



Variation in ecological interaction strength with island area: theory and data from the Bahamian archipelago

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ABSTRACT

Aim We ask empirically how the strength of the three major interactions – predation, competition and mutualism – changes with increasing island area. We review and expand current theory concerning these relationships.

Location Data for evaluating this question come from several Bahamian archipelagos and involve both experiments and observations. The latter can be especially long term; in one case data were collected over a 17-year period.

Methods We analyse the effect size of the following interactions across a range of island areas: (1) predation by lizards on spiders, (2) competition between two lizard species, (3) competition between two spider species, (4) ant–plant mutualism, and (5) plant–pollinator mutualism.

Results Effect sizes for predation and competition mostly show a hump-shaped relationship with island area. Effect sizes for ant–plant mutualism were reduced on large islands compared with smaller islands. Germination rate showed a steady increase with island area which we infer to be caused by an increase in pollinator limitation on smaller islands.

Main conclusions We argue that the effect size–area relation has rather similar aetiologies for predation, competition and to a somewhat lesser extent ant–plant mutualism. Specifically, we suggest that high species diversity, top predators, plant defences and (for predation and competition) spatial heterogeneity with respect to refuges or resource use reduce effect size on large islands, while harsh abiotic conditions, marine subsidies and stochastic events reduce effect size on small islands. Thus, for these interaction types, the greatest effect sizes are observed on intermediate-sized islands. For plant–pollinator mutualism we suggest that the monotonic increase in effect size with increasing island area is the result of interaction strength being enhanced, rather than weakened, by diversity.

Keywords

Ants, buttonwood, competition, interaction strength, island area, lizards, mutualism, predation, sea daisy, spiders.

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INTRODUCTION

Species interactions have been called the ‘invisible fabric of nature’ (Travis *et al.*, 2014) and they underlie large-scale patterns in the distribution and abundance of organisms. However, the bulk of macroecological theory treats these interactions implicitly and thus may not effectively capture important causal processes. The theory of island biogeography (MacArthur & Wilson, 1967) has been one of the most influential ideas in

macroecology in the last 50 years. Our paper extends this theory toward explicit consideration of species interactions. We start by exploring the relationship between the strength of various kinds of species interactions and one of the foundational variables in island biogeography theory, namely island area (Schoener, 2009; Spiller & Schoener, 2009). Specifically, we use extensive studies of a diverse array of species interactions in the Bahamian archipelago to ask how the strength of interactions between species varies with island area.

While the relationship between island area and species interactions has not been the subject of any synoptic theoretical treatment, certain existing theory can be brought to bear on this issue. We highlight three factors that vary with island area – biological complexity, perimeter-to-area ratio and spatial heterogeneity – and consider how these factors influence species interactions.

First, biological complexity increases with island area. For example, larger islands are occupied by more species, and a higher species diversity implies a more reticulate food web, which has been argued to weaken trophic cascades (Strong, 1992; Polis & Strong, 1996). In contrast, because species–area curves tend to be steeper for specialists than for generalists (Steffan-Dewenter & Tscharntke, 2000; Steffan-Dewenter, 2003), and specialization is often associated with greater interaction strength in mutualisms (Heil & McKey, 2003; Ehinger *et al.*, 2014), increasing biological complexity on larger islands may enhance the strength of some kinds of interactions. The length of food chains also increases with island size (Schoener, 1989; Takimoto *et al.*, 2008), and the addition of top predators can have major impacts on prey species and important consequences for the strength of species interactions at lower trophic levels (Terborgh & Estes, 2010).

In contrast to biological complexity, the perimeter-to-area ratio of islands decreases with island area. This change in habitat geometry may increase the importance of abiotic stressors on smaller islands. Bertness & Callaway (1994) proposed that positive interactions are stronger, and antagonistic interactions weaker, in environments that are more physically stressful. In addition, edge habitats are more likely to be exposed to disturbance, which can remove predators and intensify competition (Menge & Sutherland, 1976). Finally, higher perimeter-to-area ratios are associated with greater inputs of aquatic subsidies, which can alter the strength of species interactions by increasing consumer abundance (Polis & Hurd, 1996) and changing consumer behaviour (Nakano *et al.*, 1999).

The third factor that varies with island area is spatial heterogeneity. Larger islands feature more different habitats, greater structural complexity and additional types of resources. Multiple habitat types and greater structural complexity can increase the availability of refuges, which can decrease the strength of predation (e.g. Crowder & Cooper, 1982). In addition, the availability of different types of resources may reduce the strength of competition by minimizing the degree of overlap in resource use.

Our procedure in the present paper is to ask, for a system of subtropical islands in the Bahamas, how the strength of species interactions varies across a gradient of island area. We examine five different interactions, one representing predation and two each representing competition and mutualism. Many of the data are derived from experimental studies that were not explicitly designed to test hypotheses about island size. Because of this, our analyses should be regarded as exploratory, and our main goal in this paper will be to clarify ideas and refine hypotheses that will facilitate more specifically directed studies integrating species interactions into the theory of island biogeography.

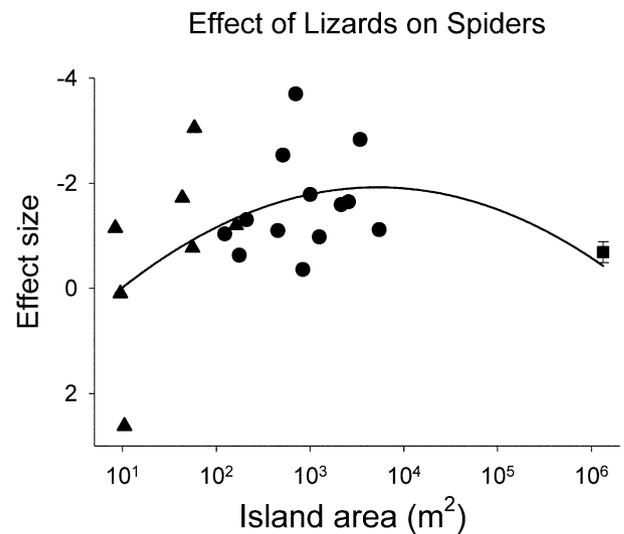


Figure 1 Relationship between effect size (natural log of response ratio) of lizards on spiders and island area compiled from three different studies: an experimental study in Abaco (triangles), a long-term comparative study in the Exuma Cays (circles), and an experimental study on a relatively large island, Staniel Cay, in the Exumas (square). The Staniel Cay point is the overall mean of three different experiments with attached standard error; note that only the overall mean was used in the regression.

METHODS

Predation by the lizard *Anolis sagrei* on spiders

We analysed the effect size of this interaction by compiling the results of three different studies ranging from tiny to large islands. The first was an experimental study conducted on islets on the eastern shore of Great Abaco from 1988 to 1995. We began the study with 14 islands without lizards and divided them into two blocks; one block had six very small islands (vegetated areas 3–35 m²) and the other block had eight slightly larger islands (vegetated areas 40–179 m²). Within each block we introduced lizards (*Anolis sagrei*, two males and three females) onto half (chosen randomly) of the islands. The results for the effect of lizards on spiders derived from the block of larger islets were consistent and dramatic (details in Schoener & Spiller, 1996, 1999a). In contrast, the results derived from the block of tiny islets were inconsistent; we decided not to publish these results because they were considered to be influenced primarily by stochastic events and therefore not appropriate for testing the effect of lizards on spiders. However, the inconsistent effects found on tiny islands are a major component of our thesis in this paper. To examine the relationship between island area and effect size, we paired each island with introduction of lizards (lizard islands) with the nearest-sized island with no lizards (no lizard islands) and the effect size for each pair was measured as the natural log of the ratio of the mean spider density 1990–95 on the lizard islands to the no-lizard islands. Then we plotted in Fig. 1 the effect size against the average area of the two islands in each pair.

The second study was a long-term survey of numbers of spiders on numerous islands with and without lizards (*A. sagrei*) in the Exuma Cays. The methodological details and results of this study showing that lizards have a major effect on spiders are in Spiller & Schoener (1996) and Schoener & Spiller (1999b). For this paper, we found 13 pairs of small to intermediate-sized islands (119–5444 m²), each consisting of a lizard and no-lizard island with similar area and structure (height) of vegetation. We computed the effect size as the log ratio of mean spider density (1981–97) on the lizard to the no-lizard islands. Then we plotted in Fig. 1 the effect size against the average area of the two islands in each pair.

The third study was a series of three experiments in which lizards were manipulated within large enclosures on Staniel Cay, a much larger island (1.3 × 10⁶ m²) than those in the previous survey study. The first experiment ran from 1985 to 1988 (Spiller & Schoener, 1988), the second from 1989 to 1994 (Spiller & Schoener, 1998) and the third from 1995 to 1997 (Spiller & Schoener, 2001). Although the full design of the experiments differed, each one contained treatments with lizards removed and controls with lizards present at natural densities, allowing the effect of lizards on spider density to be measured. For each experiment we computed the mean of the mean spider density (the average over the course of the experiment) in the removal and control enclosures and computed the effect size as described above. Effect sizes for the three experiments were consistently low: natural log ratios = -1.12, -0.60 and -0.36. We plotted the mean of these three values in Fig. 1. The entire process ensures that each point in Fig. 1 is derived from different (and therefore statistically independent) islands.

Competition in lizards: effect of *Anolis sagrei* on *Anolis carolinensis*

Losos & Spiller (1999) conducted an experimental study from 1993 to 1996 in which each species was introduced onto five islands with the congener and onto five islands without the congener. The experiment revealed that *A. sagrei* had a significant effect on *A. carolinensis* but *A. carolinensis* did not have a significant effect on *A. sagrei*. To assay the relationship between island area and effect size of *A. sagrei* on *A. carolinensis*, we paired each island containing both species with the nearest-sized island containing only *A. carolinensis*, creating five pairs of islands with and without *A. sagrei*. For each pair we computed the effect size of *A. sagrei* on *A. carolinensis* by taking the natural log of the ratio of the density of *A. carolinensis* on the island with *A. sagrei* to the density of *A. carolinensis* on the island without *A. sagrei*. Then we plotted the effect size against the average area of the two islands in each of the five pairs (Fig. 2a).

Competition in spiders: effect of *Metepeira datona* on *Eustala cazieri*

Schoener and Spiller counted the number of each orb spider species annually on c. 100 islands from 1981 to 1997.

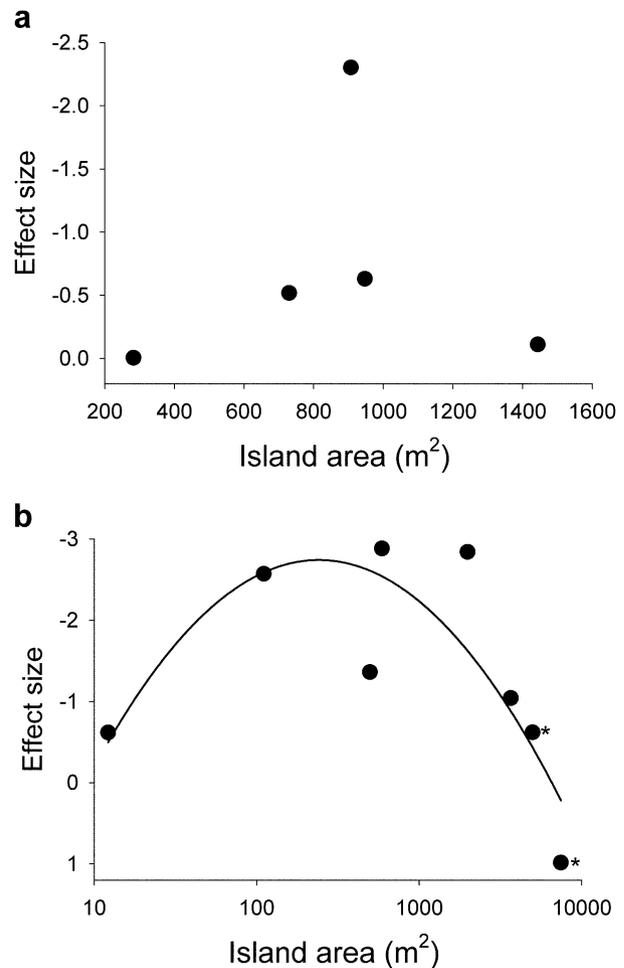


Figure 2 Relationship between the effect size (natural log of response ratio) of interspecific competition and island area. (a) Competition between two lizard species, *Anolis sagrei* and *Anolis carolinensis*, on experimental islands near Great Exuma. (b) Competition between two spider species, *Metepeira datona* and *Eustala cazieri*, in a long-term comparative study of islands in the Exuma Cays. The two points with asterisks denote islands with lizards present; lizards were absent on all other islands.

Eustala cazieri was ubiquitous and found on most islands. *Metepeira datona* was less common but occasionally found at very high densities, where they often connected their webs together to form colonies; such areas rarely contained *E. cazieri*. To assay the relationship between the effect size of *M. datona* on *E. cazieri* and island area, we selected eight islands containing populations of *M. datona* throughout the study period and paired each with the nearest-sized island containing only *E. cazieri*. For each pair we computed the effect size of *M. datona* on *E. cazieri* by taking the natural log of the ratio of the mean annual density (from 1981 to 1997) of *E. cazieri* on the island with *M. datona* to the density of *E. cazieri* on the island without *M. datona*. Then we plotted the effect size against the average area of the two islands in each of the eight pairs (Fig. 2b).

Ant–plant mutualism: effect of ants on *Conocarpus erectus*

Buttonwood (*C. erectus*) plants possess extrafloral nectaries on their leaves and petioles which attract ants which, in turn, protect the plants from herbivores. To assess the beneficial effect of these ants on buttonwood plants, we conducted ant-exclusion experiments on both large and small islands using Tanglefoot, a sticky resin, to prevent ants from accessing a plant (or part of a plant). Two experiments were conducted on large islands (vegetated area > 10,000 m²). One took place from 2006 to 2007 and compared plants defended by a thick layer of trichomes on the leaf surface with those without a dense trichome layer (Piovia-Scott, 2011b); the other took place from 2007 to 2008 and compared plants that had been pruned to simulate hurricane damage with unpruned plants (Piovia-Scott, 2011a). A third ant-exclusion experiment was conducted on small islands (vegetated area 165–955 m²) in 2008 and 2009, exploring how lizards and marine subsidies influenced the effect of ants on buttonwood (Piovia-Scott *et al.*, 2011).

In the current study, we compare the effects of ants on small and large islands across the three ant-exclusion experiments described above. Because lizards influence the strength of ant–plant interactions (Piovia-Scott *et al.*, 2011) and were present on all large islands, we used data only from small islands that had lizards, thereby excluding small islands without lizards. The trichome experiment and the island experiment used a paired-branch design, in which a focal plant contained two study branches, one of which was randomly selected for ant exclusion while the other served as a control. The pruning experiment featured a paired-plant design, in which one of a pair of plants was selected for ant exclusion (from the entire plant) while the other served as a control. We calculated the effect of ants on herbivory by taking the natural log of the ratio of mean leaf damage on ant-exclusion branches/plants to that on their paired controls. We compared the ant effect on small islands with that on large islands using linear mixed models. Island identity, experiment (trichome, pruning or island) and plant (for paired-branch experiments) or plant pair (for paired-plant experiments) were used as random effects in the model. Ant treatment (exclusion versus control) was used as a fixed effect. Likelihood-ratio tests were used to test hypotheses for fixed effects.

Plant–pollinator mutualism: germination in *Borrchia arborescens*

We examined the efficacy of pollination in the sea ox-eye daisy (*Borrchia arborescens*), a common shrub in shoreline habitats in the Bahamas (M. Keller and D.A.S., in prep.). While there is little research on pollination in *B. arborescens*, a study of *Borrchia frutescens*, a congener with which *B. arborescens* is known to hybridize (Semple & Semple, 1977), found evidence of outcrossing and insect pollination (Antlfinger, 1982).

Unlike the above studies in which predators, competitors and mutualistic ants are manipulated, or where natural variation in presence/absence allows for a direct measure of interaction

strength, we infer the strength of plant–pollinator interactions using an indirect measure of pollinator efficacy, namely germination rate. We collected large samples of *B. arborescens* seeds on 29 islands (20 islands in 2002, 9 islands in 2006) located off Great Exuma; areas varied from 357 to 7411 m². Seeds from each island were planted in separate plots and allowed to germinate in a greenhouse located at the University of California, Davis. For each island, we recorded the proportion of seeds planted that germinated along with several other variables (M. Keller and D.A.S., in prep.). We analysed the proportion of seeds that germinated (arcsine square-root transformed) using a multiple regression model with log island area and log distance to the mainland (Great Exuma) as independent variables.

RESULTS

Predation by the lizard *Anolis sagrei* on spiders

When the results of the three different studies are plotted together, the relationship between effect size and island area is curvilinear, with the strongest effects occurring on intermediate-sized islands (Fig. 1). In a quadratic regression analysis, the first-order coefficient was positive (+1.85, $t = 2.57$, $P = 0.019$) and the second-order coefficient was negative (−0.24, $t = 2.33$, $P = 0.032$), showing that the relationship was significantly hump-shaped.

Competition in lizards: effect of *Anolis sagrei* on *Anolis carolinensis*

Figure 2(a) shows that the effect size was strongest on intermediate-sized islands, suggesting a hump-shaped relationship between effect size and island area. With only five data points, obtaining a statistically significant relationship would require a very tight fit to the curve. A quadratic regression model was not significant, but we note for descriptive purposes that the first-order coefficient was positive (+50.00, $t = 1.00$, $P = 0.42$) and the second-order coefficient was negative (−8.83, $t = 0.98$, $P = 0.43$).

Competition in spiders: effect of *Metepeira datona* on *Eustala cazieri*

In this analysis, the relationship between effect size and island area was curvilinear with the strongest effects occurring on intermediate-sized islands (Fig. 2b). Note the precipitous decline in effect size on large islands, particularly those with lizards present. A quadratic regression showed that the first-order coefficient was positive (+8.33, $t = 4.05$, $P = 0.010$) and the second-order coefficient was negative (−1.66, $t = 4.12$, $P = 0.009$).

Ant–plant mutualism: effect of ants on *Conocarpus erectus*

The effect of ant exclusion on herbivory in the presence of the lizard *A. sagrei* was greater on smaller islands than it was on

Table 1 Ant effect sizes (natural log of response ratios) derived from ant-exclusion experiments conducted on buttonwood (*Conocarpus erectus*) between 2006 and 2009.

Island size class	Mean effect size	Other treatment
Large	0.113	Non-pubescent leaves
Large	0.060	Pubescent leaves
Large	0.332	Pubescent leaves
Large	0.122	Pruned
Small	0.330	Seaweed added
Small	0.848	Seaweed removed

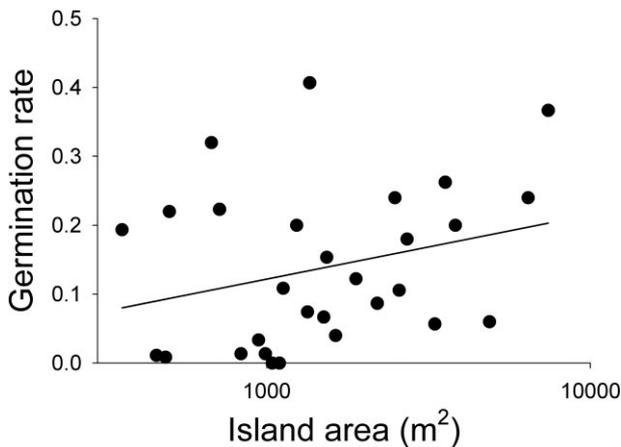


Figure 3 Relationship between germination rate (for seeds planted in a greenhouse) and island area for the sea ox-eye daisy (*Borrichia arborescens*).

large islands ($\chi^2 = 5.25$, $P = 0.02$). In addition, the greatest ant effect observed in small island treatment groups exceeded the greatest ant effect observed in large island treatment groups (Table 1; $\chi^2 = 9.51$, $P = 0.002$).

Plant–pollinator mutualism: germination in *Borrichia arborescens*

The relationship between the germination rate of *B. arborescens* and island area was positive (Fig. 3; $F_{1,26} = 21.93$, $P < 0.001$) and linear (quadratic regression showed the second-order coefficient was not significant: $F_{1,26} = 2.32$, $P = 0.14$).

DISCUSSION

Predation and competition

The weight of the present analyses for predation and competition suggest a hump-shaped relation: effect size starts small, increases to a maximum and then declines (Figs 1 & 2). We propose that this hump-shaped relationship is caused by a combination of several of the hypothesized processes mentioned in the Introduction. For both predation and competi-

tion we suggest that on the smallest islands physical factors are harsh, limiting populations and thereby reducing the strength of species interactions. This proposal is consistent with Lomolino & Weisen's (2001) rationale for species–area patterns being erratic for very small islands (Schoener, 2009; Spiller & Schoener, 2009) and with Bertness & Callaway's (1994) idea that the frequency of competitive interactions is reduced in physically stressful environments. The opposite possibility could occur, however, if disturbance intensified the effect of a particular predator by reducing the ability of other predators to compensate: for example, larger predators (e.g. lizards) on a given prey might be less vulnerable to disturbance than smaller predators (e.g. arthropods) on that prey (Schoener & Spiller, 2010). Note that only the hypothesis in which disturbance weakens species interactions is consistent with the results of the present paper, namely an ascending relation of effect size to island area over the smallest islands.

Another possible factor causing the ascending portions of the hump is marine subsidies deposited on island shores, mostly in the form of seaweed in our system (Spiller *et al.*, 2010). In theory, the effect of allochthonous subsidies should be stronger on smaller islands due to their greater perimeter-to-area ratio (Polis *et al.*, 1997). Hence, on small islands lizards may switch from eating spiders to eating marine detritivores (e.g. amphipods), thereby weakening their effect on spiders.

The right-hand portion of the hump, a descending relation of effect size to island area, is consistent with a number of hypotheses (see the Introduction and Schoener & Spiller, 2010). A hypothesis common to both predation and competition is the absence of predators at or near the top of the food web on small islands. Predators act in a similar way to disturbance, reducing population sizes of species of their prey and thereby reducing the strength of interactions in which those prey are not involved. Effects of lizards on spiders (mainly involving predation, e.g. Spiller & Schoener, 1990) were relatively weak in the enclosure experiments on Staniel Cay, the largest island by far included in Fig. 1. Staniel Cay contains many larger carnivores that eat lizards, such as birds, snakes, rats and feral cats, thereby reducing the impact of lizards on spiders. Similarly, experiments on competition in the enclosures on Staniel Cay failed to detect a significant competitive effect of the spider *M. datona* on a second spider *E. cazieri* (Spiller & Schoener, 2001). Yet on smaller islands these two species show a hump-shaped relationship (Fig. 2b) for effect size, supporting the idea of competition being strongest on islands of intermediate area; such islands lack many of the above-mentioned predators that occur on the much larger Staniel Cay.

Spatial heterogeneity is also greater on larger islands, and this can weaken both predation and competition, but in somewhat different ways. First, larger islands are more likely to have spatial refuges from predators, for example spiders can be abundant on thin spits of land where lizards do not occur, or spiders can occur on (the often high) narrow-diameter twigs and leaves that are unfavourable for lizard locomotion. Such spatial refuges

contribute to reducing the island-wide average effect size; they also allow for areas depleted by predators to be repopulated, including the areas involved in experiments. Second, the greater habitat heterogeneity of larger islands is one way in which those islands have greater resource heterogeneity, and that in turn leads to more opportunities for species coexistence via minimal overlap of their niches (resource utilization). Thus *A. sagrei* and *A. carolinensis* co-occur on large islands of the Exumas; the first perches at or near the ground and the second in higher vegetation, often large trees. In the experiment in which the two species were introduced or not to a set of islands, the effect of *A. sagrei* on *A. carolinensis* was probably weak on small islands because the scrubby habitat there was not suitable for *A. carolinensis*, so that species was sparse whether or not *A. sagrei* was present. Large islands in the experiment contained some trees, allowing the species to partition by vegetation structure. Intermediate islands were suitable for *A. carolinensis*, but the lower vegetation increased habitat overlap and thereby increased the effect of *A. sagrei* on *A. carolinensis*. Finally, vegetation height (along with island area and distance) is a significant predictor of spider species diversity (Toft & Schoener, 1983; Spiller & Schoener, 2009). This is consistent with both versions of the spatial heterogeneity hypothesis: higher perches are less accessible to many lizard predators, and existence of a greater range of heights for web placement allows spider species to more effectively partition prey resources by height.

Why did the previous analyses for predation (Schoener & Spiller, 1999b, 2010) conclude that the strength of trophic cascades, including predation, decreases with island area? The present study examines interaction strength as it varies continuously with area. In contrast, previous analyses compared summary interaction strengths for three sets of data grouped by area: very small Abaco islands, small to intermediate-sized Exuma islands, and the very large island of Staniel Cay. For the first, as explained in Methods, we omitted the tiny island block in the original treatment as these islands were considered to be influenced primarily by stochastic events and therefore not appropriate for testing the effect of lizards on spiders. Without this block, the trend is as in previous papers: the smaller the island, the stronger the effect. Note also that Schoener & Spiller (1999b) used results from only two of the experiments on very large islands; we included a third experiment here, published in 2001, and it showed the smallest effect size of the three.

Ant–plant mutualism

We found that the mutualistic effect of ants on plants (in the presence of lizards) was greater on small islands than it was on large islands. This pattern is consistent with observations of small islands versus large islands for predation and competition (i.e. the right-hand side of the hump). Unfortunately, we lack studies of the effects of ants on islands in the ‘tiny’ range, forestalling a determination of whether the hump-shaped pattern described above extends to ant–plant mutualisms.

Why does the effect of ants differ between small and large islands? The most abundant ant on buttonwood plants,

Camponotus tortuganus, can attain very high densities on small islands, perhaps due to the absence of predators and competitors. We hypothesize that *C. tortuganus* is among the more beneficial ants for buttonwoods, and that a high density of *C. tortuganus* on small islands drives greater ant effects.

In some cases, specific predators are known to enhance or reduce the effect of ants on plants. For example, lizards can enhance the effects of ants on buttonwood, a synergy which may be explained by temporal niche separation – lizards are diurnal while *C. tortuganus* is nocturnal (Piovia-Scott *et al.*, 2011). Lizards attain higher densities on small islands than large islands (Schoener & Spiller, 2010), which may contribute to greater ant effects on small islands. In contrast, cursorial spiders may compensate for ants by increasing in abundance when ants are excluded (Piovia-Scott, 2011a). The abundance of cursorial spiders can be reduced by lizards (J.P.-S. *et al.*, in prep.), which provides an alternative explanation for the enhancement of ant effects by lizards on small islands.

Plants can have fewer physical anti-herbivore defences on smaller islands. This could result from the absence of certain herbivore species, as proposed in Schoener & Spiller (2010). It could also result from an increased frequency of disturbance/stress causing fewer physical defences in plants (Spiller & Agrawal, 2003; Piovia-Scott, 2011a). Buttonwoods, with fewer physical defences, tend to produce more extrafloral nectaries and attract more ants (Piovia-Scott, 2011a,b), which is likely to enhance the ant effect on small islands. A similar pattern has been observed in other ant–plant mutualisms – reduced direct anti-herbivore defences (e.g. chemicals, spines, trichomes) are often associated with increased reliance on mutualistic ants for defence (Janzen, 1966; Koricheva & Romero, 2012). Hence, reduced direct anti-herbivore defences on smaller islands could also be responsible for increases in the beneficial effect of ants.

Marine subsidies could either enhance the ant effect by increasing ant densities (i.e. a numerical response) or reduce it by decreasing the frequency of ant foraging on buttonwood (i.e. a behavioural shift). While there is evidence for the latter (Piovia-Scott *et al.*, 2011), it is not yet clear whether the numerical responses of ants to marine subsidies can enhance ant effects. Hence, we have no evidence to support the hypothesis that marine subsidies contributed to greater ant effects on small islands.

While we have not conducted any ant exclusion studies on tiny islands, we have reason to believe that ant effects might be reduced (i.e. the hump-shaped pattern of interaction strength might hold). The smallest islands are usually only occupied by *Brachymyrmex obscurior* and *Dorymyrmex pyramicus* (Morrison, 1998), which do not visit buttonwood foliage as frequently as *C. tortuganus* (Piovia-Scott, 2011b). Hence, ant effects may be reduced on islands smaller than those examined in the current study (all of which were occupied by *C. tortuganus*). A reduction in the intensity of ant–plant mutualisms on islands lacking key mutualistic ants has been observed in other systems (Janzen, 1973; Rickson, 1977).

Plant–pollinator mutualism

In contrast to the other interactions discussed so far, the monotonic increase in the germination rate of *B. arborescens* across a broad range of island sizes suggests that the mutualistic effect of pollinators on plants increases consistently with island size. Why is the germination rate for *B. arborescens* seeds lower on smaller islands? In greenhouse experiments on *B. arborescens* collected from large and small islands, artificial pollination trials between flowers on the same plant produced no seeds that germinated (M. Keller and D.A.S., in prep.), indicating that they are obligate outcrossers; therefore we infer that the low germination rate on small islands is due to pollinator limitation.

When compared with mainlands, island pollinator communities tend to have reduced diversity (e.g. Olesen & Jordano, 2002) and a greater degree of generalization (e.g. Olesen *et al.*, 2002), which can result in reduced pollination on smaller islands (e.g. Linhart & Feinsinger, 1980; Spears Jr, 1987). In addition, smaller islands are also characterized by smaller plant population sizes, which can limit the efficacy of animal-mediated pollination (Knight *et al.*, 2005). Further support for reduced interaction strength in plant–pollinator mutualisms on smaller islands comes from studies of habitat fragmentation. For example, a meta-analysis of pollination in fragmented habitats shows a negative effect of fragmentation on pollination and plant reproductive success, with the latter appearing to be a result of pollen limitation (Aguilar *et al.*, 2006).

Comparison and conclusion

How similar are the results among the three major kinds of interactions concerning the relation of effect size to island area? Perhaps the most striking similarity is the often hump-shaped plots (Figs 1 & 2) in which the points are individual-island pairs, found for both predation and competition. Unfortunately, as elaborated above, similar plots are not available for ant–plant mutualism. However, the difference in ant–plant mutualism between small to intermediate islands and large islands is consistent with patterns for predation and competition (i.e. the right-hand portion of the hump). The most striking contrast we uncovered was that between plant–pollinator mutualisms and all of the other interactions. Like predation and competition, the effect of pollinators appeared to be weakest on the smallest islands. However, instead of reaching a maximum strength at intermediate island sizes and then declining, the effect of pollinators continued to increase across the entire range of island areas sampled.

That all of the interactions (for which we have appropriate data) showed reduced interaction strength on the smallest islands may largely result from an inescapable correlate of reduced island size, namely increased perimeter-to-area ratio. Smaller islands are more influenced by the surrounding aquatic habitat in three ways. First, organisms on smaller islands are more likely to experience physical stress and disturbance associated with being close to the shoreline, which can reduce interaction strength by limiting population density. Second,

organisms on smaller islands are more likely to utilize resource inputs from the surrounding aquatic habitat, which can reduce interaction strength by decreasing the frequency of interactions with other components of the terrestrial community. Third, demographic stochasticity in small populations on very small islands may obscure species interactions.

Of the five specific interactions we examined, four showed reduced interaction strength on the largest islands. We suggest that this reduction in interaction strength is largely due to biotic factors associated with a more complex ecological community (e.g. top predators, compensating predators, additional guilds of competitors) and increased habitat heterogeneity. The exception was plant–pollinator mutualisms – why might they continue to strengthen with island area? Perhaps because our study plant has the capacity to be pollinated from a wide array of floral visitors (M. Keller and D.A.S., in prep.), increases in pollinator diversity with island area may provide continual increases in benefits to the plant. If correct, then this hypothesis is the opposite of the species–diversity hypothesis for predation, suggesting that the response of an interaction to increasing levels of diversity may in part determine whether or not its strength peaks on intermediate-sized islands.

In summary, some of the differences among interactions in the relation of effect magnitude to island area are likely to be real, and to some extent these can be accounted for by existing theory. However, data herein were not gathered specifically to test for a relation of interaction magnitude to island area. A direct test would be to identify islands with varying areas and experimentally stage interactions on one member of a matched pair with the other as a control. In addition, underlying mechanisms could be investigated by varying their magnitude independently of area, for example the range of natural densities of marine subsidies associated with a range of island areas could be introduced on similarly sized islands. Such experiments could falsify the hypothesized mechanisms we give here as well as suggest new ones. Because interaction strengths may relate to the likelihood of extinction, knowing how they vary with island area is of interest in its own right. Yet determining the underlying mechanistic bases of an area relation would lead to deeper understanding, allowing a more finely tuned programme directed at preventing extinctions.

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REFERENCES

- Aguilar, R., Ashworth, L., Galetto, L. & Aizen, M.A. (2006) Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecology Letters*, **9**, 968–980.
- Antlfinger, A.E. (1982) Genetic neighborhood structure of the salt marsh composite, *Borrchia frutescens*. *Journal of Heredity*, **73**, 128–132.

- Bertness, M.D. & Callaway, R. (1994) Positive interactions in communities. *Trends in Ecology and Evolution*, **9**, 191–193.
- Crowder, L.B. & Cooper, W.E. (1982) Habitat structural complexity and the interaction between bluegills and their prey. *Ecology*, **63**, 1802–1813.
- Ehinger, M., Mohr, T.J., Starcevic, J.B., Sachs, J.L., Porter, S.S. & Simms, E.L. (2014) Specialization–generalization trade-off in a *Bradyrhizobium* symbiosis with wild legume hosts. *BMC Ecology*, **14**, 8.
- Heil, M. & McKey, D. (2003) Protective ant–plant interactions as model systems in ecological and evolutionary research. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 425–453.
- Janzen, D.H. (1966) Coevolution of mutualism between ants and acacias in Central America. *Evolution*, **20**, 249–275.
- Janzen, D.H. (1973) Dissolution of mutualism between *Cecropia* and its *Azteca* ants. *Biotropica*, **5**, 15–28.
- Knight, T.M., Steets, J.A., Vamosi, J.C., Mazer, S.J., Burd, M., Campbell, D.R., Dudash, M.R., Johnston, M.O., Mitchell, R.J. & Ashman, T.-L. (2005) Pollen limitation of plant reproduction: pattern and process. *Annual Review of Ecology, Evolution, and Systematics*, **36**, 467–497.
- Koricheva, J. & Romero, G.Q. (2012) You get what you pay for: reward-specific trade-offs among direct and ant-mediated defences in plants. *Biology Letters*, **8**, 628–630.
- Linhart, Y.B. & Feinsinger, P. (1980) Plant–hummingbird interactions: effects of island size and degree of specialization. *Journal of Ecology*, **68**, 745–760.
- Lomolino, M.V. & Weisen, M.D. (2001) Toward a more general species–area relation. *Journal of Biogeography*, **28**, 431–445.
- Losos, J.B. & Spiller, D.A. (1999) Differential colonization success and asymmetrical interactions between two lizard species. *Ecology*, **80**, 252–258.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ.
- Menge, B.A. & Sutherland, J.P. (1976) Species diversity gradients: synthesis of the roles of predation competition and temporal heterogeneity. *The American Naturalist*, **110**, 351–369.
- Morrison, L.W. (1998) The spatiotemporal dynamics of insular ant metapopulations. *Ecology*, **79**, 1135–1146.
- Nakano, S., Miyasaka, H. & Kuhara, N. (1999) Terrestrial–aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. *Ecology*, **80**, 2435–2441.
- Olesen, J.M. & Jordano, P. (2002) Geographic patterns in plant–pollinator mutualistic networks. *Ecology*, **83**, 2416–2424.
- Olesen, J.M., Eskildsen, L.I. & Venkatasamy, S. (2002) Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists. *Diversity and Distributions*, **8**, 181–192.
- Piovia-Scott, J. (2011a) The effect of disturbance on an ant–plant mutualism. *Oecologia*, **166**, 411–420.
- Piovia-Scott, J. (2011b) Plant phenotype influences the effect of mutualistic ants on a polymorphic mangrove. *Journal of Ecology*, **99**, 327–334.
- Piovia-Scott, J., Spiller, D.A. & Schoener, T.W. (2011) Effects of experimental seaweed deposition on lizard and ant predation in an island food web. *Science*, **331**, 461–463.
- Polis, G.A. & Hurd, S.D. (1996) Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *The American Naturalist*, **147**, 396–423.
- Polis, G.A. & Strong, D.R. (1996) Food web complexity and community dynamics. *The American Naturalist*, **147**, 813–846.
- Polis, G.A., Anderson, W.B. & Holt, R.D. (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*, **28**, 289–316.
- Rickson, F.R. (1977) Progressive loss of ant-related traits of *Cecropia peltata* on selected Caribbean islands. *American Journal of Botany*, **64**, 585–592.
- Schoener, T.W. (1989) Food webs from the small to the large. *Ecology*, **70**, 1559–1589.
- Schoener, T.W. (2009) The MacArthur–Wilson equilibrium model: what it said and how it was tested. *The theory of island biogeography revisited* (ed. by J.B. Losos and R.E. Ricklefs), pp. 52–87. Princeton University Press, Princeton, NJ.
- Schoener, T.W. & Spiller, D.A. (1996) Devastation of prey diversity by experimentally introduced predators in the field. *Nature*, **381**, 691–694.
- Schoener, T.W. & Spiller, D.A. (1999a) Indirect effects in an experimentally staged invasion by a major predator. *The American Naturalist*, **153**, 347–358.
- Schoener, T.W. & Spiller, D.A. (1999b) Variation in the magnitude of a predator’s effect from small to large islands. *Monografies de la Societat d’Història Natural de les Balears 6: Ecologia de les illes*, pp. 35–66. Societat d’Història Natural de les Balears, Palma, Spain.
- Schoener, T.W. & Spiller, D.A. (2010) Trophic cascades on islands. *Trophic cascades: predators, prey, and the changing dynamics of nature* (ed. by J. Terborgh and J. Estes), pp. 179–202. Island Press, Washington, DC.
- Semple, J.C. & Semple, K.S. (1977) *Borrchia × cubana* (*B. frutescens* × *arborescens*): interspecific hybridization in the Florida Keys. *Systematic Botany*, **2**, 292–301.
- Spears Jr, E.E. (1987) Island and mainland pollination ecology of *Centrosema virginianum* and *Opuntia stricta*. *Journal of Ecology*, **75**, 351–362.
- Spiller, D.A. & Agrawal, A.A. (2003) Intense disturbance enhances plant susceptibility to herbivory: natural and experimental evidence. *Ecology*, **84**, 890–897.
- Spiller, D.A. & Schoener, T.W. (1988) An experimental study of the effect of lizards on web-spider communities. *Ecological Monographs*, **58**, 57–77.
- Spiller, D.A. & Schoener, T.W. (1990) Lizards reduce food consumption by spiders: mechanisms and consequences. *Oecologia*, **83**, 150–161.
- Spiller, D.A. & Schoener, T.W. (1996) Food-web dynamics on some small subtropical islands: effects of top and intermediate predators. *food webs: integration of pattern and dynamics* (ed. by G.A. Polis and K.O. Winemiller), pp. 160–169. Chapman and Hall, New York.

- Spiller, D.A. & Schoener, T.W. (1998) Lizards reduced spider species richness by excluding rare species. *Ecology*, **79**, 503–516.
- Spiller, D.A. & Schoener, T.W. (2001) An experimental test for predator-mediated interactions among spider species. *Ecology*, **82**, 1560–1570.
- Spiller, D.A. & Schoener, T.W. (2009) Species–area. *Encyclopedia of islands* (ed. by R. Gillespie and D. Clague). University of California Press, Berkeley, CA.
- Spiller, D.A., Piovia-Scott, J., Wright, A.N., Yang, L.H., Takimoto, G., Schoener, T.W. & Iwata, T. (2010) Marine subsidies have multiple effects on coastal food webs. *Ecology*, **91**, 1424–1434.
- Steffan-Dewenter, I. (2003) Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. *Conservation Biology*, **17**, 1036–1044.
- Steffan-Dewenter, I. & Tschardtke, T. (2000) Butterfly community structure in fragmented habitats. *Ecology Letters*, **3**, 449–456.
- Strong, D.R. (1992) Are trophic cascades all wet? Differentiation and donor control in speciose ecosystems. *Ecology*, **73**, 747–754.
- Takimoto, G., Spiller, D.A. & Post, D.M. (2008) Ecosystem size, but not disturbance, determines food-chain length on islands of the Bahamas. *Ecology*, **89**, 3001–3007.
- Terborgh, J. & Estes, J. (2010) *Trophic cascades: predators, prey, and the changing dynamics of nature*. Island Press, Washington, DC.
- Toft, C.A. & Schoener, T.W. (1983) Abundance and diversity of orb spiders on 106 Bahamian islands: biogeography at an intermediate trophic level. *Oikos*, **41**, 411–426.
- Travis, J., Coleman, F.C., Auster, P.J., Cury, P.M., Estes, J.A., Orensanz, J., Peterson, C.H., Power, M.E., Steneck, R.S. & Wootton, J.T. (2014) Integrating the invisible fabric of nature into fisheries management. *Proceedings of the National Academy of Sciences USA*, **111**, 581–584.

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