



# Knowledge of predator–prey interactions improves predictions of immigration and extinction in island biogeography

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## ABSTRACT

**Aim** MacArthur and Wilson's original formulation of the theory of island biogeography (TIB) included the corollary hypothesis that species richness might affect immigration and extinction rates. Building on this, other researchers have suggested additional top-down and bottom-up effects. We compare these hypotheses to identify the strongest candidates for inclusion in a 'trophic TIB'.

**Location** Six mangrove islands in the Florida Keys, USA

**Methods** We studied a classic island biogeography time series featuring lists of species observed on six mangrove islands during roughly 16 censuses each across 700 days. We first used this time series to determine the number of opportunities for species to immigrate to an island for the first time ( $n = 18,420$ ), to go locally extinct ( $n = 1943$ ) or to re-immigrate to an island after having previously gone extinct ( $n = 1813$ ). We then leveraged information on the predators and prey of those species to estimate the potential for top-down and bottom-up interactions during each census period. Finally, we constructed statistical models to test for species richness, top-down, and bottom-up effects on per-species immigration and extinction probabilities and validated them by comparing each model with a similar model based on the classic TIB.

**Results** We found that models including bottom-up effects gave the greatest improvement over the classic TIB models. Extinction probability in particular decreased sharply for species with both basal resources and animal prey available. Species richness and top-down effects had far weaker impacts on per-species probabilities of immigration and extinction.

**Main conclusions** Our findings suggest that incorporating information on the trophic structure of island communities – particularly the species-specific availability of resources – can substantially alter predictions of extinction probabilities. Immigration probability, on the contrary, appeared largely stochastic. Incorporating trophic information into predictions of extinction rates therefore represents the most promising and best-supported way to extend the TIB.

## Keywords

**Bottom-up effects, community assembly, food web, predator–prey interactions, species richness, theory of island biogeography, top-down effects.**

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## INTRODUCTION

The theory of island biogeography (TIB) combines elegant simplicity of formulation (Hubbell, 2010) with the ability to reliably

predict properties such as equilibrium species richness across both islands and a range of island-like habitat patches (Simberloff & Abele, 1982; Eadie *et al.*, 1986). As such, it has become one of the cornerstones of ecological theory

(MacArthur & Wilson, 1963; Hanski, 2010; Holt, 2010; Harte, 2011). In essence, the TIB supposes that immigration rates should be higher on islands that are closer to a source of immigrants and that extinction rates should be higher as islands get smaller (MacArthur & Wilson, 1963; Schoener, 2010). These two predictions were tested empirically immediately after the publication of the TIB and have generally matched observations well (Diamond, 1969; Case, 1975; Gilpin & Diamond, 1976), although some authors note important differences in immigration and extinction rates across species (Gilpin & Diamond, 1976; Whittaker *et al.*, 2000; Piechnik *et al.*, 2008).

The original TIB partially anticipated these differences by predicting variation in immigration and extinction rates as species richness changes on an island. Specifically, the authors of the TIB predicted that, as species richness on an island increases, immigration rates should decrease while extinction rates increase (MacArthur & Wilson, 1963). An effect of species richness on immigration is expected because species vary in their dispersal abilities (Simberloff & Wilson, 1969), which could bias island faunas towards the best dispersers. Once these species are already present, the pool of remaining colonists will therefore tend to contain poorer and poorer dispersers, decreasing immigration rates (Schoener, 2010). At the same time, a species-rich island may include more extinction-prone species (e.g. species with low population sizes or specialized diets) and will therefore tend to lose more species than one which is species poor (Schoener, 2010). Increasing species richness could also directly cause increasing extinction rates if increasing species richness leads to stronger inter-specific competition (Gilpin & Diamond, 1976). However, the effect of competition on island faunas is very difficult to observe experimentally (Simberloff, 1978).

Apart from competition, the presence of other species on an island could affect immigration and extinction rates through top-down and/or bottom-up effects (Knops *et al.*, 1999; Piechnik *et al.*, 2008; Holt, 2010; Gravel *et al.*, 2011). Top-down effects of predators on their prey may increase extinction rates either directly (Savidge, 1987; Hanna & Cardillo, 2014), by causing trophic cascades (Spiller & Schoener, 1994, 2007; Ryberg & Chase, 2007) or by reducing population sizes such that stochastic extinctions are more common (Ryberg *et al.*, 2012). Alternatively, the presence of predators can mediate competition between species and decrease the probability that any of them will go extinct (Caswell, 1978; Bull & Bonsall, 2010). It is intuitively less likely that there will be top-down effects on immigration rates, as this would seem to require species to adaptively immigrate depending on conditions on islands they have not yet reached. However, given the fact that any new immigrant must persist on an island for some time before being recorded, it becomes easy to envisage effects of predators on observed immigration rates following the mechanisms described above. In such a situation, the presence of predators could either reduce observed immigration rates as new arrivals are consumed before being recorded or, alternatively, it could reduce competition and thereby increase the survival of new immigrants.

Bottom-up effects of resource availability on the TIB have also been postulated. Species with no resources available should quickly go extinct while species with abundant or varied prey may be more likely to persist (Holt *et al.*, 1999; Holt, 2002, 2010; Piechnik *et al.*, 2008). It is also possible that the presence of basal resources (e.g. plants, detritus or bacteria) can affect immigration rates. In order for an island to support resident animal life it must already have some basal resource present, while the converse is not necessarily true (Holt *et al.*, 1999; Holt, 2002, 2010). Basal resources should therefore be present on all islands that support animals as well as some that do not. This might result in a greater inclination of herbivores to immigrate to new islands since doing so entails less risk of starvation. Indeed, while most islands support herbivores, species at higher trophic levels are much rarer (Terborgh, 2010). This suggests that species which cannot consume basal resources may be less likely to immigrate or establish viable populations, perhaps because islands often support fewer prey species (and smaller prey populations) than mainland habitats (Terborgh, 2010).

Finally, top-down and bottom-up effects are known to interact in structuring communities, with the strengths and directions of each type of effect varying over time and across species (Power, 1992; Gratton *et al.*, 2002; Gratton & Denno, 2003; Gripenberg & Roslin, 2007). This wide variety of potential effects of interactions between species has prompted the development of 'trophic TIB' models that incorporate community structure into island biogeography theory (Holt *et al.*, 1999; Holt, 2002; Ryberg & Chase, 2007; Gravel *et al.*, 2011). Although these models often preserve the TIB's spirit of simplicity and clarity, it is not clear whether they significantly improve on the classic version when confronted with empirical data. Further, most of these models tend to be structured in a way that complicates rigorous comparisons between them.

Rather than investigate a single mathematical model in great depth, here we use empirical data to compare and contrast multiple potential effects of community structure on island biogeography. We are especially interested in measuring the potential effects of predator-prey interactions and examining how they differ when considering immigration and extinction. To this end, we construct a statistical framework with which to test the following non-exclusive hypotheses: (1) immigration probability will decrease with increasing species richness while extinction probability will increase; (2) immigration probability will decrease with the presence of predators while extinction probability will increase; (3) immigration probability will be higher for species that can consume basal resources and extinction probability will decrease; and (4) there will be no effect of the presence of animal prey on immigration probability but extinction probability will decrease for species with prey available. By comparing similarly structured models built around each hypothesis, our approach allows us to isolate models with little support and to demonstrate which hypotheses explain similar variation in empirical data. Together, we argue that these two endeavours reveal the strongest candidates for future efforts to extend the TIB.

## METHODS

### Dataset

We studied a classic island biogeography time series for arthropod immigration and extinction on six mangrove islands (Simberloff & Wilson, 1969) of known diameter (11–25 m) and distance from the mainland (2–533 m). In these experiments, each island was artificially defaunated and then censused 16–18 times during the following 2 years for a total of 96 post-defaunation censuses. Over the course of the experiment, five basal resources (mangrove trees, fungus, lichens, detritus, algae) and 231 arthropod species were observed, with most resolved to the species level.

Using this dataset, we were able to directly estimate when the different species immigrated to islands after defaunation. Specifically, for a given island during a given census  $k$ , we considered all species that were not observed to be potential immigrants. Note that we did not consider species that were present before defaunation but never returned during the experiment as part of this mainland species pool. All potential immigrants were counted as successful if they were observed during the next census ( $k + 1$ ) or as failed otherwise. As it is possible that different mechanisms affect species that are frequent immigrants than those that more rarely leave the mainland, we considered initial immigration (i.e. for a given species  $s$  and island  $i$ , all censuses up to and including the first successful immigration to island  $i$  by species  $s$ ) and repeat immigration (i.e. all immigration opportunities after species  $s$  had previously gone extinct from island  $i$ ) separately. Note that this distinction allowed us to examine factors affecting species which immigrate relatively frequently without defining this set of species a priori.

We estimated extinctions on each island in the dataset using a similar procedure. For a given island  $i$  during a given census  $k$ , any species present could potentially go locally extinct and those not observed during the following census ( $k + 1$ ) were considered to have done so. Species observed again in census  $k + 1$  were considered to have persisted. Table 1 shows the numbers of

potential and observed immigrations and extinctions across the complete time series.

In order to relate these species-occupancy lists to the potential interactions between species on a given island at a given time, we combined them with a published list of potential prey for each species based on interactions observed or inferred on the mainland (see Piechnik *et al.*, 2008, for details on the construction of this list). Potential prey were restricted to other arthropods (hereafter ‘animal prey’) which had been observed on at least one of the islands during the time series, plus the basal resources that were assumed to be present on all islands throughout the experiment (Piechnik *et al.*, 2008). As basal resources were assumed to be omnipresent throughout the experiment (Piechnik *et al.*, 2008), the ability of a species to consume basal resources (or not) was recorded as one measure of resource availability. The presence of animal prey, on the contrary, varied between censuses. To determine the potential for bottom-up interactions involving animal prey, we compared the list of potential prey for the focal species with the occupancy list for that island and census. If any of a species’ mainland prey items were present, that species was assumed to be able to prey on the same species on the island. Similarly, if the focal species featured in the prey lists of any other species on the island at the same time, there was potential for top-down interactions (i.e. predation on the focal species) to occur. Determining the potential for top-down and bottom-up effects on each species on each island at each census allowed us to directly examine the effects of predator–prey interactions on initial immigration, repeat immigration and extinction probabilities. Table 1 gives further details of the typical values and ranges of these predictors.

### Statistical models

Based on the aforementioned data, we created parallel sets of candidate models for the probability of a given species immigrating to, re-immigrating to or going extinct from a given island at a given census. For each model, we estimated parameters using the function `glmer` from the `lme4` library (Bates

**Table 1** The number of opportunities for initial immigrations, repeat immigrations and extinctions (i.e. sample size), number of successes and proportion of successes in each case, and minima, maxima and means for model predictors. As each set of models was based on slightly different data, we present the means and ranges for each separately.

Model	Initial immigration			Repeat immigration			Extinction		
Response									
Opportunities	18,420			1,813			1,943		
Successes	476			127			461		
Proportion of successes	0.026			0.070			0.237		
Predictor	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean
Distance	2	533	213	2	533	154	2	533	164
Diameter	11	25	14.9	11	25	15.1	11	25	14.8
Time between censuses	10	400	36.5	10	400	68.9	10	400	41.5
Species richness	2	47	18.8	11	47	32.3	2	47	30.7
Predators	0	1	0.782	0	1	0.933	0	1	0.956
Ability to eat plants	0	1	0.578	0	1	0.536	0	1	0.600
Animal prey available	0	1	0.440	0	1	0.523	0	1	0.514

*et al.*, 2014) in R (R Development Core Team, 2014) with binomial distributions and logit link functions. We then used these models to test our hypotheses relating to the effects of species richness, top-down effects, bottom-up effects and their interactions using a null model and a model based on the TIB for comparison.

#### *Null models*

The simplest models for initial immigration, repeat immigration, and extinction (henceforth referred to as our initial immigration null model, repeat immigration null model and extinction null model, respectively) included an intercept and two random effects (Appendix S1 in Supporting Information). The first random effect was for focal census (that is, the census from which predictor data were drawn, specific to a particular island). It accounted for variation in time between censuses as well as other hidden variables such that the predicted immigration or extinction probability for each census is expected to match that observed empirically.

The second random effect was intended to account for pseudoreplication within the data created by repeated observations of population-level behaviour of the same species across the experiments. For initial immigration, this was a species-by-island random effect as all potential immigrations of a given species to a given island were drawn from the same mainland population. On average, there were 8.2 pseudoreplicates per level of this random effect.

For repeat immigration and extinction, we further distinguished between different 'event windows' to produce a species-by-island-by-window random effect. That is, we considered repeat immigration opportunities for species *s* to island *i* after the species' first extinction on island *i* up to and including the first successful repeat immigration – the first event window – to be independent of opportunities for species *s* to re-immigrate to island *i* after it had gone extinct a second time up to and including the second successful repeat immigration – the second event window. For extinction, we distinguished between opportunities for extinction associated with different event windows for species *s* on island *i* (e.g. potential extinctions after an initial immigration, potential extinctions after the first repeat immigration and so on). These two models included fewer pseudoreplicates per random effect (mean 4.7 and mean 3.6, respectively) than did the initial immigration model.

#### *Theory of island biogeography models*

We next tested initial immigration, repeat immigration and extinction TIB models based on the original formulation of island biogeography. The two immigration TIB models each included terms for distance, diameter and their interaction. The extinction TIB model included only the diameter term as isolation was not hypothesized to affect the extinction of established populations (MacArthur & Wilson, 1963). In addition, each model included a term for the time between the focal census and the next census (i.e. the amount of time a species would have to

immigrate or become extinct) since this interval varied across censuses (Table 1). To account for potential differences in the strength of the time effect on different islands, we also included all interaction terms between diameter, distance (immigration models only) and time between censuses (Table S1 in Appendix S1). As in the null models, random effects of census and source population were also included.

#### *Species-richness models*

We then extended the TIB models to test the hypotheses that initial and repeat immigration probability will decline and that extinction probability will increase with increasing species richness. To do this, we studied statistical models including all terms in the corresponding TIB models, species richness during the focal census and interactions between species richness and all other terms in the TIB models (Table S1 in Appendix S1).

#### *Top-down models*

Next, we tested the hypotheses that top-down effects decrease the probability that a new immigrant survives for long enough to be observed and increase extinction probabilities for species that have already been observed. This was done by adding a term quantifying the presence of any of the focal species' predators during the focal census to the corresponding TIB models. We also included interaction terms between the presence of predators and all terms in the TIB models. In order to ensure that any observed effect of top-down interactions was distinct from the effect of species richness, we further compared each top-down model with a similar top-down and species-richness model which included all terms in the top-down model, as well as terms for species richness and interactions between species richness and all other terms in the top-down model (Table S1 in Appendix S1).

#### *Bottom-up models*

To test the bottom-up hypothesis that the ability to eat basal resources, having access to animal prey, or both, will increase a species' initial or repeat immigration probability, we created a statistical model that combined all of the terms in the corresponding TIB model with new terms that quantify whether or not the focal species consumes basal resources, whether or not any of the focal species' animal prey were available during the focal census, and their interaction. The bottom-up model also included interactions between terms in the TIB model and the terms describing bottom-up effects. As with the top-down model, we ensured that species richness and bottom-up effects were distinct by comparing each bottom-up model with a bottom-up and species richness model including all terms in the bottom-up model, terms for species richness and interactions between species richness and all other terms in the bottom-up model (Table S1 in Appendix S1).

#### *Top-down and bottom-up models*

Finally, we tested the possibility that top-down and bottom-up effects act synergistically. To do this, we examined a top-down

and bottom-up model including all of the terms in the bottom-up model as well as terms for the presence of predators and interactions between the presence of predators and all terms in the bottom-up model. In keeping with the spirit of elegant simplicity of the original TIB, we did not include terms for species richness in this model (Table S1 in Appendix S1). This decision was supported by our finding that the trophic and species richness models described above were all very similar to the trophic-only models (see Appendices S4 & S5).

### Model simplification

For each of the aforementioned statistical models, we started by fitting the most complex models including all interactions. Where a full model was non-convergent (i.e. parameter estimates could not be robustly determined, an indication of overfitting), we removed all interactions of the highest order (e.g. six-way interactions) and attempted to refit the model; we repeated this procedure (i.e. removing five-way interactions, etc.) until we obtained a convergent model from which we could proceed with simplification. We then measured the Akaike information criterion (AIC) of these 'full' models as well as each of the suite of potential simplified models. Simplified models were obtained by systematically removing all possible combinations of terms from the full model. When an interaction term was included in a simplified model, all main effects involved in that interaction term were also retained.

Once the AIC of each model had been calculated, we selected the model with the lowest AIC as the best-fitting model. We performed this simplification automatically using the R (R Development Core Team, 2014) function dredge from package MuMIn (Barton, 2014). We then used the R (R Development Core Team, 2014) function glmer from the package lme4 (Bates *et al.*, 2014) to estimate the standardized effects ( $\beta$ s) for each fixed effect in the best-fitting models as well as their corresponding *P*-values. Note that all standardized effects presented in the results reflect the per-unit (e.g. per 1 m increase in diameter) impact of each predictor on logit-transformed initial immigration, repeat immigration or extinction probability.

### Hypothesis comparison

We also wished to quantify the degree to which different hypotheses give similar predictions across the dataset. If the specific predictions of the species richness and top-down models for extinction agree, for example, this would indicate that the effect of species richness on extinction rates is capturing the same variability in the data as does the effect of predators. To compare the models and hypotheses in this way, we first generated 10,000 simulated datasets for each model using the R (R Development Core Team, 2014) function rbinom and the models' predicted probabilities of immigration or extinction. If, for example, a given model predicted that species *s* on island *i* at census *k* had an immigration probability of 0.005, approximately 50 of the simulated immigration events would be successful. Next, we used the best-fit parameters of the various

models (when fitted to the empirical data) to calculate the likelihood of observing each simulated dataset. We repeated this procedure for each pair of initial immigration, repeat immigration and extinction models, including comparisons of every model with itself, producing 10,000 likelihoods for each pairwise comparison.

To quantify the degree of similarity between the set of likelihoods obtained when data generated using model A were fitted by model A to those obtained when the same data were fitted by a different model B, we calculated the area under the receiver operating characteristic (ROC) curve. The area under the curve (AUC) represents the probability that a randomly chosen likelihood from model A is greater than a randomly chosen likelihood from model B. When models A and B explain exactly the same variation in the data, and therefore fit data generated by A or B equally well, AUC = 0.5; as the ability of model B ability to fit data generated by model A decreases, the AUC increases towards 1. An AUC close to 0.5 therefore indicates that the two models explain very similar variation while an AUC close to 1 indicates that the models account for very different variation.

## RESULTS

### Initial immigration

The best-fit versions of all alternative models for initial immigration had significantly lower AICs than the null model and explained greater variance (Table 2a). The best-fit species richness, top-down, bottom-up, and top-down and bottom-up models all provided significantly better fits to the data than the TIB model ( $\chi^2 = 8.97$ , d.f. = 2,  $P = 0.011$ ;  $\chi^2 = 8.68$ , d.f. = 3,  $P = 0.034$ ;  $\chi^2 = 11.7$ , d.f. = 4,  $P = 0.020$ ; and  $\chi^2 = 16.425$ , d.f. = 5,  $P = 0.006$ , respectively). The top-down and bottom-up model provided the best fit to the data, and significantly improved upon both the top-down and bottom-up models ( $\chi^2 = 7.74$ , d.f. = 2,  $P = 0.021$  and  $\chi^2 = 4.74$ , d.f. = 1,  $P = 0.029$ ).

In the top-down and bottom-up model, and similar to the other models, a species' probability of immigration decreased with increasing distance from the mainland ( $\beta_{\text{distance}} = -56.3$ ) and increased with increasing intervals between censuses ( $\beta_{\text{time}} = 18.1$ ; Fig. 1, Table S7 in Appendix S2). Unlike in the TIB model, a species' probability of immigration decreased with increasing island size ( $\beta_{\text{diameter}} = -0.711$ ), but this effect was overwhelmed by a positive interaction between distance and diameter ( $\beta_{\text{distance:diameter}} = 333$ ). The probability of immigration also increased for species with either predators or animal prey present. Both of these trends were stronger on larger islands ( $\beta_{\text{diameter:predators}} = 1.29$ ,  $\beta_{\text{diameter:animals}} = 1.32$ ).

Despite the statistical improvement of the other alternate models over the TIB, each model described data generated by any of the others well (Figs 2 & S2 in Appendix S5). In addition, each alternative model provided a good fit to data generated by the null model, and vice versa. This means that all models captured similar variation in the empirical data; the extra terms in the alternative models may therefore represent overfitting.

**Table 2** Terms included in the best-fit models for (a) initial immigration, (b) repeat immigration, and (c) extinction when comparing a null model (not shown), a model based on the theory of island biogeography (TIB) and models based on the TIB that also include effects of species richness (SR), top-down interactions (TD), bottom-up interactions (BU), top-down and bottom-up interactions (TD & BU), top-down interactions and species-richness (TD & SR) or bottom-up interactions and species-richness (BU & SR). Each ‘+’ indicates a positive effect, ‘-’ indicates a negative effect, and ‘0’ indicates that the effect was not included in the best-fit model. An empty cell indicates that the term was not part of the model and hence could not appear in the best-fit version. For the full list of terms included in each model, see Appendix S1. Below the individual effects, we give the Akaike information criterion (AIC) and marginal and conditional  $R^2$  values for each model, where marginal  $R^2$  is the amount of variance explained by a model’s fixed effects and conditional  $R^2$  is the amount of variance explained by both fixed and random effects (Nakagawa & Schielzeth, 2013). Sample size for all initial immigration models was 18,420 opportunities for species to immigrate, for all repeat immigration models there were 1813 opportunities for species to re-immigrate following an extinction, and for all extinction models there were 1943 opportunities for species to go extinct.

(a) Initial immigration

Effect	Model						
	TIB	SR	TD	BU	TD & BU	TD & SR	BU & SR
Distance	-	-	-	-	-	-	-
Diameter	+	+	-	-	-	+	+
Time	+	+	+	+	+	+	+
Species richness		+				+	+
Predators			+		+	0	
Animal prey				+	+		+
Distance:diameter	+	+	+	+	+	+	+
Distance:animals				+	0		0
Diameter:species		+				+	+
Diameter:predators			+		+	0	
Diameter:animal				+	+		+
Time:predators			-		-	0	
Distance:diameter:animals				+	0	0	0
AIC	4271	4266	4268	4267	4264	4266	4264
Marginal $R^2$	0.061	0.068	0.070	0.070	0.075	0.068	0.072
Conditional $R^2$	0.213	0.214	0.214	0.228	0.223	0.214	0.222

The best-fit TD & SR model was identical to the SR model.

The marginal  $R^2$  of the null model was 0 and the conditional  $R^2$  of the null model was 0.169.

(b) Repeat immigration

Effect	Model						
	TIB	SR	TD	BU	TD & BU	TD & SR	BU & SR
Diameter	-	-	-	+	+	-	+
Time	-	-	-	-	-	-	-
Basal resources				-	-		-
Diameter:time	-	-	-	-	-	-	-
Diameter:basal				-	-		-
Time:basal				+	+		+
AIC	922	922	922	912	912	922	912
Marginal $R^2$	0.026	0.026	0.026	0.060	0.060	0.026	0.060
Conditional $R^2$	0.141	0.141	0.141	0.222	0.222	0.141	0.222

The best-fit SR, TD and TD & SR models were identical to the TIB model, while the best-fit TD & BU and BU & SR models were identical to the best-fit BU model.

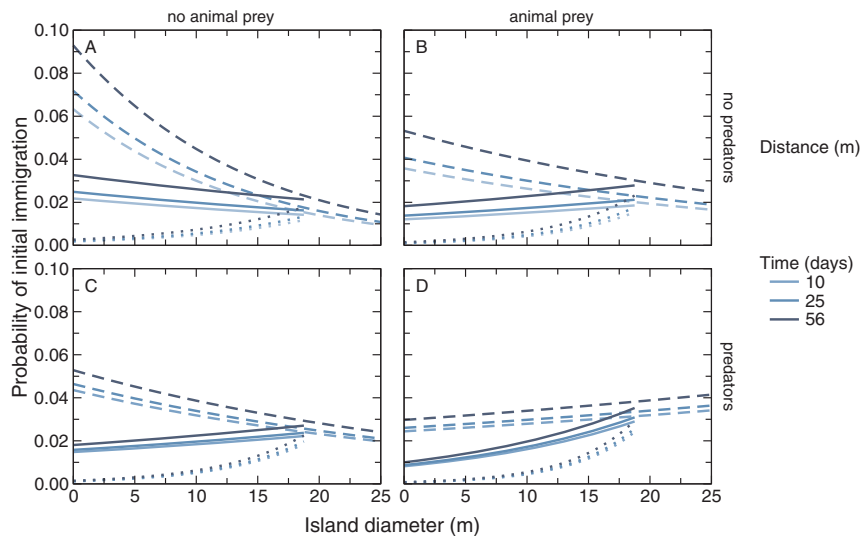
The marginal  $R^2$  of the null model was 0 and the conditional  $R^2$  of the null model was 0.148.

Table 2 Continued.

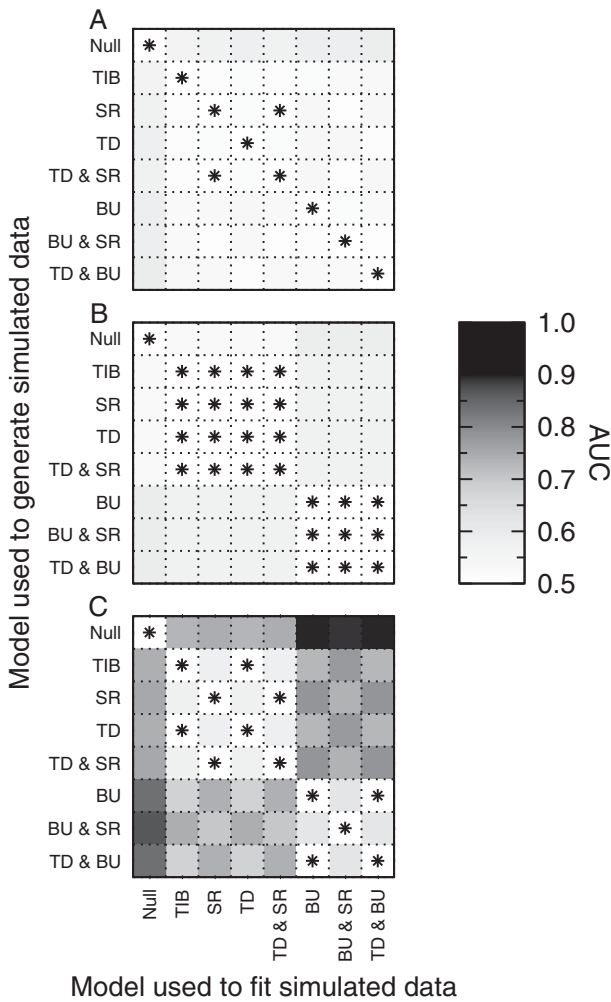
Effect	Model						
	TIB	SR	TD	BU	TD & BU	TD & SR	BU & SR
Diameter	+	-	+	0	0	-	+
Time	+	+	+	+	+	+	+
Species richness		+				+	+
Basal resources				-	-		-
Animal prey				+	+		-
Diameter:time	+	-	+	0	0	-	0
Diameter:species		-				-	-
Time:species		+				+	+
Time:basal				-	-		-
Time:animals				0	0		-
Species:basal							-
Basal:animals				-	-		0
Diameter:time:species		+				+	0
AIC	1912	1904	1912	1874	1874	1912	1864
Marginal $R^2$	0.114	0.153	0.114	0.231	0.231	0.114	0.251
Conditional $R^2$	0.296	0.373	0.296	0.497	0.497	0.296	0.524

The best-fit TD and TD & SR models were identical to the best-fit TIB model, while the best-fit TD & BU model was identical to the best-fit BU model.

The marginal  $R^2$  of the null model was 0 and the conditional  $R^2$  of the null model was 0.325.



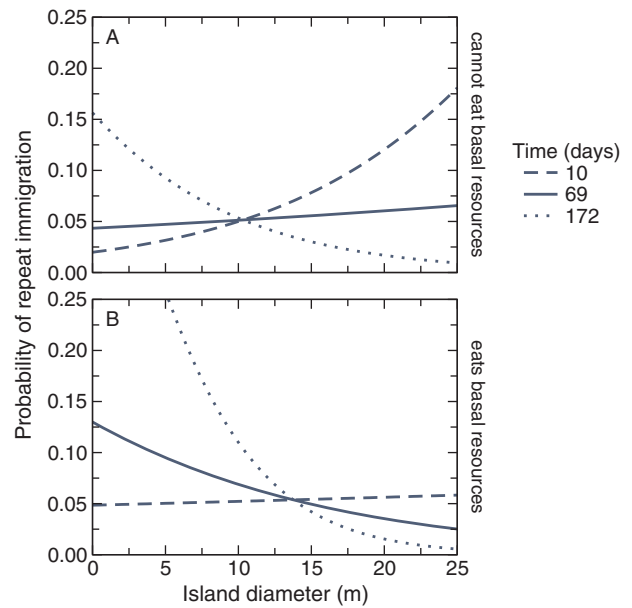
**Figure 1** Per-species probabilities of initial immigration in the top-down and bottom-up model were affected by the presence of animal prey, the presence of predators, island diameter, distance from the island and time between censuses (based on  $n = 18,420$  potential initial immigrations). In each panel we show the model predictions for different scenarios with the line colour/shade indicating island distance and line type indicating the interval between census. Light lines are for islands close to the mainland (2 m), medium lines for moderately isolated islands (163 m) and dark lines for very isolated islands (533 m). Similarly, dashed lines are for the lowest observed interval between censuses (10 days), solid lines for the mean interval between censuses (25 days) and dotted lines for the mean interval between censuses plus 1 SD (56 days). (a) When neither predators nor animal prey were present, predicted immigration probability decreased with increasing island diameter except for islands that were farthest from the mainland. (b), (c) The presence of either animal prey or predators weakened this trend such that immigration probability increased with island diameter for all islands except those closest to the mainland. (d) When both animal prey and predators were present, immigration probability increased with increasing island diameter for all islands. In all cases, increasing the time between censuses increased the probability of immigration. As no large islands were observed at moderate to high degrees of isolation, the corresponding predictions are truncated to reflect the observed range only.



**Figure 2** Hypothesis comparison of best-fit statistical models based on the area under the curve (AUC) statistic. (a), (b) All best-fit models for initial immigration generated very similar predictions, as did all models for repeat immigration. (c) Among best-fit models for extinction probability, there were two clusters of models which generated predictions that were similar to each other but distinct from those in the other cluster. In all panels, comparisons are made between a null model, a model based on the theory of island biogeography (TIB) and models based on the TIB that also include effects of species richness (SR), top-down interactions (TD), top-down interactions and species richness (TD & SR), bottom-up interactions (BU), bottom-up interactions and species richness (BU & SR) or top-down and bottom-up interactions (TD & BU). Each cell containing an asterisk indicates that two best-fit models were identical.

**Repeat immigration**

The best-fit versions of all alternative models for repeat immigration had lower AICs and explained greater variance than the null model (Table 2B), although the TIB model did not significantly improve on the null model ( $\chi^2 = 6.09$ , d.f. = 3,  $P = 0.107$ ). The best-fit species richness and top-down models were identical to the best-fit TIB model, while the best-fit top-down and



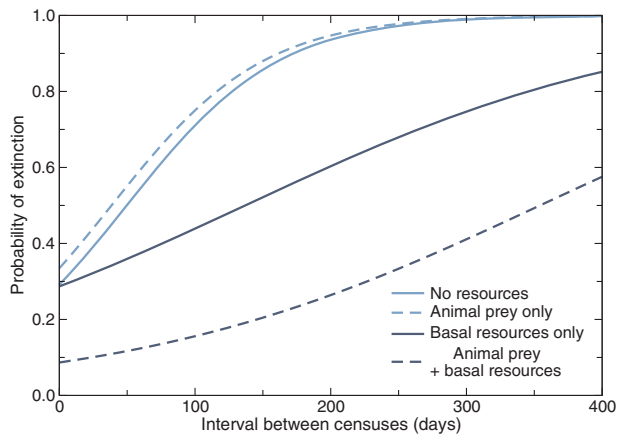
**Figure 3** Per-species probabilities of repeat immigration in the bottom-up model were affected by the ability to consume basal resources, island diameter, and the interval between censuses (based on  $n = 1813$  opportunities for species to re-immigrate). In both panels, we show model predictions for different scenarios, with line type indicating the interval between censuses: dashed lines are for the lowest observed interval between censuses (10 days), solid lines for the mean interval between censuses (69 days) and dotted lines for the mean interval between censuses plus one standard deviation (172 days). (a) For species unable to consume basal resources, repeat immigration probability increased with increasing island diameter except when the interval between censuses was very large. (b) For species able to consume basal resources, repeat immigration probability increased with increasing diameter when the interval between censuses was short and decreased with increasing island diameter when the interval between censuses was moderate to large.

bottom-up model was identical to the best-fit bottom-up model (Appendix S2). Contrary to our expectations, none of the best-fit alternative models included any effects of distance from the mainland on repeat immigration. The bottom-up model provided the best fit to the data, significantly improving upon the fits of the null and TIB models ( $\chi^2 = 22.4$ , d.f. = 6,  $P = 0.001$ , and  $\chi^2 = 16.0$ , d.f. = 3,  $P = 0.001$ , respectively).

Again contrary to our expectations, a species' probability of repeat immigration in the bottom-up model decreased as the interval between censuses increased ( $\beta_{time} = -76.8$ ; Fig. 3, Table S8 in Appendix S3). This effect was stronger on larger islands, but weaker for species able to consume basal resources ( $\beta_{diameter:time} = -431$ ;  $\beta_{time:basal} = -2.52$ ). Species able to consume basal resources were, however, less likely to immigrate to larger islands ( $\beta_{diameter:basal} = -2.52$ ).

Despite the statistical improvement of the bottom-up model over the null and TIB models, all models captured very similar variation in the empirical data (Fig. 2). Similarly, while the bottom-up model explained significantly greater variance than





**Figure 4** Per-species probabilities of extinction in the bottom-up model were affected by the presence of animal prey, the ability to eat basal resources and time between censuses (based on  $n = 1943$  opportunities for species to go extinct). (a) For species unable to eat basal resources, extinction probability increased rapidly with the interval between censuses. Extinction probability saturated near 1 after roughly 300 days. Species with animal prey available were slightly more likely to go extinct. (b) Species able to eat basal resources had lower probabilities of extinction overall, and the probability of extinction increased more slowly with interval between censuses. Species with both basal resources and animal prey available were least likely to go extinct.

the null model (Table 2b), this increase was relatively small. This suggests that the additional terms in the bottom-up model may indicate over-fitting, and that its counterintuitive predictions may be spurious.

### Extinction

Compared with the initial and repeat immigration models, the best-fit alternative models for extinction showed much greater improvements over the extinction null model (Table 2c). The best-fit top-down model was identical to the best-fit TIB model and the best-fit top-down and bottom-up model was identical to the best-fit bottom-up model (Appendix S2). In addition, the best-fit species richness and bottom-up models both improved significantly on the best-fit TIB model ( $\chi^2 = 16.6$ , d.f. = 4,  $P = 0.002$  and  $\chi^2 = 41.9$ , d.f. = 2,  $P < 0.001$ , respectively).

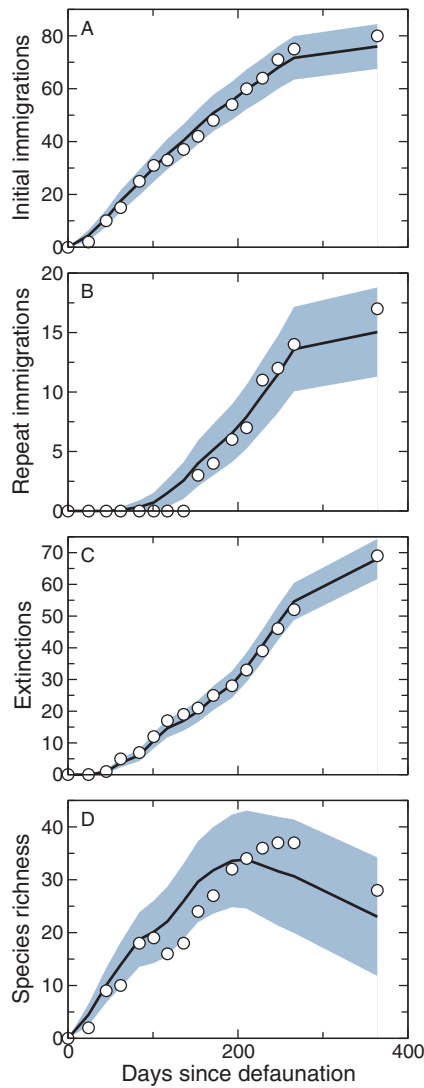
The effects included in the alternative extinction models varied a great deal. Notably, the bottom-up model did not include any effects of island diameter while the TIB and species richness models both did, although the TIB model predicted that species were more likely to go extinct on larger islands while the species-richness model predicted the opposite trend (Table S8 in Appendix S3). The bottom-up model predicted that the probability of extinction would be lower for species able to eat basal resources, especially those which also had access to animal prey, but that species with access to animal prey only would be more likely to go extinct ( $\beta_{\text{basal}} = -0.470$ ,  $\beta_{\text{animals}} = -1.64$ ,  $\beta_{\text{basal:animals}} = 0.201$ ; Fig. 4).

As a consequence of the significant trophic effects included in the bottom-up model, it described data generated by the null, TIB and species richness models poorly, and vice versa (Fig. 2). This suggests that adding bottom-up effects and removing the effect of diameter allowed this model to capture different variation in the data than that accounted for by the other models. While the model containing both bottom-up and species richness effects provided a significantly better fit to the data than the bottom-up model ( $\chi^2 = 19.5$ , d.f. = 5,  $P = 0.002$ ), it nevertheless captured very similar variation in the data (average pairwise AUC = 0.618; Fig. S5 in Appendix S5). As such, we expect that the extra terms in the bottom-up and species-richness model may constitute over-fitting.

### DISCUSSION

We compared statistical models based on several factors predicted to affect per-species probabilities of initial immigration, repeat immigration or extinction in the context of the TIB. In our dataset, species richness generally had little impact on immigration or extinction. Top-down and/or bottom-up effects, however, were included in each best-fit model. When directly compared with the empirical data, it is apparent that each of our best-fit models provides an excellent fit to the observed sequence of initial immigrations, repeat immigrations, and extinctions on all islands (Fig. 5, Appendix S6). This success of our trophic TIB models therefore stands in contrast to previous examinations of these same data where, when focusing on changes in species richness over time, it has been suggested that stochastic models of immigration and extinction may accurately describe the system (Simberloff, 1969; Simberloff & Wilson, 1969) and that colonization as a whole does not depend on trophic interactions (Simberloff, 1976). These differences also suggest that considering immigration and extinction separately provides an extra level of detail which allows us to better disentangle the underlying ecology of island biogeography.

Although the best-fitting initial and repeat immigration models showed varying structures (e.g. there was evidence that initial immigration varied with the availability of animal prey and repeat immigration with the ability to consume basal resources), they generated very similar predictions for patterns of immigration. This indicates that our expectations that island characteristics and interactions between species would affect immigration probabilities were incorrect. In particular, the prediction – based on the TIB (MacArthur & Wilson, 1963) – that immigration probability would decline with increasing distance from the mainland was ultimately not supported in this system. One possible explanation is that many of the arthropods in this system are highly mobile and could easily reach all of the mangrove islands in this study (Simberloff & Wilson, 1969). This scenario would appear even more likely because potential colonists were restricted to arthropods that were observed on the islands prior to defaunation (Wilson & Simberloff, 1969), meaning that they were all previously successful immigrants.



**Figure 5** Initial immigrations, repeat immigrations, extinctions and species richness over time for a representative island (island E9, 18 m in diameter, 379 m from the mainland). (a)–(d) The cumulative values for the observed experiment (white circles) along with the equivalent values as predicted by the the best-fitting models for initial immigration, repeat immigration and extinction (i.e. species richness, top-down and bottom-up, bottom-up, and bottom-up, respectively). We obtained the model predictions for total species richness at each census by adding predicted immigrants and subtracting predicted extinctions. In all panels, the solid line indicates the mean prediction while the shaded area corresponds to 1 SD. Comparable figures for all other islands can be found in Appendix S6.

Alternatively, it is possible that immigrants in this system are not arriving from the mainland but rather from other mangrove islands. There are many small mangrove islands in the area of the study islands that could serve as sources of colonists in addition to the mainland (see maps in Wilson & Simberloff, 1969). As the source of arthropod immigrants was not determined, the distance from each island to the mainland may not

always be the best reflection of the distance immigrants actually travelled. In this regard, the mangrove islands in this study are quite different from isolated oceanic islands but similar to habitat patches which interact both amongst each other and with a larger source habitat. Limitations of the TIB when dealing with complex geographies are well known (Hanski, 2010), and the inability of the TIB to account for multiple sources of colonists (Hanski, 2010), the existence of predator-free refuges (Ryberg *et al.*, 2012) or varying island–mainland geographies (Taylor, 1987) may all contribute to the relatively poor fit of TIB-based immigration models to this dataset and might also help to explain the apparently stochastic immigration patterns observed here.

Just as the expected distance effects were not observed in the immigration models, the best-fitting extinction model did not include the expected effect of island diameter. It is possible that the islands in this study were similar enough in size that arthropod population sizes did not vary greatly between islands, or that other factors had stronger effects. For example, populations on small islands might be maintained by occasional arrivals from the mainland (i.e. the ‘rescue effect’), preventing extinctions. While the bottom-up model for extinction did not include any effect of island diameter, it did include effects for the ability to consume basal resources and the presence of animal prey, which suggest that, all else being equal, having access to both plant and animal prey makes extinction less likely than having access to only one type of resource.

The synergistic effects of basal and animal resources are surprising in light of the fact that many arthropod species form part of the aerial plankton in the region (Simberloff & Wilson, 1969) and others such as *Diptera* that were seen on the islands were not recorded during the experiment (Simberloff & Wilson, 1969). As such, recorded animal prey may have been only a small part of the diet of even obligate insectivores. The strength of the observed effects therefore strongly suggests that bottom-up effects provide a promising avenue for extending the TIB, in agreement with previous work (Gravel *et al.*, 2011). The reduction in extinction probability where both types of resources were available also suggests that prey switching between basal resources and animal prey may be particularly important in determining extinction probabilities (Murdoch, 1969; Coll & Guershon, 2002) as well as potentially influencing immigration order (Piechnik *et al.*, 2008). It is also possible that the availability of many prey species might encourage further migration from the mainland and provide stronger rescue effects for these species.

Overall, our results suggest that incorporating bottom-up interactions provides the greatest improvement over the classic TIB. However, we note that our relatively weak results for top-down effects contrast with the strong effects of predators observed in other island systems (Spiller & Schoener, 1994, 2007; Kotiaho & Sulkava, 2007). The apparent weakness of top-down effects in this system could be due to the presence of transient predators which were observed visiting the islands during the experiment but not recorded in the censuses because they do not breed on mangroves (Simberloff &

Wilson, 1969). The effects of these predators cannot be measured from the available data, but could potentially be large. As a further complication, the effects of *resident* arthropod predators are difficult to detect in this system because they were almost always present (Table 1), making the effects of predators a 'black box' in this system. Given these caveats, and because a rich record exists of top-down and bottom-up effects acting simultaneously to structure mainland communities (Power, 1992; Amarasekare, 2008), we advocate that the potential for top-down effects still be considered along with bottom-up effects in any further attempts to combine food-web ecology and island biogeography: 'two of the most important conceptual frameworks in community ecology' (Holt, 2010).

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

**Appendix S1** Full initial immigration, repeat immigration and extinction models.

**Appendix S2** Best-fit initial immigration, repeat immigration and extinction models.

**Appendix S3** Summary tables for best-fit models.

**Appendix S4** Details of models not described in the main text.

**Appendix S5** Hypothesis comparison figures.

**Appendix S6** Cumulative species richness plots for islands not shown in the main text.

## BIOSKETCHES

**Alyssa R. Cirtwill** studies how species characteristics (including trophic level, taxonomy and mode of life) relate to food-web structure as a whole and species roles within that structure.

**Daniel B. Stouffer** works on a range of problems in community ecology, but is particularly interested in the role of species–species interactions in driving emergent ecological phenomena.

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