

Island Biogeography of Food Webs

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Abstract

To understand why and how species invade ecosystems, ecologists have made heavy use of observations of species colonization on islands. The theory of island biogeography, developed in the 1960s by R.H. MacArthur and E.O. Wilson, has had a tremendous impact on how ecologists understand the link between species diversity and characteristics of the habitat such as isolation and size. Recent developments have described how the inclusion of information on trophic interactions can further inform our understanding of island biogeography dynamics. Here, we extend the trophic theory of island biogeography to assess whether certain food web properties on the mainland affect colonization/extinction dynamics of species on islands. Our results highlight that both food web connectance and size on the mainland increase species diversity on islands. We also highlight that more heavily tailed degree distributions in the mainland food web correlate with less frequent but potentially more important extinction cascades on islands. The average shortest path to a basal species on islands follows a hump-shaped curve as a function of realized species richness, with food chains slightly longer than on the mainland at intermediate species richness. More modular mainland webs are also less persistent on islands. We discuss our results in the context of global changes and from the viewpoint of community assembly rules, aiming at pinpointing further theoretical developments needed to make the trophic theory of island biogeography even more useful for fundamental and applied ecology.



1. INTRODUCTION

1.1 Island Biogeography

Islands have always fascinated ecologists. Since the earliest stages of ecology as a scientific discipline, the fauna and flora of islands have been considered as objects worthy of study because they capture the essence of colonization-extinction and coevolutionary dynamics shaping natural systems (Whittaker and Fernández-Palacios, 2007). Among the iconic rules of ecology, the “island rule” (Lomolino, 1985) suggests that the span of body sizes found on islands is much narrower than on continents, reflecting the remarkable examples of gigantism in small herbivores/granivores and of dwarfism in predators observed. Simple, general theoretical models of faunal build-up on islands were proposed some 50 years ago (Levins and Heatwole, 1963; MacArthur and Wilson, 1963). More recently, extensions and applications of these models have been made, constituting what has been dubbed “eco-evolutionary island biogeography” which incorporates trophic, functional and local adaptation information into the island biogeography framework (Farkas et al., 2015; Gravel et al., 2011b). Empirically, islands have provided ecologists with a

playground to understand community assembly (Piechnik et al., 2008; Simberloff, 1976; Simberloff and Abele, 1976), species diversity (Condit et al., 2002; Ricklefs and Renner, 2012; Volkov et al., 2003) and metapopulation dynamics (Hanski, 1999; Ojanen et al., 2013).

The historical “theory of island biogeography” (TIB), presented independently by Levins and Heatwole (1963) and MacArthur and Wilson (1963), and summarized in the well-known book of the same name by MacArthur and Wilson (1967), is based on the idea that the ecological communities found on islands are a sample of those found on continents. The size of this “sample” results from two opposing processes: island colonization by external species and their local extinction on the island (see also Preston, 1962). The original formulation of the model by MacArthur and Wilson (1963) takes the form of a master equation linking the probability $P_S(t)$ that the focal island has exactly S species (from the original T total number of species found on the mainland) at time t to the rate of colonization by a new species (λ_S) and the rate of species extinction (μ_S):

$$\frac{dP_S}{dt} = \lambda_{S-1}P_{S-1} + \mu_{S+1}P_{S+1} - (\lambda_S + \mu_S)P_S \quad (1)$$

Adding the assumption of constant colonization and extinction rates (i.e. $\lambda_S = (T - S)c$ and $\mu_S = Se$, where c is the species colonization rate and e , their extinction rate), this naturally leads to the following equation on the expected species richness \bar{S} at time t :

$$\frac{d\bar{S}}{dt} = \sum_S S \frac{dP_S}{dt} = c(T - \bar{S}) - e\bar{S} \quad (2)$$

Solved at equilibrium, Eq. (2) yields the expected number of species on the island at any given time:

$$\bar{S}^* = T \frac{c}{c + e} \quad (3)$$

Eq. (3) lends itself to the interpretation of species–area and species–distance curves (i.e. curves linking the number of species present on an island to the area of the island or its distance from the continent) as the log–derivative of Eq. (3) with respect to e/c yields:

$$\frac{d \log \bar{S}^*}{d(e/c)} = -\frac{1}{1 + e/c} \quad (4)$$

For large e/c , Eq. (4) reads approximately as:

$$\frac{d \log \bar{S}^*}{d(e/c)} \approx -1 \quad (5)$$

As long as e and c are supposed to be monotonic functions of area and distance, with the intuitive slopes (i.e. c increases with area and decreases with distance, and the opposite relationships hold for e) from the continent respectively, Eq. (5) yields species–area and species–distance curves compatible with observed patterns (MacArthur and Wilson, 1963, 1967).

The TIB is a cornerstone of invasion biology for several reasons. First, it is very likely that colonization by external species is a strong component of the forces shaping community composition on long time scales for islands, whereas for mainland communities random species extinction and larger population sizes make coevolution more likely to be the dominant factor structuring communities on the same time scales. In a sense, remote islands can be seen as complete population sinks for all species (i.e. black-hole sinks or nearly so) and, as such, have very little to no impact on the overall coevolutionary patterns observed in species (Holt et al., 2003; Kawecki, 2004; Massol and Cheptou, 2011; Rousset, 1999), except for island endemics. From an other point of view, islands can also be considered as natural experiments for understanding biological invasions. The dynamics of successive species colonization from the mainland to the island constitutes an “accelerated” version of what could happen in other less extinction-prone habitats. Understanding how waves of colonization events can take place on an island, depending on island and mainland community characteristics, will give information on the conditions favouring the invasibility of habitats by exotic species—be they habitat characteristics or species traits. In the case of the TIB, colonizing species are not assumed to be fundamentally different in terms of their ability to invade an island; thus, the variability in diversity on islands predicted by the TIB boils down to variability in colonization and extinction parameters among islands, which in turn is assumed to only depend on island remoteness and area (MacArthur and Wilson, 1963, 1967).

Predictions from the TIB can be tested in different ways. First, the species–area curves can be fitted to infer underlying extinction-to-colonization ratios and/or to test whether such ratios are indeed constant across different areas, during a given period or among taxa (Cameron et al., 2013; Guilhaumon et al., 2008; Triantis et al., 2012). While this approach has produced some success in the past, it is not a strong test per

se as different theories can produce the same curves. Second, the TIB also predicts the value of the variance-to-mean ratio of species richness to be about one in species-poor island communities (MacArthur and Wilson, 1963). Indeed, taking the original master Eq. (1) and plugging $\lambda_S = (T - S)c$ and $\mu_S = Se$, one finds that:

$$\frac{d\bar{S}^2}{dt} = 2c(\bar{S}T - \bar{S}^2) - 2e\bar{S}^2 + c(T - \bar{S}) + e\bar{S} \quad (6)$$

which, combined with Eq. (2), yields the differential equation for the variance $V[S]$ of S :

$$\frac{dV[S]}{dt} = \frac{d\bar{S}^2}{dt} - 2\bar{S}\frac{d\bar{S}}{dt} = c(T - \bar{S}) + e\bar{S} - 2(c + e)V[S] \quad (7)$$

Taken at equilibrium, Eq. (7) entails the following relation between mean and variance of S :

$$V[S] = \frac{c(T - \bar{S}) + e\bar{S}}{2(c + e)} \quad (8)$$

Plugging Eq. (3) into Eq. (8), one finally finds:

$$\frac{V[S]}{\bar{S}} = 1 - \frac{\bar{S}}{T} \quad (9)$$

which is approximately equal to 1 when $\bar{S} \ll T$.

A third prediction of the TIB concerns the distribution of species richness in equally small and remote islands: by taking the equilibrium solution of Eq. (1), iterating from the equation of P_0 and getting up to P_T , one finds:

$$P_S = \frac{c(T - S + 1)P_{S-1}}{eS} = \dots = \binom{T}{S} \left(\frac{c}{e}\right)^S P_0 \quad (10)$$

where $\binom{T}{S}$ is the binomial coefficient $\frac{T!}{S!(T-S)!}$. With the sum of all P_S being equal to one, Eq. (10) leads to:

$$P_S = \binom{T}{S} \left(\frac{c}{c+e}\right)^S \left(\frac{e}{c+e}\right)^{T-S} \quad (11)$$

which is simply a binomial distribution with parameter $c/c + e$. Eq. (11) can also be found by considering that, at equilibrium, each species presence/absence is a Bernoulli-distributed random variable, thus summing over all

species ends up having species richness follow a binomially distributed random variable. Eq. (11) can be used to estimate the ratio $\alpha = c/e$ using different observations of species richness on the same island over time, with sufficiently temporally distant observations to remove the effect of temporal autocorrelation, or comparing the species richness of several equally small and remote islands.

Finally, a fourth prediction of the TIB comes from looking at the dynamics of P_S in vector format:

$$\frac{d\mathbf{P}}{dt} = \mathbf{M} \cdot \mathbf{P} \quad (12)$$

where \mathbf{P} is the vector (P_0, P_1, \dots, P_T) and \mathbf{M} is the matrix given by:

$$\mathbf{M} = \begin{pmatrix} -cT & e & 0 \\ cT & -c(T-1) - e & \\ & c(T-1) & \ddots & Te \\ 0 & & c & -Te \end{pmatrix} \quad (13)$$

Following Eq. (12), the solutions for $\mathbf{P}(t)$ beginning in state \mathbf{P}_0 at $t=0$ are given by:

$$\mathbf{P}(t) = e^{t\mathbf{M}} \cdot \mathbf{P}_0 \quad (14)$$

It is easy to check that the vector \mathbf{P}^* given by Eq. (11) is in the kernel of \mathbf{M} , i.e. that $\mathbf{M} \cdot \mathbf{P}^* = \mathbf{0}$. As such, $e^{t\mathbf{M}} \cdot \mathbf{P}^* = \mathbf{P}^*$ at all time and thus one recovers that \mathbf{P}^* is indeed the equilibrium distribution of species richness on the island. The nonzero eigenvalues of \mathbf{M} are exactly equal to the sequence $\{-(c+e), -2(c+e), \dots, -T(c+e)\}$, which entails that the typical time of convergence to steady state is $\tau_S = 1/(c+e)$; meanwhile, each species, once present on the island, has a typical time to local extinction equal to $\tau_X = 1/e$. Thus, based on Eq. (3), the TIB predicts the following relation between species richness at equilibrium and the ratio τ_S/τ_X :

$$\bar{S}^* = T \left(1 - \frac{\tau_S}{\tau_X} \right) \quad (15)$$

Such a prediction, which is equivalent to Eq. (3), can be tested based on time series of species colonization and extinction on islands, such as obtained from experimental defaunation data (Wilson and Simberloff, 1969) or long-term surveys.

Thus, as initially envisaged by its first proponents (Levins and Heatwole, 1963; MacArthur and Wilson, 1963, 1967), the TIB tries to explain species–area and species–distance curves on islands using a simple theory that assumes species accumulate due to colonization from the mainland and die out on islands at a constant rate. Although precisely formalized in mathematical terms, the TIB is not a mechanistic model per se as it assumes that extinction decreases with island area and that colonization decreases with distance between island and mainland. While these assumptions seem justified in general, the underlying mechanisms generating these relationships are omitted from the TIB. In particular, the links between island area, its underlying habitat heterogeneity (and hence its diversity in terms of potential species niches) and species carrying capacities (and thus extinction probabilities) have opposite effects on extinction rate, because habitat heterogeneity trades off with habitat size in an island of limited size (Allouche et al., 2012). Moreover, the TIB does not take species interactions into account in the sense that colonization and extinction rates are independent from current species composition on the island. Species are considered equivalent, but the model differs from neutral theory in that there is no competitive interaction (Hubbell’s model assumes very strong preemptive competition). As a consequence, the TIB cannot predict any aspect of community structure based on species-specific attributes, such as the dominance by generalists, functional composition or successional sequence. Gravel et al. (2011b) therefore introduced an extension to the classic TIB called the trophic theory of island biogeography (TTIB) with the aim of predicting the variation in food web structure with area and isolation. When trying to model empirical data akin to mainland-islands datasets such as Havens’ (1992), they found that the TTIB performs significantly better (in terms of statistical goodness-of-fit indicators) without introducing any new parameter into the TIB.

1.2 Spatial Food Webs

To understand how species coexist, it is necessary to understand how they interact. At the simplest level, species can be considered as competing under limiting factors (resources, predators, etc.). Competition need not be as simple as scramble resource competition. Indirect interactions through shared natural enemies (Holt, 1977; Leibold, 1996) or more generally any other species’ abundances or occurrences (e.g. species recycling nutrients from detritus; Daufresne and Hedin, 2005) can also be experienced as limiting factors and result in “apparent” competition *sensu lato*. Competition is

the only kind of interaction taken into account in most metacommunity models (Hubbell, 2001; Leibold et al., 2004; Massol et al., 2011). In general, however, species interactions are not only competitive. Food webs, i.e. networks of species that feed on one another, represent antagonistic trophic interactions among species and, as such, have to be taken into account as a structuring force behind coexistence patterns within communities. While other types of ecological interaction networks do exist (e.g. mutualistic trophic networks between plants, fungus and soil microbes, or antagonistic nontrophic networks among antibiotic-producing bacteria), food webs are ubiquitous and their complexity seems to be tightly associated with species richness, abundances, functioning and dynamics of communities (Chase et al., 2000; Cohen and Briand, 1984; Cohen and Łuczak, 1992; Downing and Leibold, 2002; Dunne et al., 2004; Kéfi et al., 2012; Pimm et al., 1991; Post et al., 2000).

Inspired by the work of Huffaker, recent work on the subject of food web dynamics has emphasized the necessity to consider food webs as spatialized entities (Duggins et al., 1989; Estes and Duggins, 1995; Estes et al., 1998; Huffaker, 1958; Huffaker et al., 1963; Polis and Hurd, 1995; Polis et al., 2004) in order to understand patterns such as species turnover, species richness, food chain length or nutrient recycling dynamics (Calcagno et al., 2011; Gravel et al., 2011a; Massol et al., 2011; McCann et al., 2005; Pillai et al., 2010, 2011; Takimoto et al., 2012). Considering food webs only as local, spatially disconnected entities may lead to misunderstanding, e.g. not recognizing population sinks because populations are maintained by the dispersal of detritus among habitat patches (Gravel et al., 2010). However, all species do not perceive space with the same grain, with habitat patches for one species not being the same as for another species at a different trophic level (Massol et al., 2011; McCann et al., 2005). Taking into account the spatial aspect of food webs is thus a necessity that requires understanding the complexity of spatial scales of species interactions. Acknowledging this spatial component of food webs is also a prerequisite to fully grasp the concept of limiting factors (Gravel et al., 2010; Haegeman and Loreau, 2014; Massol et al., 2011): when species and abiotic nutrients move from habitat patch to habitat patch, the effective “limitation” of species growth by an environmental factor depends not only on the local conditions but also on conditions in nearby patches contributing to influxes of organisms and nutrients into the focal patch. For these reasons, considering the spatial aspect of food webs is an important issue worthy of both theoretical and empirical development.

When considering food webs as spatialized entities, the fluxes of organisms and abiotic material between different locations present a duality of perspective of ecological fluxes (Massol and Petit, 2013; Massol et al., 2011): on the one hand, these fluxes contribute to the demographics of all species present in the different locations under study through immigration and emigration; more generally, such fluxes participate in the shaping of species and abiotic material stocks through source-sink dynamics (Loreau et al., 2013), while, on the other hand, the movement of plants, animals or simply abiotic material can be translated in fluxes of energy and nutrients that, together with other energy/nutrient fluxes due to local species interactions, represent the dynamics of nutrients and energy at large scales, flowing through trophic levels and between spatially distinct locations (in a manner rather reminiscent of Ulanowicz' ascendant perspective; Ulanowicz, 1997). Under this second perspective, there are common currencies (energy, carbon, nitrogen, phosphorus, etc.) behind each and every flux of organisms across the spatial food web that must comply with basic conservation laws (mass balance), thus constraining the possibilities of source-sink patterns among trophic levels (Loreau and Holt, 2004). Coupled with a consideration of species stoichiometric needs in terms of C:N:P ratios, such a perspective can potentially help us understand the spatial dynamics of nutrient enrichment through, for example death, reproduction, excretion and the foraging of organisms in different habitats (Hannan et al., 2007; Helfield and Naiman, 2002; Jefferies et al., 2004; Nakano and Murakami, 2001).

In the case of the TIB, the necessity of taking into account the spatial aspects of food webs has been construed as mandating the use of food web information in TIB models. The first model bridging food web theory and TIB was named the TTIB and makes use of trophic information for which species preys on what to correct effective colonization and extinction rates (Cazelles et al., 2015b; Cirtwill and Stouffer, 2016; Gravel et al., 2011b). In this first model, this correction takes a very simple form: species cannot colonize an island when they have no prey on the island, and the extinction of the prey species of a colonizer will also extirpate it from the island (Holt, 2002). More generally, this framework can be extended to account for arbitrary changes in colonization and extinction probabilities that depend on the presence or absence of other species on the island (Cazelles et al., 2015b). Thus, the TTIB can represent a complex picture of rates of transitions from one community state (i.e. the set of species occurring on the island) to another, through species colonization and extinction (Morton and Law, 1997; Slatkin, 1974). As illustrated in Fig. 1, the TIB and

TTIB are extremes of a continuum of approaches that weight differently transitions among possible community states.

1.3 Invasions in Food Webs, Eco-evolutionary Perspectives

Community assembly, broadly envisioned as the accumulation of species diversity over time in a novel habitat, has been modeled, classically, as an ecological process driven by sequential colonizations of species from a regional pool. This approach effectively considers species as having fixed characteristics and traits (e.g. prey range, feeding preferences, antipredator defences, etc.). This form of community assembly produces what are often called “invasion-structured” food webs (Rummel and Roughgarden, 1985). Invasion-structured food webs may be an adequate concept for ecosystems that are well connected to mainland, in which immigration events and invasions occur at a frequent pace. However, when considering more isolated areas, such as remote islands characterized by a very low colonization rate (low c value in the TIB framework), species may undergo a significant amount of evolutionary change in the interval of time between successive species arrivals. In such conditions, it is no longer legitimate to consider community assembly as a purely ecological process, and one needs to consider the effect of species evolution as well. The process of community assembly should thus be considered as involving three different timescales:

- (i) a rapid ecological timescale corresponding to community dynamics following species invasion;
- (ii) a slow immigration timescale corresponding to the arrival of individuals from the main source of species;
- (iii) a slow timescale corresponding to species (co)evolution in-between immigration events.

The relative speed of the last two timescales will be contingent on the level of isolation of the focal community directly through the rate of species colonization and indirectly through the amount of gene flow (slowing down local adaptation in the colonized community) and local selective pressures.

We can consider two extreme cases of community assembly: (i) where immigration events are common enough to completely outpace the effects of in situ coevolution, we recover the classic “invasion-structured” food webs; and, (ii) where evolution has plenty of time to proceed in-between invasion events, we may obtain “adaptive radiations”, i.e. the in situ formation of new species by evolution (see also Vanoverbeke et al., 2016). This second extreme case is sometimes called “evolutionary community

assembly” (Bonsall et al., 2004; Brännström et al., 2012; Doebeli and Dieckmann, 2000; HilleRisLambers et al., 2012; Loeuille and Leibold, 2014; Pillai and Guichard, 2012; Tokita and Yasutomi, 2003). Evolutionary community assembly has been mostly applied to competitive communities, but some studies have considered evolutionary diversification in the context of food webs. Doebeli and Dieckmann (2000) have shown how coevolution could yield diversification and greater specialization in predator–prey interactions. In the same vein, Loeuille and Leibold (2008) explored how the evolution of specific vs nonspecific (but costly) plant defences affects the topology of plant–herbivore food web modules. While these approaches treated trophic positions as fixed, and evolution occurred within trophic levels, more general approaches have also been employed. Rossberg et al. (2006) considered the coevolution of foraging and vulnerability traits in an abstract set of species and could reproduce interaction matrices similar to that of natural food webs (see also Drossel et al., 2004 for similar approaches). Loeuille and Loreau (2005) and Allhoff et al. (2015), using dynamical models of trophic interactions based on body mass, have studied how the level of trophic structuring and a number of trophic levels emerge from single ancestor species. In the case of mutualistic networks, Nuismer et al. (2013) assessed how the coevolution of mutualistic partners along a phenotypic trait continuum that governs both local adaptation and partner match/mismatch affected the topology of the mutualistic network.

Although studying the two extreme cases of community assembly is useful, it should be kept in mind that most natural food webs are likely not assembled by only invasions or only evolution, but probably by a combination of the two forces. Hence most ecosystems should harbour “coevolution–structured” food webs, using the terminology coined by Rummel and Roughgarden (1985). Unfortunately, comparatively few studies have examined the simultaneous action of sequential invasions and in situ coevolution on the dynamics of community assembly. Moreover, these studies have either only considered generalized Lotka–Volterra (or replicator) equations (Tokita and Yasutomi, 2003) or competitive interactions (Rummel and Roughgarden, 1985) and not trophic interactions. To some extent, predictions from models of asymmetric competitive interactions might be extrapolated to trophic interactions, but more work is needed to explore the interaction of invasion and coevolution (both directional evolution and diversification) in assembling food webs.

A few general conclusions can nevertheless be drawn. First, invasion- and coevolution-assembled communities can possess very different

characteristics (Rummel and Roughgarden, 1985; Tokita and Yasutomi, 2003). It is therefore crucial to understand how the type of assembly history affects the resistance/resilience of food webs, in particular their susceptibility to invaders and their ability to sustain functioning following invasions (Romanuk et al., 2017). Second, the impact of evolution in-between invasion events is threefold:

- (i) the evolution of species traits (e.g. body mass) can result in a rewiring of the network of ecological interactions (e.g. greater specialization/clustering, less generalism and omnivory);
- (ii) these changes of interactions might, ultimately, cause (delayed) species extinctions throughout the food web;
- (iii) on longer timescales, coevolution might cause species diversification, and thus entail (delayed) species additions throughout the network.

Finally, a general finding is that coevolutionary trajectories will feature more “loops”, i.e. would more often engage in cyclic successions of community states (for a theoretical example, see Loeuille and Leibold, 2014). This tendency of coevolution to generate sustained change in species traits and composition is a general property of asymmetric competition models (“taxon-cycle”; Nordbotten and Stenseth, 2016; Rummel and Roughgarden, 1985) that seems to extend to trophic interactions (Allhoff et al., 2015; Dieckmann et al., 1995) and that relates to the well-known Red Queen dynamics between hosts and parasites/pathogens (Boots et al., 2014; Gandon et al., 2008; Salathé et al., 2008).

Returning to the assembly trajectories depicted in Fig. 1, this would mean that taking into account the effect of species coevolution could: (i) alter the number and identity of species that go extinct following an invasion; (ii) allow more than one species to appear following an invasion, thus introducing longer upwards links; and (iii) introduce more cycles in the assembly graphs. All these effects seemingly make the assembly-trajectory graphs more complex, adding to the challenge of analysing and predicting food web dynamics. However, evolutionary changes might also make certain pathways much more likely than others, thus making assembly trajectories in effect less variable, more predictable.

1.4 Invasions in Other Spatially Structured Networks

Despite focusing here on trophic interactions, we must acknowledge that other types of networks can result in particular colonization/extinction dynamics when merged with the TIB (MacArthur and Wilson, 1963) or

with Levins' metapopulation model (Levins, 1969). For instance, Fortuna and Bascompte (2006) have argued that representing patch-occupancy dynamics of plant–animal mutualistic networks can help understand the effects of habitat loss on the observed structure of those networks (see also Astegiano et al., 2015; Fortuna et al., 2013). In practice, these effects stem from the asymmetry in the mutualistic network, in which one type of mutualistic partners mandatorily needs the other type to be able to colonize a patch (e.g. pollinators in need of plants as local trophic resources), while the other type of partners benefits from the interaction at a larger scale through an increase in its colonization ability (e.g. plant reproduction enhanced by animal-mediated pollination).

More generally, we can analyse the potential effects of species interaction on TIB-like dynamics through a translation of Nee and May's (1992) generalization of Levins' (1969) model to the case of island biogeography dynamics. We can describe the dynamics of the probability p_i that a given species i is present on the focal island as:

$$\frac{dp_i}{dt} = c_i(h_i - p_i) - e_i p_i \quad (16)$$

where c_i denotes species colonization rate, h_i denotes the probability that the island is hospitable to species i and e_i is species extinction rate once present on the island. Any type of species interaction can influence Eq. (16) for any species by making these three parameters depend on the expected state of the network on the island. For instance, in the case of the TTIB (Gravel et al., 2011b), h_i and e_i both change in time due to expected successive colonizations of the island by different species—successive arrivals of species increase h_i for species at all trophic levels (the more species are present on the island, the more likely it is that any species not yet present on the island will find a suitable prey species), while increase in species richness with time tends to decrease expected e_i for all species.

In the case of mutualistic networks, one must distinguish the effect of network structure on obligate vs facultative mutualistic partners (Fortuna and Bascompte, 2006). For obligate mutualistic partners, network structure is usually expressed through a strong dependency of h_i on current island network, i.e. an obligate mutualist cannot invade an island that does not contain at least one its partners. It also underlies a strong dependency of e_i on current island network structure because, as with predators in the TTIB, obligate mutualists are expected to go extinct with their last mutualistic partner on the island. In the case of facultative mutualists, the weak dependency

of the species on the presence of mutualistic partners on the island could be translated in one of two ways, either in: an increase in c_i when mutualists are present on the island (e.g. plants more likely to invade an island on which the animal seed dispersers are already present); and/or a decrease of e_i in the presence of beneficial partners (e.g. hermaphroditic plants on an island with pollinators can maintain larger, more genetically diverse, and thus less extinction-prone, populations). It is remarkable that, in the case of Levins' metapopulation model describing the dynamics of plant–pollinator interaction networks (Astegiano et al., 2015; Fortuna and Bascompte, 2006), a natural choice for the effect of pollinators on plant parameters is to consider that patches with pollinators contribute more to the pool of propagules (i.e. increase their contribution to the overall colonization \times occupancy rate).

In the particular case of networks of competitive interactions, TIB dynamics might be altered through four different mechanisms. First, the presence of competitors, especially dominant competitors, can drive other species out of the island, i.e. by increasing their extinction rate e_i . This would mimic competitive exclusion dynamics on the island. An early attempt at understanding how competition would affect species occurrence patterns in a TIB framework was made by Hastings (1987). A second possibility is that there is a priority effect, affecting those species colonizing the island, so that certain species might exclude other species from colonizing the island when they are present, i.e. effectively decreasing h_i for the other species (Shurin et al., 2004). A third possibility is to make habitat quality change with current community composition, as a consequence of ecosystem engineering (Wright et al., 2004). Finally, there might be a gradient of competitive and colonization abilities in the pool of species, so that species more likely to colonize the island first would also be more likely to be displaced by more competitive species afterwards, causing “ecological succession-like” assembly trajectories. Although the competition–colonization trade-off has been traditionally used in the context of Levins' (1969) metapopulation model (Calcagno et al., 2006; Hastings, 1980; Tilman, 1994), it can also be incorporated in an island biogeography context to describe community transitions before and after colonization by a superior competitor, e.g. borrowing from Slatkin's (1974) model and adapting it to the TIB.

For the remainder of this chapter, we cast the TTIB in terms of classic food webs, i.e. networks of species feeding on one another through predator–prey interactions. However, we would note that integrating host–parasite (or more generally, host–symbiont) interactions within this context is feasible, provided Eq. (16) accommodates the effect of the

network structure on symbiont colonization and extinction dynamics. One modelling choice is to consider that obligate symbionts cannot colonize if their host is absent, so that the symbiont can: (i) colonize the island together with its host; or, (ii) colonize the island once its host is already there (through some immigration of infected hosts which is not accounted for in the dynamics of the host occupancy because it has already colonized the island). In the case of facultative symbionts, this modelling option can be combined with the possibility of a symbiont-only colonization event, possibly occurring at a different (lower) rate. Regarding extinction rates, obligate symbionts will inevitably die out when their host goes extinct on the island, while facultative symbionts could persist (but possibly with an increased extinction rate) after their last host species disappears from the island.



2. ISLAND BIOGEOGRAPHY OF FOOD WEBS

2.1 The Model

2.1.1 Explaining the TTIB With a Simple Example

The TTIB can be understood using a simple example consisting in five species (A, B, C, D, E), arranged in three trophic levels, with species C and E being basal species, species B and D primary consumers and species A the top predator (Fig. 2). The core idea of the TTIB is that colonization and extinction of species on the island obey the principle of “at least one prey species per predator”. In practical terms, this principle can be translated as follows:

1. Colonization of a given species can only take place when at least one of its prey species is present (Fig. 3). This means that the colonization rate is now modulated by the probability that the island food web contains at least one prey species for the focal species;

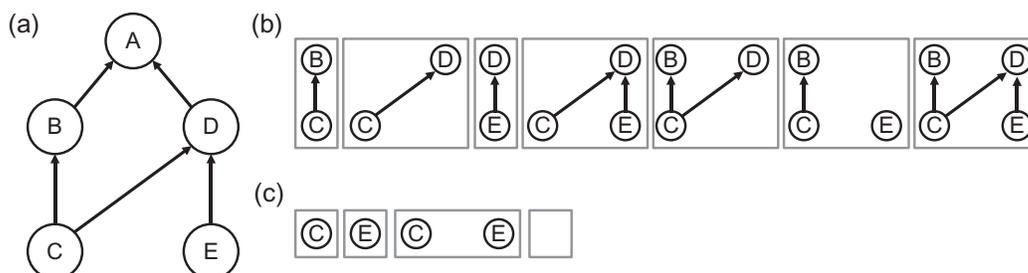


Fig. 2 Simple food web used to illustrate the Trophic Theory of Island Biogeography. (a) The complete food web (on the mainland) consists in five different species (A, B, C, D, E), (b) subfood webs that species A can colonize and (c) subfood webs that species A cannot colonize.

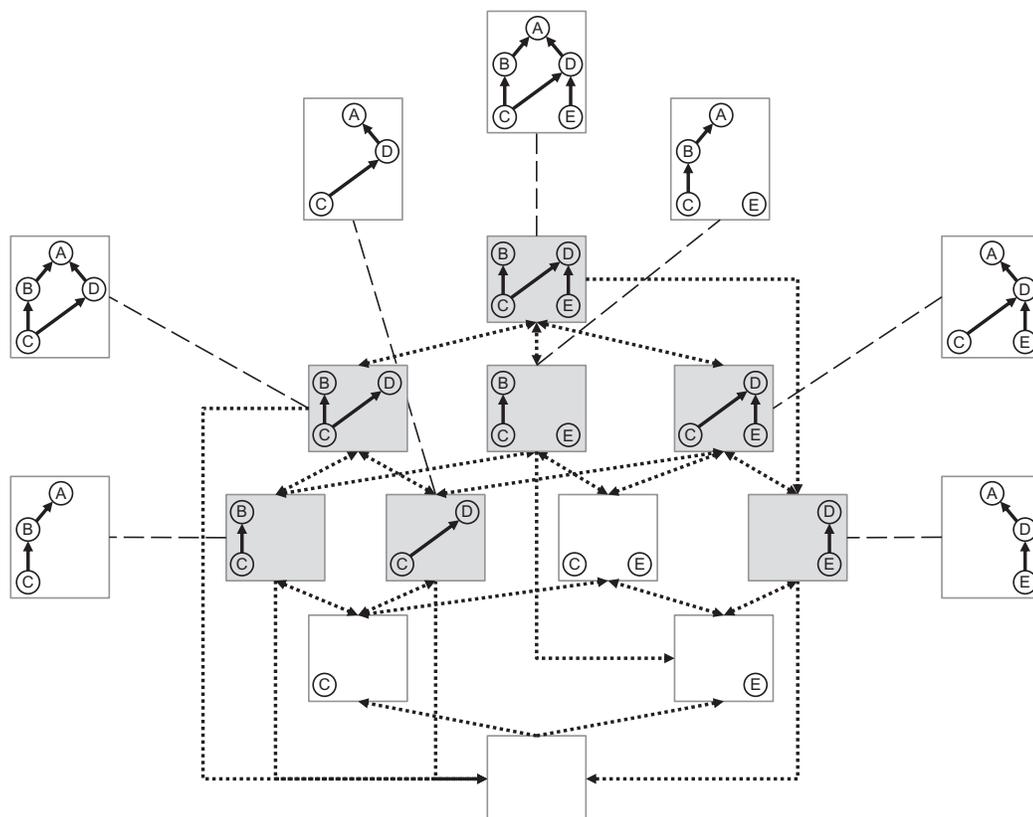


Fig. 3 Restriction of colonization under the TTIB. Transitions among community states that do not include species A are depicted by *dotted arrows*, as in Fig. 1. Communities in grey represent communities that can be colonized by species A (i.e. the fraction $h_A - P_{X_A=1}$ of the possible island communities). The associated species A-colonized communities (the “outer communities”, i.e. the fraction $P_{X_A=1}$ of the possible island communities) are linked to them with a *thick dashed l.*

- Extinction of a given species now depends not only on the single-species extinction rate of the focal species, but also on the rate at which the focal species gets caught in an “extinction cascade” (Fig. 4). Extinction cascades happen when a species “down”, or lower, in the local food web supports a whole portion of the food web and goes extinct (e.g. species C in the (A, B, C, D) community in Fig. 4).

For a general idea of the TTIB dynamics, we can write that the probability of occurrence of a given species Z obeys the following differential equation (rewriting Eq. 16):

$$\frac{dP_{X_Z=1}}{dt} = c(h_Z - P_{X_Z=1}) - e_Z P_{X_Z=1} \quad (17)$$

where h_Z is the probability that island community is hospitable to species Z (i.e. community contains at least one prey of species Z) and e_Z is the effective

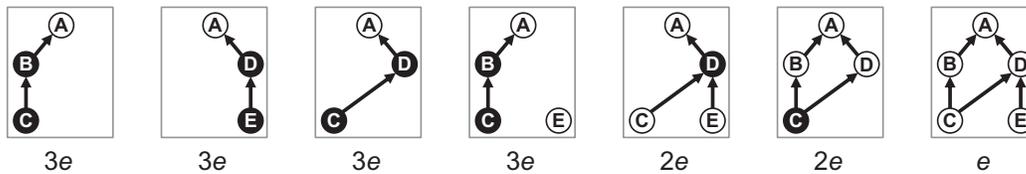


Fig. 4 Increase in the extinction rate of species A as a result of cascading extinctions. Each of the panels represents one the community that includes species A (the “outer communities” in Fig. 3). Species in *black dots* are species that contribute to the additional extinction rate of species A. For instance, in the (A, B, C) community, if species B or species C goes extinct, species A must also go extinct. The mention under each panel is the extinction rate of species A in the configuration depicted in the matching panel, e.g. in the above mentioned example, the rate of extinction of species A is $3e$ because it goes extinct at its own rate plus that of species B and that of species C. In this particular case, the total extinction rate of species A can be deduced from that of species B because if species C goes extinct, then species B must also go extinct. Thus, in this instance, the extinction rate of A is simply that of species B plus e . However, this additivity of extinction rate is not always in place. For instance, in the (A, B, C, D) community, species B and species D both experience a “ $2e$ ” extinction rate, but species A only experiences a “ $2e$ ” extinction rate as well because the single extinction of either species B or D has no effect on A, while the extinction of C makes the whole food web collapse.

extinction rate of species Z computed using e , the number of ways it can go extinct through a single-species extinction in the island food web and the weights associated with these extinction events (which are computed from the occurrence probabilities of species “down” the food web).

Let us start this example using the mainland food web given in Fig. 2a. Species A can only colonize a restricted set of island food webs (Figs 2b and 3). In other island food webs, it simply cannot settle because there is neither prey species B nor D (Fig. 2c). Once species A is on the island, the community must be in one of the “outer community” states of Fig. 3. The extinction rate of species A when established in one of these outer communities depends on how many species down the food web may provoke an extinction cascade affecting species A (Fig. 4). For instance, when only one species down the food web can provoke the extinction of species A through cascading extinction, then the extinction rate of species A is $2e$; if two species can provoke such an extinction (e.g. if the community is (A, B, C)), then the extinction rate of species A is $3e$.

Although the graphical representation of transitions among communities and colonization-prone communities for a focal species is useful to fully grasp the principles of the TTIB, a more quantitative approach can be obtained by focusing on the master equation behind food web dynamics.

The following explanation starts with the corresponding master equation in the TIB and then introduces an equivalent formulation in the case of the TTIB.

The TIB model, as expressed using Eqs (1) and (2), does not distinguish species based on any feature. However, the underlying random variable describing the number of species present on the island, S , can be decomposed as a sum of indicator variables X_i which describe the presence/absence of species i , so that at all times:

$$S(t) = \sum_i X_i(t) \quad (18)$$

Under the TIB, each of the $X_i(t)$ is a random variable the value of which changes from 1 to 0 with rate e and from 0 to 1 with rate c . The corresponding master equation for a single species is thus given by two coupled differential equations (indices i are omitted for the sake of clarity):

$$\frac{dP_{X=0}}{dt} = eP_{X=1} - cP_{X=0} \quad (19a)$$

$$\frac{dP_{X=1}}{dt} = cP_{X=0} - eP_{X=1} \quad (19b)$$

Noting $P_{X=1} = p$ and $P_{X=0} = 1 - p$, we obtain the well-known equation for the occupancy of islands by a single species under MacArthur and Wilson's framework:

$$\frac{dp}{dt} = c(1 - p) - ep \quad (20)$$

When compared with the framework set by Eqs (16) or (17), Eq. (20) means that: (i) there are no effects of network structure on any one of the three parameters of Eq. (16); and (ii) the probability that an island is hospitable to colonization is always 1 (i.e. there is no restriction to species colonization potential).

The stationary distribution of X following Eq. (19) is a Bernoulli distribution of parameter $c/(c + e)$, associated with the eigenvalue 0 of the matrix defining the process defined in Eq. (19). In other words, solving for the equilibrium of Eq. (19) is equivalent to finding the eigenvalues and eigenvectors of a 2×2 matrix, and the equilibrium is given by the eigenvector associated with the eigenvalue 0. The other eigenvalue, $-(c + e)$, is associated with the eigenvector $(-1, 1)$ (i.e. any discrepancy in the probability of occurrence of

the species from the stationary distribution of X), so that an initially absent species at time $t=0$ has a probability of occurrence at time t equal to:

$$P_{X(t)=1|X(0)=0} = \frac{c}{c+e} \left(1 - e^{-(c+e)t} \right) \quad (21a)$$

while an initially present species at time $t=0$ has occurrence probability:

$$P_{X(t)=1|X(0)=1} = \frac{c}{c+e} + \frac{e}{c+e} e^{-(c+e)t} \quad (21b)$$

Now let us proceed with the simple four species community (B, C, D, E) given in Fig. 1 under the TIB, i.e. without using the principle of “at least one prey species per predator species” on the island. Each of the P_X , where X now represents a community, obeys a differential equation similar to Eq. (19b), with losses due to both extinction of local species and colonization by new species, and gains due to “upwards” transitions from species-poor communities and “downwards” transitions from species-rich ones. For instance, the equation for the community (D, E) is:

$$\frac{dP_{DE}}{dt} = c(P_D + P_E) + e(P_{BDE} + P_{CDE}) - 2(c+e)P_{DE} \quad (22)$$

More generally, noting \mathbf{P} the vector of all P_X , the master equation can be written as:

$$\frac{d\mathbf{P}}{dt} = \mathbf{G} \cdot \mathbf{P} \quad (23)$$

where \mathbf{G} is a matrix describing all the coefficients of the master equation. In the case of the TIB acting on the food web described in Fig. 1a, matrix \mathbf{G} is given in Table 1.

Solving the equation $\mathbf{G} \cdot \mathbf{P} = \mathbf{0}$ (i.e. finding a vector of sum equal to 1 associated with the eigenvalue 0 of matrix \mathbf{G}) yields the probability of finding the food web in the different states. In the case of the TIB, the result is somehow easy to find without having to resort to the study of matrix eigenvalues and eigenvectors; Eq. (11) already gives the probability of finding a community with exactly S species present. Dividing this expression by the number of combinations of S species among T yields the following general formula:

$$P_X = \left(\frac{c}{c+e} \right)^{|X|} \left(\frac{e}{c+e} \right)^{T-|X|} \quad (24)$$

Table 1 Matrix **G** of Eq. (23) in the Case of the TIB Acting on the Food Web Presented in Fig. 1
From

	Empty	B	C	D	E	BC	BD	BE	CD	CE	DE	BCD	BCE	BDE	CDE	BCDE
To Empty	$-4c$	e	e	e	e											
B	c	$-3c-e$				e	e	e								
C	c		$-3c-e$			e			e	e						
D	c			$-3c-e$			e		e		e					
E	c				$-3c-e$			e		e	e					
BC		c	c			$-2(c+e)$						e	e			
BD		c		c			$-2(c+e)$					e		e		
BE		c			c			$-2(c+e)$					e	e		
CD			c	c					$-2(c+e)$			e			e	
CE			c		c					$-2(c+e)$			e		e	
DE				c	c						$-2(c+e)$			e	e	
BCD						c	c		c			$-c-3e$				e
BCE							c	c		c			$-c-3e$			e
BDE								c	c		c			$-c-3e$		e
CDE									c	c	c				$-c-3e$	e
BCDE												c	c	c	c	$-4e$

Empty cells are equal to zero (omitted for clarity). Columns indicate “giver” community states, rows indicate “receiver” community states. The sum of each column equals zero because the sum of incoming and outgoing state transition rates must balance (the sum of the probability of all states must always be equal to 1). A single equation such as Eq. (22) can be retrieved by following the matching row of the matrix and adding/subtracting appropriate terms based on matrix coefficients on that row.

where $|X|$ is the cardinality of community X (i.e. its species richness). The probability that a single species, say C , is present on the island can be obtained by summing Eq. (24) over all communities that include species C :

$$\begin{aligned} P_{X_C=1} &= \sum_{C \in X} P_X = \sum_{k=0}^T \sum_{\substack{C \in X \\ |X|=k}} \left(\frac{c}{c+e}\right)^k \left(\frac{e}{c+e}\right)^{T-k} \\ &= \sum_{k=1}^T \binom{T-1}{k-1} \left(\frac{c}{c+e}\right)^k \left(\frac{e}{c+e}\right)^{T-k} = \frac{c}{c+e} \end{aligned} \quad (25)$$

We now shift to the case of the TTIB, using the example given in Fig. 1b, i.e. the same food web as the one used above, but with an intrinsic dependency between species occurrences due to the underlying TTIB principle. In this context, certain communities cannot exist, i.e. (B), (D), (B, D), (B, E), (B, D, E) (grey communities in Fig. 1b). The associated \mathbf{G} matrix is given in Table 2.

Solving $\mathbf{G} \cdot \mathbf{P} = \mathbf{0}$ using the \mathbf{G} matrix given in Table 2 yields complicated expressions. However, the same type of computations as the ones used to go from Eq. (24) to Eq. (25) can be applied to this stable distribution of community states to obtain the stable distribution of each species occurrence probability. For instance, one obtains that the probability of observing species B is given by:

$$P_{X_B=1} = \frac{c^2}{(c+e)(c+2e)} \quad (26)$$

The food chain (B, C) being particularly simple (see also Section 2.2.1), this result is easy to interpret: the probability of occurrence of species B relies on species C being present (with probability $c/(c+e)$ as species C is a basal species), and species B having colonized (rate c), and the whole food chain not collapsing (rate of species B extinction $2e$).

2.1.2 A More General Presentation of the TTIB

A simple consequence of the rules governing the dynamics of the TTIB is that the two variables needed to compute the dynamics of a given species Z , h_Z and e_Z (Eq. (17)) can be obtained based only on the probability of occurrence of species “down” the food web. In other words, looking “up” the food web (i.e. at species that depend on Z for colonization) or “laterally” (i.e. at species that have no dependence relation with Z for their colonization or for species Z colonization) is not needed when assessing h_Z and e_Z . This

Table 2 Matrix **G** of Eq. (23) in the Case of the TTIB Acting on the Food Web Presented in Fig. 1

		From									
To	Empty	C	E	BC	CD	CE	DE	BCD	BCE	CDE	BCDE
	Empty	$-2c$	e	e	e	e	e	e	e	e	e
	C	c	$-3c-e$	e	e	e					
	E	c	$-2c-e$			e	e	e			
	BC	c		$-2(c+e)$				e	e		
	CD	c			$-2(c+e)$			e		e	
	CE	c	c			$-2(c+e)$			e	e	
	DE	c	c				$-c-2e$			e	e
	BCD			c	c			$-c-3e$			e
	BCE			c		c			$-c-3e$		e
	CDE				c	c	c			$-c-3e$	e
	BCDE							c	c	c	$-4e$

Empty cells are equal to zero (omitted for clarity). Interpretation of this table follows the same legend as Table 1.

means that, when focusing on species Z , we can focus on species Z and the species it depends on to colonize (the ones “down” the food web), and thus describe the dynamics of community states forgetting about the occurrence of all the other species in the mainland food web. For instance, following the example given above (Fig. 3), if we were to focus on species B, the only community states to focus on would be the empty community, the one with species C and the one with species (B, C). When forgetting about the rest of the food web, the “empty state” refers to any state in which both species B and C are absent, the “C community” refers to all states in which species C is present but not species B, and the “(B, C) community” refers to all states in which both species are present. In this instance, the (B, C, D) community would “count” under the (B, C) modeled community state. In the following, we present a new analytical derivation of the expressions for h_Z and e_Z under the assumptions of the TTIB, which was not provided by Gravel et al. (2011b).

This can be formalized more rigorously using notations that will help us navigate the set of possible communities:

- Species Y is a **foundation species** for species Z if Y is part of at least one path linking a basal species to species Z . The set of all foundation species for species Z is noted F_Z .
- Among foundation species for species Z , we note G_Z the set of prey species of species Z . For convenience, we also note $H_Z = F_Z \cup \{Z\}$, i.e. the set of foundation species and the focal species itself. The intuitive notion of species being “up” or “down” the food web can be understood through the following statement: species Y is in H_Z if and only if H_Y is included in H_Z .
- We will call a community, K , **TTIB-compatible** when all species in the community are connected to at least one basal species in the community by at least one path of species present in the community.
- The trimmed community, $[K]$, is obtained by removing the minimal number of species from community K so that the community obtained is TTIB-compatible.
- We note Ω the **set of all TTIB-compatible communities** containing from 0 to T species of the mainland food web.
- We note Ω_Z the set all TTIB-compatible communities that include species Z .
- For TTIB-compatible community K , we note Φ_K its **TTIB-compatible combination set**, i.e. the set of all TTIB-compatible communities consisting only of combinations of species in K . Naturally, $K \in \Phi_K$.

- **The expansion set** of TTIB-compatible community K , noted $\langle K \rangle$, is the set of all TTIB-compatible communities that naturally expand community K with the addition of any number of species not found in K . K is always in its expansion set and it is the smallest community in this set.
- By extension, we will note the expansion set of species Z , $\langle Z \rangle$, the set consisting in the union of all expansions of TTIB-compatible communities containing Z . Quite intuitively $\langle Z \rangle = \Omega_Z$ as any TTIB-compatible community containing species Z is in its own expansion set.
- The expansion set of K constrained by community D (not necessarily TTIB-compatible), noted $\langle K \rangle_D$, corresponds to natural expansions of K that do not include species that are part of D . As a special case, $\langle \emptyset \rangle_D$ refers to the D -constrained expansion of the empty community, i.e. the set of all communities that do not include species in community D .
- Extending the probability measure introduced on communities, the **measure P_U of the set of communities U** is equal to the sum of the P_C of all communities K in the set U .
- Finally, we introduce the indicator function for species Z in community K , noted $\mathbf{1}_Z(K)$, which is equal to one if and only if species Z is part of community K .

A consequence of the bottom-up control of species presence-absence under the TTIB framework is that the probability of species Z presence, also equal to $P_{\langle Z \rangle}$, can be computed based on the knowledge of all the $P_{\langle K \rangle_{H_Z}}$ for all communities K in Φ_{F_Z} . Taking again the example given above (Figs 2–4), assessing the probability that species A occurs on the island can be done by acknowledging that (B, C, D, E) is the set of foundation species of A , F_A (and thus $(A, B, C, D, E) = H_A$), and working on the measures (probabilities) of $\langle \emptyset \rangle_{H_A}$, $\langle (C) \rangle_{H_A}$, $\langle (B, C) \rangle_{H_A}$, etc., to find the measures of $\langle (A, B, C) \rangle_{H_A}$, $\langle (A, D, E) \rangle_{H_A}$, etc., which, together, yield $P_{\langle A \rangle}$, also equal to $P_{X_A=1}$.

Using the above notations, the probability that an island contains at least one prey of species Z , h_Z , is given by:

$$h_Z = P \bigcup_{Y \in G_Z} \Omega_Y = P \bigcup_{Y \in G_Z} \langle Y \rangle \tag{27}$$

Indeed, $\bigcup_{Y \in G_Z} \Omega_Y$ corresponds to the union of all sets of TTIB-compatible communities that include at least one prey species of species Z . It is also equal to the union of expansion sets of all species in G_Z , $\bigcup_{Y \in G_Z} \langle Y \rangle$. Eq. (27) can also

be rewritten by separating all communities K that allow colonization by species Z , i.e. all communities, possibly expanded (with a constraint on species in F_Z to avoid counting a community more than once), which are in Φ_{F_Z} but not in $\Phi_{F_Z \wedge G_Z}$ (consisting in Z -foundation species but with at least one prey species of species Z):

$$h_Z = \sum_{K \in \Phi_{F_Z} \setminus \Phi_{F_Z \wedge G_Z}} P_{\langle K \rangle_{F_Z}} \quad (28)$$

In other words, to find a community that is hospitable to species Z , one must first find a TTIB-compatible community made only of species that are foundation species for species Z and which include at least one prey of species Z , and then expand this community with species that are not foundation species for species Z (i.e. “decorative species” with respect to species Z colonization capacity).

In the same way, the extinction rate of species Z , e_Z , is given by:

$$e_Z = e + e \sum_{K \in \Omega_Z} \frac{P_C}{P_{\langle Z \rangle}} \sum_{Y \in K \cap F_Z} (1 - \mathbf{1}_Z[\{(K \cap H_Z) \setminus \{Y\}\}]) \quad (29)$$

In Eq. (29), species Z can go extinct by itself (the first e term) and also by losing a species that is necessary for its maintenance (the sum term). Enumerating these cases is made on all communities that contain Z (i.e. on $C \in \Omega_Z$); the probability to be in community state K , given that species Z is present, is $P_K/P_{\Omega_Z} = P_K/P_{\langle Z \rangle}$. Once we know that the community state is K , then we have to enumerate all the ways in which species Z can go extinct through an extinction cascade; this can only happen when one of the foundation species of species Z , i.e. a species $Y \in F_Z$ which is also present in community K (hence, $Y \in K \cap F_Z$), is such that removing it would also remove species Z from $K \cap H_Z$ after trimming “dead branches” in the ensuing community. Working on $K \cap H_Z$ (and not $K \cap F_Z$) is necessary. Indeed, one can think of situations in which removing one species from $K \cap F_Z$ might make community K TTIB-incompatible, but not by severing the path between Z and basal species. For instance, if we take species B in the last panel of Fig. 4 and imagine that a chain of species are linked to species B as their “support” species; removing species B would not affect species A in this instance, but it would sever the link between this chain of species and species C, and thus make it TTIB-incompatible. However, this should not increase the effective extinction rate of species A. As we deduced with Eq. (28) from (27), we can simplify the writing of Eq. (29) by restricting the sum to

communities in $\Phi_{H_Z} \setminus \Phi_{F_Z}$, i.e. TTIB-compatible communities consisting of species in F_Z and always including species Z :

$$e_Z = e + e \sum_{K \in \Phi_{H_Z} \setminus \Phi_{F_Z}} \frac{P_{\langle K \rangle_{H_Z}}}{P_{\langle Z \rangle}} \sum_{Y \in C} (1 - \mathbf{1}_Z[[K \setminus \{Y\}]]) \quad (30)$$

By acknowledging that:

- the sets $\Phi_{H_Z} \setminus \Phi_{F_Z}$ and $\Phi_{F_Z} \setminus \Phi_{F_Z \cap G_Z}$ are isomorphic (a community in the first set becomes one in the second by removing species Z , a community in the second set becomes one in the first by adding species Z);
- the set $\langle Z \rangle$ can be exactly decomposed as the disjoint union of the H_Z -constrained expansions of communities in $\Phi_{H_Z} \setminus \Phi_{F_Z}$, i.e. any TTIB-compatible community including Z must be an expansion of a community in $\Phi_{H_Z} \setminus \Phi_{F_Z}$ (the constraint on expansion makes it impossible to count a community twice in the union of expansions, and hence make them disjoint);
- the difference between h_Z and $P_{\langle Z \rangle}$ is a variation of Eq. (28) in which the expansions of communities are constrained by H_Z rather than by F_Z , i.e.:

$$h_Z - P_{\langle Z \rangle} = \sum_{K \in \Phi_{F_Z} \setminus \Phi_{F_Z \cap G_Z}} P_{\langle K \rangle_{H_Z}} \quad (31)$$

and expressing the dynamics of $P_{\langle Z \rangle}$ using Eqs (17), (28), (30) and (31), we get:

$$\frac{dP_{\langle Z \rangle}}{dt} = \sum_{K \in \Phi_{H_Z} \setminus \Phi_{F_Z}} \left[cP_{\langle K \setminus \{Z \rangle}_{H_Z}} - e \left(1 + \sum_{Y \in K} (1 - \mathbf{1}_Z[[K \setminus \{Y\}]]) \right) P_{\langle K \rangle_{H_Z}} \right] \quad (32)$$

Although more compact than Eqs (28) and (30), Eq. (32) is still no closer to an analytical approximation of the TTIB. In the supplementary information of Gravel et al. (2011b), an approximation of the TTIB was derived to analytically compute $P_{\langle Z \rangle}$ for any species Z . This approximation, which we do not reiterate here, is based on many assumptions. First, it is assumed that the presence of any prey within the diet of a predator on the island is independent from the presence of other prey species from the predator diet on the same island. Second, it is assumed that the absence of a predator on the island induces no statistical distortion of the probability that its prey species are present on the island. Third, the case of cascading extinction is limited to

the extinction of species within the immediate diet of the focal predator, i.e. the extra extinction rate incurred by species A in the case of community (A, B, C, D) in Fig. 4 is ignored. Overall, all these assumptions can be translated as follows: for any species Z , the identity $F_Z = \bigcup_{Y \in G_Z} H_Y$ is considered as a union over disjoint sets, with empty intersections between any two H_Y 's among the predator's prey species.

2.2 Simple Insights

In this section, we apply the rationale of the TTIB to very simple food web topologies in order to gain insight into the interaction of colonization/extinction dynamics with the position of species within food webs on species occurrence.

2.2.1 A Linear Food Chain

Let us first focus on a simple food chain consisting in N different species, noted Z_1, Z_2, \dots so that Z_1 is a basal species, Z_2 preys on Z_1 , etc. If we note P_i the probability of occurrence of species i , the following equations define the TTIB dynamics for this food chain:

$$\frac{dP_1}{dt} = c(1 - P_1) - eP_1 \quad (33a)$$

$$\frac{dP_2}{dt} = c(P_1 - P_2) - 2eP_2 \quad (33b)$$

...

$$\frac{dP_k}{dt} = c(P_{k-1} - P_k) - keP_k \quad (33c)$$

The equilibrium solution to the system (33) is given by

$$P_i = \frac{c^i}{e^i \binom{c+i}{i}} = \frac{\alpha^i}{(\alpha+i)_i} \quad (34)$$

where $(x)_i = x(x-1)(x-2)\dots(x-i+1)$ is the falling factorial or Pochhammer symbol and $\alpha = c/e$. As in the case of food chains in the met-community context (Calcagno et al., 2011), the take-home message of Eq. (34) is that constraining predator occurrence by the occurrence of its preys limits food chain length on islands (Fig. 5). This is also visible in

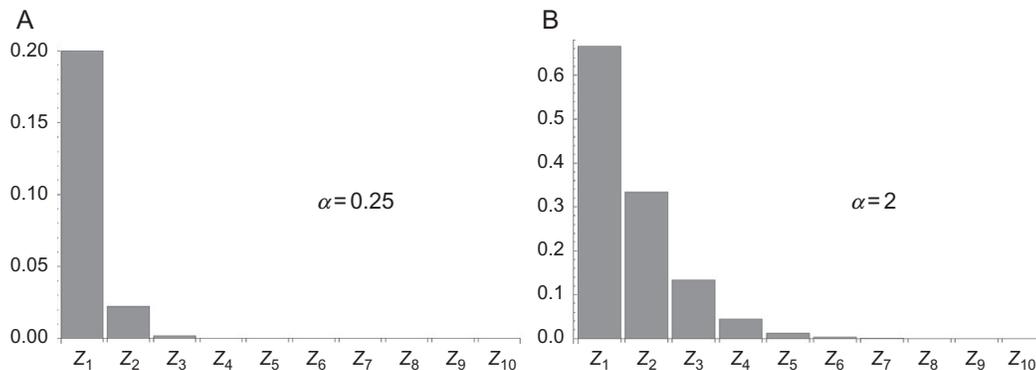


Fig. 5 Probabilities P_i to find species Z_1, Z_2, \dots from the mainland food chain on the island. Probabilities never go to zero according to Eq. (34), but are negligible at trophic levels higher than three when $\alpha = 0.25$ (A) or higher than five when $\alpha = 2$ (B).

the measure of the average trophic level on the island, \widehat{TL} , which is given by summing Eq. (34) over all trophic levels with weights equal to i :

$$\widehat{TL} = \sum_i iP_i = \alpha \tag{35}$$

In other words, in a food chain, the expectation for the average trophic level of species that have colonized the island is simply the colonization-to-extinction ratio. To close on the topic of food chain length, the expected species richness of a food chain on an island is given as:

$$S = \sum_i i(P_i - P_{i+1}) = \frac{\alpha}{1 + \alpha} + \frac{e^\alpha \alpha^{-\alpha}}{1 + \alpha} \gamma(2 + \alpha, \alpha) \tag{36}$$

where γ is the lower incomplete gamma function and the size of the mainland food chain is assumed infinite. In contrast with the TIB (Eq. 3), the expectation of species richness is not proportional to the number of species on mainland in the case of a food chain.

2.2.2 One Predator, Several Prey

We now turn our attention towards the case of one predator preying on N different prey species. As the different prey species are not identifiable (no difference in colonization or extinction rates), the TTIB can be understood as “the presence/absence of the predator” \times “the number of prey species on the island”. The probability of occurrence of the different communities will be noted as:

- P_i for the probability of finding i prey species but not the predator (i can be equal to 0);

- Q_i for the probability of finding i prey species and the predator ($i \geq 1$). The equations defining the TTIB in such a case are:

$$\frac{dP_0}{dt} = e(P_1 + Q_1) - cNP_0 \quad (37a)$$

$$\frac{dP_i}{dt} = c(N - i + 1)P_{i-1} + e(i + 1)P_{i+1} - [c(N - i) + ei]P_i - cP_i + eQ_i \quad (37b)$$

$$\frac{dQ_i}{dt} = c(N - i + 1)Q_{i-1} + e(i + 1)Q_{i+1} - [c(N - i) + ei]Q_i + cP_i - eQ_i \quad (37c)$$

Solving system (37) in the general case is quite complicated. The path to a complete (but difficult to express) solution lies in rewriting system (37) for quantities $F_i = P_i + Q_i$ and $D_i = P_i - Q_i$, identifying the dynamics of F_i as those of the TIB (and hence its probabilities are known and given by Eq. 11), simplifying the recursions on D_i and finally expressing D_i in terms of the F_i 's. We found no general form for this solution, but an interesting relationship between the expected number of prey species present to support a predator and the probability of predator occurrence emerges at equilibrium:

$$\sum_{k \geq 1} kQ_k = \frac{N\alpha^2}{2} + \frac{N\alpha}{4} \sum_{k \geq 1} Q_k \quad (38)$$

where $\alpha = c/e$. Eq. (38) always holds exactly for this system (i.e. it is not an approximation).

To obtain a general formula for the probability of predator occurrence, i.e. $\sum_{k \geq 1} Q_k$, we can assume that $\alpha \ll 1$. As the colonization by the predator

species entails a colonization event on top of the ones already needed for the prey species to occur, we assume that the quantities $F_k = P_k + Q_k$ are asymmetrically separated, i.e. we assume that the Q_k 's can be written as:

$$Q_k = a_k \alpha F_k \quad (39)$$

Developing Eq. (37c) in powers of α , we find that:

$$a_1 = \frac{N}{2} \quad (40a)$$

$$a_i = \frac{1 + ia_{i-1}}{1 + i} \quad (40b)$$

Solving recursion (40b), we finally have the following expression for the a_i 's:

$$a_i = \frac{i - 1 + N}{1 + i} \quad (41)$$

Plugged into Eq. (39) and summed over all k 's, Eq. (41), take at the first available order in α , yields:

$$\sum_{k \geq 1} Q_k \approx \frac{N^2 \alpha^2}{2} \quad (42)$$

Plugged into Eq. (38), Eq. (42) implies:

$$\frac{\sum_{k \geq 1} k Q_k}{\sum_{k \geq 1} Q_k} \approx \frac{1}{N} + \frac{N\alpha}{4} \quad (43)$$

What Eqs (42) and (43) mean is that: (i) the probability of occurrence of the predator at low α is proportional to the square of its degree (i.e. the number of preys it can feed on); and, (ii) the expected number of prey species occurring with the predator, conditionally on its occurrence, is proportional to its degree when it is not too low. Eq. (42) can also be reinterpreted given that, when α is low, $\sum_{k \geq 1} F_k \approx N\alpha$:

$$\sum_{k \geq 1} Q_k \approx \frac{N\alpha}{2} \sum_{k \geq 1} F_k \quad (44)$$

Hence, a predator only occupies a ‘‘fraction’’, $N\alpha/2$, of the probability space given by its preys.

2.2.3 Multipartite Network as a Food Web

We now extend Eqs (42)–(44), i.e. assuming that $\alpha = c/e$ is small and consider a multipartite food web in which each and every species can be assigned a precise trophic level and only prey on species at the immediate trophic level down the web. We will note D_k the random variable giving the degree (as a predator, i.e. the in-degree) of species at trophic level k in the mainland food web. We assume that there are many species at each trophic level and we note N_k the number of species at trophic level k in the mainland food web. We will also note S_k the number of species at trophic level k on the island.

Following the TIB, we know that the expected number of basal species on the island is:

$$\mathbb{E}[S_1] \approx N_1 \alpha \quad (45)$$

Using relation (42), we find that the expected number of species of the second trophic level occurring on the island is given by:

$$\mathbb{E}[S_2] \approx \frac{N_2 \alpha^2}{2} \mathbb{E}[D_2^2] \quad (46)$$

Generalizing approximation (46) to the next trophic levels, we finally get:

$$\mathbb{E}[S_k] \approx \frac{N_k \alpha^k}{2^{k-1}} \prod_{i=1}^k \mathbb{E}[D_i^2] \quad (47)$$

When the distribution of degrees is the same across trophic levels (i.e. $\mathbb{E}[D_i^2] = \mathbb{E}[D^2]$ for all i), noting $T = \sum N_k$ the total number of species on the mainland and $S = \sum S_k$ the equivalent on the island, we can transform Eq. (47) using $\beta = \alpha \mathbb{E}[D^2]/2$:

$$\mathbb{E}[S] \approx \alpha T \sum_{k \geq 1} \beta^{k-1} \frac{N_k}{T} \quad (48)$$

Eq. (48) expresses the relationship between $\mathbb{E}[S]$ and T as a function of α (as in the classic TIB) and the distribution of degrees across the food web (through β) and the distribution of trophic levels in the food web (through N_k/T). The approximation remains valid as long as $\mathbb{E}[D^2] = \text{Var}[D] + \mathbb{E}[D]^2$ remains small compared to $1/\alpha$, ensuring a relatively low degree of dependence between species occurrence within the same trophic level.

2.3 Interpretation in Terms of Food Web Transitions

2.3.1 Reformulation in Terms of Transitions Between Community States

As suggested in Section 2.1.2, an analytical alternative for the study of the TTIB is to derive a master equation for community states rather than individual species. The mathematical object is then the random process $C_{t>0} = \cup_{i=1}^T X_i$ which is a vector of 0 and 1 describing the presence and absence of all species at any time t . For T species, there are 2^T community states. Table 3 provides an example for species B, C, D and E presented in Fig. 2.

Table 3 Community States Associated to the (B, C, D, E) Network, i.e. All the Combinations of Presence and Absence of Species (Columns B, C, D, E)

Community States	B	C	D	E	TTIB-Compatible
S_0	0	0	0	0	Yes
S_1	0	0	0	1	No
S_2	0	0	1	0	Yes
S_3	0	0	1	1	Yes
S_4	0	1	0	0	Yes
S_5	0	1	0	1	Yes
S_6	0	1	1	0	Yes
S_7	0	1	1	1	No
S_8	1	0	0	0	No
S_9	1	0	0	1	No
S_{10}	1	0	1	0	No
S_{11}	1	0	1	1	Yes
S_{12}	1	1	0	0	Yes
S_{13}	1	1	0	1	Yes
S_{14}	1	1	1	0	Yes
S_{15}	1	1	1	1	Yes

At any time t , $C_{t>0}$ represents the species composition of the island and thus is in one of the 16 possible S_k states. Here all communities are considered regardless of whether they are TTIB-compatible as highlighted in the *rightmost* column.

Deriving the equation associated to a given community state S_k requires study of the transition probabilities between community states between t and $t + dt$ (dt is assumed to be short enough to permit only one transition). As all community states are included in the set $S_k, k \in \{1, 2, \dots, 2^T\}$, following the law of total probability, for any community state:

$$P_{C_{t+dt}=S_k} = \sum_{l=0}^{2^T-1} P_{C_{t+dt}=S_k|C_t=S_l} P_{C_t=S_l} \quad (49)$$

The transition probabilities $P_{C_{t+dt}=S_k|C_t=S_l}$ are assumed to be linear functions of dt , when dt is small enough. For $k \neq l$, the transition matrix \mathbf{G} , similar to the one presented in Eq. (23), is defined by:

$$P_{C_{t+dt}=S_k|C_t=S_l} = g_{kl} dt \quad (50)$$

and, as $\sum_l P_{C_{t+dt}=S_l|C_t=S_k} = 1$:

$$P_{C_{t+dt}=S_k|C_t=S_k} = 1 - \sum_{l \neq k} g_{lk} dt \quad (51)$$

g_{kl} reflects the rate at which community state switches from state S_l to state S_k , and it can be greater than one as long as $g_{kl} dt < 1$. The TTIB acknowledges the existence of trophic interactions by assuming:

1. $g_{kl} = 0$, when the transition from S_l to S_k involves the colonization of a predator without any prey,
2. $g_{kl} = e$, when removing a species from S_l and then successively removing all predators not sustained by any prey species transforms the community into state S_k .

Plugging Eqs (50) and (51) in Eq. (49), we obtain:

$$\frac{P_{C_{t+dt}=S_k} - P_{C_t=S_k}}{dt} = - \left(\sum_{l \neq k} g_{lk} \right) P_{C_t=S_k} + \sum_{l \neq k} g_{kl} P_{C_t=S_l} \quad (52)$$

When $dt \rightarrow 0$, this approach provides the master equation that can be written in vector format to integrate the dynamics of all community states $\mathbf{P} = (P_{S_1}, P_{S_2}, \dots, P_{S_{2T}})$:

$$\frac{d\mathbf{P}}{dt} = \mathbf{G} \cdot \mathbf{P} \quad (53)$$

This equation is the same as Eq. (23); \mathbf{P} includes all community states and the coefficients of the matrix \mathbf{G} generally depend on the community. Nevertheless, the form of the solution remains equivalent:

$$\mathbf{P}(t) = e^{t\mathbf{G}} \mathbf{P}_0 \quad (54)$$

This approach describes a continuous-time Markov chain. When all the community states communicate (i.e. the Markov chain is irreducible), their probabilities reach an equilibrium \mathbf{P}^* given by the vector in the kernel of \mathbf{G} the elements of which sum to one.

2.3.2 Reasonable Approximations

The formulation above allows the study of nonindependence between species occurrences, but suffers from its generality: for T species, the matrix

\mathbf{G} must be filled with $(2^T - 1) \times (2^T - 1)$ coefficients (the “ -1 ” acknowledges that at any time t the elements of $\mathbf{P}(t)$ sum to one). Even if the knowledge of a particular network may help find these coefficients, reasonable assumptions can be made to decrease the complexity of \mathbf{G} .

- First, community compositions between t and $t + dt$ cannot differ in more than one species, i.e. $g_{kl} = 0$ when $||S_k| - |S_l|| > 1$. This turns \mathbf{G} into a sparse matrix: at most $T \times (2^T - 1)$ of its coefficients are not equal to zero. This assumption is not possible under the TTIB as the extinction of a prey can lead to multiple extinctions. However, this issue is easy to circumvent by allowing the predator to survive a (very) short period alone on the island. This can be done using large value for g_{kl} that measures the transition of a community with a predator to the same community without it.
- A second assumption is that colonization processes may be independent of interactions. That is, a predator can actually colonize an island without any prey. This is reasonable if the extinction probability of this predator on such an island is high, as is recommended to comply with the first assumption. Therefore, we can assume $g_{kl} = c$ when $|S_k| - |S_l| = 1$. This assumption is also useful to integrate variability in dispersal capacities among species (Cazelles et al., 2015b).

Table 4 presents matrix \mathbf{G} for species C, D and E of the example presented in Figs 2–4, i.e. community states from S_0 to S_8 . Once the colonization probability is determined, the remaining $T \times (2^T - 2)$ coefficients can be found based on the biological knowledge of species studies, e.g. the nature and the strength of interactions.

2.3.3 Deriving Species Richness

The solution \mathbf{P}^* contains the probabilities of all community states at equilibrium. This information is actually more than the knowledge of individual species presence and species richness. Indeed the probabilities of species occurrence are particular unions of community states; therefore, \mathbf{P}^* is sufficient to derive them at equilibrium. The probability of a species being present at equilibrium is given by:

$$P_{X_i=1} = \sum_{k|S_{k,i}=1} \mathbf{P}_k^* \quad (55)$$

where $S_{k,i} = 1$ means that species i is in community state S_k and \mathbf{P}_k^* is the k th component of \mathbf{P}^* . Similarly, the species richness is given by the sum of \mathbf{P}^* weighted by the cardinality of the community states it refers to:

Table 4 The Transition Matrix \mathbf{G} of the Continuous-Time Markov Chain Associated with All Combinations of C, D and E Species

S_0	S_1	S_2	S_3	S_4	S_5	S_6	S_7
S_0	$-3c$	g_{01}	g_{02}	g_{04}			
S_1	c	$-2c - g_{01}$	g_{13}		g_{15}		
S_2	c	$-2c - g_{02}$	g_{23}			g_{26}	
S_3	c	c	$-c - g_{13} - g_{23}$				g_{37}
S_4	c			$-2c - g_{04}$	g_{45}	g_{46}	
S_5	c			c	$-c - g_{15} - g_{45}$		g_{57}
S_6		c		c		$-c - g_{26} - g_{46}$	g_{67}
S_7			c		c	c	$-g_{37} - g_{57} - g_{67}$

See Figs 2–4 for details on this simplistic food web. The present table is of intermediate density between Table 1 (the classic TIB model, dense transition matrix) and Table 2 (the TTIB model, sparse matrix involving cascading extinctions but no colonization in the absence of prey species).

$$S = \sum_{k=0}^{2^T-1} |S_k| \mathbf{P}_k^* \quad (56)$$

In a similar fashion, many probabilities can be derived regarding either a particular set of species or a particular property of the community. For instance, this framework allows deriving the probability of finding a given set of predators but also the mean trophic level expected and even the probability of having a trophic chain of at least p levels. In all these situations, computation of probabilities requires the identification of the community states to be summed.



3. EFFECTS OF MAINLAND FOOD WEB PROPERTIES ON COMMUNITY ASSEMBLY

In this section, our aim is to explore how the structural properties of mainland food webs affect the colonization/extinction dynamics and the resulting structural properties of island food webs. We first assess the effects of the degree distribution, the network size, the network connectance and the proportion of primary producers on island food web structural properties. In a second stage, we assess the effects of modularity in the mainland food web on island food web properties.

The degree distribution (i.e. the distribution of the number of links per node) is known to be a fundamental property of real-world, complex networks (Barabási and Albert, 1999; Newman et al., 2001) and will have important implications for their stability (Allesina et al., 2015; May, 1972). Food web models classically used in ecology—the niche model (Williams and Martinez, 2000), the cascade model (Cohen and Newman, 1985), etc.—are able to reproduce some properties of real food webs. However, they do not constrain the degree distribution, and typically display distributions of links that follow an exponential law for which there is mixed evidence in empirical data (Camacho et al., 2002; Dunne et al., 2002a). Moreover, those models do not control for the connectance or the proportion of basal species, contrary to the model used by Thébault and Fontaine (2010), for example. In the same vein, classic network generation models used in network science—the Erdős-Rényi model (Erdős and Rényi, 1959), the preferential attachment algorithm (Barabási and Albert, 1999; De Solla Price, 1976), etc.—are able to generate different degree distributions but in a stochastic way. Furthermore, one version of the Erdős-Rényi

model allows the number of links to be fixed, but this is not the case for the Barabási–Albert algorithm in which network topology arises through a growth process (i.e. preferential or random attachment) and in which each vertex is added with a certain number of links. Finally, the growth process of the Barabási–Albert algorithm could lead to particular features in the resulting networks other than just the degree distribution (Newman, 2005; Stumpf and Porter, 2012). We therefore use a network generation algorithm based on degree sequence (Bollobás et al., 2001; Chung et al., 2003; Kim et al., 2009; Miklós et al., 2013).

3.1 Simulating the Model

3.1.1 Generating Directed Networks With Given Structural Properties

Because we want to assess the effects of different structural properties of the mainland food web on the colonization/extinction dynamics of island food webs, we need a network generation model that is able to be constrained by different properties. In particular, we want to fix the size of the network, the number of edges, the proportion of primary producers and the degree distribution. The typical size of food webs and other ecological networks is at least several orders of magnitude below that of network datasets from physics or computer science. For this reason, we want to use a network-building algorithm that yields a food web with properties (size, connectance, degree distribution, etc.) set at exact values, in order to remove the noise that could result from working with food webs that only obey “expected” constraints.

The sequence of degrees, which lists the total number of links of each node, allows the simultaneous fixing of three different metrics: the degree distribution, the network connectance and the size of the network. Thus, we generated the sequences of degrees in a deterministic way, using the procedure of Astegiano et al. (2015), adapted for unipartite networks, which was based on the algorithm of Chung et al. (2003).

3.1.1.1 Generating the Sequence of Degrees for a Given Degree Distribution

We want a degree sequence $w = \{w_1, w_2, \dots, w_n\}$ representing the number of undirected links per node in a decreasing order, i.e. such that $w_i \geq w_{i+1}$ for all i , with n the total number of vertices, and such that the sequence of degrees follows a given probability density function f . One way of deriving such a sequence can be found by solving for w_i :

$$\frac{i}{n} \approx 1 - F(w_i) \quad (57a)$$

or equivalently

$$w_i \approx F^{-1} \left(1 - \frac{i}{n} \right) \quad (57b)$$

where F is the cumulative distribution function associated with the probability density function f . Given a fixed connectance C , the parameters of the probability density function have to be selected such that:

$$2C \approx \frac{1}{n(n-1)} \sum_i w_i \quad (58a)$$

with C the desired directed connectance;

$$C = L/n(n-1) \quad (58b)$$

and L the number of directed links in the network. The denominator in Eq. (58) is $n(n-1)$, because we consider that there is no self-loop (i.e. cannibalism) to avoid species that would stay on an island without any prey except itself. One can adjust the degree distribution (i.e. through f) to obey this constraint by setting the average undirected degree to be exactly $2C(n-1)$. We target twice the desired connectance ($2C$) because the algorithm for directed links leads to a loss of half of the links (due to the passage from undirected to directed links). Finally, this sequence has to be feasible (i.e. the sequence has to be graphic) for a simple connected graph (with no cannibalism, i.e. self-reference, or multiple edges, and with a unique component). In other words, at least one simple connected graph must exist which satisfies the degree sequence (Berger, 2014; Brualdi and Ryser, 1991; Ryser, 1957).

We use truncated degree distributions, and so do not allow node degrees to be below or over certain predetermined limits. Indeed, the maximal degree of a vertex within a community of n species is $n-1$, in the absence of cannibalism, and the minimal degree is one because we target simply connected graph (i.e. without disconnected species). When high values of network connectance are targeted with a Power law for the degree distribution, obtained degree sequences are generally not graphic. In those cases, distributions are left-truncated in order to obtain graphic sequences that maintain a heavy tail. We also round degrees obtained for exponential distribution, because this law is continuous. This is not needed for Poisson and Power law (Zipf law) distributions, which are discrete. It should be noted that Power law distributions have been included mostly for the sake of

comparison, even though it is very difficult to evidence the existence of such distributions in data unless the distribution of degrees spans at least three orders of magnitude (e.g. with degrees spanning the whole 1–1000 interval; [Clauset et al., 2009](#); [Stumpf and Porter, 2012](#)).

3.1.1.2 Generating a Graph With a Prescribed Degree Sequence

If the sequence is graphic, the second step is to generate random undirected connected simple graphs that satisfy the sequence of degrees (and therefore the other desired properties as well), drawn uniformly from all the possible sets of graphs. To do so, we use the procedure described in [Viger and Latapy \(2005\)](#), which improves the MCMC algorithm from [Gkantsidis et al. \(2003\)](#) and is implemented in the R package `igraph` ([Csardi and Nepusz, 2006](#)).

3.1.1.3 Directing the Links

Finally, the generated networks have to be directed in order to be construed as food webs. There is, to our knowledge, no method currently available to direct a graph such that it has a fixed number of primary producers and to ensure that all vertices can be reached from a basal species (there are of course methods to generate directed graphs from undirected ones obeying certain constraints, e.g. [Stanley, 1973](#), but these algorithms were not designed to keep certain nodes as incoming or outgoing ends of the graph, as is needed in the case of food webs with controlled number of basal species).

To do this, we first randomly selected the desired number of basal vertices. These vertices have to be disconnected. Indeed, if two vertices are connected, necessarily one of them cannot be a primary producer. Because of constraints on connectance and degree distribution, some proportions of basal species seem to be unreachable. To confirm that there is no solution in those instances, we use a graph colouring algorithm ([Blöchliger and Zufferey, 2008](#)). This algorithm tries to find the minimal number of colours necessary to colour each vertex such that two adjacent vertices have a different colour. Thus, a set of disconnected vertices is associated to each colour. If this algorithm finds not a single colour-associated set containing at least the desired number of primary producers, then we consider that our basal species assignment problem has no solution. In fact, all parameter sets are not possible, especially for degree distributions following a Poisson law (see later), or when connectance reaches relatively high values (~ 0.1). Then, the network is directed by an algorithm inspired from breadth-first search on graphs (see [Appendix](#)). The basic idea is that, at each time step, one proceeds from the current “trophic level” to the next up the food chain by exploring

the graph from each of the node of the current trophic level, taking all nodes that can be reached in one step from all the nodes in the current trophic level. The next trophic level consists of all nodes thus explored that were not explored earlier; all links between the current level and the next are directed “upwards” (i.e. from current to the next), while links between nodes in the next trophic level are randomly directed. The next step of the algorithm then takes place after taking the next trophic level as the current one.

3.1.2 Generating Modular Networks

Modularity, i.e. the propensity of nodes to form densely connected clusters with few links between them, has been suggested as a potential explanation for properties such as ecological network stability (Thébault and Fontaine, 2010), persistence (Stouffer and Bascompte, 2011) and feasibility (Rozdilsky and Stone, 2001). In the context of the TTIB, our objective is to assess whether the modular structure of a mainland food web affects expectation on islands and, if so, how?

Modular networks are generated with a stochastic block model (SBM; Govaert and Nadif, 2008). Vertices are grouped into groups, and edges are added following the Erdős–Rényi model (Erdős and Rényi, 1959), with a probability q_w of finding an edge between two vertices in the same group, and a probability q_b between two vertices in different groups. If all modules have the same size, the expected network connectance is:

$$E[2C] = \left[\frac{1}{m} - \frac{1}{n-1} \left(1 - \frac{1}{m} \right) \right] (q_w - q_b) + q_b \quad (59)$$

with m is the number of modules. Note that when n (number of vertices/species) is large enough, the expected connectance can be approximated by the following equation:

$$E[2C] \approx \frac{q_w - q_b}{m} + q_b \quad (60)$$

As described in Section 3.1.4.4, modularity is computed with the `walktrap` algorithm (Pons and Latapy, 2006), and with the flow-based `infomap` algorithm (Rosvall and Bergstrom, 2008). Modularity cannot be controlled exactly, but can be approximated through generations of networks with different q_w and q_b such that the connectance stays constant.

An approximate log-linear relation can be found between the logarithm of modularity and the ratio $\beta = q_b/q_w < 1$ (at a constant connectance C):

$$\log(Q) \approx a_C \beta + b_C \quad (61)$$

Using a linear regression, a and b values can be computed. Based on approximations (60) and (61), we can approximately control both the expectation of the connectance and the modularity of the network.

3.1.3 Defining a Null Model

When we compare the properties of local food webs on islands relative to their mainland counterpart, there can possibly be two confounding effects. On the one hand, observed differences could be due to the sequential dependence of colonization/extinction events. On the other hand, differences could arise just because local food webs are limited subsets of the mainland food webs. In particular, some network properties could vary in a systematic way with the size of local networks (Poisot and Gravel, 2014).

In order to disentangle these two confounding effects, we use a null model, which is simply MacArthur and Wilson's TIB model, i.e. without any interaction. For each of the 50 replicates of each parameter set, and for each value of the colonization-to-extinction ratio ($\alpha = c/e$), we randomly draw a sample of species on the mainland. It is noteworthy that to get a broad range of local web sizes, we had to use a wider range of α values for the null model than for the simulations with interactions. The size of the sample is a proportion of the total number of species on mainland, whose value is determined by the value predicted by MacArthur and Wilson's model (i.e. Eq. 3). In this case, all species have the same colonization and extinction rates and are thus considered sampled with the same probability. We do not add any constraint on this random sample, which can thus lead to unrealistic local food webs (e.g. an intermediate species in the mainland food web could appear as a "basal" species in the island network generated by the null model, or a large proportion of species could end up being completely disconnected from the island network, especially for small α , weak connectance and small size of the mainland food web).

3.1.4 Network Properties of Interest

3.1.4.1 Connectance

We consider the directed connectance, which is the number of directed links found in the network relative to the maximal number of directed links possible, given by Eq. (58b).

We have to note that connectance for the null model is computed considering all species on the island, be they connected or not. When α is small (i.e. $c \ll e$), the proportion of disconnected species (i.e. species with no link) increases and thus, the connectance rapidly decreases.

3.1.4.2 Trophic Levels

We use the notion of the shortest trophic level (Williams et al., 2002), which is, the shortest path from a species i to any basal species. This metric is computed using the adjacency matrix (\mathbf{A} , with $a_{ij} = 1$ when there is a link going from species j to species i) of the food web in the following way; for a species i , its trophic level is one plus the smallest τ such that:

$$\mathbf{x}_i^T \cdot \mathbf{A}^\tau \cdot \mathbf{b} \neq 0 \quad (62)$$

where \mathbf{b} is the vector of basal species (i.e. if species j is a basal species, then $b_j = 1$, else $b_j = 0$) and \mathbf{x}_i is a vector of zeroes with a single “1” at position i . Noting τ_i the shortest path from a species i to basal species, the mean shortest trophic level over the whole island food web is:

$$\widehat{TL} = \frac{1}{n} \sum_i (1 + \tau_i) \quad (63)$$

where n is the number of species in the food web. The maximal trophic level in the same food web is:

$$TL_{\max} = \max_i (1 + \tau_i) \quad (64)$$

3.1.4.3 Degree Distribution

Identification of degree distribution is done by fitting several models (Uniform, Poisson, Exponential and Power law) and retaining the one with the lowest Akaike Information Criterion (AIC). Likelihood and parameter estimates are computed with the R package `fitdistrplus`. When this is done on mainland webs, in which the degree distribution is imposed, the best-fit distribution does not always correspond to the desired distribution. For example, relatively small networks with a weak connectance tend to be characterized by uniform or Poisson distributions. Similarly, Power law-constructed networks can appear as following an exponential distribution of degrees when there are not enough well-connected nodes (Newman, 2005; Stumpf and Porter, 2012). For results about degree distributions, we consider the distribution given by the best-fit model rather than the

distribution used to create the input networks so as to better relate our findings to the type of information empiricists have access to.

3.1.4.4 Modularity

As previously noted, modules can be defined as a set of nodes that interact significantly more with each other than with nodes in the rest of the network (Newman, 2004, 2006a,b; Newman and Girvan, 2004). The identification of modules relies on partitioning the nodes of a given network in different modules such that this partition maximizes a property named *modularity*. In ecology, the definition commonly used is the one of Newman and Girvan (2004). With this definition, directed links (i.e. arrow from one species to another) in ecological networks are generally considered as undirected (but see Arenas et al., 2007; Leicht and Newman, 2008, for ways to extend classic modularity to directed networks). As food webs present directed links that represent energy or matter fluxes, this information could be important for constructing modules. Thus, we also use a flow-based approach, the `infomap` algorithm (Rosvall and Bergstrom, 2008) to partition food webs. With this approach, the network is decomposed into modules by optimally compressing a description of a random walk (representing information, matter or energy) on the network. This method could be more capable of detecting modules associated with energy channels (as in Rooney et al., 2006) than the classic optimization of modularity. A value of modularity can be obtained with the partition of the food web obtained by the `infomap` algorithm. However, we instead use the compression rate, i.e. one minus the ratio of description length after/before compression, the description lengths being given in bits necessary to describe typical random walks on the network, as a proxy for modularity.

3.1.5 Running Simulations

As many properties are susceptible to scale with the complexity of the network (Wood et al., 2015), simulations are done with mainland food webs of different sizes (100, 250, 500 nodes/species) and connectance values (0.01, 0.025, 0.05 and 0.1) as well as for different proportions of basal species (5%, 10%, 20%, 40%), since this could alter the outcome of the process by forming a more or less solid foundation for food chain construction. Three different degree distributions are used: Zipf (Power law), Poisson and Exponential (geometric) distributions. Thirty-two combinations of parameter sets are not feasible because they either lead to food webs that do not consist of a single component (disconnected webs) or are unable

to host the targeted proportion of basal species. Fifty networks are constructed for each of the 112 feasible parameter sets.

Two connectance values (0.05 and 0.1) and four approximate levels of modularity (~ 0.1 , ~ 0.25 , ~ 0.45 , ~ 0.6) are used for simulations of modular networks. Food web size ($n=200$), the proportion of primary producers (10%) and the degree distribution (detected as Poisson) are constant among these simulations. Fifty food webs are generated for each parameter set.

All simulations start with empty islands which are then colonized by species from the mainland species network, in which the size, connectance, degree distribution and number of basal species are controlled, as explained earlier.

Simulations are done in continuous time following the Gillespie algorithm for the simulation of Poisson processes (Gillespie, 1976, 1977). The colonization rate, c , is fixed to 0.1 per capita, and the extinction rate, e , varies such that $\alpha = c/e$ takes the following values: $\alpha = \{0.16, 0.25, 0.5, 0.75, 1, 1.5, 2, 4\}$. Given that consumers must have at least one prey present on the island to colonize and species present on the island go extinct with their last prey species, at each moment, the global colonization rate is:

$$\tilde{c} = \sum_{i \in S_C \setminus S_L} c Y_i \quad (65)$$

where $Y_i = 0$ if species i has no prey on the island and $Y_i = 1$ if species i has at least one prey on the island; S_C and S_L are, respectively, the set of species on the mainland and on the island. In the same vein, the global extinction rate is:

$$\tilde{e} = \sum_{i \in S_L} e = |S_L|e \quad (66)$$

The waiting time between two consecutive events is drawn from a negative exponential law of parameter $\lambda = \tilde{c} + \tilde{e}$. This event is a colonization with probability \tilde{c}/λ or otherwise an extinction. If it is a colonization event, a species is randomly selected from the set of species which are not already on the island and which have at least one prey on the island. If it is an extinction, a species is randomly selected from the set of species on the island.

Each simulation runs for 5000 events. The local network structure is saved every 50 events. At each time step, the local diversity and the number of secondary extinctions is recorded. Only networks recorded after 2500 events are analysed (2500 events is large enough to attain the stationary state).

3.2 Results Obtained When Controlling Mainland Food Web Richness, Connectance, Degree Distribution and the Proportion of Primary Producers

3.2.1 Effects on Species Diversity on the Island

The incorporation of trophic interactions into the theory of island biogeography generally leads to a reduction in the species richness observed on islands. This effect is stronger for smaller and less connected mainland food webs and effectively vanishes for large and well-connected networks (Fig. 6).

The shape of the mainland degree distribution does not seem to have a significant effect on the mean diversity observed on islands (Fig. 6). The proportion of basal species has a positive effect on species richness for small and poorly connected mainland food webs (Fig. S1 (doi:10.1016/bs.aecr.2016.10.004)): the more primary producers in those networks, the closer the species richness is from the null expectation (i.e. from MacArthur and Wilson's prediction). These results agree with expectations from the analytic model of Gravel et al. (2011b).

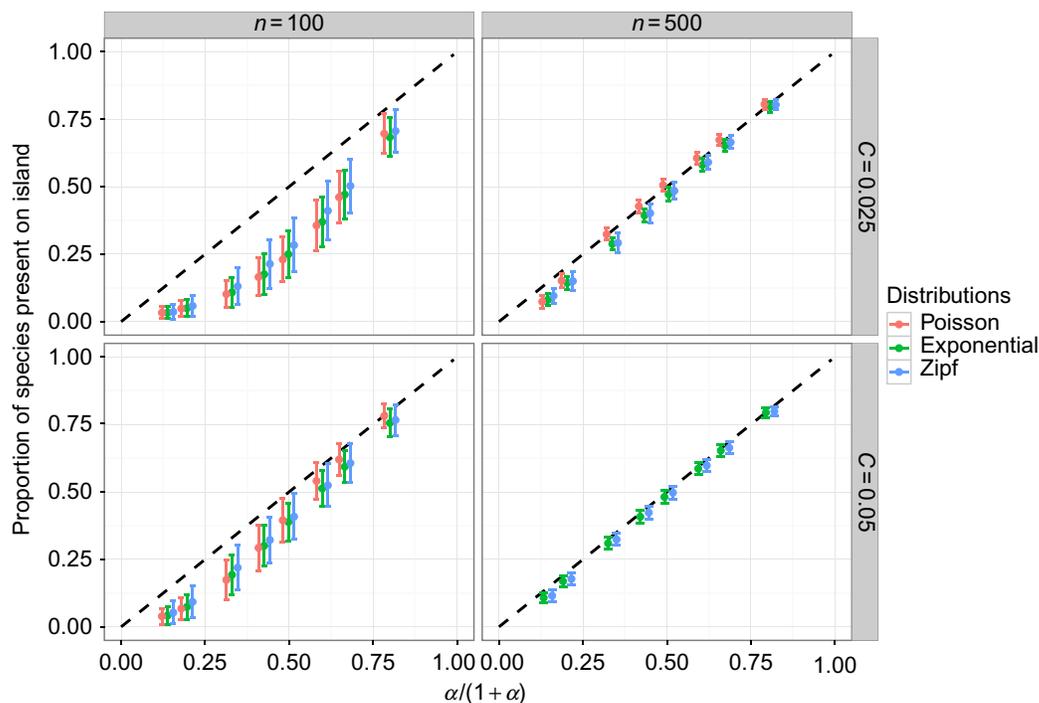


Fig. 6 Species richness observed on islands relative to the size of the mainland food web as a function of the colonization-to-extinction ratio (α , abscissas) compared to the species richness predicted by MacArthur and Wilson's model (the dotted line), for different sizes (columns; $n = 100$ or $n = 500$) and connectance values (rows; $C = 0.025$ or $C = 0.05$) of the mainland food web. Different colours correspond to the different degree distributions of the mainland network. Error bars represent the variance among replicates; points are slightly jittered for clarity. Here, proportion of primary producers is 10%.

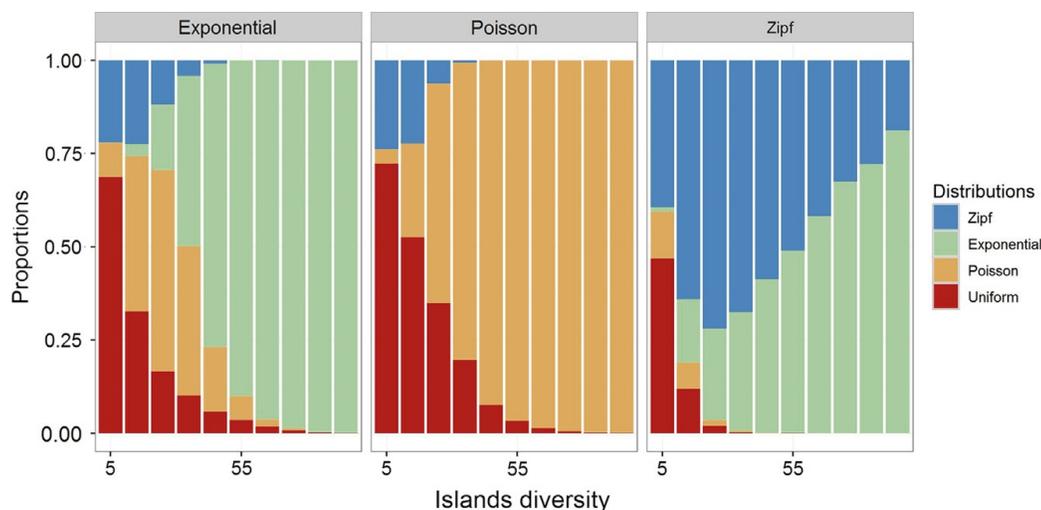


Fig. 7 Fitted degree distributions for island food webs as a function of diversity on islands (abscissas) and mainland degree distributions (from *left to right panel*: exponential, Poisson and Power law). Mainland food webs have 250 species, and a connectance of 0.025. All proportions of primary producers are merged. *Colours* correspond to fitted distributions (legend on the right of the three panels).

3.2.2 Effects on the Degree Distribution on the Island

Regardless of the parameter sets, all simulations show the same pattern when local diversity is low. Indeed, when the number of species on the island is less than a few dozen species, the local degree distribution tends to be statistically identified as uniform, Poisson or Power law, independently of the shape of the mainland degree distribution (Fig. 7). This pattern is stronger when mainland connectance and mainland diversity decrease. However, it can be attributed to a statistical power issue. Indeed, the proportion of cases in which the second best-fit degree distribution is less than 2 units of AIC away from the best model (Fig. 8) decreases with species diversity on the island and with mainland connectance and mainland diversity, but tends towards higher values for small local food webs. Thus, it is difficult to identify a degree distribution with certainty, especially when networks are small.

It is noteworthy that these situations correspond to colonization-to-extinction ratios near or inferior to 0.25, which is large enough when compared to empirical estimations, e.g. from species–area curves (Preston, 1962). For example, from the 50-lake dataset of Havens (1992), the mean local diversity is 38.8 ± 14.8 , while the “mainland” food web has 210 species. This corresponds to a mean colonization-to-extinction ratio close to 0.23 following the original TIB (Eq. 3). Similarly, from the Simberloff and Wilson (1969) dataset on islands (after a defaunation experiment), mean local diversity is 26.8 ± 7.4 for a mainland diversity of 250. This corresponds

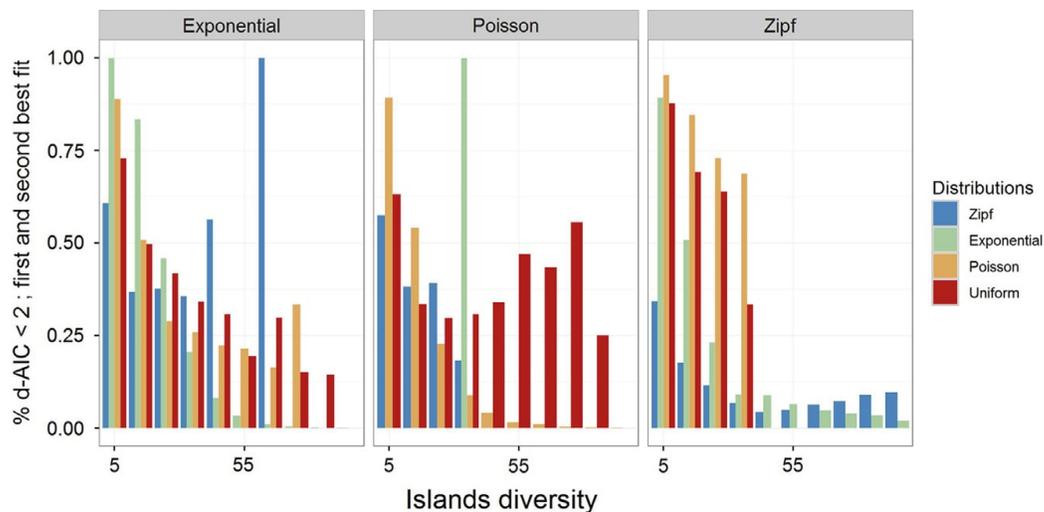


Fig. 8 Proportion of ΔAIC less than 2 units away from the best model. Abscissas represent species richness on the island. Bars represent the proportions of simulated island networks of a certain size for which the second best fit for degree distribution is less than two units of AIC away from the best-fit degree distribution and is given by the distribution associated with the colour of the bar. Parameter values are as in Fig. 7. Mainland degree distribution changes between panels (from left to right: exponential, Poisson and Zipf distributions).

to a colonization-to-extinction ratio close to 0.12. Thus, from our results with colonization-to-extinction lower than 0.25, mainland degree distribution does not seem to be predictable from a sample observed on a local food web (at least, from the comparison of AIC values).

When the number of species on the island increases (which is not necessarily a realistic situation, as mentioned earlier), the local degree distribution tends to become more similar to the mainland distribution (Figs 7 and 8). However, this similarity is not so high when the mainland food web is characterized by a heavy-tailed degree distribution (i.e. a Zipf distribution; see Fig. S2 (doi:10.1016/bs.aecr.2016.10.004)). In this case, a large proportion of local networks are identified to have exponential distributions. For intermediate values of connectance ($0.025 \leq C \leq 0.05$), the majority of island networks follow an exponential degree distribution, especially for intermediate sizes of the local networks. When connectance is relatively strong ($C \approx 0.1$), the larger the size of the local network, the higher the proportion of networks with a degree distribution detected as heavy tailed (Fig. S2).

3.2.3 Effects on Secondary Extinctions on the Island

The size and the frequency of cascading extinctions in the local networks following the extinction of a species are affected by the degree distribution

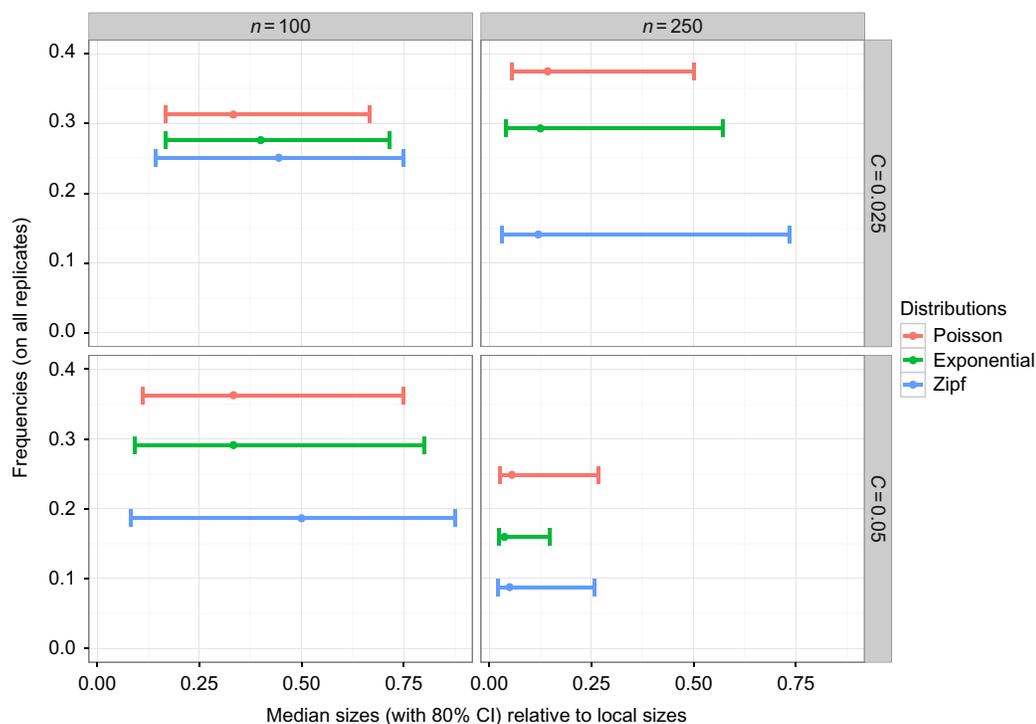


Fig. 9 Median size (with 80% CI) relative to local sizes and frequencies of secondary extinctions, as function of mainland fixed degree distribution and for different size (*columns*) and connectance (*rows*) of the mainland food web. Here, proportion of primary producers is 5%, and alpha ratio is 0.25.

of the mainland network. Indeed, secondary extinctions are less frequent, but generally more variable in size, on islands that are being colonized from mainland food webs with more heavily tailed degree distributions (Fig. 9). This pattern is reinforced in small and poorly connected mainland webs. These results are consistent with previous work on “virtual removal experiments” in networks (Albert et al., 2000; Cohen et al., 2000, 2001; Dunne et al., 2002b), although the processes involved are slightly different (removal of vertex/species vs colonization/extinction process, see also Curtsdotter et al., 2011).

A higher proportion of primary producers on mainland is positively linked to a more robust base for network construction: communities with a high proportion of basal species are less prone to undergo secondary extinctions, and when secondary extinctions do occur, their results are less catastrophic (Fig. S3 (doi:10.1016/bs.aecr.2016.10.004)).

It is interesting to note that, even if some different mainland degree distributions are statistically detected as the same distribution (e.g. Zipf and Exponential laws could both be identified statistically as Exponential), the median size and frequencies of secondary extinctions depend on the “ideal”

distribution (Fig. S4 (doi:10.1016/bs.aecr.2016.10.004)), not on the fitted one. In other words, secondary extinctions occurred according to the degree distribution the mainland food web was supposed to resemble, not according to the degree distribution that best fitted the generated degree sequence.

3.2.4 Effects on Food Web Connectance and Average Degree on the Island

For all parameter sets, directed connectance on islands decreases with the local size of the network and rapidly reaches the same value as the mainland web at intermediate to large network sizes. The proportion of basal species in the mainland web affects this relation. Indeed, with a larger proportion of basal species in the mainland web, the local directed connectance is lower and reaches the mainland connectance faster. Overall, connectance is roughly constant in large enough island food webs.

Comparing the connectance of the island food webs obtained with or without taking into account the trophic interactions (i.e. comparing results following the TTIB vs the TIB), the observed connectance does not seem to be only driven by size. Indeed, island food webs built following the TTIB always show a higher connectance than those following the null model. This difference is slightly more important when the mainland food web displays a heavy-tailed degree distribution.

We find that the TTIB agrees roughly with Martinez' constant connectance hypothesis (Martinez, 1992; Fig. 10). The scaling of links per species, however, tends to look more like the Cohen Link-Species scaling law for mainland food webs of low connectance (Briand and Cohen, 1984; Cohen and Briand, 1984), especially in island networks with few primary producers (see Fig. S5 (doi:10.1016/bs.aecr.2016.10.004) for comparison).

3.2.5 Effects on the Number of Trophic Levels on the Island

When the mean trophic level on the islands is compared to the mean trophic level on the mainland, several patterns are observable (Fig. 11):

- When mainland connectance and/or species richness take low to intermediate values, and island diversity is low, the mean trophic level on the island is below that on mainland;
- When diversity on the island increases, mean trophic level increases too and quickly exceeds mean trophic level of the mainland food web. This difference with the mainland web increases as connectance and size of mainland food web increase;

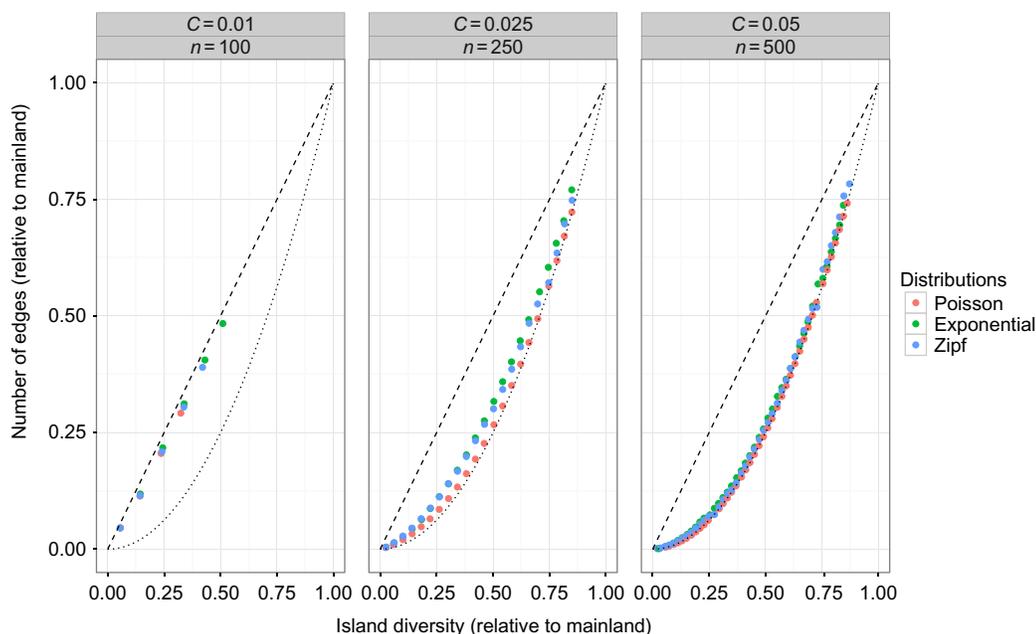


Fig. 10 Number of edges on island (relative to number of edges on mainland), as a function of the diversity on island (relative to mainland) and for different size (n) and connectance (C) along *columns*; points are slightly jittered for clarity. The *dashed line* represents the link-species scaling law and the *dotted line*, the constant connectance hypothesis. Here, proportion of primary producers is 5%. Point colour refers to mainland degree distribution.

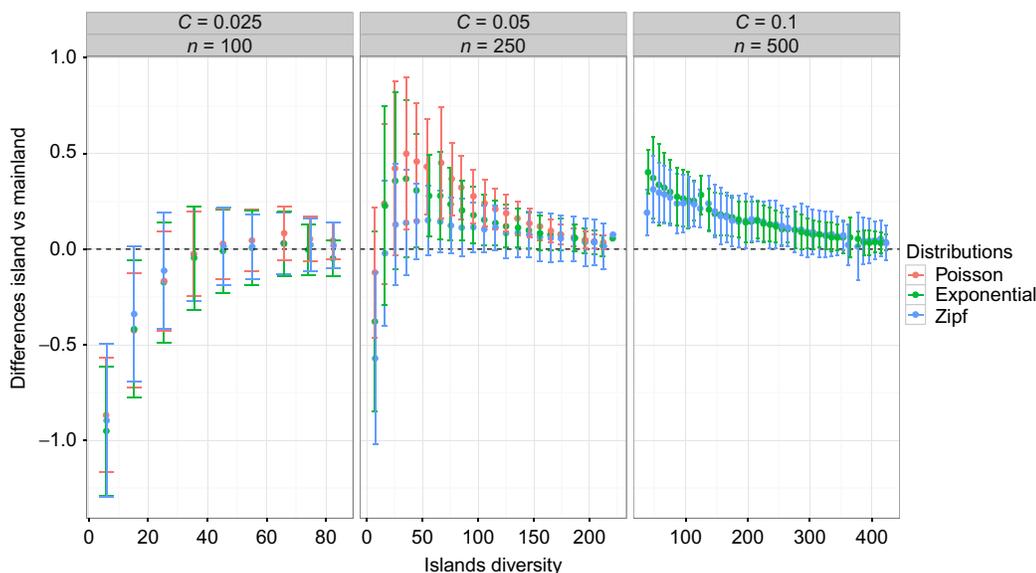


Fig. 11 Island mean trophic level minus mainland mean trophic level for different size (n) and connectance (C) of mainland food web along *columns*. Here, the proportion of primary producers is set at 10%. Points are slightly jittered for clarity and their colour refers to mainland degree distribution. There is no Poisson distribution in the rightmost panel, because we could not generate such a network with a single connected component.

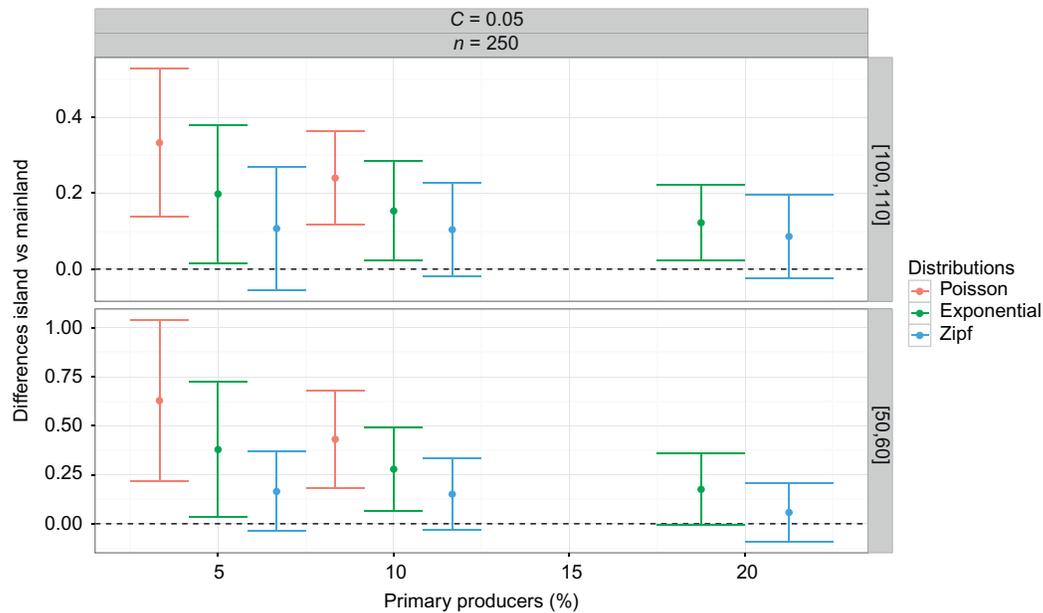


Fig. 12 Difference between island and mainland mean trophic levels as a function of the proportion of primary producers within the food web (*x*-axis), for different mainland degree distributions (colours), fixed characteristics of the mainland food web ($C=0.05$ and 250 species), and different values of species richness on the island (*top panel*: ca. 105 species; *bottom panel*: ca. 55 species).

- When diversity on the island approaches that of the mainland, the mean trophic level also becomes similar to the one on mainland. Thus, mean trophic level changes with island species richness according to a hump-shaped, right-skewed curve.
 - Absolute difference between island and mainland mean trophic levels is higher when the proportion of primary producers decreases (see also Fig. 12);
 - In the same vein, the absolute difference with the mainland web is weaker for heavy-tailed distributions of degree in the mainland food web.
- Thus, in a first phase of colonization, the mean trophic level is lower than in the mainland food web. Shorter trophic chains at low species diversity on the island could be explained by: (i) the sequential dependence of predators on their prey, because at low local diversity, the number of prey species present for a predator is only a subset on the predator's prey on mainland, and thus, it is more difficult for the former to colonize and stay sustainably on the island, thus eventually leading to lower mean trophic level; and, (ii) similarly, because only a subset of prey is present, predators are more prone to undergo cascading extinctions, and this is even more pronounced when the predator trophic level is high. These two effects are already known to limit the length

of food chains in the metacommunity framework (Calcagno et al., 2011). Point (i) matches hypotheses about resource limitation, energetic constraints (Hutchinson, 1959) and level of perturbation. Indeed, low colonization-to-extinction ratios correspond to small and/or isolated islands or strongly disturbed habitats (i.e. high extinction rates). The size of island could also be related to notions of productive space and habitat heterogeneity which are known to limit food chain length (Post, 2002, but see Warfe et al., 2013). Isolated islands should present the same pattern (i.e. low species richness should lead to less productive ecosystem, and should reduce habitat heterogeneity—e.g. fewer engineer species, fewer microhabitats, etc.). Point (ii) relies more on the dynamical constraint hypothesis (May, 1972; Pimm and Lawton, 1977), under which longer food chains are less stable. However, here, like in Calcagno et al. (2011), these effects arise through spatial processes.

Mean trophic level on islands rapidly exceeds the one on mainland (especially in big and well-connected mainland webs) as species diversity on the islands increases. This could be explained by the presence of generalists, which are often also omnivorous in our framework. Such generalist/omnivores can readily colonize islands (Holt et al., 1999; Piechnik et al., 2008), even with a small subset of their usual prey, and then, could present higher realized trophic levels because prey at low trophic levels were absent (see also Pillai et al., 2011). The same effect exists in principle for all species, but decreases with the level of specialization. Moreover, mean degree on islands increases linearly with the number of species, initially (Fig. 10), so that species are ever more connected as diversity increases on the island. Thus, with more links, a species has more chance of being connected to a low trophic level species, which tends to reduce its trophic level. When species richness tends towards the level of the mainland, island webs increasingly resemble the mainland webs and therefore all properties also tend to be similar.

The fact that webs built from heavy-tailed mainland degree distributions deviate less than others from the mainland mean trophic level could be explained by the presence of intermediate trophic level super-generalists, which prey on a large proportion of species on mainland and are in turn consumed by a large proportion of species. When one or more such super-generalists are present, they can link many species together in a way very similar to the mainland web because super-generalists are always associated with primary producers and they assume trophic levels similar to their trophic level in the mainland web.

3.2.6 Effects on Food Web Modularity on the Island

In the first set of simulations, modularity was not controlled when generating the food webs. However, interesting results arise by looking at changes in modularity among network topologies. In mainland food webs, modularity scales with connectance and size of the mainland webs (Fig. S6 (doi:10.1016/bs.aecr.2016.10.004)). Networks characterized by heavy-tailed distributions are less modular than those characterized by lighter-tailed distributions, and the proportion of primary consumers has no effect on modularity (results not shown). This highlights the fact that numerous properties of networks are correlated (Fortuna et al., 2010; Orsini et al., 2015; Vermaat et al., 2009), and disentangling the effects of each property, or deducing that a property results from a particular process is a difficult task, which needs appropriate tools (Orsini et al., 2015).

Modularity on island food webs is generally superior or equal to the one on mainland, except when island food webs are obtained from a poorly connected and small mainland web. Island food web modularity displays a hump-shaped curve along the gradient of species richness (Fig. 13). The number of species (relative to the mainland) required to reach mainland modularity seems to decrease with the size and the connectance of the

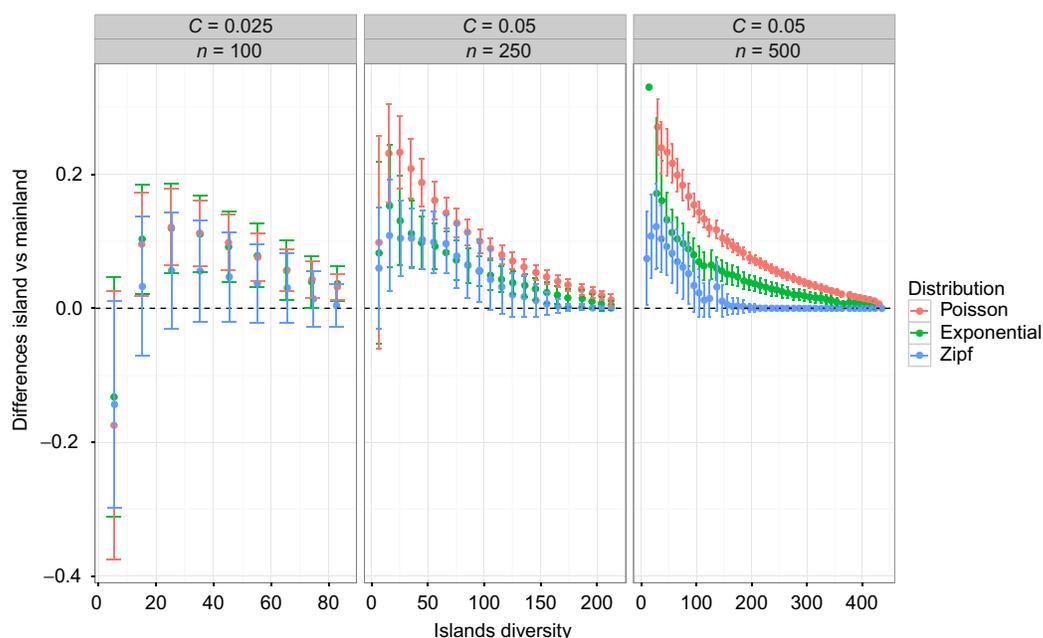


Fig. 13 Differences between island and mainland modularity as species richness increases on island (abscissas), for different size (n) and connectance (C) along columns. Here, the proportion of primary producers is 5%. Points are slightly jittered for clarity and their colour refers to mainland degree distribution.

mainland web, especially with Power law degree distributions. Food webs constructed from complex mainland webs ($C=0.05$) with heavy-tailed degree distributions deviate less and reach the mainland web modularity faster. Again, this is only true when the mainland web is large and well connected. A large proportion of primary producers increases the difference in modularity between mainland and island, but only for small and poorly connected mainland webs (Fig. S7 (doi:10.1016/bs.aacr.2016.10.004)).

It should be noted that modularity is always lower under the TTIB than under the classic TIB (results not shown). Indeed, species samples obtained through the classic TIB are not necessarily simply connected; every connected component of the food web then automatically amounts to another module, hence increasing modularity. However, as empirical measures of modularity are always obtained on simply connected networks (i.e. a single connected component with no disconnected species), results obtained with the null model are not at all comparable with empirical measures on island food webs.

It is remarkable that modularity has more or less the same response to island diversity as mean trophic level. In the first stages, only a few numbers of primary producers are present, and then, trophic chains are constructed independently from each basal vertex by adding new species with higher trophic levels. This leads to several compartments based on different primary producers (different “channels”) and could be seen as a niche-based construction of food webs, assimilating each channel as a different niche. When the diversity on the island increases, with higher colonization-to-extinction ratio, the different trophic “chains” tend to progressively merge together, thus finally leading to a unique component.

Food webs built from heavily tailed mainland degree distributions deviate less and reach the mainland modularity faster, as noted earlier. This could be a consequence of the presence of super-generalist species, which tend to merge the different compartments faster than expected under a more homogeneous degree distribution.

3.3 Results Obtained Using the SBM to Generate Mainland Food Web

3.3.1 Effects of Modularity on Species Richness

Modularity is often considered as a property that enhances the stability and robustness of trophic networks by limiting the diffusion of perturbations through the web (Thébault and Fontaine, 2010) and is often found in empirical data (e.g. Krause et al., 2003). Here, we investigated its effects on food

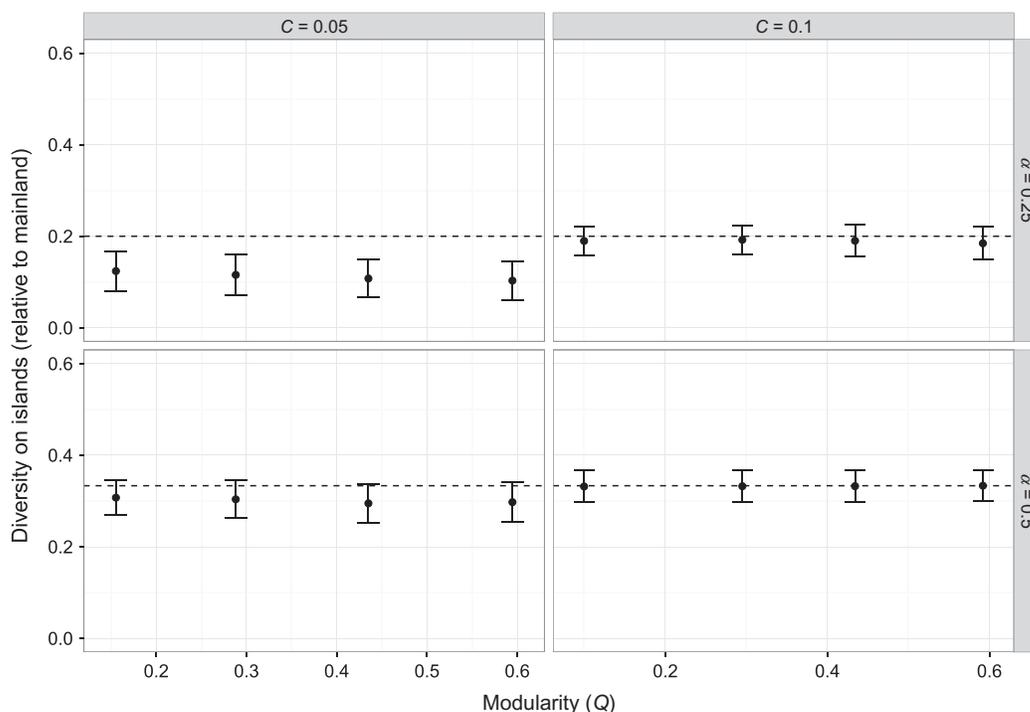


Fig. 14 Species richness on islands as a function of network modularity on the mainland (from Newman and Girvan's method), with mainland food webs built using a stochastic block model algorithm. Mainland connectance changes along *columns* and colonization-to-extinction ratio (α) along *rows*.

web assembly on islands. When looking at the influence of modularity on species richness under the TTIB framework, modularity, computed either with Newman and Girvan's or with Rosvall and Bergstrom's method, does not have any effect on species richness observed on the island (Fig. 14). Thus, more modular mainland food webs are not more easily reconstructed on islands (see also Fig. S7). This observation relates to early studies of Pimm (1979) which suggested that high levels of compartmentalization are not stabilizing. Thus, the origin of compartmentalization in food webs could be unrelated to a stability/robustness issue, but rather to the niche-based organization of food webs (Guimera et al., 2010).

3.3.2 Effects of Modularity on Secondary Extinctions

As for species richness, the modularity of the mainland food web does not really affect the frequency or the size of cascading extinctions on islands (Figs 15 and S8 (doi:10.1016/bs.aecr.2016.10.004)). Contrary to what we expected, frequencies and sizes of secondary extinctions even show a slight increase with modularity. Thus, in our framework, food web compartmentalization does not assure against cascading extinctions.

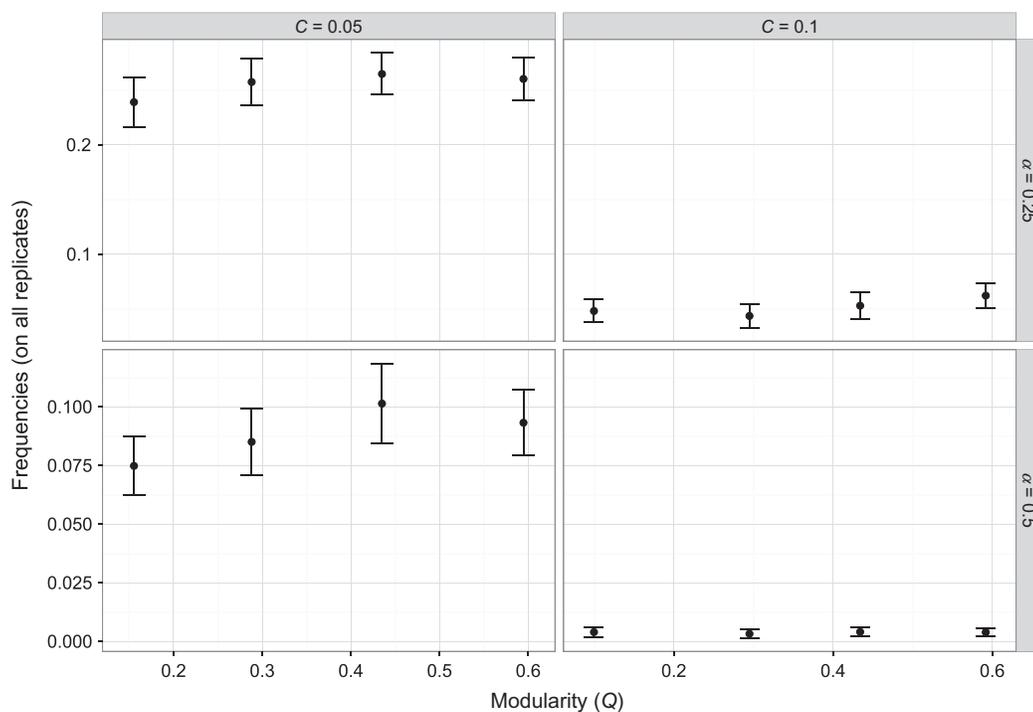


Fig. 15 Frequencies of secondary extinctions as a function of modularity (from Newman and Girvan's method) of mainland food webs. Mainland connectance changes along *columns* and colonization-to-extinction ratio (α) along *rows*.



4. DISCUSSION

4.1 Legacies of Island Biogeography Theory

MacArthur and Wilson's TIB (1963, 1967) has contributed to several conceptual revolutions that are still important in current theoretical ecology. These were originally proposed because of the particularities of insular habitats, but now it is well recognized that they also concern other ecological systems (Warren et al., 2015). First, because islands are discrete habitats harbouring small populations, they are subject to important demographic stochasticity and elevated extinction risk. Consequently, it is essential to consider the impacts of colonization and extinction dynamics and that biodiversity is never at equilibrium. Second, because of their isolation, community composition on islands is strongly contingent on the regional species pool and the ability of species to reach the islands. These two features of insular habitats lead to a different perspective of community assembly, in which macroscopic properties of communities are deterministic, despite considerable stochasticity in local community properties.

The neutral theory of biodiversity (Bell, 2000, 2001; Etienne and Alonso, 2005; Hubbell, 2001; Volkov et al., 2003) is perhaps the best example to illustrate the legacy of the TIB on today's theoretical ecology. As with the TIB, the neutral theory of biodiversity assumes that some meaningful predictions about community organization can be made without detailed knowledge of the natural history (Wennekes et al., 2012). The neutral theory integrates the dynamical balance between colonization and extinction dynamics and then adds competitive interactions. While it maintains the main predictions of the TIB (species abundance–rank curves and species turnover), it also expands the range of predictions owing to its individual-based formulation (e.g. species abundance distributions, range–abundance relationship). Neutral theory is, however, not the endpoint of the story, as we have argued in this chapter in which we developed theory for nonneutral interactions. While the TIB and neutral theory were originally concerned with competitive interactions, recent developments have also paved the way to a network theory of biogeography. Extending the TIB to several trophic levels also reveals different species–area relationships for prey and predators (Holt et al., 1999) and the reciprocal feedback between insular dynamics and network structure (Gravel et al., 2011b). We discuss here how the TIB can be used as a template to add complexity in species interactions and contribute to the integration of community ecology and biogeography.

4.2 The Future of Island Biogeography Theory

4.2.1 A General Theory for Sampling the Regional Species Pool

The TIB establishes the principle that a local community is a sample of the regional species pool. The size (i.e. species richness) and the composition of this sample depend on the probability of each species to be sampled from the regional pool. In the TIB, and incidentally in neutral theory as well, this probability is only influenced by two abiotic variables, that is island size and isolation. The model supposes that all species are functionally equivalent and have the same probability to compose the regional pool. All species are treated as equal and consequently they all have the same occupancy. At any time, a local community of a random sample of S species drawn from the regional pool can be described using the following general stochastic model:

$$P(R_i, X_i = 1) = P(R_i)P(X_i = 1|R_i) \quad (67)$$

where $P(R_i, X_i = 1)$ is the probability of observing a species i with characteristics R_i on an island, $P(R_i)$ represents the probability of sampling a species

with such characteristics and $P(X_i = 1|R_i)$ is the occupancy function for such a species, conditional on its characteristics. The classic TIB assumes that $P(X_i = 1|R_i)$ is independent of R_i and consequently the distribution of species characteristics on an island is only driven by their distribution in the regional species pool.

The trophic extension of the TIB introduced the idea that the sampling could be biased by trophic interactions, and indirectly by the traits driving these interactions (Gravel et al., 2016). Here, we derived a model in which diet breadth and trophic position with respect to primary resources determine species-specific occurrence probabilities. In this model, generalist species located at low trophic levels are more likely to find prey species at colonization and thereafter persist. Compared to the mainland species pool, local community composition is biased towards more generalist species, as described by:

$$P(X_i = 1|R_i) = \frac{c(R_i)}{c(R_i) + e(R_i)} \quad (68)$$

where c and e are colonization and extinction functions based on the characteristics of the species, R_i . In addition, we have shown that these characteristics are not stationary. In other words, the diet of a species on an island, and so its colonization and extinction probabilities, is a function not only of its position in the mainland food web, but also of the local community composition (see e.g. Fig. 11 on trophic levels). The inclusion of species-specific equilibrium occurrence probabilities, developed in the TTIB, therefore paves the way to the integration of functional ecology, community ecology and biogeography. This approach could indeed be extended to further sets of biogeographical models that incorporate biotic variables related to species dispersal capacities (e.g. symbionts, see Amsellem et al., 2017) and extinction probabilities.

Such an example is provided by the investigation of body mass distribution on islands. Body mass appears to be a fundamental trait that percolates through all aspects of community dynamics and ecosystem processes, from productivity to energy flows (Brown et al., 2004; Cohen et al., 2003; Etienne and Olf, 2004; Otto et al., 2007; Peters, 1986; Woodward et al., 2005). Body mass has also been successfully used to parameterize models of food web topology (Allesina et al., 2008; Eklöf et al., 2013; Gravel et al., 2013; Petchey et al., 2008; Rohr et al., 2010; Williams et al., 2010). At the biogeographical scale, body mass is likely to

influence both colonization and extinction rates (Bradbury et al., 2008; Soininen, 2016). The scaling of colonization and extinction rates with body mass could be easily integrated into the TIB and the TTIB, leading to an allometric theory of island biogeography with species-specific and mass-dependent occurrence probabilities. Owing to the negative relationship between abundance and body mass (Blackburn and Gaston, 1999; Cohen et al., 2003; Damuth, 1981; Nee et al., 1991; White et al., 2007), we would expect extinction rate to correlate positively with body mass (Gotelli and Taylor, 1999; Petchey et al., 2004). However, empirical evidence for this assumption is weak (Gaston, 2000), while the supposed higher abundance of small-bodied species might be balanced by other factors that make them more prone to extinction, like their higher dependence on habitat complexity (Graham et al., 2011). In contrast, the scaling of colonization rate, dispersal and space use with body size is supported by many empirical studies, in particular in marine systems (Jetz et al., 2004; Peters and Wassenberg, 1983; Wieters et al., 2008). All life-history traits increasing the rate of colonization, such as fecundity, home range, mobility or diet generality are indeed positively correlated to fish body size (Kulbicki et al., 2015; Luiz et al., 2013; Mora et al., 2003; Nash et al., 2015). The scaling of colonization rate with body size is, however, less straightforward in taxonomic groups in which these traits scale differently. For example, fecundity decreases with body size for birds and mammals while mobility increases (Marquet et al., 2005). In terrestrial and semiterrestrial animals, a positive relationship between dispersal and body size is generally supported by existing data (Stevens et al., 2014), although exceptions do exist. Even if single large individuals might disperse further away than small ones, the larger number of offspring produced by populations of smaller organisms could also lead to inverse scaling relationships. Allee effects might also affect the establishment success of immigrants, and we do not have clear expectations of how it might scale with body size. While intuitive at first, the integration of allometric constraints into the TIB and the TTIB will require direct empirical investigation of colonization and extinction rates.

4.2.2 Abundance and Energy

In the TTIB, the consequences of ecological interactions are only perceptible when a predator cannot find any prey. However, the consequences of interactions may actually be perceptible for any change in the composition

of the community when analysing species abundances. Thus, extinction rate should vary more smoothly with community composition (i.e. not sharply increase when the underlying food web is weakened by extinction of a keystone species) because of the role of trophic regulation on population size (Hairston et al., 1960; Oksanen et al., 1981; Persson et al., 1992). Moreover, fluctuations of individual species numbers due to interactions may further influence extinction rates when driving populations to very low densities. It is also the rationale on which the results pertaining to the stability of ecological networks are based (Allesina and Tang, 2012; May, 1972, 1973). Hence, introducing species abundance in the TTIB, and their link to dynamical stability, is a promising avenue towards a more mechanistic and integrated TIB.

Species abundances are also key to introduce energetic constraints in a mechanistic framework (Trebilco et al., 2013). In the TIB, the existence of such limits lies in considering the extinction rate as a decreasing function of the island area. In the TTIB, energetic constraints actually restrict the diversity of primary producers which in turn reduces species richness at higher trophic levels. Therefore, as in the TIB, rich communities are precluded, but in the TTIB, species are not equally affected: the higher their trophic level, the more affected they are. Furthermore, the energetic consumption of an entire island community at equilibrium can be computed based on the relationships between the body mass and the metabolic rates. This measurement can then be used to determine if the community may persist on the island or if imminent extinctions are expected due to the lack of available energy. Integrating species abundances and energetic constraints in the TTIB may provide new insights into the abundance–body mass relationship that remains poorly understood (Blackburn and Gaston, 1999; Blackburn et al., 1993; Damuth, 2007; Trebilco et al., 2013). It also promises the investigation of biodiversity distribution over large temperature gradient and might prove useful at explaining the widely documented relationship between energy and species richness (Currie, 1991; Currie et al., 2004; Hurlbert, 2004). Also, taken from an evolutionary perspective, these considerations might possibly come up with new explanations of gigantism and dwarfism on islands.

4.2.3 Environmental Heterogeneity

Kadmon and Allouche (2007) proposed a model unifying niche and metapopulation theories under the area-heterogeneity trade-off hypothesis

(see also [Allouche et al., 2012](#)). The niche theory proposes that species coexistence occurs because a differentiated response to the environment reduces the interspecific competition below intraspecific competition ([Chesson, 2000](#)). Assuming species packing along niche axes, species richness should be proportional to the range of these axes and inversely proportional to the niche width of individual species. The TIB, on the other hand, proposes that species richness in a locality is a dynamical equilibrium between stochastic colonization and extinction events. The TIB predicts a positive relationship between area and species richness because larger islands will have lower extinction rates. [Kadmon and Allouche \(2007\)](#) proposed to unification of these concepts with a single assumption: for a given region, the average area of favourable habitats should decrease with increasing environmental heterogeneity because each extra portion of a novel habitat reduces the surface occupied by other ones. There are, therefore, two contrasting forces acting on species richness with increasing environmental heterogeneity: a positive effect of niche diversity and a negative effect of increased extinction rate ([Allouche et al., 2012](#)). The theory consequently predicts a hump–shape relationship between environmental heterogeneity and equilibrium species richness, which has been partly supported by empirical data ([Hurlbert, 2004](#); [Tews et al., 2004](#)). The last missing piece of information is the scaling of environmental heterogeneity with area. A positive relationship, which is generally expected, would further strengthen the scaling relationship between area and species richness.

It could be feasible to extend this theory further to account for species-specific colonization and extinction probabilities, contingent on the environmental heterogeneity. With such an approach, results might differ as some species could benefit from increasing environmental heterogeneity because they are more likely to find their niche, or alternatively they could be increasingly maladapted with more environmental heterogeneity ([Farkas et al., 2015](#)). Overall, it is likely that a large portion of model deviations from the classic TIB would be linked to the variance of environmental conditions, and the average conditions relative to the average niches of the mainland species pool. With such extensions, we could find flat, positive, negative and hump-shaped relationships between average conditions and species richness.

The TIB has been established and tested for islands, but the vision provided in the early sixties goes beyond the scope of islands. The TIB can indeed be regarded as the simplest metacommunity model with two patches.

The first patch has an infinite area (the continent) and contains all the species. The second patch has a finite area (the island) and contains a sample of species present in the first patch. The TIB describes the occupancy dynamics of the latter given colonization of species from the former. Although this vision is applicable in many situations, regardless of the insular nature of patches considered, it has often been restricted to islands and fragmentation studies (Losos and Ricklefs, 2009). Among the limitations hampering the application of the TIB to other contexts, there is the paucity of predictions regarding abiotic conditions, such as temperature and precipitation, which are at the core of the theory of biogeography (Peterson et al., 2011). This apparent gap in the TIB is not surprising given that on many islands, abiotic conditions can reasonably be assumed similar between islands and the continent, i.e. the latitudinal range of colonization from the continent is restricted. However, this assumption prevents the TIB from being used to study species richness along environmental gradients.

Recently, Cazelles et al. (2015b) have developed a framework inspired from the TTIB that integrates abiotic constraints. According to their work, introducing an environmental gradient in the TTIB requires an explicit statement for how the local conditions prevailing on the island affect species differently, i.e. modulating the extinction rate, the colonization rate or both according to the values of the environmental gradient. The authors highlight the potential of such an integration for examining the interplay between biotic and abiotic constraints, which is often neglected in models used to predict species distributions (Thuiller et al., 2013). For instance, they hinted at the importance of positive covariation in the response to the environment between interacting species. Independent environmental requirements between interacting species might result in a dislocation of local networks. Broadly speaking, such an extension of the TIB corresponds to the introduction of the abiotic niche in the TTIB and the possibility of studying the relationship between the fundamental niche and the realized one (Cazelles et al., 2015a).

4.2.4 Network Macroevolution

The isolation of oceanic islands provides an ideal setting to investigate diversification dynamics in a context of limited immigration and gene flow (Gillespie, 2004; Losos et al., 1998; Warren et al., 2015). Island biogeography theory has been influential to the study of macroevolution and community phylogenetics (Warren et al., 2015). Fairly simple extensions to the

modelling approach described in this study might allow investigation of the macroevolution of network structure. The model of colonization–extinction dynamics is analogous to speciation–extinction models of macroevolution, with the distinction that in macroevolutionary models the regional pools emerges from the dynamics and is not fixed in time.

There is currently an intense debate about the effect of ecological interactions on diversification rates (Harmon and Harrison, 2015; Rabosky and Hurlbert, 2015), and it is possible that an evolutionary extension of trophic island biogeography could perhaps address these issues. Except for a few mechanistic endeavours (e.g. Hubert et al., 2015), the bulk of current quantitative approaches considers a phenomenological model to represent the effect of species diversity on diversification, under which the net diversification rate (speciation and extinction) slowly decays with diversity, in a manner similar to a logistic growth model (Ricklefs, 2007). Following the dynamics of the TTIB, one could consider that a successful speciation event will occur provided that a mutant finds at least one prey species, and accordingly it goes extinct on losing its last prey (see also Quince et al., 2002). Such a model would predict an exponentially increasing diversification rate in absence of top–down control because the more species there are, the more successful mutants will be and the lower the extinction rate. On the other hand, diversification is expected to saturate at a stable equilibrium species richness in the presence of negative effects of predators on the extinction rate of the preys since higher species richness will result in stronger top–down control (Rabosky and Hurlbert, 2015). Such a model could be used to investigate a much larger range of predictions than typical birth–death models do (Ricklefs, 2007), with predictions on diversification rates as well as phylogenetic structure of trophic interactions (Peralta, in press).

4.2.5 Biological Invasions

A recurring question in the field of biological invasions is to understand the determinants of invasion success and impacts (David et al., 2017; Mollot et al., 2017; Pantel et al., 2017). Historically, approaches to solve this question have first relied on species-centred, static attributes (i.e. not variable among populations of the same species and/or considered absolute measures of species “invasiveness”) such as fecundity, generation time, growth and development trajectories, etc. (Van Kleunen et al., 2010, 2015) and include “classic laws” e.g. Baker’s law (Baker, 1955, 1967)—self-compatible plants should have an edge as invaders of areas disconnected from

their native distribution. However, multiple traits are often required to obtain good predictions of species invasiveness (Kuster et al., 2008). A second approach has been to compare trait values to those of native species within the invaded ecosystems, i.e. to look at the similarity (or dissimilarity) of the potential invader with the rest of the local community, based on trait values, functional groups and/or phylogeny (Gross et al., 2013; Leffler et al., 2014; Minoarivelo and Hui, 2016; Pearse and Altermatt, 2013b). Other approaches have also used the opposite approach, i.e. looked at native traits or functions which could prevent invasion by a repetitive invader (Byun et al., 2013). However, in all these approaches, the structure of the underlying interaction networks—the invaded network and the network which natively hosts the invading species—is rarely taken into account.

The TTIB could be used as a simple null model of the invasibility of food webs, insofar as it could account for the trophic levels of both native and invasive species, and thus generates predictions for the probability of species occurrence “on the island” given its position within the interaction network (mostly its trophic level and degree as predator) and colonization/extinction parameters. As a dynamic model of species occupancy, the TTIB could also be used to predict temporal invasion sequences based on the position of invaders within the network. Whereas most models tend to predict invasion success independently of other invasions in the system, the TTIB could help design a more realistic model of network invasion through its built-in mechanism of sequential colonization dependence. In place of predicting the probability of a single invasion success, it would therefore give the probability that a given series of invasions occurs, or the probability that a given species invades before another potential invader.

4.3 Using the TTIB to Model Species Distribution

Since the pioneering study of Davis et al. (1998), there is growing evidence for the role of ecological interactions in community response to climate change (Harmon et al., 2009; Suttle et al., 2007). Treating species as isolated entities when predicting their future geographic distribution will likely result in erroneous predictions (Clark et al., 2014). To make such an assumption, we must understand how interactions influence species distributions (Holt, 2009) and also how environmental gradients affect the strength of interactions (Poisot et al., 2012). Adding abiotic constraints into the TTIB

yields an adequate theoretical model to scrutinize the relative contribution of trophic interactions and individuals response in the context of climate change (Cazelles et al., 2015b). In this framework, a species colonizes a patch according to its abiotic requirements and survives only if it becomes embedded in a network that is assumed to be feasible. Hence, a predator whose prey cannot survive during the warming up will go extinct. This provides a simple model that reflects observed extinctions under climate changes mainly caused by changes in network structure (Cahill et al., 2013; Pearse and Altermatt, 2013a; Säterberg et al., 2013). This application of an extended TTIB could be the key to renewal of the theoretical foundations of species distribution models, but it will demand significant effort to turn this theoretical model into a statistical tool (see Gravel et al., 2011b).

4.4 From Theory to Data

Extensions of the TIB, such as the incorporation of trophic interactions, not only introduce more realism but also considerably enrich the range of predictions and our ability to test theory with empirical observations. The species–area relationship is one of the best-documented observations in ecology (Preston, 1962), but it also has several competing explanations for which there is currently no agreement (Lomolino, 2000). In such a case of conflicting theories with common predictions, distinguishing them does require testing them from different perspectives (Chave et al., 2002; McGill, 2003). It is of course a challenge to increase model complexity without facing a trade-off with the number of parameters to evaluate. But, the development and evaluation of the TTIB with empirical data has shown it is possible to keep a model relatively simple, without the addition of extra parameters, owing to some realistic assumptions (Gravel et al., 2011b). As presented earlier, the biggest advantage of the approach developed in this chapter is to derive species-level predictions, in comparison to the community aggregated predictions of the classic TIB. It is possible to fit the occupancy functions using maximum likelihood methods (Gravel et al., 2011b). The next step is perhaps to evaluate the capacity of the theory to predict finer aspects of network structure, such as the distribution of motifs (Stouffer et al., 2007). The frequency distribution of the motifs could be derived using approximate Bayesian computing (Beaumont, 2010) or exponential random graph models (Snijders et al., 2006), and compared to empirical data. Unfortunately, we still lack appropriate data to go beyond what has been done so

far. Doing so will require specific data on realized interactions at different locations and, for now, there are only few candidate datasets with replicated network sampling that could allow it.

Surprisingly, despite the simplicity of the approach, we are not aware of any attempt to directly measure colonization and extinction processes, and then comparing quantitative predictions of expected species richness to observations. Doing so would require time-series data, such as the one collected by [Simberloff and Wilson \(1969\)](#) in their classic experiment, measuring the colonization and extinction probabilities for different islands and then relating them to island area and isolation. One would simply seek to evaluate the probability of a colonization (and extinction) event occurring between time step t and step $t + dt$. The model could be rendered more complex, with detailed investigation of the species-specific colonization and extinction rates, trying to relate them to their position in the food web and other functional traits. This is indeed what [Cirtwill and Stouffer \(2016\)](#) performed for colonization. They found that in Simberloff's experiment, the variability of colonization rates among arthropods was best understood from species diet. Time-series data for entire communities combined with knowledge of trophic interactions are hard to gather but would have immense value for the advancement of island biogeography theory specifically, and for community assembly theory and ecology more generally.

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APPENDIX. BREADTH-FIRST DIRECTING OF THE LINKS IN THE GENERATED NETWORK

For a undirected connected simple graph $\mathcal{G} = (\mathcal{V}, \mathcal{E})$, with \mathcal{V} the set of vertices and \mathcal{E} the edges set. \mathcal{V}_B (with $\mathcal{V}_B \subset \mathcal{V}$) represent the basal species set, drawn from the colouring algorithm. Capital letters are vertices set, upper-case letters represent one vertex. Finally, double arrow (\leftrightarrow) represents an

edge (directed or not), simple right arrow ($v \mapsto \omega$) is a directed edge from v to ω and simple left arrow (\leftarrow) is an affectation.

$\mathcal{V}_f \leftarrow \mathcal{V}_B$

$\mathcal{V}' \leftarrow \mathcal{V}_B$

while $\mathcal{V}' \neq \mathcal{V}$ do // While all nodes have not be done

$\mathcal{V}'_f \leftarrow \emptyset$

for v in \mathcal{V}_f do

for ω in $A(v)$ do // $A(v)$ is the set of vertices adjacent to vertex v

if $v \leftrightarrow \omega$ is undirected then // If edge between v and ω is undirected

$v \mapsto \omega$ // Edge is direct from v to ω

$\mathcal{V}'_f \leftarrow \text{add}(\omega)$

done

done

done

for v in \mathcal{V}'_f do

for ω in $A(v)$ do

if $v \leftrightarrow \omega$ is undirected AND $\omega \in \mathcal{V}'_f$ then

$v \mapsto \omega$ OR $\omega \mapsto v$ // Edge can be in one direction or the other, with the

done // same probability

done

done

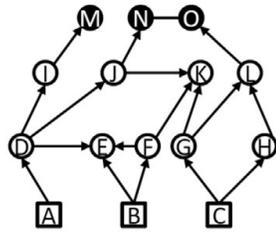
$\mathcal{V}_f \leftarrow \mathcal{V}'_f$

$\mathcal{V}' \leftarrow \mathcal{V}' \cup \mathcal{V}'_f$

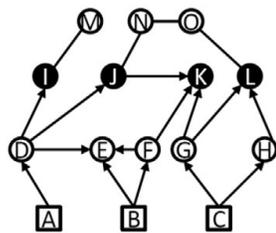
done

The above-described algorithm is illustrated in the following figure. Starting from an undirected graph (A–M) with basal species (A–C), the different steps (1–10) describe how (i) the graph is explored (steps 2, 5 and 8), (ii) the links are directed from one “trophic level” to the next (steps 3, 6 and 9) and (iii) links within a given trophic level are randomly directed (steps 4, 7 and 10).

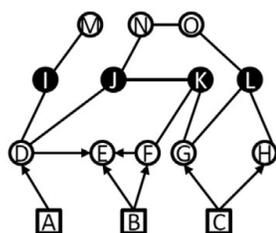
9. Direct links towards explored species



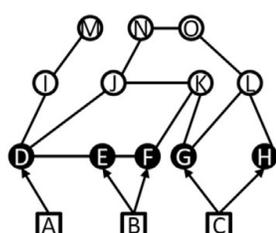
7. Randomly direct links among explored sp.



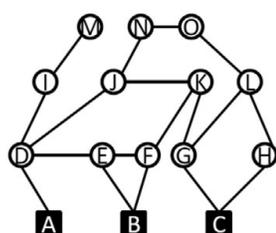
5. Explore one step further



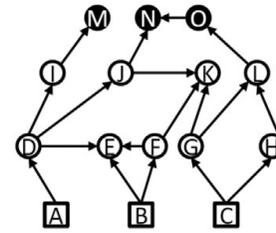
3. Direct links towards explored species



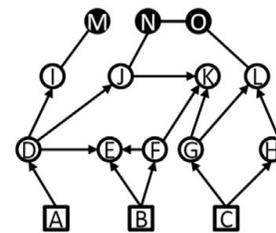
1. Undirected network with basal species



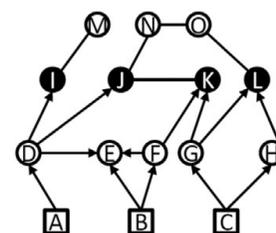
10. Randomly direct links among explored sp.



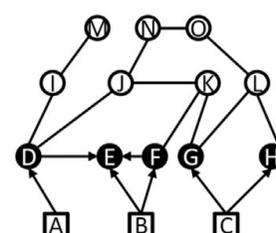
8. Explore one step further



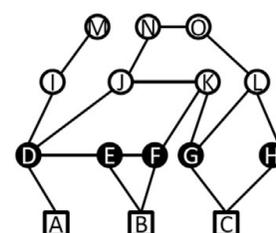
6. Direct links towards explored species



4. Randomly direct links among explored sp.



2. Explore network from basal species



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