

Patterns of introduced species interactions affect multiple aspects of network structure in plant–pollinator communities

LAURA RUSSO,^{1,2,6} JANE MEMMOTT,³ DANIEL MONTOYA,³ KATRIONA SHEA,¹ AND YVONNE M. BUCKLEY^{4,5}

¹*Pennsylvania State University, Biology Department and Interdepartmental Graduate Program in Ecology, University Park, Pennsylvania 16802 USA*

²*Cornell University, Entomology Department, Ithaca, New York 14853 USA*

³*School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG United Kingdom*

⁴*ARC Centre of Excellence for Environmental Decisions, University of Queensland, School of Biological Sciences, Queensland 4072 Australia*

⁵*School of Natural Sciences and Trinity Centre for Biodiversity Research, Trinity College Dublin, Dublin 2, Ireland*

Abstract. Species introductions have the potential to affect the functionality and stability of ecological communities, but because little is known about how introduced species form novel interactions, these impacts are difficult to predict. We quantified the impacts of species introductions on species interaction networks using five different model scenarios of how a novel species might form plant–pollinator interactions. The network structure was based on experimental manipulations on a community of plants and pollinators and shows that the community was more diverse, ordered, and compartmentalized, but less complex when an invasive plant generalist was present. Our models of species introductions reliably predicted several aspects of novel network structure in the field study. We found that introduced species that become incorporated into the community as generalists (both in the number and frequency of their interactions) have a much larger impact on the structure of plant–pollinator communities than introduced species that integrate into the community with few interactions. Average degree is strongly affected by the number of interactions the novel species forms and whether it competes for interactions, whereas connectance is affected by whether the novel species competes for interactions or adds new interaction partners. The number and size of compartments in the network change only when the novel species adds new interaction partners, while modularity and nestedness respond most to the number of interactions formed by the novel species. We provide a new approach for understanding the impacts of introduced and invasive species on plant–pollinator communities and demonstrate that it is critical to evaluate multiple structural characters simultaneously, as large changes in the fundamental structure of the community may be disguised.

Key words: community structure; invasive species; mutualistic interactions; plant invasions; plant–pollinator network; species additions.

INTRODUCTION

Range shifts, invasions, introductions, and assisted migrations (Hoegh-Guldberg et al. 2008) are all timely examples of how a new species might enter a community. After its introduction, a novel species will interact with those already present (Memmott and Waser 2002, Stokes et al. 2006, Lopezaraiza-Mikel et al. 2007, Vilá et al. 2009, Paynter et al. 2010). Such communities can be represented as networks of interacting species. Network theoretical approaches are one way to explore the impact of novel species on existing communities because changes in species composition can alter emergent network properties of species interactions (e.g., Lopezaraiza-Mikel et al. 2007, Aizen et al. 2008). For example, from an extinction-focused perspective, species

deletions have been simulated in networks to determine effects of local extinctions on network structure (e.g., Dunne et al. 2002, Memmott et al. 2004, Valvodinos et al. 2009, Campbell et al. 2012, LaBar et al. 2013). However, few studies directly model the impact of the addition of a species on network properties (but see Fedor and Vasas 2009, Romanuk et al. 2009, Devoto et al. 2012).

Though invasive species often have negative impacts on communities, they do not necessarily form only negative interactions. Many introduced species must integrate into existing mutualistic networks to establish. For example, from 78% (temperate communities) to 94% (tropical communities) of flowering plant species depend on animal pollinators (Ollerton et al. 2011). Many invasive plants will therefore require resident insects to provide pollination services and will form novel mutualistic interactions (Chittka and Schürkens 2001, Moragues and Traveset 2005, Stokes et al. 2006). Although invasive mutualists seem able to alter the

Manuscript received 4 December 2013; revised 17 March 2014; accepted 21 March 2014. Corresponding Editor: R. Mitchell.

⁶ E-mail: lrusso@cornell.edu

network structure of resident communities, the results of comparative studies are sometimes contradictory. For example, invasive mutualists can increase the nestedness of networks they invade (Bartomeus et al. 2008), but decrease connectance among resident species (Aizen et al. 2008). Other studies find little or no apparent impact of a species invasion on network structure (e.g., Vilá et al. 2009, Carvalheiro et al. 2011). It is therefore unclear how we might expect species additions to alter the original network of mutualistic interactions and what the consequences of such changes would be (Hobbs et al. 2006).

We propose models of the impact of an introduced species on the structure of interactions between plants and pollinators. We simulate the introduction of a plant species into an empirical network of resident plants and pollinators constructed from the replicated experimental manipulation of an invaded community (Lopezaraiza-Mikel et al. 2007). We simulate the impacts of a novel species along a gradient of generality, from a species that has few interactions to one that forms many interactions at high frequencies. This gradient could represent the differential impacts of species that have difficulty attracting resident mutualists vs. those that readily integrate, or the difference between a recently introduced species at low densities vs. a well-established introduced species at high densities (Aizen et al. 2008, Kaiser-Bunbury et al. 2011). There are several plausible alternative models for how a novel species may integrate into an existing ecological community: a novel mutualistic species may interact with many species or few, add or replace interactions, and/or add additional new species to the network (Fig. 1).

Thus, our objectives were to (1) use data from experimentally manipulated plant–pollinator communities in the field to develop predictive theoretical models of the impacts of novel species additions, (2) apply these models to identify the properties of networks that best reflect changes in ultimate community structure for different scenarios of novel species interactions across a generality gradient, and (3) assess the predictive power of the different models by comparing the model outputs to observed structural changes from the field experiment. We present five different models of novel species interaction formation: addition, competitive, supergeneralist, randomized pollinator matrix, and novel species substitution (Fig. 1). These models show that the impacts of a novel species addition are not limited to negative or competitive interactions, but that novel species can change the structure of the existing community solely by forming new mutualistic interactions.

METHODS

We represented communities of plant–pollinator interactions documented from a field experiment (Lopezaraiza-Mikel et al. 2007) as interaction matrices with

rows of plant species, columns of pollinator species, and values in the cells of the matrix denoting the presence or absence of an observed interaction weighted by the frequency of that interaction (Memmott et al. 2004, Russo et al. 2013). This matrix is a bipartite network of interactions between plant and pollinator species (Fig. 1A). We used this empirical system as a framework for our network analysis because random networks fail to recapture many integral aspects of real community structure (Bascompte et al. 2003). We then simulated the addition of a plant species to these networks using the program R (R Core Development Team 2008; Supplement).

We added the simulated plant species as a node in the network with a set of interactions determined by the interaction model type (see *Interaction models*). We simulated the addition of this species 1000 times for each level of generality; each time, we randomly assigned the novel species interactions to resident species. After each simulation, we calculated network properties (Table 1) and averaged these properties across all simulations to create neutral models of novel interactions (i.e., there was no a priori bias in the interactions that the novel species formed unless it was so dictated by the model). We then compared the results of the simulations to real network structures in the presence of the invader or after its removal as a form of model validation.

Data

The experiment was composed of four replicate unmanipulated sites paired with four replicate treatment sites where the flowers of an invasive species, *Impatiens glandulifera* (Himalayan Balsam), were removed from a plant community (Lopezaraiza-Mikel et al. 2007). The rest of the plant was left intact to prevent potential experimental biases from disturbance and alteration of above- and belowground competition. Insect species that visited flower species in the sites were recorded between 2 July 2003–23 September 2003, and each of the eight sites was observed eight times (see Lopezaraiza-Mikel et al. [2007]). The size of communities varied between sites. The original study compared the community structure of the control (invaded) and experimental (*I. glandulifera* flowers removed) plots (Lopezaraiza-Mikel et al. 2007). Data were collected on the frequency of visitation; we also include models using the presence or absence of interactions in the appendices as examples of the qualitative impacts of novel species addition in systems where interaction frequencies are not known (see Appendix A). For example, there is some concern about the impact of introduced managed bee species, but little is known about how they will change the interaction structure of the resident communities (Goulson 2003).

We compare the simulated invaded communities to the empirical invaded sites as a form of model

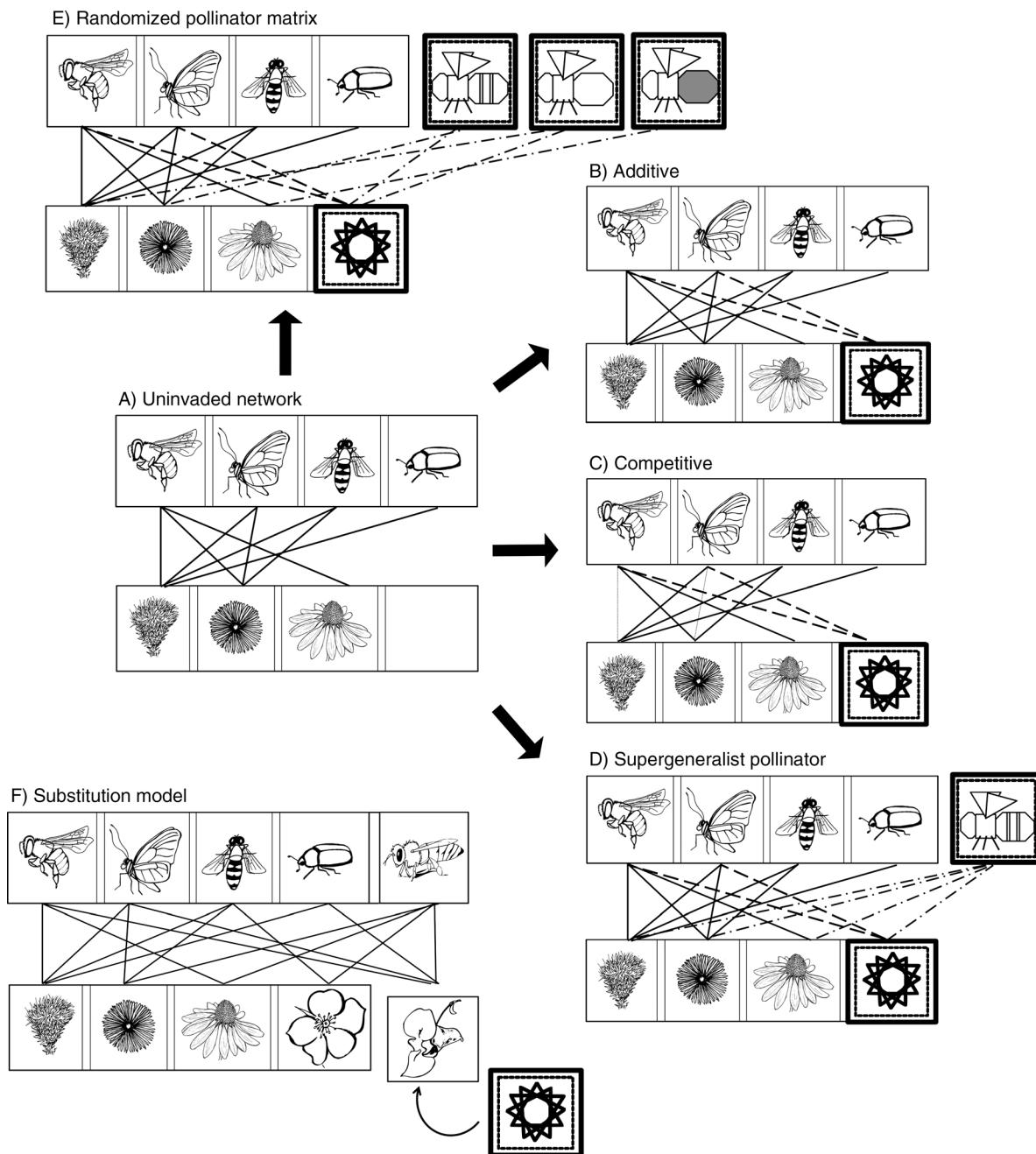


FIG. 1. A heuristic figure to demonstrate the simulated addition of a novel species to (A) an uninvaded plant–pollinator network, according to different models: (B) an additive model, where the novel species forms new interactions (dashed lines) with existing species; (C) a competitive model, where the novel species removes a proportion of the existing interaction (dotted lines) from each species with which it forms a new interaction (dashed lines); (D) a supergeneralist pollinator model, where the novel species attracts a supergeneralist pollinator that interacts with all resident plant species; and (E) a randomized pollinator matrix, where the novel species attracts a matrix of pollinator species that interact randomly with resident species. The dot-dashed lines indicate novel interactions formed by the new pollinator species. Additionally, (F) an invader substitution model replaces *I. glandulifera* in the invaded (more species rich) sites with a simulated novel species.

validation. We believe this is a valid comparison for three reasons. First, this experiment was conducted to examine short-term changes in community structure; the insect species visiting the plots were foraging opportunistically. Over this short time, the community would

likely respond similarly to abrupt changes in community composition (i.e., addition or removal). Second, the experimental plots were small (360–450 m²) relative to the surrounding plant community. Thus, they can be considered patches with a subset of a regional pool of

TABLE 1. Descriptions of network properties and predictions of how they will change in response to a species invasion.

Network properties	How we calculate it†	Description	Hypotheses
Average degree			
Unweighted	$\frac{h_i + v_i}{h + v}$	Average degree describes the average number of interactions in the community. A network with a high average degree is better connected and thought to be more stable (Dunne et al. 2002, Thébault and Fontaine 2010). Average degree can be strongly influenced by generalists.	A generalist invasive species will cause the average degree to increase.
Weighted	$\frac{h_{iw} + v_{iw}}{h + v}$	The weighted average degree accounts for the frequency of interactions and captures not only the connectedness of the community, but also the strength of the interactions.	A species with high interaction frequencies will cause weighted average degree to increase more than the unweighted degree.
Connectance			
Unweighted	$\frac{\sum \frac{h_i}{h} + \sum \frac{v_i}{v}}{h + v}$	Connectance describes the number of realized interactions; it may relate to complexity and robustness to species loss (Dunne et al. 2002), as well as stability (Thébault and Fontaine 2010).	A generalist species will cause the connectance to increase.
Weighted	$\frac{\sum \frac{h_{iw}}{h} + \sum \frac{v_{iw}}{v}}{h + v}$	The weighted connectance of the community is influenced by the interaction frequency of the species.	A generalist with high interaction frequencies will have a larger impact on the weighted connectance than unweighted connectance.
Compartmentalization			
Modularity	We measure modularity using the algorithm proposed by Newman and Girvan (2004).	Modularity splits a network into compartments that are tightly intracompartmental and weakly intercompartmental. Compartmentalization is tied theoretically to stability and robustness (Krause et al. 2003); higher modularity values may destabilize mutualistic networks (Thébault and Fontaine 2010).	A novel species may change different aspects of compartmentalization in conflicting ways; for instance, a generalist novel species may decrease the modularity and thereby increase stability.
Number of compartments	Compartments are groups of species within the network that interact more strongly with each other than with species from other compartments.	A larger number of compartments may have a stabilizing effect (Krause et al. 2003).	An introduced generalist may reduce the number of compartments in the network and may destabilize the community.
Median compartment size	This is the median number of species of the compartments.	Median compartment size allows us to track changes in the size of compartments.	A generalist species that reduces the number of compartments in the network will also increase the median compartment size.
Nestedness	We calculate nestedness using the NODF algorithm (Almeida-Neto et al. 2008).	Nestedness has been related to species and community persistence (Campbell et al. 2012) and stability and robustness (Thébault and Fontaine 2010, Pocock et al. 2012).	A generalist species will increase the nestedness of the community (Aizen et al. 2008). This may have a stabilizing effect on community structure.

Note: NODF is nested overlap and decreasing fill.

† Where h_i is the number of interactions of a host plant i , h_{iw} is the weighted interaction frequency of a host plant i , h is the number of host plant species, v_i is the unweighted interaction frequency of a visitor species i , v_{iw} is the weighted interaction frequency of a visitor species i , and v is the number of visitor species.

species in which the pollinators can forage. Third, a removal simulation (whereby the invader was removed from control sites) showed the community after the experimental removal of the invader was similar to the community after the simulated removal of the invader (see Lopezaraiza-Mikel 2006).

Interaction models

There are several ways in which a novel species might integrate into an existing community (Fig. 1). We generated five models of novel species interactions, each designed to simulate an introduction scenario. For each

model, we ran simulations across a gradient from low to high generality of the novel species. The novel plant species integrated into the community starting with a minimum of five interactions. The interactions were randomized among the resident pollinators in each of 1000 simulations. We repeated the 1000 simulations for increments of five interactions, representing a gradient of generality of the novel plant species' pollinator interactions until the novel plant was fully linked to all pollinators. For all models, we drew the frequencies of the novel species interactions (i.e., weighted interactions) from the distribution of interaction frequencies of *I. glandulifera* (but see Appendix A for unweighted models). This distribution is typical of generalist invasive plant species (Valvodinos et al. 2009, Tylianakis et al. 2010).

The simplest model of species introduction is the additive model (Fig. 1B). In this model, a novel plant species enters the community and forges new mutualistic interactions with existing pollinators. In the context of the network, we added a new plant node with randomized interactions among resident pollinators. Because we simulated across a gradient of novel species generality, we were able to compare a novel species that acted as a specialist interacting with few pollinators (i.e., a plant node with few links) to a supergeneralist that interacted with every pollinator (i.e., a fully linked node), as well as to all intermediate levels of generalism. We randomly sampled the weight of each interaction from the frequency distribution of *I. glandulifera*; thus, the weighting of the novel species interactions was independent of the generality. This model might apply best in a pollen-limited environment, where pollinators are abundant, but floral resources are scarce.

To simulate a situation where an introduced species would compete with resident plant species for pollinator services, we generated the competitive model (Fig. 1C). In this model, every interaction the novel species formed with a pollinator removed a proportion of one of the pollinator's existing interactions such that when the novel plant formed an interaction at random, the frequency of a resident plant interacting with that pollinator was lowered. The proportion removed depended on the interaction frequency of the novel species. If the frequency of the interaction formed by the novel species was greater than the frequency of the existing selected interaction, the novel species continued to remove interactions from additional resident species at random until its frequency condition was satisfied or there were no more interactions to remove. The competitive model might represent a pollinator-limited environment where there are many available floral resources, but few pollinators.

A novel plant species might also attract new mutualistic partners to the community. Because the data show that pollinator species richness was higher in invaded plots (Lopezaraiza-Mikel et al. 2007), we developed two pollinator addition models. The super-

generalist model included a novel plant, as in the additive model, as well as a supergeneralist pollinator (Fig. 1D) that interacted with every plant. The interaction frequencies of the simulated supergeneralist pollinator were selected from a distribution informed by a true supergeneralist pollinator in the field study (*Apis mellifera*). This scenario is designed to represent a facilitated invasion scenario, where one generalist invasive allows for another generalist invasive to integrate into the system (Simberloff and Von Holle 1999).

For the randomized pollinator matrix model, we added pollinators and their interactions from the invaded network to the uninvaded network (Fig. 1E). Specifically, we randomly selected pollinators from the invaded community and added them to the uninvaded community such that the two communities had the same number of pollinator species. We randomized the interactions of the added pollinators during each simulation. To this new community, we added the novel species as before. This model might best represent a situation where an extremely attractive and generalist plant species is introduced to a community of relatively specialist plant species.

In the novel species substitution model (Fig. 1F), we removed *I. glandulifera* from the invaded network, then simulated the addition of the novel plant species to the remaining network structure. We added interactions to the novel species in a similar manner to the other models, simulating its impact as its interactions increased. We randomized interactions between the novel plant species and resident pollinator species during each simulation. However, this model is distinct in that we add the novel species to the intact post-invasion interaction structure of the resident pollinators and plants. Thus, this model was intended to capture any change in network structure that occurred in the field community among the resident species, but was not captured by our other models.

To complement the quantitative weighted models presented in the main text, we include qualitative unweighted versions of the models in Appendix A. In the qualitative models, interactions can only be present or absent (1 or 0). The qualitative models demonstrate the impacts of an introduced species without accounting for the frequency of its interactions. These models are useful for systems where we expect that the introduced species interacts with different frequencies to those reported here.

Network properties

For each model and degree value (number of interactions), we ran 1000 simulations. Each simulation generated a network of plant and pollinator interactions for which we calculated six network properties, ranging in complexity and providing complementary information on community structure (see Table 1). To compare each model with the field study, we averaged each of the

TABLE 2. Values of network properties where the novel species in each model has the same number of pollinator interactions as *Impatiens glandulifera* had in the field study.

Model	Unweighted average degree	Weighted average degree	Unweighted connectance	Weighted connectance	Nestedness
Averages					
Additive	1.44 ± 0.06	3.59 ± 0.39	0.28 ± 0.07	0.66 ± 0.13	15.35 ± 1.53
Competitive	1.08 ± 0.06	2.96 ± 0.39	0.24 ± 0.05	0.54 ± 0.09	9.25 ± 1.04
Randomized pollinator matrix	1.90 ± 0.42	3.73 ± 0.61	0.31 ± 0.05	0.65 ± 0.19	14.31 ± 2.86
Substitution	1.34 ± 0.04	3.26 ± 0.33	0.18 ± 0.03	0.43 ± 0.1	10.13 ± 0.72
Supergeneralist	1.55 ± 0.08	4.48 ± 0.56	0.30 ± 0.07	0.83 ± 0.18	14.8 ± 1.56
Absolute differences					
Additive	0.28	(-) 1.07	0.14	0.06	3.45
Competitive	(-) 0.28	(-) 1.69	0.02	(-) 0.07	(-) 2.64
Randomized pollinator matrix	0.22	(-) 0.92	0.08	0.04	2.41
Substitution	0	(-) 1.40	0	(-) 0.18	(-) 1.77
Supergeneralist	0.41	(-) 0.18	0.16	0.22	2.9

Notes: The values in the top part of the table are averaged across the four sites and the standard error is included ($n = 4$). The lower half of the table includes absolute difference values (directionality indicated in parentheses) for the model outputs. The lowest absolute difference for each property is highlighted in bold. Cells with ellipses indicate that the values cannot be calculated.

six properties across the 1000 simulations where the simulated novel species had the same number of interactions as *I. glandulifera*. To find the best performing model overall, we summed the absolute differences between the predicted and observed value for each property. We used absolute differences because we were interested in the magnitude of the difference between the observed and predicted values, rather than the directionality, and the influence of interaction frequency.

We included these six network properties because it is possible for one property to change in response to the introduction of a novel species while another remains constant. For example, the compartmentalization of a network might change even when properties such as average degree and connectance remain constant (Table 1). In addition, each of these properties is thought to relate to the stability of the community in a different way. These properties might therefore have a synergistic effect on community stability. For example, it is possible for there to be a lower modularity between a higher number of compartments, resulting in a neutral effect on stability (Table 1). Another reason for including multiple network properties is that they each respond differently to network properties. For example, connectance is sensitive to small network sizes, while nestedness is very stable despite environmental stochasticity (Petanidou et al. 2008) and not sensitive to sampling effort and network size (Nielsen and Bascompte 2007). Due to their impacts on network level properties, invasive species have the potential to increase stability in mutualistic communities (Aizen et al. 2008). However, stability in this context is not necessarily advantageous to resident species. Though increased stability would make the whole network less vulnerable to collapse, vulnerable species may still be lost.

RESULTS

On average, invaded sites in the empirical network (Lopezaraiza-Mikel et al. 2007) had a higher average degree, nestedness, number of compartments, and

median compartment size, but lower connectance than their invader-removed counterparts (Appendix A: Table A2). They also had higher plant and pollinator species richness. Thus, the invaded system was more diverse, ordered, and compartmentalized, but less complex; new pollinator species attracted to *I. glandulifera* had fewer interactions on average than the original resident plant and pollinator species. By sum of the absolute differences between averaged model predictions and observations for each property, the best overall model was the randomized pollinator matrix model, while the worst was the competitive model (Table 2). This suggests that the invader in this field study, *I. glandulifera*, was more likely to add new species and interactions than remove them. Among the different network properties, unweighted connectance was the best predicted measure (Fig. 2C), while the median compartment size had the largest difference between the overall model predictions and the empirical system (Fig. 3D). In all properties and for all models, the size of the community mediated the impact, leading to the jagged appearance of the model responses, as smaller communities were saturated with novel species interactions (Figs. 2 and 3; see also Appendix B for site-based variation in model responses).

Degree and connectance

The impact of the simulated novel species on both unweighted and weighted average degree steadily increased as its generality increased for all five models (Fig. 2A, B), which was consistent with our expectation (Table 1). This trend was driven by the high number of interactions of the novel species itself and was thus moderated in the models where other species were also added; these other species tended to have a lower than average degree (Fig. 2A, B). The steepest slope in average degree occurred in the additive and supergeneralist models, while the lowest slope occurred in the competitive model, which only increased after the novel species had exhausted all extant interactions and began

TABLE 2. Extended.

Modularity	Number of compartments	Median compartment size	Weighted interaction frequency	Sum of absolute differences
0.15 ± 0.04	5.53 ± 0.9	3.34 ± 0.6	150.34 ± 40.34	...
0.36 ± 0.04	6.59 ± 0.76	3.8 ± 0.74	126.03 ± 36.74	...
0.12 ± 0.06	11.16 ± 5.56	5.47 ± 3.12	260.29 ± 61.21	...
0.32 ± 0.03	14.61 ± 1.56	1.44 ± 0.33	231 ± 38.83	...
0.13 ± 0.04	4.79 ± 0.93	5.86 ± 1.08	190.1 ± 50.57	...
(-) 0.24	(-) 2.47	(-) 4.28	(-) 180.16	386.12
(-) 0.03	(-) 1.41	(-) 3.82	(-) 204.47	430.28
(-) 0.27	3.16	(-) 2.15	(-) 70.21	162.19
(-) 0.07	6.61	(-) 6.18	(-) 99.50	235.82
(-) 0.26	(-) 3.21	(-) 1.76	(-) 140.40	299.01

adding new interactions (Fig. 2A, B). The impact of the novel species still increased with increasing generality for both unweighted and weighted connectance as we predicted (Fig. 2C, D), but in a much less linear fashion. Both unweighted average degree (Fig. 2A) and connectance (Fig. 2C) tended to be overestimated by the models (connectance by every model) because *I. glandulifera* attracted species that were more poorly linked, on average, than the simulated novel species. In contrast, weighted average degree (Fig. 2B) was underestimated by all models (*I. glandulifera* had a higher interaction frequency than the simulated novel species). In our simulations, the novel species substitution model exactly recaptured the unweighted average degree and connectance of the field study, as expected (Table 1), because the identity and frequency of the interactions were unimportant for these properties. Among the other models, the randomized pollinator matrix model best predicted the unweighted average degree of the field study, while the competitive model better predicted the unweighted connectance (Table 2). In contrast, the supergeneralist model better predicted the weighted average degree, while the randomized pollinator matrix better predicted weighted connectance (Table 2). The difference in our predictions for the weighted and unweighted versions of these properties demonstrates the importance of the interaction frequencies in the impact of an introduced species. In terms of the overall interaction frequencies of the simulated networks, the randomized pollinator matrix was closest to the field study (Table 2).

Compartmentalization

The number and size of the compartments in the network remained relatively constant in all five models, but modularity steadily decreased as the novel species became more generalist. Thus, the models predict that the compartments will become less distinct as the novel species becomes more generalist (Table 2). However, the modularity remained fairly constant in the field study (Appendix A: Table A2). Thus, all five models

overestimated the change in modularity (Fig. 3C) and the median compartment size (Fig. 3D) at the number of interactions acquired by *I. glandulifera* in the field study. Indeed, the compartmentalization of the field study was greater than predicted by any model because *I. glandulifera* formed interactions in a nonrandom pattern, while the novel species in the simulations interacted at random with resident species, generating a more diffuse community. Simply replacing the invader from the control communities with a species whose interactions were randomized (novel species substitution model) did not recapture the compartmentalization of the field study (Table 2). Of the three measures of compartmentalization, modularity, and number of compartments were better predicted by the competitive model, while median compartment size was best predicted by the supergeneralist model (Table 2).

Nestedness

The impact of the novel species on nestedness tended to increase as the novel species became more generalist, but the responses of the supergeneralist and additive models (which behaved very similarly) were nonlinear (Fig. 3A). The sudden change in slope in these models was likely due to the fact that the novel species had acquired so many interactions that the nested subgroups became less apparent. In other words, the novel species, if a moderate generalist, acted to create a more ordered system but, if a supergeneralist, created a less ordered system unless its impact was mediated by additional species. The novel species substitution model best predicted the nestedness of the field study (Table 2).

DISCUSSION

As species expand their ranges, naturally or due to anthropogenic causes (Hoegh-Guldberg et al. 2008), they begin to interact with resident species, forming novel communities (Hobbs et al. 2006). Our models demonstrate that the number of interactions formed by novel species is important, but not the only factor, for determining a novel species' network level impact. The

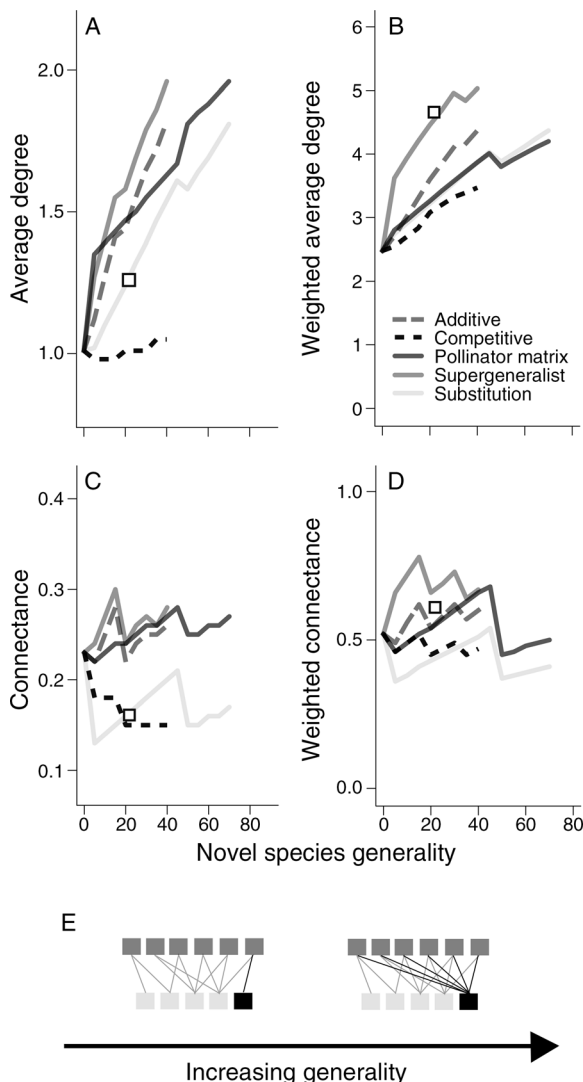


FIG. 2. The impact of simulated species addition on the (A) unweighted and (B) weighted average degree and the (C) unweighted and (D) weighted connectance of the community, across increasing novel species generality. The five models of simulated novel species behavior are represented as lines (see legend). The lines represent the average model response across the four sites, while the open square represents the properties of the field community, averaged across all four control sites. The novel species saturates the interactions available in the smaller of the sites sooner, leading to the jagged appearance of the response. Panel (E) is a heuristic diagram showing a network with pollinators (top dark gray boxes) and plants (bottom light gray boxes), which increases in both average degree and connectance as the novel species (black box) increases in generality.

way a novel species forms new mutualistic interactions (e.g., competitive or additive) and the other species it adds also determine how the network structure will change.

Model predictions of novel species impacts

In many cases our models showed that, in this system, the more generalist the introduced species, the larger its

impact. This agrees with other studies that suggest that invaders that readily form interactions with resident species or those that are present in high densities will have a greater impact on the resident community structure (e.g., Aizen et al. 2008, Kaiser-Bunbury et al. 2011). For example, the average degree and nestedness of the community tend to increase linearly, while modularity tends to decrease linearly with generality. On the other hand, some network properties are relatively constant across a broad range of novel species generality. For connectance, number of compartments, and median compartment size, the addition of other new species is more important than the number of interactions the focal novel species forms. The models show very different outcomes if the invader is competitive as opposed to adding interactions; the complexity of the interactions and the capacity to add other new species strongly affect the ultimate network structure.

Because most invasive plant species are generalists (Valvodinos et al. 2009, Tylianakis et al. 2010), our expectations were that the overall number of interactions in the community would increase after invasion in the field study. However, it was also possible to design models of species addition where this was not the case. For example, species forming interactions in novel communities might not necessarily be invaders or highly generalist, or they may exist in low densities. In addition, even highly generalist novel species failed to increase the average degree and connectance of a network if they added other new species with few interactions (randomized pollinator matrix model) or competed for interactions (competitive model).

Novel interaction formations and ultimate network structure

We hypothesized that systems where a strong generalist is introduced would become more nested but less compartmentalized. If the novel species interacts at random with mutualistic partners, interactions will be diffusely distributed among the compartments, leading to lower modularity. Because of the relationship between modularity and number of compartments (i.e., lower modularity, but a larger number of compartments, is thought to lead to stability), one might expect a relatively neutral effect on stability (Krause et al. 2003, Thébaud and Fontaine 2010). Our results show that random interaction formation and deterministic behaviors may jointly shape the network structure of invaded communities, as has been seen in with previous research on the architecture of arthropod communities (Ellwood et al. 2009).

Notably, just because we do not detect strong changes in network properties does not imply that the novel species is not changing the interaction patterns of the community. For example, in the competitive model, the novel plant species removes interactions from other plant species in the community, yet nearly all of the network properties remain constant across a range of

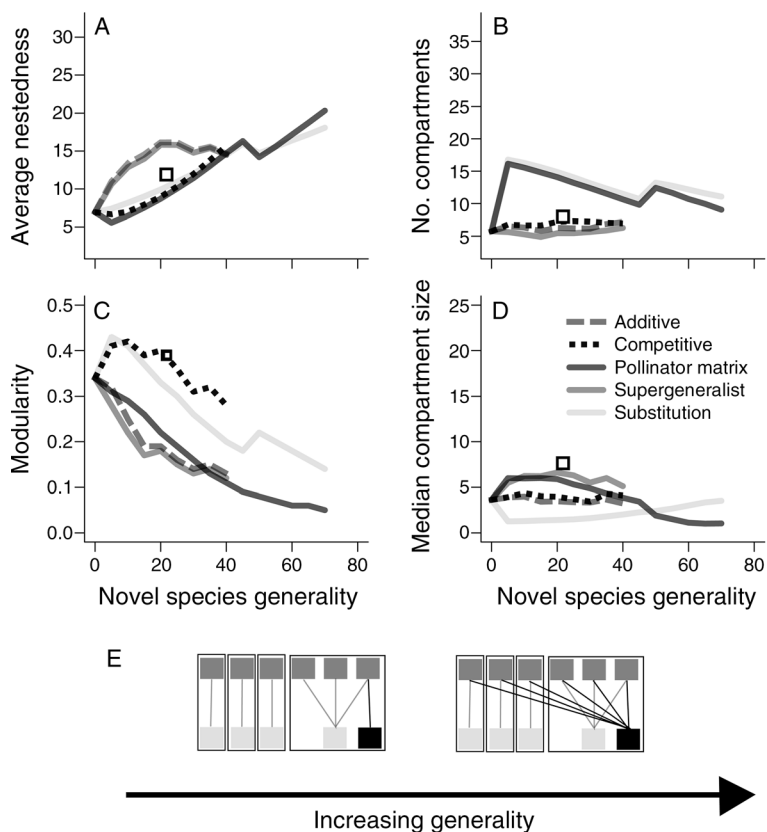


FIG. 3. The impact of the simulated species addition on (A) nestedness, (B) compartment number, (C) modularity, and (D) median compartment size. As before, the models are represented as lines (see figure legend). The lines represent the average model response across the four sites, while the open square represents the network properties of the field community averaged across the four sites. The novel species saturates the interactions available in the smaller of the sites sooner, leading to the jagged appearance of the response. Panel (E) is a heuristic diagram of a network of pollinators (top dark gray boxes) and plants (bottom light gray boxes) showing the impact of a novel species (black box) as it increases in generality. The compartments remain even when the novel species is a generalist, but they become less distinct; thus the modularity decreases.

novel species generality. The exception, in this case, is modularity, which decreases even in the competitive model. Some properties, such as median compartment size, remain fairly constant even after a suite of both plants and pollinators are added (Fig. 3). This suggests that studies that detect no or little invader impacts on a network level (e.g., Vilá et al. 2009, Kaiser-Bunbury et al. 2011) may not detect some competitive interactions that do not result in a change in network properties and highlights the importance of measuring multiple aspects of network structure. There are several ways in which one property of a network might remain constant after the introduction of a species, while other properties are affected.

Comparisons with field study

Among the five models we tested here, the model that performed the best across all properties (relative to the field study) was the randomized pollinator matrix model. This model incorporated some information about the real system (i.e., new pollinators are attracted to invaded sites), but it did not contain information

about interaction identity, as interactions were randomized for each simulation. It is promising that a simple model can predict some properties very well. In contrast, the model that performed the worst was the competitive model. This demonstrates that *I. glandulifera* is more likely to add interactions to the community than to remove them (Chittka and Schürkens 2001, Memmott and Waser 2002, Aizen et al. 2008, Bartomeus et al. 2008).

Limitations of the study

These models are limited in that they do not incorporate any interaction dynamics (see Olesen et al. 2008, Romanuk et al. 2009, Campbell et al. 2011) and the validation is done with only one system. Overcoming these limitations would improve our understanding of the process of species addition. The incorporation of dynamics would allow for exploration of the persistence of novel species through time and would show how their impacts on the interaction structure are strengthened or reduced as the system equilibrates to their presence. Interestingly, the results of the qualitative model

equivalents (Appendix A) are not very different from those presented in the main text; this shows that many properties can be approximated qualitatively even when information on interaction frequencies is lacking. Unfortunately, experiments like this one, which include not only detailed species-level interactions, but also experimental manipulation and replication, are uncommon. However, it would be very interesting to compare the behavior of these models in a larger number of empirical communities. Different results would suggest not only the importance of novel species behavior to mediate its impact, but may also suggest whether some communities are more or less resistant to invasion based on their interaction structure.

Future directions

These models have the advantage of being simple and intuitive. At the same time, they provide a range of different interaction types and novel species behaviors to explore, do not require extensive knowledge of the system a priori, and have many promising extensions. For example, with information about invader traits (e.g., corolla depth or proboscis length), these models could be used to make predictions about interaction identity as well (e.g., Stang et al. 2006, Campbell et al. 2011, Eklöf et al. 2013). These models could help to generate predictions about the impact of novel species integrating into a variety of ecological communities. For example, managers may be interested in predicting the impact of introduced managed pollinators, such as the honey bee or bumble bee, in places where they were previously absent (Goulson 2003). In addition, it may be advantageous to make predictions about the impacts of assisted migration (Hoegh-Guldberg et al. 2008).

CONCLUSIONS

These five models generate predictions of how a novel species will change the structure of an ecological community through both direct and indirect effects on mutualistic interactions. To the best of our knowledge, these are the first models to simulate the addition of a virtual species to a network constructed from real data collected through experimental manipulation (but see Olesen et al. [2008]). We demonstrate that the impact of even a highly generalist novel species can be strongly mediated by the way it forms interactions with resident species. Different hypotheses about how a novel species will interact can change our predictions. For managers of systems facing imminent species introductions or for those that seek to conserve species interactions in novel communities, these predictions might help to direct conservation objectives. More broadly, these models show that the impacts of novel or introduced species are not limited to competitive or negative interactions. Our models suggest that the addition of a new species could alter the stability of the community by forming mutualistic interactions and that the impacts of the

novel species might be concealed by compensating changes in the interactions of other species.

ACKNOWLEDGMENTS

We acknowledge B. Teller, C. Campbell, and the multispecies management group of Australian Research Council Centre for Excellence for Environmental Decisions (ARC CEED) for helpful discussions. We also acknowledge M. Lopezaraiza-Mikel for collecting the data. Support was provided by the Pennsylvania State University, USDA National Needs Program grant #2008-38420-18722, NSF grants #DEB-0815373 and DMS-1313115, the European Commission fellowship to D. Montoya (MODELECORESTORATION-FP7 Marie Curie Intra-European Fellowship for Career Development [301124]), and ARC CEED. L. Russo designed the research, performed the analyses, and wrote the initial draft of the paper; J. Memmott provided the data; Y. Buckley designed the research and assisted with the analyses; and K. Shea and D. Montoya assisted with the analyses. All authors discussed the results and wrote the manuscript.

LITERATURE CITED

- Aizen, M. A., C. L. Morales, and J. M. Morales. 2008. Invasive mutualists erode native pollination webs. *PLoS Biology* 6: e31.
- Almeida-Neto, M., P. Guimarães, P. R. Guimarães, R. D. Loyola, and W. Ulrich. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* 117:1227–1239.
- Bartomeus, I., M. Vilá, and L. Santamaría. 2008. Contrasting effects of invasive plants in plant–pollinator networks. *Oecologia* 155:761–770.
- Bascompte, J., P. Jordano, C. J. Melián, and J. M. Olesen. 2003. The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences USA* 100:9383–9387.
- Campbell, C., S. Yang, R. Albert, and K. Shea. 2011. A network model for plant–pollinator community assembly. *Proceedings of the National Academy of Sciences USA* 108: 197–202.
- Campbell, C., S. Yang, K. Shea, and R. Albert. 2012. Topology of plant–pollinator networks that are vulnerable to collapse from species extinction. *Physical Review E* 86:021924.
- Carvalho, L., R. Veldtman, A. Shenkute, G. Tesfay, C. Pirk, J. Donaldson, and S. Nicholson. 2011. Natural and within-farmland biodiversity enhances crop productivity. *Ecology Letters* 14:251–259.
- Chittka, L., and S. Schürkens. 2001. Successful invasion of a floral market. *Nature* 411:653.
- Devoto, M., S. Bailey, P. Craze, and J. Memmott. 2012. Understanding and planning ecological restoration of plant–pollinator networks. *Ecology Letters* 15:319–328.
- Dunne, J. A., R. J. Williams, and N. D. Martinez. 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters* 5: 558–567.
- Eklöf, A., et al. 2013. The dimensionality of ecological networks. *Ecology Letters* 16:577–583.
- Ellwood, M. D. F., A. Manica, and W. A. Foster. 2009. Stochastic and deterministic processes jointly structure tropical arthropod communities. *Ecology Letters* 12:277–278.
- Fedor, A., and V. Vasas. 2009. The robustness of keystone indices in food webs. *Journal of Theoretical Biology* 260:372–378.
- Goulson, D. 2003. Effects of introduced bees on native ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 34:1–26.
- Hobbs, R. J., et al. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography* 15:1–7.

- Hoegh-Guldberg, O., L. Hughes, S. McIntyre, D. Lindenmayer, C. Parmesan, H. P. Possingham, and C. D. Thomas. 2008. Assisted colonization and rapid climate change. *Science* 321:345–346.
- Kaiser-Bunbury, C. N., T. Valentin, J. Mougil, D. Matatiken, and J. Ghazoul. 2011. The tolerance of island plant–pollinator networks to alien plants. *Journal of Ecology* 99: 202–213.
- Krause, A. E., K. A. Frank, D. M. Mason, R. E. Ulanowicz, and W. W. Taylor. 2003. Compartments revealed in food-web structure. *Nature* 426:282–285.
- LaBar, T., C. Campbell, S. Yang, R. Albert, and K. Shea. 2013. Global versus local extinction in a network model of plant–pollinator communities. *Theoretical Ecology* 1–9.
- Lopezaraiza-Mikel, M. 2006. The impact of alien species on native pollination systems. Dissertation. University of Bristol, Bristol, UK.
- Lopezaraiza-Mikel, M., R. Hayes, M. Whalley, and J. Memmott. 2007. The impact of an alien plant on a native plant–pollinator network: an experimental approach. *Ecology Letters* 10:539–550.
- Memmott, J., and N. M. Waser. 2002. Integration of alien plants into a native flower–pollinator visitation web. *Proceedings of the National Academy of Sciences USA* 269:2395–2399.
- Memmott, J., N. M. Waser, and M. V. Price. 2004. Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society B* 271:2605–2611.
- Moragues, E., and A. Traveset. 2005. Effect of *Carpobrotus* spp. on the pollination success of native plant species of the Balearic Islands. *Biological Conservation* 122:611–619.
- Newman, M. E. J., and M. Girvan. 2004. Finding and evaluating community structure in networks. *Physical Review E* 69:026113.
- Nielsen, A., and J. Bascompte. 2007. Ecological networks, nestedness and sampling effort. *Journal of Ecology* 95:1134–1141.
- Olesen, J. M., J. Bascompte, H. Elberling, and P. Jordano. 2008. Temporal dynamics in a pollination network. *Ecology* 89:1573–1582.
- Ollerton, J., R. Winfree, and S. Tarrant. 2011. How many flowering plants are pollinated by animals? *Oikos* 120:321–326.
- Paynter, Q., A. Main, A. H. Gourlay, P. G. Peterson, S. V. Fowler, and Y. M. Buckley. 2010. Disruption of an exotic mutualism can improve management of an invasive plant: varroa mite, honeybees and biological control of Scotch broom *Cytisus scoparius* in New Zealand. *Journal of Applied Ecology* 47:309–317.
- Petanidou, T., A. Kallimanis, J. Tzanopoulos, S. Sgardellis, and J. Pantis. 2008. Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure, and implications for estimates of specialization. *Ecology Letters* 11:564–575.
- Pocock, M. J. O., D. M. Evans, and J. Memmott. 2012. The robustness and restoration of a network of ecological networks. *Science* 335:973–977.
- R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org
- Romanuk, T. N., Y. Zhou, U. Brose, E. L. Berlow, R. J. Williams, and N. D. Martinez. 2009. Predicting invasion success in complex ecological networks. *Philosophical Transactions of the Royal Society B* 364:1743–1754.
- Russo, L., N. DeBarros, S. Yang, K. Shea, and D. Mortensen. 2013. Supporting crop pollinators with floral resources: network-based phenological matching. *Ecology and Evolution* 3:3125–3140.
- Simberloff, D., and B. Von Holle. 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions* 1:21–32.
- Stang, M., P. G. Klinkhamer, and E. Van Der Meijden. 2006. Size constraints and flower abundance determine the number of interactions in a plant–flower visitor web. *Oikos* 112:111–121.
- Stokes, K. E., Y. M. Buckley, and A. W. Sheppard. 2006. A modeling approach to estimate the effect of exotic pollinators on exotic weed population dynamics: bumblebees and broom in Australia. *Diversity and Distributions* 12:593–600.
- Thébault, E., and C. Fontaine. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 329:853–856.
- Tylianakis, J. M., E. Lilberté, A. Nielsen, and J. Bascompte. 2010. Conservation of species interaction networks. *Biological Conservation* 143:2270–2279.
- Valvodinos, F. S., R. Ramos-Jiliberto, J. D. Flores, C. Espinoza, and G. López. 2009. Structure and dynamics of pollination networks: the role of alien plants. *Oikos* 118: 1190–1200.
- Vilá, M., I. Bartomeus, A. C. Dietzch, T. Petanidou, I. Steffan-Dewenter, J. C. Stout, and T. Tscheulin. 2009. Invasive plant integration into native plant–pollinator network across Europe. *Proceedings of the Royal Society B* 276:3887–3893.

SUPPLEMENTAL MATERIAL

Appendix A

Detailed description of the empirical study and presence/absence models of species interactions, as well as results of these simulations ([Ecological Archives E095-254-A1](#)).

Appendix B

Results including site-based variations in quantitative model responses ([Ecological Archives E095-254-A2](#)).

Supplement

R script file for the simulation models ([Ecological Archives E095-254-S1](#)).