Species interactions–area relationships: biological invasions and network structure in relation to island area

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The relationship between species number and island area is a fundamental rule in ecology. However, the extent to which interactions with exotic species and how the structure of species interactions is related to island area remain unexplored. Here, I document the relationship between island area and (i) interactions with exotic species and (ii) network structure of species interactions in the context of mutualistic interactions between ants and extrafloral nectary-bearing plants on the oceanic Ogasawara (Bonin) Islands, Japan. Pooled data contained 122 interactions among 19 plant (including five exotic) and 23 ant (including 20 exotic) species. Of the observed interactions, 82.8 per cent involved at least one exotic species, ranging from 68.2 to 86.4 per cent among islands. The number of links including exotic species increased in proportion to island area, although the number of links excluding exotic species did not. These results indicate that the number of interactions with exotic species increased in proportion to island area. Connectance, or the proportion of interactions actually observed among all possible interactions, decreased with island area. Nestedness, an asymmetry index in the species interaction network, also decreased with island area. Therefore, island area affects both the number of interactions with exotic species and the network structure.

Keywords: exotic species; island species–area relationships; mutualistic networks; native species; oceanic islands; plant–ant networks

1. INTRODUCTION

Understanding the relationship between island area and species richness is of fundamental importance in community ecology (MacArthur & Wilson 1967; Simberloff 1974; Connor & McCoy 2001; Whittaker & Fernández-Palacios 2007). Species number increases with island area because the rates of species immigration and extinction are positively and negatively related to island area, respectively (MacArthur & Wilson 1967; Simberloff & Wilson 1969; Connor & McCoy 2001; Whittaker & Fernández-Palacios 2007). The number of interaction links among species such as prey–predator and plant–pollinator interactions also increases with the total number of species (Martinez 1992; Bascompte *et al.* 2003), which suggests that the number of interaction links increases with island area; however, this prediction has not been tested using field data.

Many exotic species have recently been introduced to island communities through a variety of human activities (Elton 1958). The number of exotic species also increases with island area because large islands attract more human occupants, which increases the risk of propagule transfer, and large islands provide more diverse habitats for the establishment of introduced species (Chown *et al.* 1998;

Sax *et al.* 2002; McKinney 2006; Blackburn *et al.* 2008). Therefore, the number of interactions involving exotic species may be related to island area. Although island species–area relationships are well documented, the effects of island area on interactions with exotic species have not been explored.

Plant–animal interactions provide excellent model systems for investigating the structure of species interactions (Jordano 1987; Bascompte *et al.* 2003; Novotny *et al.* 2004; Vázquez & Aizen 2004; Lewinsohn *et al.* 2006; Bascompte & Jordano 2007). The structure of such interactions is often described using concepts such as connectance and nestedness (Jordano 1987; Bascompte *et al.* 2003; Aizen *et al.* 2008; Blüthgen *et al.* 2008). Connectance, or the proportion of interactions actually observed among all possible interactions, has been used frequently to describe the density of links in interaction networks or food webs (Blüthgen *et al.* 2008). Connectance usually represents the degree of generalization or redundancy in a system, with consequences for community stability (May 1973; Jordano 1987). Connectance has been frequently reported to decrease with the total number of species participating in mutualistic plant–animal interactions (Jordano 1987; Olesen & Jordano 2002; Blüthgen *et al.* 2007; Aizen *et al.* 2008) and food webs (Briand 1983; Schoenly *et al.* 1991; cf. Winemiller 1989; Warren 1990). However, how island area affects the connectance of species interaction webs has remained unexplored. Nestedness, which is a specific type of

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Figure 1. (a) Native (*Camponotus ogasawarensis*) and (b) exotic (*Pristomyrmex punctatus*) ant species visiting EFNs of the native plant *Terminalia catappa*. (c) *Camponotus ogasawarensis* attacking a larva of the moth *Rehimena variegata*. Scale bar, 5 mm.

asymmetrical specialization, is often observed within mutualistic plant–animal networks (Bascompte *et al.* 2003; Vázquez & Aizen 2004; Guimarães *et al.* 2006), although the concept of nestedness was originally used to analyse patterns of species occurrence and absence on a set of islands or in habitat fragments (e.g. Atmar & Patterson 1993). Nested networks are characterized by (i) generalists that all interact with each other, forming a core of interacting species, (ii) specialist species that tend to interact only with generalists, and (iii) the absence of specialists that interact only with other specialists (Bascompte *et al.* 2003; Blüthgen *et al.* 2008). The importance of native ‘super-generalists’ for nested structures of plant–animal interaction networks, particularly on islands, has been suggested (Olesen *et al.* 2002; Aizen *et al.* 2008; Sugiura *et al.* 2008). Asymmetry in mutualistic networks increases with the total number of species (Vázquez & Aizen 2004; Guimarães *et al.* 2006); thus, nestedness is predicted to be related to island area. However, how island area affects the nestedness of species interaction webs has remained unexplored.

The main goal of this study was to test the hypothesis that island area affects both interactions with exotic species and the structure of mutualistic plant–animal interactions. Although the ways in which exotic species affect the network structure of mutualistic plant–animal interactions have recently been investigated (Aizen *et al.* 2008; Padrón *et al.* 2009; Vilà *et al.* 2009), the effects of island area on interactions with exotic species and the network structure have not been examined. Since island area is indicative of many environmental factors, clarifying such effects is crucial to understanding the nature of biological invasions and the structure of species interactions within both island systems and fragmented mainland communities. In this study, I tested the following three predictions: (i) the number of species interactions increases with island area, (ii) interactions with exotic species increase with island area, and (iii) the structure (connectance and nestedness) of species interaction networks is related to island area. To accomplish this, I documented the structure of mutualistic interactions between ants and extrafloral nectary (EFN)-bearing plants on an oceanic island group, the Ogasawara (Bonin) Islands, Japan, in the northwestern Pacific Ocean. Oceanic islands that have never been connected to a continental landmass can serve as model systems for elucidating how species interactions relate to islands because the islands are isolated and independent units. Oceanic islands are also an appropriate system for clarifying how exotic species invade and influence species

interactions, particularly because these uniquely structured interactions have likely been invaded repeatedly by exotic species (Elton 1958; Olesen *et al.* 2002; O’Dowd *et al.* 2003; Aizen *et al.* 2008; Sugiura *et al.* 2008; Sugiura 2010). Interactions between ants and plants with EFNs (hereafter, EFN networks) are representative of plant–animal mutualisms because some plant species produce extrafloral nectar on organs such as leaves, stems and buds, thereby attracting ants; the ants, in turn, defend the plants against herbivores (Bentley 1977; Oliveira & Freitas 2004; Rudgers 2004; figure 1). Like plant–pollinator networks, EFN networks that involve multi-species associations offer ideal systems for investigating the structure of plant–animal interactions (Guimarães *et al.* 2006, 2007; Blüthgen *et al.* 2007).

First, I studied the structure of EFN networks on five islands (two large, inhabited islands and three small, uninhabited islands) of the Ogasawara Islands archipelago. Second, I examined the relationship between island area and the number of interaction links. To determine how exotic species become integrated into EFN networks, the relationship was analysed with and without exotic species. Third, I explored the relationship between island area and network structure (connectance and nestedness) of species interactions. Finally, I discuss the effects of island area on biological invasions and network structure of species interactions.

2. MATERIAL AND METHODS

(a) Study sites

The Ogasawara Islands are located in the northwestern Pacific Ocean, about 1000 km south of the Japanese mainland (20°25′–27°40′ N, 136°13′–153°59′ E; Ogasawara Village, Japan; figure 2a). The mean annual temperature is 23.2°C, and the mean annual precipitation is 1292 mm. The study was conducted on five islands (figure 2b): Chichi-jima (area: 23.99 km²; 0–317.9 m a.s.l.), Haha-jima (area: 20.80 km²; 0–462.6 m a.s.l.), Ani-jima (area: 7.85 km²; 0–253.9 m a.s.l.), Mukou-jima (area: 1.38 km²; 0–136.8 m a.s.l.) and Nishi-jima (area: 0.49 km²; 0–99.8 m a.s.l.). All are volcanic islands that appeared near the equator approximately 50 Ma (Shimizu 2003). The Ogasawara Islands have been inhabited since 1830 (Shimizu 2003). The large islands, Chichi-jima and Haha-jima, supported about 2000 and 400 people, respectively, in 2008, whereas the other islands are uninhabited. Chichi-jima and Haha-jima received 300–1000 and 50–750 visitors per week in 2008, respectively, whereas the uninhabited islands received only 0–10 researchers (and/or conservationists) per week.

Figure 2. (a) Ogasawara Islands (open circle); scale bar, 1000 km. (b) Study sites on Chichi-jima, Ani-jima, Nishi-jima, Haha-jima and Mukou-jima. Haha-jima Islands are located about 50 km south of the Chichi-jima Islands; scale bars, 5 km. Closed circles indicate the study sites. (c) Qualitative EFN network composed of 19 plant and 23 ant species on the Ogasawara Islands (pooled data). (d) Networks on five islands. Plant and ant species are represented by squares (right) and circles (left), respectively. The species are arranged in rank order of the frequency of interactions in pooled data. Red and blue squares and/or circles indicate exotic and native species, respectively. Code numbers next to squares and circles indicate plant and ant species codes, which are provided in tables S1 and S2, respectively, in the electronic supplementary material. Red and blue lines between circles and squares indicate associations with and without exotic species, respectively.

(b) Study organisms

I examined 14 native and five exotic species of EFN-bearing plants on the Ogasawara Islands (table S1 in the electronic supplementary material). The ecological attributes of the study plants (distributional status, position of EFN and life form) were obtained from Pemberton (1998), Toyoda (2003), Sugiura *et al.* (2006) and Keeler (2008).

Fifty-four ant species have been recorded on the Ogasawara Islands (except for the Kazan Island group; Ohbayashi *et al.* 2003; Japanese Ant Database Group 2008), and most are exotics (Terayama & Hasegawa 1991; Ohbayashi *et al.* 2003; Sugiura *et al.* 2006). Only one of the six native ant species, *Camponotus ogasawarensis*

Terayama & Satoh, is found frequently on most of the Ogasawara Islands; other native ants are rare or occur on only a few islands (Ohbayashi *et al.* 2003; Japanese Ant Database Group 2008). I encountered three native and 20 exotic ant species during visits to EFNs on the Ogasawara Islands (table S2 in the electronic supplementary material). The known distributional ranges of ants were obtained from Wilson & Hunt (1967), Wilson & Taylor (1967), Terayama & Hasegawa (1991), McGlynn (1999), The Japanese Ant Database Group (2008) and Krushelnycky *et al.* (2005). The cited studies documented species lists of the ants, which are easily introduced to many islands by humans (e.g. boats). In addition, Dr M. Terayama, a

Japanese ant taxonomist who has investigated the ant fauna of the Ogasawara Islands extensively, provided detailed information on the residency status of ants.

(c) *Sampling methods*

To ensure that I could identify most ants under field conditions, I initially collected specimens from the Ogasawara Islands and identified them by species in the laboratory using keys (Japanese Ant Database Group 2008). The number of each ant species was counted while visiting EFNs of various plant species. These surveys were conducted on five of the Ogasawara Islands from July to September 2008. To examine all EFN-bearing plant species, survey sites were selected to cover all main vegetation types on each island. The sites were established along survey routes ranging from 30 to 100 m in length. All individuals of EFN-bearing plant species were assessed along these routes (route breadth: 3 m). EFNs at heights of 0–3 m above the ground on trees, shrubs and vines were checked for the numbers and types of visiting ants. Although preliminary surveys were conducted on Chichi-jima and Haha-jima in each month (except January) from July 2005 to June 2008, few ants were found on EFNs in the winter from November to March. Ant and/or EFN activity were likely low during these months. Therefore, surveys on the islands were conducted on sunny days in summer 2008 when ant and/or EFN activity was highest (table S3 in the electronic supplementary material): Chichi-jima on 7–10 July and 6, 9, 10, 14 and 16 September; Haha-jima on 10, 11, 13 and 14 July and 11–14 September; Ani-jima on 4 and 14 July and 7 and 15 September; Mukou-jima on 12 July and 19 September; Nishi-jima on 5, 6 and 18 July and 8 September. Over the short sampling periods, all interaction data for plant and ant species were more easily collected on small islands than large ones because surveyed sites and plants were limited to smaller areas on smaller islands. Furthermore, on small islands, I was able to examine all vegetation types over only a few days, whereas on large islands, several additional days were needed to monitor all vegetation types. Therefore, so that all of the interactions on each island could be examined adequately, my sampling effort varied among the islands (table S3 in the electronic supplementary material). Field experiments were conducted to clarify the role of ants visiting EFNs and the effects of exotic ants on the visitations of native ants to EFNs (see the electronic supplementary material).

(d) *Data analysis*

To determine the proportion of ant–plant interactions that involved exotic species, qualitative and quantitative networks of links between ant and EFN-bearing plant species were constructed considering two classifications: one containing only native species and one including exotic species (Henneman & Memmott 2001; Memmott & Waser 2002; Sugiura *et al.* 2008). In the quantitative networks, the total number of visits of each ant species was used as a measure of the abundance of an ant species. I also examined the effects of island area on the proportion of interactions (ant visits) involving exotic species using a generalized linear model (GLM) with a binomial error distribution and logit link (i.e. logistic regression; JMP v. 7.0; SAS Institute, Cary, NC, USA). Island area was used as the explanatory variable and the response variable was whether an ant was exotic or native (1/0).

The numbers of links between ant and plant species were analysed in relation to island area using linear regression models (JMP v. 7.0). To determine how exotic species become integrated into EFN networks, two datasets were analysed; the first excluded associations with exotic plant and ant species (i.e. contained only native species) and the second included exotics (i.e. contained all species).

To examine how EFN network structure was related to island area, connectance and nestedness were calculated. Connectance (C) was calculated as follows (May 1973; Jordano 1987):

$$C = 100 \times \frac{I}{P \times A}$$

where P and A are the numbers of plant and ant species, respectively, and I is the number of observed links between plant and ant species. I used the software ANINHADO 3.0.3 (Guimarães & Guimarães 2006; Almeida-Neto *et al.* 2008; see the electronic supplementary material for details) to calculate nestedness (NT and $NODF$; range 0–100). These indexes have previously been used as an estimation of the plant–animal network organization (Bascompte *et al.* 2003; Guimarães *et al.* 2006; Ulrich *et al.* 2009). Relatively high values of NT or $NODF$ indicate a high degree of nestedness, whereas intermediate values are usually produced assuming random interactions among species, and low values may indicate compartmentalization. The numbers of links between ant and plant species, connectance and nestedness were analysed in relation to island area using linear regression models (JMP v. 7.0). The numbers of native species on smaller islands were insufficient to calculate nestedness. Connectance may also be influenced by small numbers of native species on smaller islands. Therefore, unlike numbers of links, network structure was analysed using only the dataset that included both exotic and native species.

To clarify the importance of native super-generalists in plant–animal interaction networks, I determined the native super-generalist ant and plant species in EFN networks. Olesen *et al.* (2002) examined the five most generalized plant and pollinator species of all species in each community and found that super-generalist plants and pollinators associate with 46–77% of potential pollinator and 44–80% of potential plant species in their networks, respectively. Following Olesen *et al.* (2002), I considered the most generalized native species, which paired with more than 45 per cent of potential partner species in EFN networks, as super-generalists.

Sampling effort varied among the islands and may have affected the number of links that were found during the study (table S3 in the electronic supplementary material). Therefore, to exclude sampling effort effects, I also examined the relationship between island area and (i) the number of links, (ii) the connectance and (iii) the nestedness using 198 observations (i.e. ant individuals) randomly sampled from the dataset for each island. Each observation was based on records of individual ants visiting EFNs. The minimum sample size among the islands that were visited was 198 (table S3 in the electronic supplementary material). Out of all the observation data on each island, 198 were randomly selected, and numbers of links, connectance and nestedness were calculated. The mean values calculated from 100 replicates were used.

Figure 3. Relationships among island area and (a) the numbers of links, (b) connectance (C), and nestedness (NT and $NODF$). (a) Closed and open circles indicate values calculated from the data with and without exotic species, respectively. (b) Closed squares, closed circles and open circles indicate C , NT and $NODF$, respectively. Lines represent best-fit linear regressions; (a) numbers of links, all species, $\log(y) = 2.9601 + 0.0506 * x$, $r^2 = 0.99$, $F_{1,3} = 266.9$, $p = 0.0005$; excluding exotic species, $\log(y) = 1.7439 + 0.0268 * x$, $r^2 = 0.54$, $F_{1,3} = 3.5$, $p = 0.16$; (b) C , $\log(y) = 3.9680 - 0.1566 * \log(x)$, $r^2 = 0.93$, $F_{1,3} = 42.9$, $p = 0.007$; NT , $y = 87.2389 - 4.4980 * \log(x)$, $r^2 = 0.80$, $F_{1,3} = 11.8$, $p = 0.042$; $NODF$, $y = 71.3601 - 5.9726 * \log(x)$, $r^2 = 0.80$, $F_{1,3} = 12.2$, $p = 0.040$.

For many organisms with limited dispersal abilities, it is more reasonable to consider large islands as comprising an ensemble of local populations coupled with in-island dispersal (Holt 1992). Therefore, for some taxonomic groups with limited dispersal abilities, the numbers of species per area (site) may be independent of island area despite strong relationships between total numbers of species and island area (Holt 1992). Additionally, large islands exhibit more diverse habitats than small ones, suggesting that exotic species have higher probabilities of establishing on large islands than on smaller ones. To cover all the vegetation types, I investigated more study sites on large islands than on small islands (table S3 in the electronic supplementary material). Considering the importance of the low dispersal abilities of ants and plants as well as the habitat diversity on large islands, I investigated the relationships between island area and species numbers and links per study site using linear regression (JMP v. 7.0).

3. RESULTS

(a) Structure of anti-plant networks

Pooled data contained 122 interactions among 19 plant (including five exotic) and 23 ant (including 20 exotic) species (figure 2c; tables S1, S2 and S4 in the electronic supplementary material). The native ant species *C. ogasawarensis* (figure 1a; code no. 6) visited 89.5 per cent of EFN-bearing plant species, making it a super-generalist, whereas other native ant species visited few native plants (figure 2c). *Hibiscus glaber* Matsumura (code no. 10) and *Callicarpa subpubescens* Hook. et Arn. (no. 17), the two native plants visited by the greatest number of ant species (figure 2c; 60.9%), can also be described as super-generalists. Of the observed interaction links, 82.8 per cent involved exotic species (figure 2c; table S4 in the electronic supplementary material), ranging from 68.2 to 86.4 per cent among islands (figure 2d; table S4 in the electronic supplementary material). Quantitative networks also showed that 43.7–90.2% of visits involved exotic species among islands (figure S1 in the electronic supplementary

material). Hence, many exotic ant species visited EFNs of both native and exotic plant species (figure 2c).

(b) Relationship between island area and numbers of interaction links

The numbers of both ant species and EFN-bearing plant species increased with island area (table S5 in the electronic supplementary material), although the numbers of species per study site were independent of island area (figure S2a–c in the electronic supplementary material). The total number of links between ant and plant species also increased in proportion to island area (figures 2d and 3a; table S4 in the electronic supplementary material), although the numbers of links per study site were independent of island area (figure S2d in the electronic supplementary material).

(c) Relationship between island area and interactions involving exotic species

Although the total number of links between ant and plant species increased with island area, the number of links excluding exotic species did not (figures 2d and 3a; table S4 in the electronic supplementary material). Differences in sampling effort among islands did not fundamentally influence these relationships (figure S3a in the electronic supplementary material). Quantitative networks also indicated that the proportions of visits involving exotic species increased with island area (GLM: $\chi^2_4 = 318.3$, $p < 0.001$; figure S1 in the electronic supplementary material). Therefore, the number of interactions involving exotic species increased in proportion to the island area.

(d) Relationship between island area and network structure

All ant species shared at least one plant species with another ant species (figure 2c,d), suggesting that EFN networks were not compartmentalized, but were highly connected. Connectance (C) ranged from 30.8 to 62.5 and decreased with island area (figure 3b). Nestedness

showed relatively high values; *NT* ranged from 70.5 to 91.2 and *NODF* from 46.7 to 74.2. Such values of *NT* and *NODF* suggest a nested structure of EFN networks on the Ogasawara Islands, although the nestedness of some islands was not significant (table S6 in the electronic supplementary material). Like *C*, *NT* and *NODF* also decreased with island area (figure 3*b*). Differences in sampling effort among islands did not fundamentally influence these relationships (figure S3*b* and table S7 in the electronic supplementary material).

4. DISCUSSION

The results of this study were concordant with the three predictions: (i) the number of species interactions increases with island area (figure 3*a*), (ii) interactions with exotic species increase with island area (figure 3*a*), and (iii) the structure (connectance and nestedness) of species interaction networks is related to island area (figure 3*b*). To my knowledge, this is the first study to demonstrate that island area affects both the number of interactions with exotic species and the network structure.

(a) *Native super-generalist ant species*

Several recent studies have shown the importance of native and exotic super-generalists in plant–animal interactions on oceanic islands (Olesen *et al.* 2002; Aizen *et al.* 2008; Sugiura *et al.* 2008). I observed that the native ant species *C. ogasawarensis* (code no. 6) visited the EFNs of almost all native plant species (figures 1*a* and 2*c*). Furthermore, *C. ogasawarensis* appeared to work as a bodyguard of EFN-bearing plants of the Ogasawara Islands (figure 1*c*; see results in the electronic supplementary material), suggesting that the relationship between *C. ogasawarensis* and native EFN-bearing plant species is mutualistic. Given that the Ogasawara Islands support a species-poor native ant fauna (Sugiura *et al.* 2006), ecological release owing to competitor-free conditions may have allowed *C. ogasawarensis* to develop into a super-generalist that is able to use a broad spectrum of host species. Furthermore, EFNs, which are open and easily accessible resources to ants, usually attract a range of largely generalist ant species (Blüthgen *et al.* 2007). This may be one reason why EFN networks are much less specialized than plant–pollinator networks (Blüthgen *et al.* 2007). Hence, the native generalist ant species (*C. ogasawarensis*) and several exotic ant species are able to make use of both native and exotic plant partners (figure 2*c*).

(b) *Effects of exotic species*

This study also revealed that the highest proportions of species interactions were those involving exotic species (figure 2*d*; table S4 and figure S1 in the electronic supplementary material). Of the observed interactions, 82.8 per cent on average involved at least one exotic species, with values ranging from 68.2 to 86.4 per cent among islands (figure 2*d*; table S4 in the electronic supplementary material). These values are higher than those previously observed in other types of mutualistic networks on other oceanic islands (e.g. 60 and 61.5% of species interactions in the plant–pollinator network on the Azores and Mauritius islands, respectively; Olesen *et al.* 2002). The highest value (86.4%) in my study is similar

to that of moth–parasitoid interactions in a community on the Hawaiian Islands (85%; Henneman & Memmott 2001). The Hawaiian moth–parasitoid interactions are one of the most invaded species interaction networks. Therefore, exotic species may have changed original EFN networks in the Ogasawara Islands, although I could not fully clarify the effects of exotic species on the network structure using network analysis owing to the small numbers of native species. Additionally, my field experiment showed that the exotic ant species *Ochetellus glaber* (Mayr) exploits the extrafloral nectar without protecting the plant (see Results in the electronic supplementary material). This suggests that some exotic ant species parasitically use the native ant–plant mutualism, although this study revealed only one such parasitic situation involving only one exotic species. Furthermore, the other field experiment showed that the exotic ant species *Pristomyrmex punctatus* (F. Smith) excludes native ants from EFNs (see Results in the electronic supplementary material). This suggests that some exotic ant species exclude native ant species from EFN networks. Indeed, the number of links excluding exotic species did not increase with island area (figures 2*d* and 3*a*; table S4 in the electronic supplementary material), suggesting that parts of native ant–plant links may have been lost owing to interference by exotic ants. Such effects of exotic ants in EFN networks have rarely been clarified (Lach 2003; cf. Sugiura *et al.* 2006), despite frequent reports of the effects of exotic ants on island fauna (Holway *et al.* 2002).

(c) *Network structure of anti-plant interactions*

Connectance is generally known to decrease with the number of species in mutualistic networks and food webs (e.g. Briand 1983; Jordano 1987; Schoenly *et al.* 1991; Olesen & Jordano 2002). My data also showed that connectance decreases with the total number of species (i.e. island area; figure 3*a*). However, as Kenny & Loehle (1991) and Blüthgen *et al.* (2008) suggested, the number of observations per species will decline with increasing numbers of possible links, as will connectance, if the same absolute effort is taken to sample larger networks (i.e. larger islands). Indeed, at the same sampling effort, the connectance decreased with increasing island area (figure S3*b* in the electronic supplementary material). However, an alternative explanation of this phenomenon is that recent introduction of ant and plant species to large islands could reduce connectance. Some exotic ant species that have not increased in population density and expanded their distribution within large islands interacted with only a few plant species on large islands (figure 2*d*).

Values of nestedness (*NT* = 70.5–91.2; table S6 in the electronic supplementary material) were similar to the values calculated from other EFN networks (mean *NT* = 71.4; Guimarães *et al.* 2006). Such nested patterns of mutualistic networks could be explained by three alternative mechanisms (Ulrich *et al.* 2009): passive sampling (abundance and/or ubiquity), asymmetric interaction strength (ecological specialization) and phenotypic complementarity (morphological specialization). In this study, abundant ant species such as *C. ogasawarensis* visited a wider range of plant species than did rare ants

(table S2 in the electronic supplementary material), and abundant plant species were visited by more numbers of ants than were rare plant species (table S1 in the electronic supplementary material). Species with low numbers of sampled individuals are likely specialist species, which interact with only one species (tables S1 and S2 in the electronic supplementary material). Different phenologies and specialized structuring of EFNs were not found on these islands. Therefore, passive sampling may have caused the nested pattern of EFN networks on the Ogasawara Islands.

Nestedness is known to increase with the total number of species in networks (Bascompte *et al.* 2003; Guimarães *et al.* 2006). However, this was not the case in this study. Rather, nestedness decreased with the total number of species (i.e. island area; table S6 in the electronic supplementary material). However, Guimarães *et al.* (2006) and Bascompte *et al.* (2003) used a dataset composed of mutualistic networks collected from different climatic and geographical areas during different periods to show that species-rich networks are more likely nested than species-poor networks. Conversely, I constructed EFN networks using data collected from the same climatic and geographical area in the same season. These differences may explain the conflicting results of the studies, although this should be further tested.

(d) Invasion process

The numbers of exotic ant and plant species have been increasing recently on the two larger islands, Chichi-jima and Haha-jima, which are inhabited. These increases may be attributable to increases in the numbers of travellers, plants and materials that are transported to Chichi-jima and Haha-jima every year. The movement of people and materials may be accelerating intentional and accidental introduction of exotic species (Ohbayashi *et al.* 2003; Toyoda 2003). Thus, the propagule pressure of exotic species is considered higher on the two inhabited islands (Chichi-jima and Haha-jima) than on the three uninhabited islands. Hence, propagule pressure may explain the difference in interactions with exotic species among islands.

Introduced ants and plants are likely to establish on these two large islands, which have a wider array of potential habitats for exotic species than do the smaller, uninhabited islands. Note that the numbers of species and interaction links per study site did not differ among small and large islands (figure S2 in the electronic supplementary material), suggesting that exotic species have more frequently established on large islands than on small islands because of higher habitat diversity. Nevertheless, some exotic ants and plants have gradually invaded uninhabited offshore islands from Chichi-jima and Haha-jima either on their own and/or via human activities. Moreover, further introduction of exotic ants will probably affect the interactions involving exotic species and the relationship between EFN network structure and island area in the Ogasawara archipelago.

5. CONCLUSIONS

Since the publication of *The Theory of Island Biogeography* (MacArthur & Wilson 1967), island species number–area relationships have been well studied for various groups

of organisms (Connor & McCoy 2001; Whittaker & Fernández-Palacios 2007). The analyses of island mutualistic plant–animal interactions presented here suggest an extension of this basic relationship to more specifically address ‘island species interactions–area relationships’. Network analyses, which have recently been used to determine the structure of species interactions such as mutualistic plant–animal interactions (Bascompte *et al.* 2003; Vázquez & Aizen 2004; Lewinsohn *et al.* 2006; Bascompte & Jordano 2007; Aizen *et al.* 2008; Blüthgen *et al.* 2008; Ulrich *et al.* 2009), are crucial for examining these more complex relationships. Biological invasions were also shown to be related to island area. Exotic species are currently increasing on islands worldwide, and the effects of exotic species on species interaction networks have been gaining attention in ecological research (Mommott & Waser 2002; Aizen *et al.* 2008; Padrón *et al.* 2009; Vilà *et al.* 2009). Therefore, through the use of network analysis, island species interactions–area relationships will help elucidate the general patterns of biological invasions.

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