hence, on extinction rates, an effect that may complement effects due to trophic specialization. The population size explanation should also apply to many trophic generalists.

Sampling effects and trophic rank.—As noted, sampling effects can provide a simple explanation for species–area relationships, particularly at small spatial scales. The range of island sizes over which sample size effects generate a species–area relationship should tend to increase as average population density in the focal taxa declines. If higher ranked taxa, on average, have lower abundances than do lower ranked taxa, sample size effects should be evident over a wider range of island sizes for higher ranked taxa, than for lower ranked taxa, This may explain some observed effects of trophic rank on z values. For instance, in Example 5, birds have the highest z and also likely have the highest average trophic ranks among the taxa recorded. However, in this case, high trophic rank is correlated with low abundance, with few individuals per species on each of these small islands. Because most of these bird species settle afresh each breeding season, it is plausible that sampling taxa of low abundance accounts for the observed high z for birds on these islands (J. Bengtsson, *personal communication*). The main effect of trophic rank, here, is upon abundance and, thus, upon the likelihood of sampling effects being pronounced in small areas.

Ecological processes that weaken the effect of trophic rank upon z

Violating any of the three qualitative assumptions that underlay the incidence model can weaken or reverse the predicted effect of rank on z.

Conditional incidence may decrease with area.—We assumed that the conditional incidence for species i increases with area. This seems reasonable but does rest upon implicit assumptions about underlying species interactions. In some plausible circumstances, conditional incidence may decrease with area. Holt (1996*a,* *b*) analyzed explicit island biogeographic and metapopulation models of food chains, in which species' incidence on islands or patches in a heterogeneous landscape emerges from the dynamic interplay of trophically driven colonizations and extinctions. One conclusion was that larger z values at higher trophic ranks are likely, if the food chain is "donor-controlled" (i.e., extinctions in level i are not driven by the presence of higher trophic levels), or when weak top-down effects are present (i.e., predators increasing prey extinction).

However, if increasing area reduces rates of predator extinctions for reasons other than prey depletion (e.g., small predator populations may be vulnerable to extinction due to inbreeding, or catastrophes, even with abundant prey), prey populations may overall be more prone to extinction on larger islands, because that is where predators, on average, persist long enough to potentially extirpate their resource species. In this case, prey species richness can actually decline with increasing island area, or have a flat relationship. Comparing the species richness of intermediate consumers to their own resources may paradoxically result in an inverted relationship between trophic rank and $z,$ because of

negative effects of higher ranked top predators on the incidence of intermediate consumers. Of the three qualitative assumptions we have made to link trophic rank and z, the one that is violated here is that conditional incidence increases with area for each trophic level. Increasing island area may, at times, be correlated with a greater likelihood of strong top-down predator effects, leading to a decline in conditional prey incidence with increasing island area. We suspect that this effect, though interesting and possible in theory, may not be widespread, both because some predators do not exert sufficiently strong top-down control on their prey, and because spatial heterogeneity (e.g., refuges) afforded by large areas can facilitate the persistence of intrinsically unstable predator–prey interactions. For instance, studies of cellular lattice models with unstable local predator–prey dynamics, multiple trophic levels, and limited dispersal among neighboring cells (Wilson et al. 1998) suggest that larger areas can more readily sustain longer food chains.

Communities may be open.—A second assumption was that a species at level i will not be present unless its required resource at level $i - 1$ is present. This is reasonable in isolated habitats, such as oceanic islands or groundwater-fed lakes. However, many communities are ''open,'' in that community composition is influenced over short time scales by individual mobility linking the local community to a larger landscape (Holt 1993). In open communities, mobile consumers may be able to very rapidly colonize, once their resource is present (leading to coincident spatial distributions, e.g., the aphid *Hyalopterus pruni* on *Phragmites*, [Tscharntke 1992]) or even occur without their required resource being present. High consumer mobility should weaken effects of trophic rank on the strength of the species–area relationship.

The effect of trophic generalization.—Possibly the most crucial assumption we made was of a ''stacked specialist'' model for community organization. Though analytically convenient, many natural communities in fact are dominated by nonspecialized consumers (Polis 1991). There are two distinct effects introduced by trophic generalization. First, depending on the detailed nature of resource dependencies, generalization could either weaken or strengthen the impact of trophic rank upon z. Second, trophic generalization can lead to a wide range of indirect interactions in the food web. We deal with each of these issues in the following paragraphs.

1. *Different kinds of generalists.*—There is an ambiguity in the term ''generalist.'' In the food web literature, this usually refers to a species linked trophically to more than a single species. Using this definition, in some circumstances trophic generalism may actually strengthen the predicted effect of rank upon z. Some species may be obligate generalists, unable to persist without an entire suite of resource populations. For instance, consumers may obtain different essential

nutrients from different resource species; or, a species with a complex life cycle (e.g., many parasites) may require distinct resource species (e.g., hosts) at different life history stages; or, in temporally varying environments, some resource populations may be rare or absent in some years (e.g., annual plants in deserts), so a consumer must be able to exploit a range of species to persist at all. In these circumstances (which pertain to many taxa), the effect of trophic rank on the species–area relationship should be magnified, because an obligate generalist consumer species will be absent unless *each* of its required resource types is present. The joint probability that all required resource types are present simultaneously is less than the average probability that any given resource type is present alone.

By contrast with obligate generalists, many generalists are opportunistic. If a consumer population can subsist on any one of n resource types, the sequential dependency embodied in Eq. 1 may be greatly weakened. For instance, a generalist may need only one or a very few resource types to be present before it can persist as a population, provided those resources are reasonably abundant. The probability that at least one (any one) resource type is present exceeds the probability that any given resource type is present. This should blur the nested distributional pattern predicted for trophic specialists and weaken spatial constraints on consumer distributions arising from resource distributions. For opportunistic generalists, if there is an observed relationship between trophic rank and z, it more likely arises from the other factors discussed above (e.g., the influence of population size on persistence).

At times, opportunistic generalists may quantitatively require multiple resource types to persist, leading to patterns reminiscent of those expected for obligate generalists (e.g., because no single resource type is very abundant). For instance, the persistence of a consumer with high metabolic requirements should be enhanced, given multiple resource populations on an island, which can collectively provide a higher or more dependable supply of resource than does any single resource population. Ritchie (1999) has demonstrated this effect in isolated colonies of a generalist grazing herbivore, the Utah prairie dog (*Cynomys parvidens*); local extinction rates decline dramatically with increasing food plant species diversity.

The conditional incidence function model can be modified to describe these disparate sorts of trophic generalization. As an example, assume that the mainland community is made up of m two-level modules (Holt 1997), each with one predator species consuming two prey species. For simplicity, assume the prey do not directly compete, the predator–prey interaction is donor-controlled, and the two prey are distributed identically and independently on islands varying in size A, with incidence function $p(\log(A))$ (for notational convenience, below we simply refer to p). Let p_i be the

conditional probability that an island has any given predator species, given that $i = 0$, 1, or 2, of its prey species are present. The total probability that this predator is present is $P = p_0(1 - p)^2 + p_1[2p(1 - p)] + p_2 p^2$. The expected number of predator species present is $S = mP$.

For isolated islands, one expects $p_0 = 0$. Two special cases are ''obligate generalists'' (ob; $p_1 = 0$, $p_2 = p'$), and ''indifferent generalists'' (ind; $p_1 = p_2 = p'$). Taking logs and evaluating z leads to

$$z_{ob} = \frac{1}{p'} \frac{\partial p'}{\partial[\log(A)]} + 2\frac{1}{p} \frac{\partial p}{\partial[\log(A)]}$$

$$z_{ind} = \frac{1}{p'} \frac{\partial p'}{\partial[\log(A)]} + \frac{1(1 - p)}{2 - p} \frac{1}{p} \frac{\partial p}{\partial[\log(A)]}$$

which imply that z is greater for obligate generalists than for indifferent generalists.

It would be interesting to examine these predictions in host–parasite assemblages. For example, parasites with obligate complex life cycles, involving several host species, could be compared with more opportunistic generalists, e.g., generalist insectivores. We predict that obligate generalists should have particularly high z values, compared to trophic specialists, which in turn should have higher z values than opportunistic generalists.

Several of the examples sketched here probably reflect the consequences of trophic generalization. In the Baja system (Example 8), for instance, within-island heterogeneity in edaphic factors seems to have a strong influence on the plant community (W. Anderson, *personal communication*), leading to an expectation of high z values at the plant trophic level (Williamson 1981). Many consumers in this system (e.g., scorpions and lizards) are highly generalized and opportunistic in diet, and input of marine detritus may directly or indirectly partially decouple land consumers from the terrestrial plant community (Polis and Hurd 1995, 1996). It seems unlikely that tight sequential dependencies of prey and predators are at all common in these Baja consumer taxa. The analysis of Havens' (1992) lake food webs (Example 7) may also illustrate how trophic generalization weakens the rank dependency of z values. There is scant evidence in freshwater systems to suggest that zooplankton and fishes are obligate generalists; instead, these taxa often seem able to persist in the face of large-scale variation in the species composition of their prey (W. J. O'Brien, Jr., *personal communication*). Hence, one might not expect a strong increase in z values with trophic rank in the lake food webs.

2. *Interaction webs.*—A second major effect of trophic generalization is to open up the Pandora's box of indirect interactions, such as exploitative competition, apparent competition, and intraguild predation. Developing theoretical models to address more formally the implications of multitrophic interactions for the spe- cies–area relationship is a challenging task, one that goes beyond the scope of this paper. Theoretical studies of webs with even small numbers of interacting species (e.g., Abrams 1993, Holt 1997) often reveal counter-intuitive effects, usually dependent upon the detailed structure of the web. Nonetheless, it is useful to briefly contemplate some likely consequences of interspecific interactions for z values in communities dominated by generalists.

Consider a mainland community with two trophic levels, with roughly equal numbers of species in both levels, and predators that are trophic generalists. This implies that many predator species will have overlapping diets, and prey species will share predators. Assume initially a distribution of these species amongst islands such that the predator z value is much less than the prey z value. Small islands will have many predator species, relative to the number of prey species present. This, in turn, makes it likely that, on small islands, predators will experience extinctions driven by exploitative competition, thus increasing the predator z value. Conversely, now assume that the initial distribution has a much higher z for predators than for their prey. On small islands, some prey may not experience predation at all, and so should increase in abundance. If prey directly compete, this can, in the end, lead to higher rates of prey extinction on small islands, thus increasing the prey z values. Or, multiple prey species may share a single predator, leading to the possibility of exclusion of some prey via apparent competition (Holt and Lawton 1994), once again increasing the prey z. Thus, given trophic generalization, interspecific interactions may tend to foster reduced variation among trophic levels in z values. These suggestions will be addressed more thoroughly elsewhere (R. Holt, *unpublished results*).

Nonequilibrium communities

Species–area curves may display a kind of ontogeny in communities far from equilibrium. In classic primary succession (Clements 1916), pioneering plants colonize first, followed by herbivores, then predators and parasites. This sequential colonization is sometimes observed (Glasser 1982); in such cases, one would expect nested distributions with increasing rank. If lags in colonization at higher ranks are reduced on larger areas, one would expect to observe (among patches all entering succession at the same time) stronger species–area relationships at higher ranks. However, in some systems, this successional pattern is not observed (Edwards 1987, Polis et al. 1995). For example, on small islands and barren ''habitat islands,'' initial colonists may be generalist predators, subsisting on wind-borne arthropods and detritus (e.g., Heatwole 1971, Edwards et al. 1986, Thornton et al. 1990, Polis and Hurd 1995, 1996). Thus, community assembly may not match tidy sequential patterns of assembly in progressing up food chains; this makes it less like that effects of trophic

rank on species–area relationships (if observed) reflect patterns of sequential colonization and trophic dependencies.

The inverse of community assembly during succession is ''disassembly,'' for instance because of habitat fragmentation. Mikkelson (1993) compiled data from several studies of anthropogenic habitat fragmentation, suggesting that trophic structure (i.e., the fraction of total species lists in defined trophic categories) may not change during habitat fragmentation. He does not directly discuss z values, but clearly if fragments vary in size and species richness, but not in trophic structure, species at different trophic ranks must necessarily have equal values of z. Early in disassembly, of course (as noted by Mikkelson [1993]), extinctions may be slow; thus, one might not expect to see marked effects on z values. Moreover, the consumers in the datasets considered by Mikkelson (1993) are vertebrates, many of which are generalized, opportunistic consumers. By the arguments presented above, one might expect these species to have weak species–area relationships relative to specialists in community disassembly. It would be interesting to examine distributional patterns of trophic specialists, such as parasitoids or herbivorous insects in fragmented habitats. We predict that such taxa would show stronger and more rapid effects of fragment size and isolation, than do trophic generalists. The data of Kruess and Tscharntke (1994) on parasitoids and herbivorous insects on alfalfa patches support this expectation. Gilbert et al. (1998) have recently described an experimental study of habitat fragmentation in an invertebrate community with rapid extinctions; such extinctions were disproportionately experienced by species at high trophic levels, leading to stronger species–area effects at high levels.

Conclusions

Trophic specialization in closed communities (e.g., on oceanic islands) has spatial consequences: an expected pattern of nested distributions of consumers and their resources. In turn, this nesting should lead to stronger species–area (and species–distance) effects as trophic rank increases. Similar patterns may emerge from very different mechanisms (e.g., from population level consequences of trophic rank, and sampling effects), so merely observing the pattern does not constitute proof that our hypothesized mechanism is responsible for it. We have identified a number of circumstances in which the predicted effect of trophic rank on the species–area relationship should not be observed, or may even be reversed. These include the following: strong top-down effects; open systems and mobile consumers; trophic generalization (in particular opportunistic generalists, able to persist flexibly on many subsets of prey species); and, communities far from equilibrium.

Data from some systems with specialized consumers tentatively supports our theoretical expectation that the strength of the species–area relation should increase with trophic rank. However, much more work needs to be done in documenting species–area relationships in a range of taxa, differing in traits such as trophic specialization, in the context of well-resolved food webs. It is difficult to assess hypotheses such as those discussed here in the absence of a broader range of food webs that are resolved to the species level (rather than more general categories). More generally, we suggest that the ideas presented in this paper provide pointers towards a conceptual framework for analyzing the implications of food web structure for the spatial scaling of species richness. All food webs exist in space, and many aspects of local food web structure surely reflect spatial dynamics in heterogenous landscapes.

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