

## LETTER

### Trophic theory of island biogeography

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#### Abstract

MacArthur and Wilson's Theory of Island Biogeography (TIB) is among the most well-known process-based explanations for the distribution of species richness. It helps understand the species–area relationship, a fundamental pattern in ecology and an essential tool for conservation. The classic TIB does not, however, account for the complex structure of ecological systems. We extend the TIB to take into account trophic interactions and derive a species-specific model for occurrence probability. We find that the properties of the regional food web influence the species–area relationship, and that, in return, immigration and extinction dynamics affect local food web properties. We compare the accuracy of the classic TIB to our trophic TIB to predict community composition of real food webs and find strong support for our trophic extension of the TIB. Our approach provides a parsimonious explanation to species distributions and open new perspectives to integrate the complexity of ecological interactions into simple species distribution models.

#### Keywords

Complexity, ecological network, food web, island biogeography, metacommunity, species–area relationship.

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#### INTRODUCTION

The elegance of the Theory of Island Biogeography (TIB; MacArthur & Wilson 1967) arises from its simplicity (Lomolino *et al.* 2009): species richness in a community is the result of a dynamic equilibrium between immigration and extinction processes, which are influenced by the area holding the local community and its connection via dispersal (MacArthur & Wilson 1967). It predicts the slope of the species–relationship, a fundamental pattern for ecology (Lomolino 2000) and conservation (May 1988; Guilhaumon *et al.* 2008; He & Hubbell 2011). This parsimonious classic theory comes, however, with some limitations: it only applies to well-defined trophic guilds, it does not explicitly consider the nature of interactions among species and it cannot predict their identity in local communities.

Ecological interactions are known to underpin species occurrence at large spatial scales (Gotelli *et al.* 2010). However, there have been surprisingly few theoretical developments on these limitations since the publication of the TIB (Holt 1996, 1997; Hanski & Gyllenberg 1997; Holt *et al.* 1999; Ryberg & Chase 2007) and development of metacommunity theory (Leibold *et al.* 2004). The success of the TIB, and its recent extension through the neutral theory of biodiversity (Hubbell 2001), is nonetheless strong assets for an elegant and synthetic theory of biogeography (Losos & Ricklefs 2009). Considering more realistic community structures and dynamics is now needed to reach process-based species distribution models (Guisan & Thuiller 2005; Araujo & Luoto 2007). Ecological communities generally display complex structures (Polis & Strong 1996) that are

challenging to integrate into a parsimonious and realistic model. Here, we show how integrating elements of food web theories (Pascual & Dunne 2006) into the TIB helps improve predictions of community structure across trophic levels and scales.

#### MODEL ANALYSIS

Following the TIB, a local community is assumed to be a random sample of species drawn from a metacommunity (Leibold *et al.* 2004). The sampling process is non-specific: every species has the same probability  $p(t)$  of being included in the local community at any time  $t$ , independently of local and regional community structures (MacArthur & Wilson 1967). This probability, named occupancy, is the result of two processes: locally absent species immigrate into the local community at rate  $c$ , and locally present ones go extinct at rate  $e$ , yielding the following dynamics (Holt 1996):

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

The equilibrium total occupancy is then  $p^* = \frac{\alpha}{1+\alpha}$ , where immigration and extinction rates are summarised under a single parameter,  $\alpha = c/e$ . The immigration rate  $c$ , and so the ratio  $\alpha$ , is hypothesised to be inversely related to the distance to the mainland (MacArthur & Wilson 1967). As the extinction rate  $e$  should be inversely proportional to population size (Hanski 1999; Lande *et al.* 2003), the ratio  $\alpha$  is also hypothesised to be related to local area or any environmental factor affecting local population density. The equilibrium local species

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richness  $S_L$  is reached when immigration equals extinction, and is given by  $S_L = P_T p^*$ , where  $P_T$  is the total species richness in the metacommunity (Fig. 1a).

The challenge of building a trophic TIB model is to use as few assumptions as possible to capture the inherent complexity of food webs, without losing the elegant simplicity of the classic TIB. We make two assumptions translating the concept of bottom-up sequential dependency, developed by Holt and others (Holt 1997, 2009; Dunne *et al.* 2002a; Calcagno *et al.* 2011; Gravel *et al.* 2011): (1) a consumer species can colonise a local community only when at least one of its prey species is already present and (2) a consumer species losing its last prey species in a local community (because of extinction or emigration processes) goes extinct. We consider a regional food web with  $P_T$  species, among which there are  $P_C$  consumer species, and which share  $L_R$  potential feeding links in the regional species pool. The number of potential prey species for a given consumer species is noted  $g$  (diet breadth). The average diet breadth of a consumer in the regional food web is  $\bar{g} = C_R P_T$ , where  $C_R$  is the regional directed connectance,  $C_R = L_R / P_T P_C$ . As the distribution of diet breadth is usually skewed (many specialists, few generalists, Dunne *et al.* 2002b), we need to take into account species-specific diet breadth. Let  $p_g$  be the occupancy of a consumer species having a diet of  $g$  prey species, we define  $q_g$  as the probability that a species with diet breadth  $g$  has one or more of its prey species present in the local community when it colonises it, and  $\epsilon_g$  the rate at which a species with diet breadth  $g$  loses its last prey species (these variables are derived in the online supporting information). The TIB can thus be modified, yielding the following occupancy dynamics:

$$\frac{dp_g}{dt} = c(1 - p_g)q_g - (e + \epsilon_g)p_g \quad (2)$$

The immigration rate  $c(1 - p_g)q_g$  increases with the probability of finding a prey in the local community ( $q_g$ ), while the extinction rate  $(e + \epsilon_g)p_g$  increases with the probability of finding no prey. Equation 2 yields the following steady-state occurrence probability:

$$p_g = \frac{cq_g}{cq_g + e + \epsilon_g} \quad (3)$$

The expected local species richness  $S_L$  at equilibrium is then obtained by averaging the equilibrium occupancies  $p_g^*$  over all diet breadths found in the regional species pool ( $S_L = \sum_{g=1}^g P_g p_g^*$ ).

We now need to express the quantities  $q_g$  and  $\epsilon_g$  to derive the solution for the equilibrium occupancies  $p_g^*$  (the detailed derivations are provided in the online supporting information, here we just provide an overview of the approach). Let the random variable  $X_i$  indicate occurrence for species  $i$ , with  $X_i = 0$  when species  $i$  is absent from the local food web and  $X_i = 1$  when it is present. We note the expected occurrence probability  $p_i = E[X_i]$ . The indicator variable  $Y_i$  equals 1 when at least one prey of species  $i$  is present.  $Y_i$  may be expressed in terms of variables  $X_j$ 's:

$$Y_i = 1 - \prod_{j \in G_i} (1 - X_j) \quad (4)$$

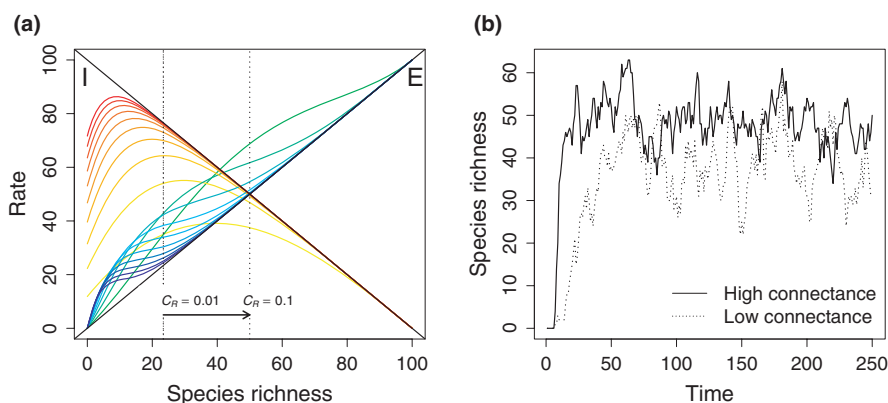
where  $G_i$  is the set of prey for species  $i$  (so that its cardinal  $|G_i|$  denotes the number of prey for species  $i$ , i.e. its diet breadth  $g$ ). Based on eqn 4 and assuming that the occurrence of a species is not affected by the occurrence of its predators and by the occurrence of species sharing its predators (similar results are obtained when relaxing this assumption), we can express  $q_i$  as the expectation of  $Y_i$  when species  $i$  is absent:

$$q_i = 1 - E \left[ \prod_{j \in G_i} (1 - X_j) \middle| X_i = 0 \right] \quad (5)$$

$$q_i = 1 - \prod_{j \in G_i} (1 - p_j) = 1 - e^{\beta |G_i| \langle \log(1 - p_g) \rangle_P}$$

where  $\beta = \langle \log(1 - p_g) \rangle_P$  is the average value of the log-probability of absence, obtained from the regional food web.

We note  $e_i = e + \epsilon_i$  to include the trophic constraint on the extinction rate for consumer species  $i$  resulting from intrinsic



**Figure 1** The trophic theory of island biogeography. (a) Adding a trophic constraint on species immigration and extinction affects the equilibrium species richness in a local community (note all consumer have the same diet breadth for the illustration). The classic TIB is depicted with the black lines. Species richness in a local community is found when the immigration rate equals the extinction rate (when the respective I and E curves cross, depicted by the vertical dotted lines). The coloured lines for the trophic TIB are obtained following the analytical approximation in the online supporting information. The connectance in the regional species pool is varied between 0.01 (yellow and green for the immigration and extinction curves, respectively) and 0.1 (red and blue curves, respectively). At connectance larger than 0.1, the trophic TIB no longer differs from the classic TIB for these immigration and extinction rates (see Fig. 2a). The parameter  $\alpha$  (ratio of intrinsic immigration to extinction rates) is set at 1 for the illustration. (b) Stochastic simulations (see online supporting information) show the assembly dynamics for local communities with low and high regional connectance ( $C_R = 0.05$  and  $C_R = 0.3$ , respectively). All consumer species have the same diet breadth  $g$  on both and the regional species pool consists of 10 primary producer species and 100 consumer species (both panels).

extinction ( $e$ ) and the extinction of its last prey species ( $\varepsilon_i$ ). The expression for  $\varepsilon_i$  is given by:

$$\varepsilon_i = E \left[ \sum_{j \in G_i} e_j X_j \prod_{\substack{k \in G_i \\ k \neq j}} (1 - X_k) \middle| X_i = 1 \right] \quad (6)$$

$$\varepsilon_i \approx \sum_{j \in G_i} e_j E[X_j] \prod_{\substack{k \in G_i \\ k \neq j}} (1 - E[X_k])$$

Solving for  $e_i$  yields:

$$e_i = e + \sum_{j \in G_i} e_j p_j \prod_{\substack{k \in G_i \\ k \neq j}} (1 - p_k) \quad (7)$$

$$e_i \approx e + \left( |G_i| \left\langle e_g \frac{p_g}{1 - p_g} \right\rangle_p e^{|G_i| \langle \log(1 - p_g) \rangle_p} \right)$$

Using eqns 3 and 6, taking expectations over the whole food web and replacing species indices by diet breadths, we obtain the following expression which links the probability  $p_g^*$  that a species with diet breadth  $g$  occurs in a local community (using  $\alpha = c/e$ ):

$$p_g^* = \frac{\alpha(1 - e^{\beta g})}{1 + \alpha(1 - e^{\beta g})(1 + g e^{\beta g})} \quad (8)$$

Equation 7 cannot be solved in closed form, but a numerical solution can be found easily given  $\alpha$  and the distribution of  $g$  in the regional food web. The species richness for a diet breadth  $g$  is then simply  $S_g = \sum_{i=1}^S p_i$  (where  $S_g$  is the number of species with diet breadth  $g$  in the regional species pool). Note that this analytical derivation is a mean-field approach that does not consider food web topology. Previous metapopulation studies established that persistence and occupancy of a consumer is influenced by its trophic position (Holt 1997; Holt *et al.* 1999; Calcagno *et al.* 2011; Gravel *et al.* 2011). We thus performed stochastic simulations to better assess how topology influences predictions on occupancy (see Simulation Model).

Following this model, we found that trophic interactions fundamentally alter the way species richness varies with immigration and extinction rates. Under the classic TIB, the equilibrium species richness occurs when immigration and extinction rates are equal (in Fig. 1a: when the immigration and the extinction curves cross). We found that the immigration rate is lower for the trophic TIB than for the classic TIB, but increases with regional connectance (Fig. 1a) because immigrating consumers struggle to find a prey. Conversely, the extinction rate is increased at low connectance relative to the classic TIB because of secondary extinctions occurring when specialised consumers lose their last prey. The trophic TIB thus predicts that decreasing regional connectance reduces equilibrium species richness (Fig. 1a). Stochastic simulations illustrate the effect of trophic structure on immigration-extinction dynamics (see Supporting Information Data S1): a low regional connectance slows the assembly dynamics as primary producers, generalists and then specialists arrive sequentially (Piechnik *et al.* 2008; Fig. 1b) and also increases the temporal variability of assembly dynamics (Dunne *et al.* 2002a; Fig. 1b).

Regional food web structure has considerable effects on the resulting species–area relationship (Fig. 2a). The trophic TIB predicts that at a given area (proportional to  $\alpha$ ), local species richness increases with connectance of the regional food web because the average diet breadth increases with connectance, and thus fewer species are

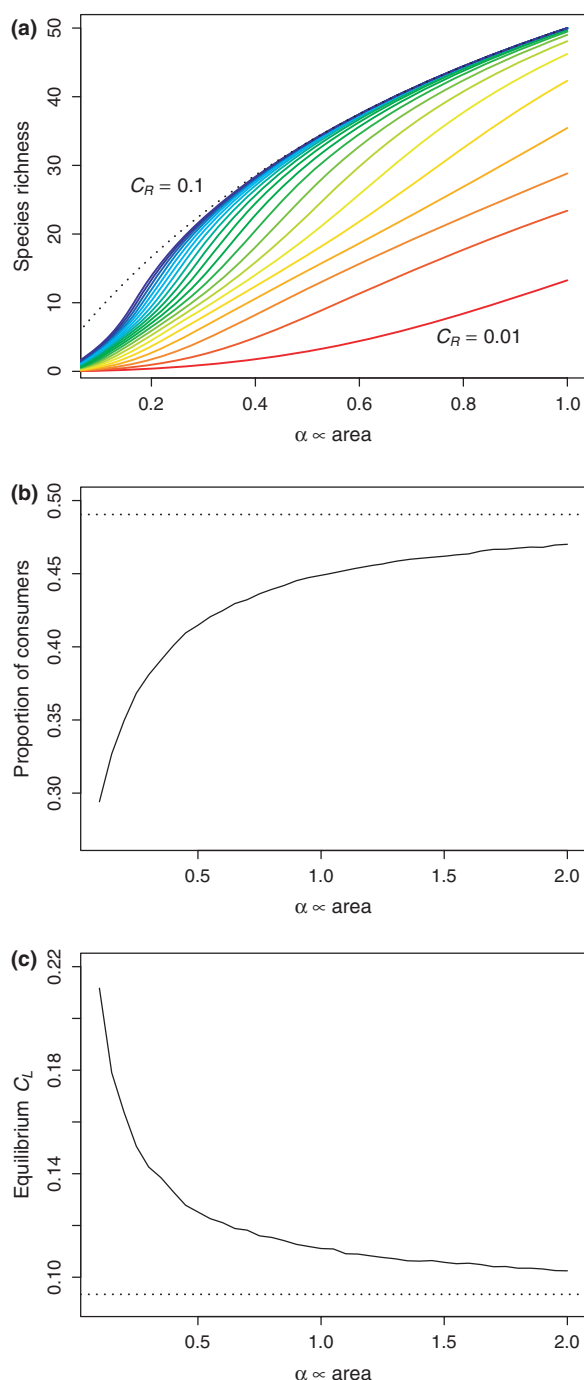
constrained to find a prey in the local community. It also predicts that the proportion of consumers increases with  $\alpha$  (Fig. 2b) because it is easier for them to find at least one prey in larger local communities with higher species richness. The species–area relationship displays a sigmoid shape (Fig. 2a) with a first phase dominated by primary producers (Fig. 2b), followed by a build-up of the consumer species richness. Immigration-extinction dynamics favour greater occupancy of generalists in small areas, so local directed connectance ( $C_L = L_L/S_L S_C$ , where  $S_C$  is local consumer species richness) is predicted to decline with area (Fig. 2c). As community complexity depends on both species richness (Fig. 2a) and connectance (Fig. 2c), our model provides a process-based prediction for the complexity–area relationship that has been derived from the combination of link–species and species–area scaling relationships and observed for various systems (Brose *et al.* 2004).

## TESTING THE THEORY

We investigated how the trophic TIB performs compared with the classic TIB to predict local community structure and composition using two published datasets of insular food webs. We collected local and regional food web data for pelagic organisms of 50 lakes of the Adirondacks (Havens 1992) and for the arthropod community from a classic defaunation experiment performed in the Florida Keys (Simberloff & Wilson 1969; Piechnik *et al.* 2008). The lake dataset has a lower regional connectance (0.09) than the island dataset (0.21). The trophic TIB thus predicts that the former will be more constrained by trophic interactions (Figs 1a and 2a). Starting with coarse analyses at the community-level scale and then moving to the species-level, we tested the following predictions derived from the trophic TIB: (1) link density and connectance in local food webs is higher than the expectation from the classic TIB, (2) connectance in local food webs increases with the extinction rate, (3) occupancy increases with species diet breadth.

The complete methodology for the sampling of the 50 lakes can be found in Sutherland (1989). The lakes were sampled once during the summer 1984. The potential predator–prey interactions among the 210 species of the regional food web were determined by Havens (1992) from the literature, precluding the potential effect of regional abundance (Krishna *et al.* 2008) and sampling effort on network structure (Martinez 1991). A feeding link between two species found in the regional food web was automatically assumed to occur when both species were present in a given lake. Each of the 50 lakes comprised 13–75 species, with 17–577 feeding links (Table 1). There are 2020 feeding links in this regional food web.

The methodology for the sampling of the island data is described in Simberloff & Wilson (1969) and Piechnik *et al.* (2008). Six islands from the Florida keys, 11–25 meters in diameter, were defaunated with insecticide. The arthropods were first censused before the experiment and then on a regular basis approximately once every 3 weeks during the first year and again 2 years after defaunation. We restricted our analysis to the first census because it is the only one that is definitely at equilibrium. Piechnik *et al.* (2008) determined the trophic interactions among 250 arthropod taxa of the dataset using scientific literature and expert opinions. The regional food web is thus independent of local food webs, similar to the lake data. Each island comprised between 15 and 38 species, with 32–331 feeding links (Table 1). There are 13 068 feeding links in this regional food web.



**Figure 2** Predicted effect of island area on the equilibrium food web structure on islands. (a) Effect of the regional food web complexity on the species–area relationship where  $\alpha$  is the immigration-to-extinction ratio, which should increase monotonically with area. The regional connectance varies between 0.01 (red) and 0.1 (blue). The regional species pool contains 10 primary producers and 100 consumer species. All consumer species have the same diet breadth  $g$ . The black line corresponds to the classic TIB. (b) Heterogeneity in the distribution of consumers' diet breadth is introduced into the analytical model to show the predicted relationship between  $\alpha$  and the proportion of consumers in local food webs. The regional food web is taken from Havens (1992) (see Testing the Theory) and has 107 primary producers, 103 consumer species and 2010 links. (c) Predicted local connectance–area relationship assessed from stochastic simulations with Havens' regional food web. The local connectance ( $C_L$ ) asymptotes with the regional connectance (dotted line) in large communities. The dotted black line represents the prediction of the classic TIB.

The high number of sites for the lake data also allowed us to test if the connectance scales with lake size (volume). We controlled for lake pH because this variable is known to have a strong effect on the community structure in these lakes (Brose *et al.* 2004). Moreover, because the pH reduces population size, we hypothesise that this environmental variable could also control the extinction risk and thus community structure. We tested the relationship between connectance, pH and lake volume (also considering the interaction pH  $\times$  lake volume) with a linear model.

### Maximum likelihood comparison

We investigated through likelihood-based goodness-of-fit measures over the whole dataset the ability of the trophic TIB to predict species-specific occupancies and compared it with the null expectation of the classic TIB. The log-likelihood for the observation of a species' presence in a lake is simply the log of its predicted occupancy  $p_i$  and  $\log(1 - p_i)$  for its absence. Under the trophic TIB, the predicted occupancy of a species with diet breadth  $g$  is computed following the analytical approximation given in the online supporting information, while it is simply local species richness divided by the size of the regional species pool under the TIB. We also considered the predicted occupancies of stochastic simulations of the trophic TIB because the analytical solution did not explicitly consider the food web topology but only the distribution of diet breadths. We estimated the parameter  $\alpha$  for all 50 lakes and six islands for the three models (TIB, trophic TIB analytical approximation and stochastically simulated) by maximum likelihood. Note that for both the analytical prediction and the simulations, the likelihood function has a single peak.

### Simulation model

The analytical derivation of the occupancy assumes a random food web structure and does not consider the network topology. Previous metapopulation studies have established that persistence and occupancy of a consumer are influenced by its trophic position (Holt 1997; Holt *et al.* 1999; Calcagno *et al.* 2011; Gravel *et al.* 2011). Basically, for a predator to occupy a patch, it needs the herbivore it feeds on to be present, which also needs a primary producer to feed on, etc. This constraint has dramatic consequences for the occupancy of the highest trophic levels. We wondered if the assumption of a random food web structure could alter the predicted community composition in local communities and consequently compared the analytical derivation with results of a simulation model taking explicitly into account the topology of the regional food web. We simulated the dynamics of occupancy in local communities with a stochastic model. The regional food web we considered is based on the compilation of the regional food webs for both the lake and the island datasets. The model approximates the continuous dynamics described by equation by discretising it into small time steps ( $\Delta t$ ). At each time step, the probability that a consumer species absent from the local community colonises it is 0 if it has no prey already present (among the potential ones in the regional food web) and  $c\Delta t$  if there is at least one prey present. The probability that a primary producer colonises the local community is  $c\Delta t$ , irrespective of community composition. The probability that a consumer species present in the local community goes extinct is  $e\Delta t$  if it has at least one prey present and 1 if its last prey went extinct at the previous time step. The probability that a primary producer present goes extinct is  $e\Delta t$ , independent of



**Table 1** Comparison of food web properties between the regional food web and the observed food webs. Expectations from the classic TIB are based on random sampling of the regional pool for  $S_L$  species, yielding a constant fraction of non-trophically constrained species and connectance. Expectations of from the trophic TIB are based on simulations of the insular dynamics for each local community using the parameters estimated by maximum likelihood (see Table 2). Correlations are provided to indicate the goodness of fit of the parameter estimation for the trophic TIB

Statistics	Dataset	Regional food web	Observed food webs	Expectation from classic TIB	Expectation from trophic TIB	(r pred. vs. obs.)
			mean $\pm$ SD	mean $\pm$ SD	mean $\pm$ SD	
Species richness	Lakes	210	38.8 $\pm$ 14.8	38.8 $\pm$ 14.8	50.9 $\pm$ 18.2	(0.62)
	Islands	250	26.8 $\pm$ 7.4	26.8 $\pm$ 7.4	28.1 $\pm$ 11.3	(0.99)
Fraction of non-trophically constrained species*	Lakes	0.51	0.49 $\pm$ 0.10	0.51 $\pm$ 0	0.61 $\pm$ 0.03	(0.56)
	Islands	0.48	0.49 $\pm$ 0.07	0.48 $\pm$ 0	0.49 $\pm$ 0.005	(0.99)
Number of links $L$	Lakes	2020	168.5 $\pm$ 130.9	78.5 $\pm$ 58.3	152.4 $\pm$ 97.9	(0.64)
	Islands	13 068	192.0 $\pm$ 109.4	161.4 $\pm$ 90.8	199.8 $\pm$ 150.3	(0.96)
Connectance $C$	Lakes	0.09	0.2 $\pm$ 0.03	0.05 $\pm$ 0	0.14 $\pm$ 0.02	(0.33)
	Islands	0.21	0.25 $\pm$ 0.03	0.21 $\pm$ 0	0.23 $\pm$ 0.01	(-0.48)
Fraction of isolated consumer species†	Lakes	0	0 $\pm$ 0	0.36 $\pm$ 0.11	0 $\pm$ 0	(1)
	Islands	0	0.07 $\pm$ 0.05	0.20 $\pm$ 0.00	0 $\pm$ 0	(0)

\*Primary producers are not constrained to find their food in the lake dataset, while the herbivores feeding on mangrove trees and detritivores are not constrained in the islands dataset.

†For each of the lakes and islands of  $S_L$  species richness, we calculated the null expectation with 10 000 artificial communities of  $S_L$  randomly drawn species from the regional species pool.

community composition. We calculated the expected occupancy for each of the 210 species of lake data and of the 250 species of the island data for a wide range of values (at interval of 0.0001). We fixed  $c\Delta t$  at 0.1 and varied  $e\Delta t$  with the parameter  $\alpha$  following the relation  $e = c/\alpha$ . For each value, we started with a bare local community and ran the model 1000 time steps to reach equilibrium and then ran the model for another 250 000 time steps to record the average occupancy (number of time steps present/total number of time steps). We obtained a large table with the expected occupancy for all species from the regional pool in rows and the different  $\alpha$  values in columns. We used this table to estimate the parameter  $\alpha$  for each of the 50 lakes and the six islands by maximum likelihood.

## RESULTS

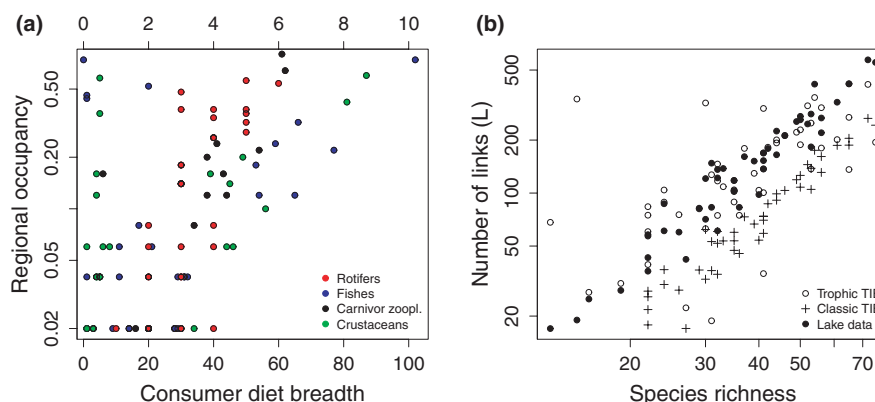
The classic TIB is a null model where local webs are random samples from the regional food web and thus predicts no association between diet breadth and island area. The trophic TIB instead predicts that, in small islands, species with larger diet breadth are more likely to occur than more specialised consumers. We found a much higher number of links per local food web for both the lakes and the islands, and a higher connectance than under the hypothesis of random sampling (Table 1). These results suggest a selection process in favour of consumers with larger diet breadths. Previous work has shown that the number of feeding links in the lake dataset scales with lake volume (Brose *et al.* 2004). We also found for this dataset (the island dataset does not have enough sites to test this hypothesis), with a multiple regression linear model, that once accounting for the interaction with pH, the number of trophic links significantly increases with lake volume and connectance significantly decreases with lake volume (Table 2), as predicted by our trophic TIB.

Connectance is a global descriptor of food web properties averaging the distribution of species' diet breadth (Dunne *et al.* 2002b). The fundamental prediction of the trophic TIB is, however, a species-specific relationship between diet breadth and occupancy. The positive relationship between diet breadth and regional occupancy is illustrated in Fig. 3a for the lake dataset. We thus investigated the

effect of trophic constraints on insular dynamics by comparing the ability of the classic and trophic TIB to predict species-specific occupancies. Our model is a likelihood function for occurrence probability that we used to estimate the parameter  $\alpha$  for each lake and island from the empirical diet breadth and occurrence data (details in the Supporting Information Data S1). This parameter was estimated for the classic and trophic TIB models and we compared their goodness-of-fit through maximum likelihood. We found a significantly larger log-likelihood for the trophic TIB in comparison to the classic TIB for the lakes and a similar one for the islands (Table 3; see also correlations between observed and predicted food web statistics in Table 1 for an assessment of the goodness-of-fit). The trophic TIB well predicts the link–species relationship, while the classic TIB underpredicts the number of trophic links (Fig. 3b). We also expected a better fit from the trophic TIB to the lake dataset than to the island dataset because of their differences in regional connectance and maximum food chain length (the island dataset contains fewer trophic levels among more connected species). The trophic TIB predicts that the effect of trophic constraints on occupancy should decrease with regional connectance to a point where occupancy is similar to the classic TIB (Fig. 1a). The occupancy for given immigration and extinction rates is predicted to reach an asymptote at  $c$  10–30 prey species, depending on the parameter  $\alpha$ , because at larger diet breadth consumers are no longer constrained to find their prey. The fraction of consumers having fewer than 10 prey species is indeed much higher in the lake dataset than for the islands (40% versus 8% respectively). This comparison between datasets suggests that the classic TIB could

**Table 2** Summary results for linear models between food web properties (species richness, link density and connectance) and lake characteristics (pH and volume)

Variable	Estimate ( $P$ -value)			$R^2$
	pH	log volume	pH $\times$ log volume	
Species richness	1.29 (<0.001)	-10.59 (0.793)	1.98 (0.068)	0.61
Link density	-83.15 (<0.001)	-158.86 (0.138)	31.43 (0.002)	0.59
Connectance	-0.06 (0.006)	-0.04 (0.590)	0.008 (0.003)	0.29



**Figure 3** Empirical investigation of the theory. (a) The relationship between diet breadth and regional occupancy across the 50 Adirondack lakes. Note the diet breadth for rotifers is given by the top axis. The linear regression between the occurrence probability, the log of the number of trophic links ( $g$ ) per consumer and the trophic rank (TR) is highly significant ( $P < 0.001$ ) for all four groups, but not significant when all species are considered together. The  $R^2$  for the carnivorous zooplankton is 0.52 ( $g$ ) and 0.59 ( $g + \text{TR}$ ); for rotifers is 0.56 ( $g$ ) and 0.77 ( $g + \text{TR}$ ); for fishes is 0.15 ( $g$ ) and 0.18 ( $g + \text{TR}$ ) and for crustacean zooplankton is 0.19 ( $g$ ) and 0.75 ( $g + \text{TR}$ ). (b) Scaling relationship between species richness and the number of trophic links for the lake dataset and predictions from the classic TIB and the trophic TIB (based on maximum likelihood parameter estimation).

**Table 3** Log-likelihood comparison for the different models and datasets

Dataset	Classic TIB	Trophic TIB (analytical)	Trophic TIB (simulations)
Adirondack lakes	-2428.2	-2416.8	-2392.4
Florida islands	-259.3	-259.9	-260.0

be a sufficient approximation to insular dynamics for less trophically constrained systems.

We also considered a simulation model because our analytical derivation of occupancy does not explicitly consider network topology. We found a significantly larger log-likelihood for the simulations with the trophic TIB for the lake dataset (Table 3), telling us that knowledge of food web topological details, such as trophic rank and food chain length, improves predictions on species-specific occupancy.

## CONCLUSION

MacArthur and Wilson were among the first to envision that species richness could be the result of processes occurring at a large scale, independent of the details of local ecological interactions. With no impinging on model parsimony, our model improves MacArthur and Wilson's TIB in two ways: (1) with the inclusion at a macroscopic level of the basics of ecological interactions through information on food web structure, (2) by providing richer predictions (species-specific occupancies and descriptors of community structure that can be derived from diet breadth-based occupancies). Remarkably, our model remains as simple to parameterise as the classic TIB, but it greatly improves its estimation. Our results suggest that trophic constraints contribute to the diversity of islands, nonetheless we might underestimate their importance to insular dynamics: indeed, we have considered neither the need for multiple preys, e.g. because of seasonality or to maintain nutrient homeostasis, nor top-down control of prey extinction rates by their predators (Ryberg & Chase 2007; Holt 2009; Calcagno *et al.* 2011; Gravel *et al.* 2011). Other concurrent processes related to generalist/specialist distinctions, such as increased colonisation rates, behavioural plasticity or the ability to feed on

allochthonous inputs (Polis & Hurd 1995; Massol *et al.* 2011), should also be considered further.

Ecologists need better models to understand the interplay of the environment and species interactions in the shaping of species distributions at macro-ecological scales (Araujo & Luoto 2007; Gotelli *et al.* 2010). An important challenge is to predict which species might become extinct and the functional consequences of their loss. A major issue remains the prediction of future species geographic distributions from which we may infer extinction rates (Thomas *et al.* 2004), changes in biodiversity patterns (Thuiller *et al.* 2011) and ultimately the loss of ecosystem services (Mooney *et al.* 2009). Such predictions classically rely on spatial modelling methods that only use environmental variables to predict species occupancy but that rarely include population dynamics (Keith *et al.* 2008) or species interactions (Araujo & Luoto 2007). However, there is growing evidence that the next generation of coarse-grained macro-ecological models will need to account for biological interactions and trophic relationships among species to reach accurate predictions of species distributions and biodiversity patterns (Schweiger *et al.* 2008; Gotelli *et al.* 2010; Lavergne *et al.* 2010). The ongoing challenge is thus to include information about species interactions while keeping the parsimony of macro-ecological models used to predict species occupancy on large scales, i.e. without complexifying the biogeographical background beyond our analysing and parameterisation abilities. Our trophic TIB provides such a simple theoretical framework to include interactions into species distribution models. Our model has focused on food webs, but it could be easily extended to apply to other interaction networks, e.g. plant-pollinator or plant-disperser networks. The integration of species interactions into distribution models, as exemplified in the present work, should improve our ability to predict the consequences of global change for communities with complex structures.

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## AUTHOR CONTRIBUTIONS

D.G., F.M., E.C., D.M. and N.M. designed research; D.G., F.M., E.C. conducted research and contributed to the model, analytical tools; D.G., F.M. and N.M. wrote the paper; D.G., F.M., E.C., D.M. and N.M. edited the paper.

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### Appendix S1 Trophic theory of island biogeography.

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