12 · *On the Interface of Food Webs and Spatial Ecology: The Trophic Dimension of Species–Area Relationships*

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12.1 Introduction

A hidden dimension of food web ecology almost since its inception has been a concern with space and spatial dynamics. One of the first food webs ever scribbled onto paper was a hand-drawn diagram Charles Elton sketched as an undergraduate, during an expedition to the Svalbard region north of Norway (Summerhayes & Elton, 1923). The food web he drew for Bear Island depicts spatial interactions among the marine realm, terrestrial habitats and bodies of freshwater, mediated by the movement of colonial seabirds from their foraging grounds to their nesting arenas (a process now called 'spatial subsidy'; Polis et al., 1997; Graham et al., 2018). Elton maintained an interest in the spatial aspects of communities through his life. One of his last publications, the rarely read tome *The pattern of animal communities* (Elton, 1966), contained two essential spatial insights about food webs. Elton noted that 'The pyramid of numbers, really a pyramid of consumer layers [trophic levels], is matched by . . . the inverse pyramid of habitat'. Namely, species at higher trophic levels often range further and so have to be examined at larger spatial scales. This means species at higher trophic ranks can spatially couple dynamics of communities at lower trophic ranks, an insight that resonates to the present day (e.g. McCann et al., 2005). Moreover, echoing his youthful excursion to the frigid Arctic, he states 'no habitat component with its animal community is a closed system . . . the structural boundaries . . . are constantly passed by population movement . . . every community unit is partly interlocked with others, not necessarily its nearest neighbours . . .'. This statement could be viewed as a harbinger of

today's concern with metacommunity processes (Holt, 1997; Leibold et al., 2004; Leibold & Chase, 2018).

However, for most of its history, food web ecology has largely focussed on local interactions. Amarasekare (2008) notes 'scant empirical evidence of spatial effects in food webs'. Even the fine recent volume *Adaptive food webs* (2018) only marginally deals with food webs in a spatial context. Montoya and Galiana (2018), however, do provide a useful perspective on how to relate species interaction networks to biogeography. They note several distinct modalities of spatial processes at play in food web ecology. First, there now exist preliminary attempts to explicitly integrate island biogeography and food web theory via influences of food web interactions on the colonization and extinction processes generating species' occupancy patterns (Holt, 1996, 1997, 2010; Gravel et al., 2011; Massol et al., 2017). Second, there is growing recognition that taxa at different trophic levels can have distinct spatial strategies, for example the coupling of spatially separated habitats by mobile consumers (e.g. McCann et al., 2005; Rooney et al., 2008), related to the broader theme of spatial subsidies and spatial ecosystem ecology (Polis et al., 1996; Massol et al., 2011). Third, dispersal in metacommunities can permit the persistence of otherwise unfeasible configurations of species interactions (Amarasekare, 2008); area effects on species persistence can reflect within–island spatial dynamics (Holt, 1992), which can be particularly important in fostering the persistence of strong food web interactions (e.g. see Wilson et al., 1998 for a food chain example). Yet these three components of merging food web and spatial ecology have yet to be comprehensively integrated.

Montoya and Galiana (2018) note that one potential approach to integrating food web ecology with biogeography is to examine how food web properties vary along major environmental gradients. Preeminent among such gradients are those spatial attributes of habitats at the heart of island biogeography theory (MacArthur & Wilson, 1967; Whittaker & Fernández-Palacios, 2007) – the area of islands or isolated habitat patches and their distance to potential sources of colonists. Baiser et al. (2012) examined the food webs of pitcher plants (*Sarracenia purpurea*) and showed that food web attributes – food chain length, total species richness, linkage density and incidence of omnivores – increased with pitcher volume. Gravel et al. (2018) point to the rapidly growing evidence that the structure of ecological networks varies by habitat, through time and across gradients. A systematic understanding of how area influences network attributes – such as the number of species in each

trophic rank – is clearly emerging as a key desideratum for current research. Species coexistence mechanisms can also be scale dependent (Holt, 1993; Chesson, 2018) and variation in species richness with area could reflect the breakdown of such mechanisms at small spatial scales. For example, Orrock and Fletcher (2005) showed that the respective roles of stochasticity and competitive ability in driving competitive outcomes can change with habitat size. The principal ingredient of quantitative, dynamical food webs – interaction strength – can itself vary with island area (e.g. Schoener et al., 2016). Martinson and Fagan (2014) carried out a meta-analysis of plant–insect herbivore interactions in fragmented landscapes and found that plants on small, isolated fragments enjoyed almost 50 per cent less herbivory than plants in large patches. Across a range of island and patch sizes, Connor et al. (2000) observed that animal densities are higher in larger areas. Ecological interactions are typically 'dosage-dependent', so for instance competition intensity increases with the densities of competitors, implying a likely systematic signal of area on interspecific interaction strength (as found in parasitoid–host interactions by Fenoglio et al., 2013) – with implications for the spatial scaling of species richness.

Island biogeography has dealt with trophic interactions and food web structure, but not as a central theme. As Holt (2010) noted, MacArthur and Wilson (1967) do not directly discuss food webs at all, but do obliquely hint at how local food web interactions can govern colonization and extinction and, thus, island community structure. The synthesis of island biogeography by Whittaker and Fernández-Palacios (2007) touches on predation and food chains several times. Two telling examples they cite from classic island studies are: i) that Thornton (1996) ascribed several extinctions of birds on Anak Krakatau to top avian predators (whose numbers were sustained, it appears, by the ability of raptors to move among several islands, an example of the spatial scaling of movement with trophic rank hypothesized by Elton in 1966) and ii) that Lomolino (1984) demonstrated that the carnivorous shrew *Blarina brevicauda* drove extinctions of a mammalian prey species, *Microtus pennsylvanicus*, on islands in the Thousand Island region of the St. Lawrence River. Harold Heatwole (Heatwole & Levins, 1972; Heatwole, 2018) examined islands in the Caribbean and off Australia and argued that insular trophic structure (the relative proportion of species in major trophic groups such as detritivores, herbivores and predators) can be relatively stable, even if species composition is in continual flux. Piechnik et al. (2008) re-examined the classic Simberloff-Wilson experimental

defaunation of mangrove islets and reported a signature of trophic breadth in the order of colonization, with generalist consumers arriving first in community assembly (see also Cirtwill & Stouffer, 2016). These examples show that the presence or absence of predators and trophic attributes such as dietary specialization can influence the primary drivers of community assembly on islands – extinction and colonization – an issue we examine more closely in Sections 12.3 and 12.4.

A principal goal of the theory of island biogeography was to develop a dynamic explanation for the species–area and species–distance relationships on true islands. There are many kinds of species–area relationships (SARs), including for instance different kinds of species accumulation curves within contiguous land masses (Scheiner, 2003) and we touch on several below. In island biogeography and analyses of habitat fragmentation, the focus is typically on the Type IV curves of Scheiner (2003), which describe species richness across 'true' or 'habitat' islands or distinct geographical domains varying in area (also termed island species–area relationships or ISARs, see Chapter 1). Over some spatial scales, ISARs nicely fit the classic power law, $S = cA^{z}$, where c is a parameter representing a kind of carrying capacity per unit area and z is a parameter that indicates how area (A) boosts species richness (S) (Triantis et al., 2012; Matthews et al., 2016). Equivalently, we have $z = \frac{\partial \log (S)}{\partial \log (A)}$. This expression usefully characterizes the strength of the relationship between species richness and area, even if the power law does not hold (i.e. z can vary with A).

A null expectation might be that the parameters defining the strength of the species–area relationship are not influenced by trophic rank or interactions. Indeed, Drakare et al. (2006) reviewed species–area relationships (largely for nested or contiguous species–area curves) from a wide range of systems and concluded that there was no significant signal of trophic guild '. . . across autotrophs, herbivores, omnivores, carnivores, microbivores, parasites and decomposers'. So maybe this chapter could end right here!

But we won't do that; instead we will revisit these issues. We will build simple models of SARs across multiple trophic levels, beginning from the unlikely starting point of ecological neutral theory (Hubbell, 2001), which at its core shares the assumption that trophic position is an unimportant predictor of spatial variation in biodiversity. After presenting this novel bit of theory, we then examine some decidedly non-neutral models, including communities with tightly specialized food
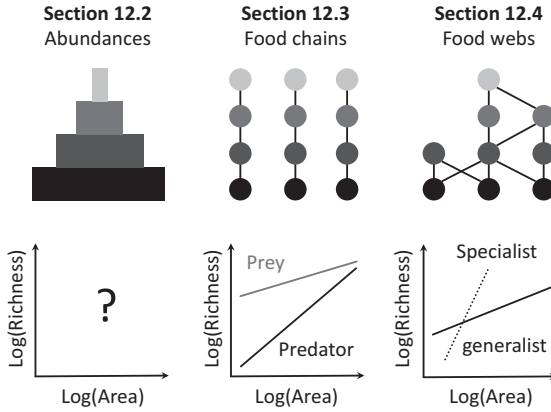
Section 12.2
Abundances

Section 12.3
Food chains

Section 12.4
Food webs

Log(Richness) | ?
Log(Area)

Log(Richness) | Prey / Predator
Log(Area)

Log(Richness) | Specialist / generalist
Log(Area)

Figure 12.1 The three scenarios considered in this chapter. Left: a trophic abundance pyramid, with lower abundances at higher trophic ranks. Centre: a community comprised of 'stacked specialists', where each plant sustains a specialist consumer, which in turn supports a specialist hyper-consumer. Right: a community with a mixture of trophic specialists and generalists within trophic levels.

chains and mixtures of specialist and generalist predators, complementing several important reviews and theoretical advances which have recently appeared (e.g. Gravel et al., 2011; Massol et al., 2017; Galiana et al., 2018). Figure 12.1 shows schematically the three aspects of community structure we explore in the three main sections of this chapter: trophic pyramids (Section 12.2), food chains (Section 12.3) and more complex food webs (Section 12.4).

12.2 Trophic Pyramids and the SAR

Ecological neutral theory assumes an individual's chances of reproduction and death are independent of its species identity. This may seem an extreme simplification of a richly complex reality, especially in the context of food web interactions. However, the merits of neutral theory (like the theory of island biogeography) lie in its ability to act as a minimal starting point on which more complex ideas or inferences can be built, a 'yardstick' for assessing implications of additional biological assumptions. Furthermore, neutral theory actually does an excellent job of predicting SARs, both on islands and on contiguous mainland (see Chapter 11). In the simplest neutral community model there is a 'zero–sum' competitive game at play: the total size of the community is fixed so that the abundance of one species can only

increase when another decreases. This fixed total abundance is set by unexamined factors, such as total resource supply or top-down effects of higher trophic levels acting to constrain total abundance at lower levels. In each time step, one individual is chosen at random to die and another is comparably chosen to reproduce, filling the 'gap' left in the community by the death. Relative abundances of species drift over time and species go extinct. Based on these rules alone, the community would drift eventually to monodominance of one species. To maintain diversity, an input of new species is required to counterbalance extinction, either by speciation or immigration from an external species pool or both. One can use neutral theory to construct species–area relationships in either case (see Rosindell & Cornell, 2007; Chapter 11). To do so over the full range of spatial scales requires a fully spatially explicit model in which individuals occupy a precise location in space. The ubiquitous power-law relationship emerges at intermediate sample areas from these models and is especially prominent when dispersal across space follows a fat-tailed distribution in which long-distance dispersal events are common (Rosindell & Cornell, 2009).

What could possibly be neutral about food webs? In some systems, trophic levels or guilds are cleanly delineated, so that one can discern distinct trophic levels. Interactions across trophic levels are obviously not neutral. But maybe interactions *within* trophic levels or 'guilds' could be treated as if governed by neutral dynamics, at least as a simplification (see Krishna et al., 2008 for a comparable approach to mutualistic networks; see Chave, 2004 and Adler et al., 2007 for more discussion on the equivalence assumption). This has previously been done to provide a neutral model of predator–prey interaction networks (Canard et al., 2012) and later in host–parasite systems (Canard et al., 2014). Here we consider the simpler question of SARs in linked neutral models across two or more trophic levels. One could imagine for the sake of argument that the total number of individuals (across all species) in a given trophic level is determined by trophic interactions, whilst dynamics among species within a trophic level are a competitive, zero-sum game. If all species are competitively equivalent on the same trophic level, their numbers should drift, comparable to Hubbell's neutral tree community model (Hubbell, 2001). In a food web diagram, all species (or alternatively, all individuals) on one trophic level would be equally connected to all species (or individuals) in levels below and above. In later sections, we explore the implications of more specialized interconnections across trophic levels.

We first explore the consequences of trophic levels for a non–spatial neutral model, which is suitable for capturing SARs on isolated islands or at very large continental scales. The species richness S in a community containing J individual organisms and having a per capita speciation rate of v can be described by (Etienne & Alonso, 2005):

$$S = \theta(\psi_0(\theta + J) - \psi_0(\theta)). \tag{12.1}$$

Here ψ_0 is the digamma function and the quantity θ is the 'fundamental biodiversity number' (Hubbell, 2001) given by $\theta = \frac{(J-1)v}{1-v}$ (see also Chapter 11).

Now consider a system with n trophic levels; trophic level i has a total community size of $J_i = A \cdot \rho_i$, where A is area and ρ_i is the density of individuals per unit area for trophic level i. Total community size is thus assumed to be proportional to area; more complex relationships between density and area are known (Connor et al., 2000) and could straightforwardly be accounted for. The SAR for species from trophic level i is given by an extension of Equation (12.1):

$$S_i(A) = \theta_i(A)(\psi_0(\theta_i(A) + \rho_i A) - \psi_0(\theta_i(A))), \tag{12.2}$$

where $\theta_i(A) = \frac{(\rho_i A - 1) v_i}{1 - v_i}$ (see also Chapter 11). The SAR incorporating species from all n trophic levels is a sum over Equation (12.2):

$$S(A) = \sum_{i=1}^{n} \theta_i(A)(\psi_0(\theta_i(A) + \rho_i A) - \psi_0(\theta_i(A))). \tag{12.3}$$

Two patterns emerge from these formulas. First, very small metacommunities will harbour only a single species in each trophic level. Second, once metacommunity size (area) becomes larger, the SAR becomes linear. This is consistent with an approximation of Equation (12.2) in which, provided species richness is not small, $\theta_i \gg 1$, we can write

$$S_i(A) \approx A \frac{\rho_i v}{1 - v} \log\left(\frac{1}{v}\right). \tag{12.4}$$

These findings essentially restate the results of Chisholm et al. (2016), who studied an extension of neutral theory, in the context of ISARs, where the community consists of multiple niches and where within each niche multiple species interact neutrally. Here, we simply replace 'niches' with 'trophic levels'.

Note that this SAR for large A is only consistent with the classic power law $S = cA^z$ when $z = 1$. This does not match typical observations

for small to moderate-sized oceanic islands, but resembles the SAR of some isolated islands which receive very limited immigration, so that all species richness emerges from in situ diversification; every island is then an independent evolutionary arena (Losos & Schluter, 2000; Chisholm et al., 2016).

We now use the above machinery to examine SARs as a function of trophic rank. A general rule of thumb is that predators, collectively, are rarer than their prey. Charles Elton, in his *Animal ecology* (1927), referred to this as the 'pyramid of numbers', which often (not always, see figure 3.15 in Odum, 1971) describes how total abundance varies with trophic rank (when such ranks are cleanly delineated). Let us imagine that species in different trophic ranks are demographically equivalent and have the same speciation rates, but that trophic ranks differ in total community size. For illustration, we make the simplifying assumption that the number of individuals declines by a factor of 10 with each increase in trophic level. This assumption has no effect on our qualitative conclusions.

At sufficiently large areas, where the relationship is effectively linear, one expects the relative species richness of two trophic ranks to match their relative abundances, or

$$\frac{S_{i+1}}{S_i} \approx \frac{J_{i+1}}{J_i}. \tag{12.5}$$

In an earlier era of food web theory, it was suggested that the relative richness of top, intermediate and basal trophic species within communities are relatively invariant across communities (Cohen, 1977; Cohen & Briand, 1984; Cohen & Newman, 1991). Where this is the case, the null expectation might be that SARs (after accounting for differences in individual densities) would match, across trophic levels. Combined with our conclusions from the above simple neutral model, it might appear that Drakare et al. (2006) are correct and that trophic rank or guild are not informative relative to SARs.

But organisms at different trophic levels can differ in many important ways, for instance in body size and mobility. Genetic estimates suggest substantial variation in dispersal across trophic levels (Kinlan & Gaines, 2003). McCann et al. (2005) argued that, in oceanic food webs, there is an allometric relationship between body size and dispersal ability, so top-ranked predators roam widely and link distinct ecosystems (Figure 12.2). For example, in coral reef fish communities, predator dispersal scale increases with increasing body size (Stier et al., 2014a). We build on
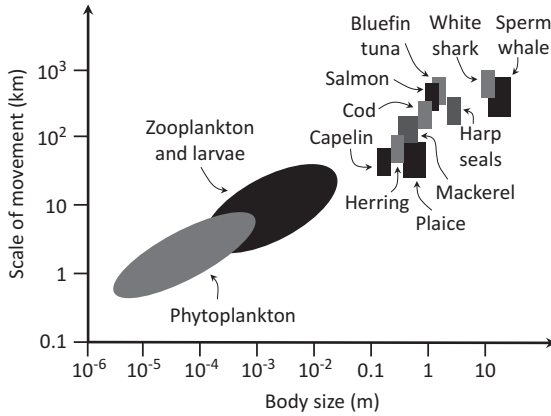
Figure 12.2 The spatial scale of movement increases with body size, which is correlated with trophic rank (redrawn using data from a figure in McCann et al., 2005; under license from John Wiley and Sons). The shades used are for graphic clarity only and are not intended to map to any property of the system.

results in Chapter 11 to provide a spatially explicit neutral SAR for mainlands (SAR types I, IIA; Scheiner, 2003) across multiple trophic levels. We assume, as a starting point, that the primary drivers are trophic level, abundance and dispersal ability, rather than the precise interaction structure of the food web.

First we state the density of individuals δ_i in trophic level i using the '10 per cent' rule of thumb given by

$$\delta_i = 0.1 \cdot \delta_{i-1}, \ \delta_1 = \delta. \tag{12.6}$$

Next, we determine the individual body mass m_i of an individual in trophic level i using a scaling law (Cohen et al., 2003)

$$\delta_i = N_0 \cdot m_i^{-\beta}, \tag{12.7}$$

which can be rearranged to produce

$$m_i = (N_0/\delta_i)^{1/\beta}, \tag{12.8}$$

where $\beta = \frac{3}{4}$ or $\beta = \frac{2}{3}$ are typical (Cohen et al., 2003); we assume $\beta = \frac{3}{4}$ in our results.

In many systems, dispersal range scales with body size, which increases with trophic rank (Figure 12.2). We use individual body mass in a further scaling law to predict total lifetime dispersal distance σ_i for each trophic level

$$\sigma_i = B_0 m_i^{\alpha}. \tag{12.9}$$

The allometric relationship itself is well supported (Brown et al., 2000), but the value of the scaling exponent α may be hard to determine in this case. For example, 0.21 was inferred for scaling of active dispersal velocity in terrestrial mammalian carnivores (Rizzuto et al., 2018) and 0.48 was used more generally for scaling of passive dispersal in the Madingley model (Harfoot et al., 2014). However, neither is quite the same as total lifetime dispersal (in general, the precise scaling of dispersal with body size and how it interacts with other factors such as fertility and lifespan is unknown and an important desideratum for future research). Dispersal distance σ_i can be multiplied by $\sqrt{\delta_i}$ to give dispersal measured in units of individual widths at their natural density, rather than in units of geometric distance.

We will use a spatially explicit neutral model for which the SAR on a contiguous mainland is closely approximated by an analytical formula (see Chapter 11):

$$S_i\left(A, \nu, \sigma_i^2\right) \sim \delta_i \sigma_i^2 \, \Psi\left(\frac{A}{\sigma_i^2}, \nu\right). \tag{12.10}$$

Here A is area (measured in the same units as σ_i^2), ν is a per capita speciation rate and Ψ is the 'Preston Function' (Chisholm et al., 2018; Chapter 11), which can be approximated analytically (O'Dwyer and Cornell, 2018). This can be written with substitutions from Equations (12.6), (12.8) and (12.9) into Equation (12.10) to obtain

$$S_i(A, \nu, \sigma_i^2) \sim x \cdot \delta^{1-2\alpha/\beta} 0.1^{(i-1)(1-2\alpha/\beta)} \cdot \Psi(A \cdot x^{-1} \cdot \delta^{2\alpha/\beta} \cdot 0.1^{2\alpha(i-1)/\beta}, \nu), \tag{12.11}$$

where $x = B_0^2 \cdot N_0^{2\alpha/\beta}$. The total SAR across multiple trophic levels is given by the sum across all trophic levels of the individual SARs:

$$S(A) = \sum_{i=1}^{n} S_i\left(A, \nu, \sigma_i^2\right). \tag{12.12}$$

Figure 12.3 depicts what happens when dispersal rates are assumed equal across trophic levels ($\alpha = 0$). As area increases, food chain length increases (upper left; the minimal number of species cannot drop below one). However, the spatial dependence of richness on area (the value of z) is the *same* across trophic levels (upper right). Thus, in the simplest neutral model that is spatially explicit, where all individuals disperse in the same way, we conclude: trophic rank has no effect on the SAR. This may
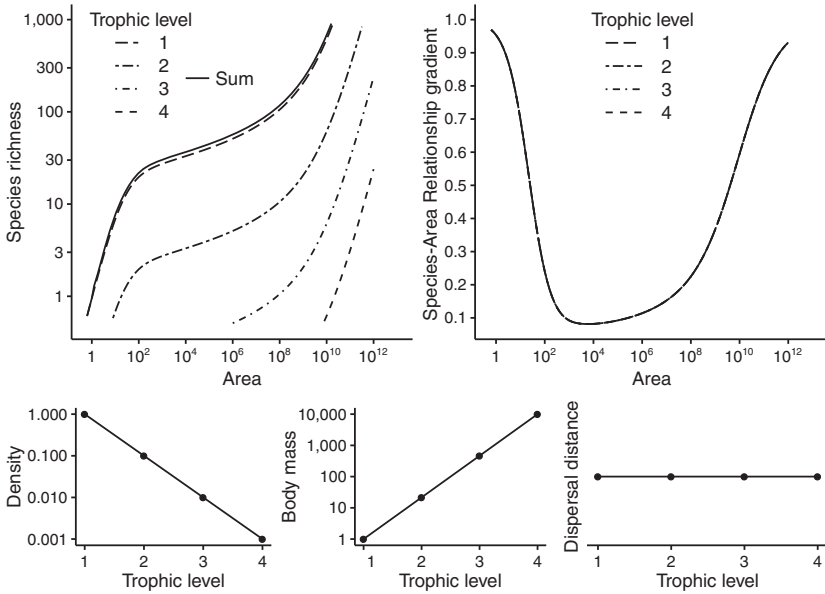
Figure 12.3 Top left: the species–area relationship on a contiguous mainland for multiple trophic levels. The data come from an independent spatially explicit neutral model for each trophic level and are based on an analytical solution (the Preston Function) for the mean total number of species in different sized (nested) areas. It is assumed that there are several trophic levels which differ systematically by a factor of 10 in total abundance, but with equal dispersal ability. Top right: the species–area relationship gradient, $z = \frac{\partial \log(S)}{\partial \log(A)}$ as a function of log area. The strength of the species–area relationship depends on the spatial scale in question – but does not differ by trophic level. Bottom panels: underlying allometric relationships between trophic level and density (bottom left), body mass (bottom centre) and dispersal (bottom right). The parameters used were $\nu = 10^{-9}$, $\delta = 10^{6}$, $N_0 = 10^{-3}$, $\beta = \frac{3}{4}$, $\alpha = 0$, $B_0 = 3$.

seem surprising, but it happens because dispersal limitation is the key driver of spatial distribution in a neutral model and in this first example this has been assumed fixed across all trophic levels.

Figure 12.4 shows a more interesting observation, where now we assume that individuals at higher trophic rank disperse further (with exponent $\alpha = 0.25$). The gradient of the SAR in logarithmic space is now dependent on spatial scale as a function of trophic level. At smaller spatial scales, higher trophic levels are predicted to have *steeper* SAR gradients. However, at larger spatial scales the opposite is predicted, with higher trophic levels having *shallower* SAR slopes. Thus, the effect of trophic level on the strength of the SAR exponent is predicted to be scale dependent.
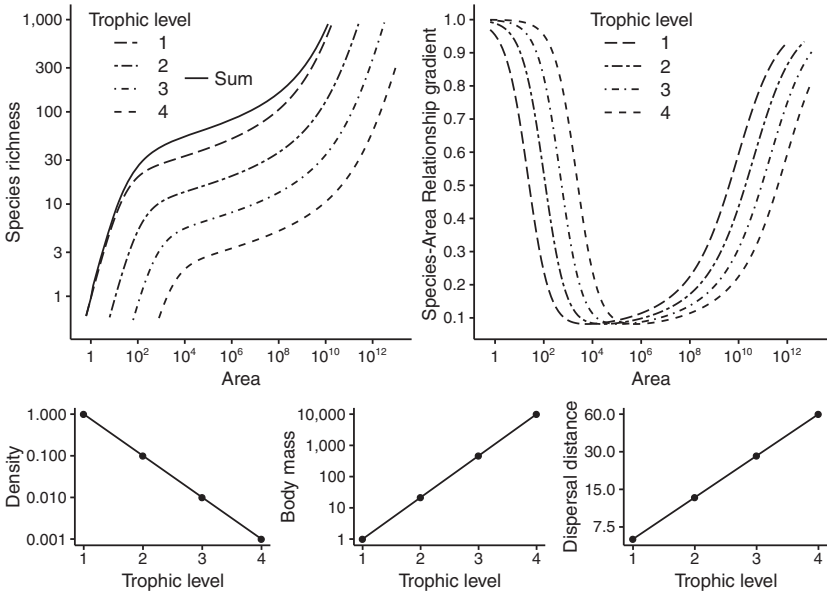
Figure 12.4 As in Figure 12.3, but now dispersal distances increase with trophic level α = 0.25. This implies that species–area relationships can vary by trophic level, but in a manner that is scale dependent.

12.2.1 Beyond Neutrality

There are several ways to relate trophic interactions and the species–area relationship that go beyond these neutral expectations (Holt, 2010). First, trophic status might be correlated with individual or population-level attributes which influence extinction or colonization rates or evolutionary rates. Alonso et al. (2015) provided an excellent example from coral reef fish experiencing mass mortality events: extinction rates increase at higher trophic ranks. Jacquet et al. (2017) showed that including trophic position improved predictive accuracy of occupancies in tropical coral reefs, using a MacArthur-Wilson style model. Stier et al. (2014a) convincingly argued that colonization rates should be higher at higher trophic ranks in fish communities, because predators with relatively larger body sizes in their larval stages can disperse further through longer larval durations, a factor that we have taken into account in the analyses leading to Figure 12.4 because trophic levels are treated as having different dispersal abilities. Colonization makes rescue effects more likely, dampening extinction. This may help explain the observation that predator:prey richness ratios increase with distance from sources across

the Pacific Ocean (Stier et al., 2014a). Top fish predators have highly generalized diets and so are not likely to be constrained by the occurrence of particular prey species; together with high mobility, this should flatten SARs in contrast to specialist enemies, as we will investigate later.

12.3 Food Chains and the SAR

Trophic interactions themselves could directly drive extinction and colonization, via 'bottom-up' and 'top-down' forces. Trophic interactions can be complex (nonlinear functional responses, predator–prey cycles, chaos and the like) and in the future it would be valuable to link the rich body of theory that exists on food web ecology more explicitly to the spatial processes that underlie SARs. But it is useful to start with simpler, more schematic models, a 'minimalist' community ecology that goes beyond neutral theory, but does so by utilizing the simpler abstraction of MacArthur and Wilson (1967), which focuses on the extinction and colonization of entire species. The simplest, non-interactive island biogeographic model (where the rate parameters for each species do not depend upon other community members) can be viewed as a limiting niche model, where each species potentially has its own separate niche on an island.

A fundamental descriptor in spatial ecology is 'occupancy' – the fraction of habitat patches or islands occupied by a species. Occupancies expressed as a function of area are called 'incidence functions'. Given incidence functions, one can construct SARs for entire communities (Ovaskainen & Hanski, 2003). Interactions among species, including food web interactions, can be built into incidence functions. It is an ecological truism that all species require resources and a food web at the very least describes asymmetrical resource dependencies among species. We start by assuming 'donor-control', so that predators need prey, to colonize and avoid extinction, but do not themselves alter prey colonization or extinction. This sequential trophic dependency, all by itself, has consequences for community structure, including species–area relationships. In empirical studies of extinction, specialist herbivores usually go extinct before their required host plants (e.g. Sang et al., 2010) and differences in establishment by basal host species constrain colonization by specialist trophic guilds dependent upon those hosts (Harvey & MacDougall, 2014; Cirtwill & Stouffer, 2016). We will first consider simple communities of multiple unbranched food chains – 'stacked specialists' (e.g. host plants, with specialist herbivores, sustaining specialist

parasitoids; Figure 12.1). Take a single such food chain and consider a taxon at trophic rank i. A mainland community is assumed to have n such food chains.

Previous papers by one of us (Holt, 1993, 2010; Holt et al., 1999) developed simple models incorporating sequential dependencies among specialist consumers and their biotic resources, drawing out implications for the species–area relationship built on this 'bottom-up' effect. These models include static incidence function models and dynamic patch occupancy models; we here just sketch the former. The incidence function for a given species of rank i is the percentage of islands that are occupied, as a function of area and rank, $p(i)$ (we leave the functional relationship on area, A, implicit and for simplicity assume all species of a given rank have the same incidence function). The expected number of species of rank i on a given island is $S_i = np(i)$.

Given tight specialization up food chains, a species of rank i cannot persist on any island lacking its resource species of rank $i - 1$, but it might not persist even if that resource is present. Colling and Matthies (2004) provided an example of an incidence function for a specialist fungal pathogen, which is not sustained on small host populations. Small islands often contain the host, but not the pathogen. This sequential dependency leads to nested spatial distributions, which we can formalize as follows.

A resource species of rank $i - 1$, which a species of rank i requires, has its own incidence function, $p(i - 1)$. If we focus on one food chain, we expect nested distributions across islands, for populations that persist without recurrent immigration: if species $i - 1$ is absent, so too should be any dependent consumer, species i, $i + 1$, etc.

Define the conditional incidence function of species i as the probability it will be present, given that its required resource is present, $p(i|i - 1)$, as a function of (say) area. The unconditional incidence for species i can be written as a compounding of such conditional incidence functions

$$p(i) = p(i|i - 1)p(i - 1)\ldots = p(1)\prod_{j=2}^{i} p(j|j - 1) \qquad (12.13)$$

If we assume that there are n stacked specialist food chains on a mainland, on the islands the expected number of species of rank i is $S_i = np(i)$. On a log–log plot, the strength of the SAR across trophic ranks is as follows

$$z_i = \frac{\partial \log (S_i)}{\partial \log (A)} = \frac{\partial \log (p(i))}{\partial \log (A)} = \frac{\partial \log (p(i-1))}{\partial \log (A)} + \frac{\partial \log (p(i|i-1))}{\partial \log (A)}$$

$$= z_{i-1} + \frac{\partial \log (p(i|i-1))}{\partial \log (A)}, \tag{12.14}$$

implying $z_1 < z_2 < z_3$, etc., if the rightmost term is positive. Thus, if conditional incidence increases with area, the z-value increases with trophic rank. As a limiting case, conditional incidence might be independent of area, in which case z-values across trophic levels will match. Similar results emerge for dynamic occupancy models given donor control with sequential colonization and linked extinction dynamics. The basic idea is that a specialist consumer cannot colonize an island unless its required resource is present and if that resource goes extinct – so should it and, in turn, any species depending solely on it. Based on these simple models, Holt et al. (1999) and Holt (2010) argued that on islands relatively closed to immigration, specialist consumers (which attack just a single prey species) with weak top-down effects on their prey should often have stronger SARs (i.e. higher z-values) than do their prey. Because the same argument holds at each trophic level, this suggests that z-values should increase, as one marches up higher trophic ranks through specialist food chains in a community. Roslin et al. (2014) provided a fine empirical demonstration of this prediction, using a system where the natural history fits the model assumptions – herbivorous insects on an island archipelago in the Baltic, where those insects sustained primary parasitoids, which in turn supported secondary parasitoids. Each trophic level was comprised of relatively specialized consumers (herbivores on their plant hosts, parasitoids on their insect hosts, etc.). Consistent with theory, the slope of the log–log ISAR '...steepened from plants through herbivores and primary parasitoids, to secondary parasitoids'.

12.4 Food Webs and the SAR

The tightly specialized food chains explored in Section 12.3 are an abstraction; few, if any, natural communities will show such marked specialization across trophic levels. Holt et al. (1999) suggested circumstances in which trophic rank might not systematically affect the SAR, if for instance communities are open with rapid, recurrent immigration at high trophic levels, or if consumers are generalists, so their

populations can be sustained by any of a number of lower-level prey species. If some consumers are generalists, but others specialists, there could be differences in the strength of the SAR associated with the degree of trophic specialization.

12.4.1 'Bottom-up' Effects

Holt (2010) developed a variant of the classic MacArthur–Wilson island model, to suggest that generalists could even have lower SARs (i.e. lower z-values) than their prey. There is growing evidence that trophic specialization versus generalization does influence colonization and persistence. Bagchi et al. (2018) reviewed evidence that specialist plant–herbivore interactions are differentially absent on the small, isolated patches that characterize fragmented landscapes, leading to steeper SARs for specialist, compared to generalist, herbivores. As they note, this reflects the fact that the abundance of dietary specialists depends on host plant availability, whereas generalists do not show such strong dependency. Cirtwill and Stouffer (2016) revisited the mangrove island experiment of Simberloff and Wilson and showed that knowledge of species-specific resource requirements increased predictability of extinctions. In butterfly and moth assemblages on islands, dietary specialists have higher z-values (Franzen et al., 2012). This matches earlier results by Steffan-Dewenter and Tscharntke (2000) for butterflies of meadows in central Europe: polyphages, strongly oligophagous and monophagous species, respectively, have z-values of 0.07, 0.16 and 0.22. In other words, small meadows are dominated by trophic generalists. This has been detected in oceanic island studies. For instance, Santos and Quicke (2011) showed that oceanic island parasitoid faunas are more typified by generalists than are continental parasitoid assemblages. Gravel et al. (2011) have extended the sequential dependency approach of Holt to more complex food webs and demonstrated that the model successfully predicts several patterns in an Adirondacks lake dataset: small areas are dominated by primary producers and generalist predators are relatively more prevalent on islands of intermediate size. The same held for coral reef fishes, but these patterns were not observed in the mangrove arthropod communities examined by Cirtwill and Stouffer (2016).

Bottom-up effects can percolate up multiple trophic levels. Fenoglio et al. (2012) reported how forest fragment area influences parasitism on leafminers by interlocked changes in plant, herbivore

and parasitoid diversity, largely reflecting the differential loss of specialist parasitoids in small fragments. Even for generalists, trophic rank sometimes strongly influences the strength of SARs, for example Noordwijk et al. (2015) showed that the richness of zoophagous carabid beetles increased with the area of calcareous grassland, but phytophagous carabids did not. This contrasts with some of the examples cited in Holt et al. (1999), where an absence of a trophic rank effect on z was ascribed to generalization; these carabids are generalists, but nevertheless show the predicted pattern of stronger species–area relationships with trophic rank. Noordwijk et al. (2015) sensibly suggested that even generalist predators are likely scarcer than their prey, so are prone to higher extinction risks, and that generalization is no buffer against extinction, if prey numbers fluctuate synchronously (e.g. in response to major climatic events). Prairie dogs for instance have highly generalized diets, yet show a strong effect of plant species richness on local extinction rates (Ritchie, 1999). An ineffective generalist or one that draws different nutrients from different species might need a diverse array of prey types in order to gain a foothold and persist on an island.

Holt and Hoopes (2005) and Holt (2010) developed a model of bitrophic 'donor-controlled' island assembly, extending the classic immigration-extinction model of MacArthur and Wilson (1967). They assumed a prey trophic level colonizes from a mainland source pool, with non-interactive colonization and extinction rates dependent on island area. A predator trophic level likewise colonizes but, in addition to direct effects of area on its colonization and extinction rates, there are indirect effects, because increased prey species richness can facilitate predator colonization or reduce extinction. If predators are specialists, these effects should be strong (the sequential dependency effect discussed in Section 12.3). But if predators are generalists, they might well be weaker, depending on the details of trophic generalization. Generalist predators may be able to plastically use prey types that are not even part of their regular diet on the mainland, for instance, thereby promoting colonization and lowering extinction. The model made plausible that one might expect to see heterogeneous SARs by trophic rank. This theoretical prediction matched a finding in the Steffan-Dewenter and Tscharntke (2000) study: the z-value of the host plants was 0.14, even higher than that of the generalist butterflies, but lower than that of the specialists.

12.4.2 'Top-down' Impacts of Natural Enemies on Species–Area Relationships

The models summarized in Section 12.4.1 neglect the widespread observation that predators and other natural enemies alter the population sizes of their victims, with likely consequences for colonization, extinction and, thus, SARs. In the Bahamas, predatory lizards greatly lower the abundance of spider prey, boosting extinction risks (Toft & Schoener, 1983). Top-down effects in principle could have divergent impacts on SARs at lower trophic levels. Predators and parasites can at times facilitate coexistence among competing prey (e.g. Holt et al., 1994) or keep in check mesopredators that can wreak havoc at lower trophic levels. There are indications that elimination of top predators can often lead to extinction cascades at lower trophic ranks (Donohue et al., 2017). If these natural enemies are found mainly on large islands, prey diversity may collapse on smaller islands. Large islands may also harbour more refuges from predation or disturbance, reducing extinction (Schoener & Spiller, 2010). This should steepen SARs in the prey.

Conversely, strong, generalist predators can elevate extinctions in their prey, particularly if prey are not competing and some prey species are better able to withstand predation (Holt, 1977). Predators can prevent colonization, with systematic effects on SARs in the prey trophic guild (Ryberg & Chase, 2007; Holt, 2010). Strong predation can reverse positive impacts of island area on occupancy for vulnerable species (Grainger et al., 2017). In the island-like glades of the Ozarks, the eastern collared lizard is a top predator with a generalized insectivorous diet and is largely found within larger glades. Its prey had depressed z-values among glades harbouring the collared lizard, compared to glades without it. Ryberg and Chase (2007) developed a simple model where predators were assumed to increase extinction rates by a constant additive amount across islands and showed that this should depress z-values. This result does not hold in all systems. For instance, a test of the hypothesis that predators affect the SAR in coral reef systems found no evidence that predators affected the slope of the SAR in coral reef fish ecosystems in the South Pacific (Stier et al., 2014b). Moreover, at times, predators may exert stronger negative effects on their prey on larger islands. In the Bahamas, islands with lizards have fewer spider species than islands without, and this effect is strongest on large islands (Spiller & Schoener, 2009), leading to a lower value of z (0.16) for lizard islands than for lizard-free islands (0.4). This is consistent with a model presented in Holt (2010), where predators are assumed to have a multiplicative effect on

prey extinction. Murakami and Hirao (2010) reported similar impacts of lizard predation upon z-values in insects, for a different suite of Bahamian islands. Such results could arise if predators are differentially more abundant, on larger islands. Ostman et al. (2007) suggest that heterogeneity of spatial distribution of predators and the strength of their impacts of predation could help explain variation in SARs among systems, particularly given that top predators often may be absent from small, isolated islands or habitat patches (Holt & Hoopes, 2005).

12.5 Conclusions and Future Directions

In an early foray toward linking food web ecology and island biogeography, Holt et al. (1999) presented simple theory suggesting that z-values should increase with trophic rank, particularly for specialist consumers, but sometimes also for generalists. They reported examples which fit this expectation, but also counter-examples. They suggested the latter might reflect several factors: '(1) ... strong top-down interactions leading to prey extinction; (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' (p. 1495).

In this chapter, we have presented new neutral theory that emphasizes how differences in dispersal rates among trophic ranks could influence species–area relationships in a scale dependent way, matching one idea broached in Holt et al. (1999). Leaving aside neutrality, we then summarized past theory and touched on illustrative empirical examples. When trophic interactions are relatively specialized, species–area relationships tend to be steeper at higher trophic ranks. Overall, specialist consumers have steeper species–area relationships than do generalists. Top-down effects of predation on their prey can have a diverse range of impacts on such relationships.

There are many directions one could envisage for further development at the interface of food web ecology and the spatial scaling of species richness. One realistic complication in multi-trophic systems is that cascading effects across multiple trophic levels can lead to non-monotonic relationships between predation pressure on a focal taxon and area. For example, if top predators are restricted to large islands, their prey can grow to larger numbers on smaller islands, imposing greater pressure on lower trophic levels (e.g. Genua et al., 2017). In principle, patch occupancy models built to include trophic influences on

colonization and extinction can also include top-down and lateral competitive effects (Lafferty & Dunne, 2010; Pillai et al., 2010; Massol et al., 2017), although even seemingly simple models can rapidly become analytically intractable. This line of thought should be extended to incorporate a richer array of trophic phenomena, such as interference competition among consumers, apparent competition among prey, intraguild predation increasing extinction risk for consumers of intermediate rank, the influence of food web structure and predator behaviour on local population stability and thus extinction risk, and so on. The approach developed in Gravel et al. (2011) and Massol et al. (2017) could, in principle, provide a springboard to consider such effects.

One real-world complication is that, along the gradient from small to large islands, it may be insufficient to monitor occupancy on islands taken as a whole. As one of us observed long ago (Holt, 1992), organisms may have limited dispersal capacity *within* islands, so that one might view area as a proxy for, for example, lattice size, where cells in the lattice are domains of local interactions, connected by within-island dispersal. Large islands correspond to large lattices and small islands correspond to small lattices. Chase et al. (2019) make useful suggestions about how to use rarefaction at different scales within islands to discern possible mechanisms for area effects. This perspective is particularly important given strong natural enemy–victim interactions, which tend to self-destruct. Ever since the classic experiments of Huffaker (1958) it has been clear that predator–prey persistence can be enhanced by colonization among patches (Hastings, 1977) and other spatial effects such as refugia may also be important (Lampert & Hastings, 2016). Wilson et al. (1998) demonstrated that local instability could lead to strong area effects in the persistence of tritrophic (host–parasitoid–hyperparasitoid) food chains. On large islands, metacommunity processes operating within the island may buffer the many disparate ways species-rich and interconnected food webs can be unstable in their local dynamics (LeCraw et al., 2014; Wang & Loreau, 2014; Liao et al., 2017).

An important task for future work will be to articulate how the stabilizing attributes of space – against a backdrop of habitat heterogeneity and island ontogeny (Scherber et al., 2018) – in food web interactions help contribute to realized species–area relationships. One key factor affecting persistence is movement behaviour of species at different levels in the food web. Top predators can be highly mobile, coupling different local communities within a large island, modulating species coexistence at lower trophic ranks. Guzman et al. (2019) have recently

argued that understanding spatial use properties is necessary to characterize spatially distributed food web dynamics, and outlined key ingredients in an emerging predictive framework. Articulating how dispersal varies across a food web will be crucial for a more precise characterization of how trophic rank influences SARs.

The importance of considering food webs and more broadly network development in the context of island biogeography is becoming increasingly recognized as an exciting direction for current research (Warren et al., 2015). Gravel et al. (2011; see also Massol et al., 2017) creatively extended the sequential dependency model proposed earlier by Holt to include generalist consumers, such that colonization required at least one suitable resource species (among an array of alternatives) to be present already and extinction was mandated if all potential resources went missing on an island. With these reasonable assumptions, they crafted predictions about food web structure and found that their predictions held in empirical datasets: consumers accumulate at larger areas, compared to primary producers, and small areas are dominated by generalist consumers (which experience only weak sequential dependency). Network relationships are implicit, not explicit, in the model of Holt (2010) mentioned above. It would be an instructive exercise to tie this minimalist model more directly to the generalized sequential dependency models developed by Gravel et al. (2011) and Massol et al. (2017).

Further integration of food webs and biogeography theories should also consider the role of trophic interactions in driving the turnover of species. Specifically, how do factors such as island size and isolation drive the turnover of predator and prey species? What is the role of top–down and bottom–up processes in governing the rate at which the species composition of prey communities turn over across a landscape? And does trophic specialization alter the effects of island characteristics on species turnover? Ryberg et al. (2012) developed a model that predicts how predators can alter the diversity of organisms within a patch as well as the rate of species turnover among patches. Yet empirical tests of this model remain absent and additional theory is required to understand how different types of predator foraging (i.e. generalists or specialists) alter the effects predators have on patterns of prey diversity within and among patches. An additional issue of great current importance is integrating humans as natural enemies into trophic biogeography. Humans act as top predators and also as agents mediating interjections of other natural enemies (e.g. rats, goats) onto even desolate, isolated oceanic islands.

There are likely to be substantial shifts in the form of SARs, concordant with the magnitude of such top-down anthropogenic influences.

Additionally, we need to explicitly consider the importance of spatial scale in the development and testing of theory linking island biogeography to food web ecology. The neutral model presented in Section 12.2 provides a first pass at this, since it shows that if dispersal rates vary systematically with trophic rank, the ranking of z-values with trophic rank shifts with increasing scale. Naturally, experiments testing new theory necessarily tend to operate at much smaller spatial scales than that for which theory is often developed, presenting challenges in rigorously testing theory. Moreover, the role of migration between patches, in addition to how predator–prey interactions alter patterns of biodiversity across patchy landscapes, remains poorly understood. There is a growing body of literature on predator–prey interactions in patchy landscapes (see e.g. Schmitz et al., 2017), yet this literature has yet to be integrated with the literature linking food web ecology and island biogeography, or SARs more broadly. We need theory linking island biogeography to food web ecology that better accounts for movements of animals among patches or sites at a range of spatial and temporal scales.

Another key direction for future research is to examine the joint influences of food web interactions, other kinds of ecological networks, non-trophic interactions and cross-system subsidies on species richness as a function of island area. There is increasing recognition that food web structure and dynamics cannot be fully understood without paying attention to interactions such as mutualism, ecological engineering and information flows (Olff et al., 2009). Specialists are differentially lost from mutualism networks on small fragments or islands, doubtless with consequences for the remaining food webs (Aizen et al., 2012). Spatial subsidies (Polis et al., 1997) are likely more important in small islands, because of their greater perimeter:area ratio, altering colonization or extinction rates for consumers directly or indirectly capable of exploiting those subsidies (Anderson & Wait, 2001), with consequences for the strength of top-down effects (Piovia-Scott et al., 2017). A particularly important avenue for future research will be tying trophic island biogeography more explicitly to modern coexistence theory, which increasingly recognizes the importance of food web interactions for maintaining coexistence in complex assemblages (Chesson, 2018). Some coexistence mechanisms may be ineffective on small islands (e.g. any that involve patch dynamics across a metacommunity) and this surely contributes to shaping the form of realized SARs. Understanding the interplay of

coexistence mechanisms and space in maintaining diversity and in contributing to SARs is becoming ever more important in our world, so increasingly dominated by the relentless hammers of anthropogenic habitat destruction and fragmentation (among other drivers of global change) and the looming risk of mass extinctions.

Finally, all these issues should be given an evolutionary spin. Several authors have observed that trophic cascades play out very differently on isolated oceanic islands than in continental areas (Oksanen et al., 2010; Terborgh, 2010) and suggest that this reflects dramatically different evolutionary histories. On islands without top predators, herbivores can exert strong consistent selective pressure that leads to adaptations such as heterophylly and alters the allocation of plant resources to different anti-herbivore defences, depending on the suite of herbivores that are present. This evolutionary dimension at the interface of trophic interactions and species–area relationships has yet to be explored in any depth in the literature.

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