



Food-web assembly during a classic biogeographic study: species' "trophic breadth" corresponds to colonization order

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Ecologists have found many patterns in food-web structure. Some, like the constant connectance hypothesis, lack definitive explanatory mechanisms. In response, we investigated whether community assembly mechanisms could explain why trophic complexity consistently scales with species richness among ecosystems. We analyzed how food-web structure developed during the community assembly recorded in Simberloff and Wilson's classic biogeography experiment. Using their arthropod surveys, we constructed six time series of food-webs from pre- and post-defaunation censuses of six experimental islands, and synthesized trophic information for 250 species from the literature and expert sources. We found that the fraction of specialist species increased and the fraction of generalists decreased during food-web assembly. Directed connectance initially declined over time, despite an increase in species richness, but eventually leveled off as predicted by the constant connectance hypothesis of diversity-complexity scaling. The initial decline was explained by later colonization by trophic specialists, probably due to limited resource availability during early colonization. Late-colonizing super-generalists maintained constant connectance at later dates. This relationship between colonization success and trophic breadth helps explain food-web patterns and corroborates assertions that community assembly is systematically influenced by species' trophic breadths.

Community assembly research has formulated generalities or assembly rules to predict community structure (Diamond 1975, Belyea and Lancaster 1999, Keddy and Weiher 1999). However, explaining factors responsible for assembly patterns and community structure can be complicated by environmental factors that act simultaneously (Weiher and Keddy 1995), or obfuscated by the temporal changes of multiple factors. Stochastic processes have emerged as an alternative explanation for species associations and community assembly (Ulrich 2004), however others have recognized repeated patterns during community assembly which argues for further research into biotic mechanisms (Diamond 1975, Belyea and Lancaster 1999, Gotelli and McCabe 2002, Fukami 2004). Our research addresses the role of species' trophic breadth in community assembly.

Ecologists now look to community assembly processes and patterns to detect mechanisms responsible for complex community structure and effects (Keddy 1992, Weiher and Keddy 1995, Holt et al. 1999, Fukami 2004). With MacArthur and Wilson's (1967) first description of the Equilibrium theory of island biogeography, investigators began to examine community assembly mechanisms like colonization and extinction dynamics, and how such factors as island size and degree of isolation became important to community structure, including trophic structure. For

example, Heatwole and Levins (1972) added trophic information to mangrove arthropod survey data (Simberloff and Wilson 1969) to demonstrate that trophic structure does return to an equilibrium-like state, or a state similar to one observed before a major disturbance (e.g. defaunation) (Heatwole and Levins 1972). However, Simberloff (1976) discounted any biotic effects during arthropod re-colonization, claiming that Heatwole and Levins' trophic classifications were too broad, and because randomly generated or "null" species collections also exhibited patterns of trophic equilibrium.

Though understanding constancy within multi-species communities constitutes a rather complex analysis, examining trophic structure during community assembly is a simpler approach which can suggest mechanisms that operate during the assembly process. For example, Holt et al. (1999) assert that a species' ability to colonize an island is likely constrained by the presence of its food resources. That is, predators show 'sequential dependence' on their prey. Holt et al. (1999) constructed a conditional incidence function model which predicted that specialist predators at high trophic levels were less likely to be present on small, species-poor islands than on large, species rich islands because their prey were less likely to be present on smaller islands. They also mentioned that opportunistic

generalists are less constrained by sequential dependencies than specialists. We generalized from this model to predict that sequential dependencies would cause patterns in species' trophic breadths during the community assembly process, as species richness increased or biotic interactions proceeded. We also analyzed how the average species' trophic breadths changed during community assembly, to gain insight into the empirical pattern of "constant connectance" observed across food-webs of differing species richness (Martinez 1992, Beckerman et al. 2006).

Food-web theory uses a conceptual map of who eats whom among species to describe diversity patterns within local assemblages (Schoener 1989, May 1973, Dunne 2006). Structural food-web theory uses binary links between predators and prey to detect larger-order patterns within multi-species communities. The term "directed connectance" ($C = L/S^2$, Martinez 1991) is a measure of community complexity that equals the fraction of all possible links that are realized. This fraction (C) equals the number of observed feeding links (L) divided by species richness (S) squared. S^2 links would be observed only if every species ate all species including its cannibalistic self. C appears to scale independently with S because with increasing species richness the linkage density (L/S) also increases; with more species present in a community, the more (potential) prey are also present (Martinez 1992). Multiple analyses have revealed that C is remarkably constrained below 0.4 (Martinez 1991, 1992, Martinez et al. 1999, Fox and McGrady-Stead 2002, Dunne et al. 2004, Srinivasan et al. 2007), but few plausible mechanisms have been advanced to explain this surprising regularity.

Our aim was to determine if patterns of colonization order and community complexity could be detected and explained using species trophic breadth. We used common structural food-web parameters as measures of individual species' trophic breadth, and the overall trophic community complexity (directed connectance, C). Following Holt et al.'s (1999) concept of sequential dependency and their observation that opportunistic omnivores have fewer constraints, we hypothesized that generalists should colonize before specialists, because they are more likely to be able to consume any early-arriving prey. If specialists do colonize later, connectance should decrease as a function of time because links per species will decrease as specialists colonize. If instead generalists colonize later, then connectance will remain constant during the colonization process. Because Simberloff (1976) suggested that stochastic abiotic and physical factors rather than biological factors likely govern recolonization processes of these mangrove islands, we tested this assertion using Monte Carlo simulations. We randomly assembled species from this same species pool to assess whether these food-webs based on published censuses

were random draws from the same species pool. Thus, we tested three main hypotheses: 1) specialists will colonize later due to sequential dependencies and therefore C will decrease over time; 2) constant connectance will occur as communities assemble, therefore species' trophic breadths will increase over time; and 3) there will be no patterns in species' trophic breadths or connectance over time.

Methods

Data source

Simberloff and Wilson (1969, 1970) selected six islands (E1, E2, E3, ST2, E7 and E9) in the Florida Keys, 11–25 m in diameter, and located 2–533 m from the nearest colonization source (Table 1). These six islands were first censused and then defaunated with methyl bromide (Wilson and Simberloff 1969). During the first year following defaunation, arthropods were censused approximately once every three weeks for a total of 15–17 times for each island (Wilson and Simberloff 1969). Four of the six islands (E1, E2, E3 and ST2) were censused again two years after defaunation (Simberloff and Wilson 1970). Censuses are likely bias-free with respect to trophic guilds on the mangrove islands because the "extremely small size of the experiment islands" made it possible to extensively study the microhabitats (Wilson and Simberloff 1969). Most of the islands had only "arboreal substrate", but taxa associated with supra-tidal areas were not included if this habitat was exposed during sampling (see Wilson and Simberloff 1969 for these taxa). The arboreal habitats surveyed throughout the experiment included: hollow twigs, living branches and twigs, dead bark and tree holes, leaves and flowers, green shoots, and fruits (Wilson and Simberloff 1969). Care was taken to not disturb or destroy animals or potential microhabitats during the post-defaunation surveys.

From 102 censuses (6 pre-defaunation and 96 post-defaunation), Simberloff and Wilson (1969) identified 278 taxa which they considered 'propagules', specified to include adult females, adult indeterminate sex, and immatures. In our analyses, we used 250 of the 278 recorded taxa (exclusions are justified below). Among these 250 taxa (Supplementary material Appendix 1), 44% were identified to the species level, 39% to the genus level, and 17% to the family level. The only taxon identified at the order level was a pauropod (Class Myriapoda: Order Pauropoda), an insect-like arthropod that dwells in moist soil and wood (Brusca and Brusca 1990). Table 2 shows the identity of the 22 arthropod orders censused and used in our analyses.

Table 1. Summary of mangrove island traits (Simberloff and Wilson 1969).

| Island | Diameter (m) | Distance (m) | Closest landmark (Key) | SF Pre-defaunation survey | SF final survey |
|--------|--------------|--------------|------------------------|---------------------------|-----------------|
| E1 | 11 | 533 | Squirrel | 0.68 | 0.55 |
| E2 | 12 | 2 | Snipe | 0.51 | 0.66 |
| E3 | 12 | 172 | Rattle Snake Lumps | 0.52 | 0.58 |
| ST2 | 11 | 154 | Saddlebunch | 0.48 | 0.58 |
| E7 | 25 | 15 | Manatee Creek | 0.52 | 0.52 |
| E9 | 18 | 379 | Colusa and Bob Allen | 0.50 | 0.47 |

Table 2. Diversity of taxa used in this analysis.

| Orders | Families | Genus/genera | Taxa (unit) |
|--------------|----------|--------------|----------------------|
| Acarina | 13 | 19 | 21 |
| Araneae | 15 | 33 | 42 |
| Chelonethida | 1 | 1 | 1 |
| Chilopoda | 1 | 1 | 1 |
| Coleoptera | 13 | 27 | 32 |
| Collembola | 1 | 1 | 1 |
| Dermoptera | 1 | 1 | 1 |
| Diplopoda | 1 | 1 | 2 |
| Diptera | 2 | 2 | 2 |
| Embioptera | 1 | 2 | 2 |
| Hemiptera | 10 | 16 | 16 |
| Homoptera | 4 | 6 | 8 |
| Hymenoptera | 14 | 44 | 57 |
| Isopoda | 1 | 1 | 1 |
| Isoptera | 1 | 2 | 2 |
| Lepidoptera | 10 | 12 | 14 |
| Neuroptera | 1 | 1 | 3 |
| Orthoptera | 3 | 7 | 11 |
| Pauropoda | 1 | 1 | 1 |
| Psocoptera | 9 | 16 | 29 |
| Thysanoptera | 1 | 2 | 2 |
| Thysanura | 1 | 1 | 1 |
| Totals | 105 | 197 | 250 taxa in food-web |

Trophic information

Trophic habits were determined for all life stages of the 250 arthropod taxa using primary publications, monographs, textbooks, and expert opinions (Table 2; Supplementary material, Appendix 1–3). Five basal (autotrophic) taxa were assumed present on all islands and in every survey: the red mangrove (*Rhizophora mangle*; Rhizophoraceae), and four less specific taxa identified as “algae,” “fungi,” “lichens,” and “detritus.” We found two or more literature references describing trophic habits for the majority (72%) of the consumer taxa. For most taxa, we described their trophic resource organisms to order, but a few species had more specific diet descriptions. For example, Arnett (1985) describes the diet of larval *Orgyia detrita* (Lepidoptera: Lymantriidae; Supplementary material Appendix 1, sp. no. 228) as “feeding on foliage of trees and shrubs avoiding herbaceous plants.” We designated this species to consume red mangrove, the only tree species known to be present (Rhizophoraceae: *Rhizophora mangle*; sp. no. 263). A predator’s (or parasitoid’s) diet, such as *Nesepyrus floridanus* (Hymenoptera: Bethyilidae; sp. no. 167), was described as “probably parasitic on borers in twigs or bark”, (Krombein 1979), and as “eating Lepidoptera and Coleoptera” (Goulet and Huber 1993). Therefore, *Nesepyrus floridanus*’s diet included all twig-boring or bark-dwelling Coleoptera and Lepidoptera.

Predators typically consume smaller prey than themselves (Elton 1927, Memmott et al. 2000), so we used adult and larval body sizes of predators to identify their likely prey (Gertsch 1979, Arnett 1985, Borror et al. 1989). Some commonly known exceptions to this assertion are ants (Hymenoptera: Formicidae) and jumping spiders (Araneae: Salticidae). We also used natural history information such as habitat preference, prey flight ability, and web-type to infer spider diets (Gertsch 1979, Wise 1993, G. B. Edwards pers. comm.).

Speculative metaweb

We assumed all taxa co-occurred spatially and temporally to construct a speculative community food-web which included both diet and natural history information (Supplementary material, Appendix 2). After excluding 28 (10%) of the 278 censused taxa, our resulting speculative metaweb contained 250 arthropod taxa. These 28 taxa were excluded because they were either identified to order and designated as “Family unknown” making their diet determination too uncertain (11 taxa), their prey were absent in the original census (9 taxa; e.g. hematophagous insects that parasitize birds or vertebrates), or their diet description was unknown or too vague (8 taxa; e.g. some Thysanoptera “thrips”). Furthermore, we excluded additional species from the Monte Carlo simulations if their prey species were absent in a randomly assembled food-web (see Analyses). Usually <5% of the species were disconnected in moderately-sized observed food-webs ($S > 10$). Because arthropod co-occurrence is quite low in mangrove communities (Simberloff 1978), our speculative metaweb should overestimate actual species co-occurrences and also contain some feeding links unrealized in nature. This level of estimation combined with infrequent species occurrence would cause broad, literature-based diets to become more specific because only one or a few co-occurring species from a particular census fit a predator species’ broad diet description. Following Havens (1992), we constructed one food-web per census period on each island, establishing trophic links between co-occurring taxa if links between the taxa were present in the speculative community food-web. One food-web was constructed for each of the 6 pre-defaunation and 96 post-defaunation censuses for a total of 102 food-webs.

Analyses

Food-web attributes

For each food-web, we analyzed effects of time and species richness (S) on food-web properties including directed connectance (C) (Gardner and Ashby 1970, Martinez 1991) and trophic generality, or the fraction of species that are specialists (SF; Schoener 1989, Williams and Martinez 2000). Directed connectance ($C = L/S^2$) hereafter connectance, is the total number of observed links (L) divided by the number of possible links including cannibalism (S^2) (Martinez 1991). Measured in this way, C is the average fraction of species in a community consumed by the average species. When no species consume one another, $C = 0$, but $C = 1.0$ when all species consume all other species and themselves. To determine the relationship between S and C (L/S^2), we regressed log S against log L rather than C, because a ratio regressed against its denominator can lead to a negative correlation (Pimm 1982).

Generality (G_i) describes a species’ trophic breadth within a food-web. G_i is calculated by summing a species’ prey (a_{ij}) from a predator(i)-prey(j) matrix, and then normalizing by the average prey count of the food-web (L/S) (Schoener 1989, Williams and Martinez 2000):

$$G_i = \sum_{j=1}^S a_{ij} \frac{1}{L/S}$$

Normalizing by L/S makes it possible to compare the standard deviations of generality among food-webs independent of variation within C and S because the average species' G_i equals 1. Thus multiplying G_i by C means the average species consumes the proportion of the community equal to C . Therefore, C is the threshold for determining which species are generalists and which are specialists. We define the specialist fraction (SF) and generalist fraction (GF) as those fractions of species in a food-web consuming less and more, respectively, than the average connectance value of all the food-webs. We applied an average threshold (C) to all food-webs, equaling 0.2, calculated by averaging the C 's for all 102 food-webs (6 pre-defaunation and 96 post-defaunation food-webs, excluding disconnected species). We examined the sensitivity of our results to this choice by using a SF/GF threshold less than the average (0.10). "Super-generalists" fractions (SGF), the subset of generalists that consumed $\geq 0.50 S$ within their food-web, were also analyzed for relative arrival time and species richness among taxonomic groups, because these should be least constrained by sequential dependence on particular prey.

Simulations

We used Monte Carlo simulations to explore whether observed species colonizations may be primarily governed by stochastic abiotic and physical factors (Simberloff 1976). We did this by randomly assembling food-webs whose S equaled the observed food-web's S . First we included all five basal species and then randomly selected (without replacement) additional non-basal species from the speculative metaweb. Random species selection continued until the S species in the simulated food-web equaled the S in the observed food-web, and then disconnected species were removed. This process mimicked null colonization sequences for each of the 96 post-defaunation island food-webs. Repeating the same process, we sampled 999 more sets of the 96 food-web collection, from the observed post-defaunation island food-webs. Each set of 96 food-webs were pooled and analyzed as a single entity for response of SF with time, but for the relationship of C to S , they were analyzed individually. To test for significant variation of C , we calculated the standard deviation for C among the simulated "null" food-webs. Disconnected species were also removed from these simulated food-webs, which sometimes reduced simulated S to below observed S . This was especially problematic for the smallest food-webs ($S \leq 4$) because low species richness decreased the number of trophic connections between species. However, only 5 out of the 96 observed post-defaunation food-webs had $S \leq 4$.

Statistics

To account for correlations of observations taken on the same island, repeated measures ANOVAs (SYSTAT 11.0.0, Systat Software, Inc.) were used to test for changes in food-web properties (e.g. C , SF, SGF, standard deviation of

generality). We used multiple least squares regressions (SYSTAT 11.0.0) to test for relationships between food-web properties (C and SF) and island area, distance to the nearest colonization source, and S in the observed food-webs. The relationship between connectance and S was analyzed by comparing $\log L$ to $\log S$ to determine whether links vary with species richness (Link-species scaling law, Cohen et al. 1990). To examine food-web properties (SF and C) in the simulated food-webs sets, we used a Kendall's rank correlation (τ), to test for temporal relationships (Campbell 1989).

We used the first 15 post-defaunation surveys (i.e. including day 21–day 720) for the Repeated measures ANOVA (hereafter RANOVA). After the last one or two censuses were removed from four of the islands (six censuses total), observations were binned into five periods, with three observations per period. Combining censuses into fewer sampling periods allowed us to meet statistical requirements for running the RANOVA. The Greenhouse-Geisser (G-G) correction was used to provide a conservative test of the period effect. Contrasts were used to assess the statistical significance of changes between subsequent periods. Model aptness was assessed via Greenhouse-Geisser epsilon and residual analysis techniques. We used a log-likelihood ratio analysis (G-test; Sokal and Rohlf 1995) to test for differences in SF between pre-defaunation and two-year post-defaunation surveys for islands E1, E2, E3 and ST2, and the final one-year post-defaunation surveys for islands E7 and E9. We also used a G-test to examine the variation of all the observed food-webs about the mean of the simulated food-webs.

Results

Food-web attributes

The fraction of specialists (SF) that consumed $< 0.20 S$ within the food-webs increased with time since defaunation (within subjects $F = 9.69$, $DF = 4$, G-G corrected $p = 0.002$; p_{G-G} hereafter; Fig. 1a–f), and increased with species richness ($R^2 = 0.095$, $p = 0.002$). SF also significantly increased with time using a lower threshold (0.1) than the observed C ($C = 0.2$) (Table 3). After defaunation, variation in arthropod trophic breadths showed an increasing trend (standard deviation of Generality: $F = 3.095$, $DF = 4$, $p_{G-G} = 0.078$). By the last census date, all islands' specialist fractions (SF) were similar to pre-defaunation values ($G = 3.946$, $n = 12$, $DF = 5$, $0.75 < p < 0.5$, Table 1). SF was negatively correlated to island size ($R^2 = 0.17$, $p = 0.0002$), but not at all with distance. Because the biogeographic analyses explained little or none of the variation within the food-web attributes, these results are not discussed further.

For each set of 96 randomly generated food-webs ($n = 1000$ sets), SF was calculated and tested for correlation with the days since defaunation published by Simberloff and Wilson (1969). SF was positively correlated with time in only eleven of 1000 simulated food-web sets using the observed C threshold ($C = 0.20$, where Kendall's $\tau = 0.135$ when $\alpha = 0.05$, $n = 96$) (Table 3). Using the lower

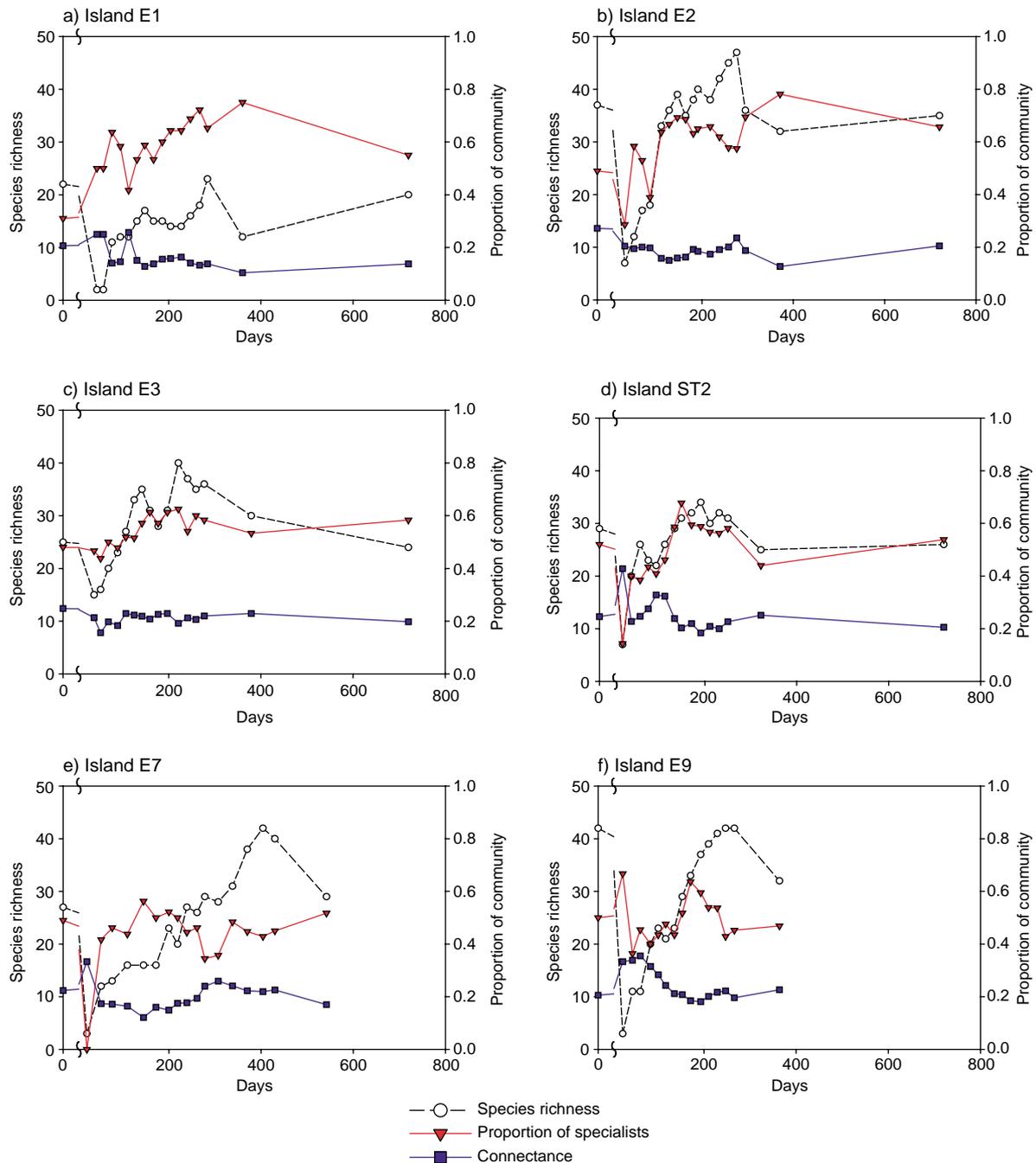


Fig. 1. Food-web attributes plotted against time (days). Species richnesses (circles) correspond to the first y-axis, and the second y-axis corresponds to both the proportion of the community made up of specialists (triangles), and the mean generality (i.e. connectance; squares). Individual island attributes are in Table 1.

specialist/generalist thresholds (0.1) for the same analysis suggests the increase in SF is also significant (Table 3).

The fraction of super-generalists increased over time ($F = 7.040$, $DF = 4$, $p_{G-G} = 0.007$). After defaunation, there were 46 super-generalist taxa belonging to four taxonomic groups: 15 ants (Hymenoptera: Formicidae), 15 wasps (Hymenoptera: 5 families), 13 spiders (Araneae: 4 families), 2 beetles (Coleoptera: Cantheridae and Lampyridae), and 1 true bug (Hemiptera: Anthorcoridae, *Dufouriellis afer*) (Supplementary material Appendix 1). Ants were the most

common super-generalist taxa (93 sampling periods), followed by wasps (63 sampling periods), and spiders (27 sampling periods) ($n = 96$). Super-generalist beetles and true bugs were found in only four and two surveys, respectively. Averaging the super-generalists' species richness over all six islands and all surveys, ants had the highest average species richness (8.17 species/island, $SD = 2.32$) followed by parasitoids (6.33 species/island, $SD = 3.08$), and spiders (3.67 species/island, $SD = 2.34$). Including all taxonomic groups, the mean number of super-generalist colonizers per island

Table 3. Summary of sensitivity analysis of generalist/specialist criterion. Disconnected species were included in these food-webs. Due to autocorrelation in the data, a repeated measures ANOVA was used for the observed data, and a Kendall's rank correlation (τ) was used for the simulated food-webs since there was no implicit data structure, and the simulated food-webs were random draws from the metaweb with replacement between sampling for each food-web.

| Food web set type | Trophic specialist/generalist cut-off (proportion of community consumed) | |
|--|--|--|
| | 0.10 | 0.20 |
| Observed RM-ANOVA | F = 8.47, DF = 4 $p_{G-G} = 0.003^*$ | F = 9.69, DF = 4, $p_{G-G} = 0.002^*$ |
| Simulated τ ($\alpha = 0.05$) | $\tau = 0.239^*$ | $\tau = 0.135^*$ |
| No. of randomly generated sets out of 1000 occurring in distribution tail. | 20 sets | 11 sets |

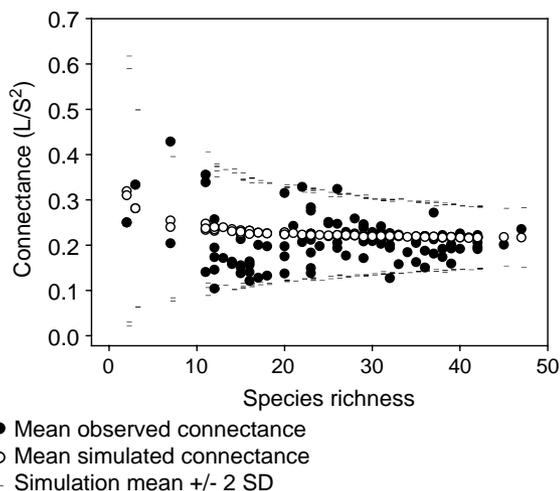
* =statistically significant ($\alpha = 0.05$).

was 19 species (SD = 7.87, $n = 6$). The number of super-generalists ranged from 7 (island E1) to 27 taxa (islands E2 and E9).

The mean C among all observed food-webs was 0.209 ($n = 102$, SD = 0.058). Post-defaunation C was negatively correlated with time ($F = 6.808$, $DF = 4$, $p_{G-G} = 0.005$, Fig. 1). However, C had a mixed response to time as it decreased by 26% between sampling periods one and three, but maintained the same level from sampling period 3 to 5 ($C = 0.18$). The slope of regression Log L vs Log S is very close to 2 both including (slope = 1.940, SE slope = 0.004, $R^2 = 0.980$, $p = 0.0001$) and excluding (slope = 2.130, SE slope = 0.0008, $R^2 = 0.967$, $p = 0.0001$) the six food webs with $S < 10$. These results support the constant connectance hypothesis that “the exponent of [this] link-species relationship is approximately two” (Martinez 1992). This indicates that species did, on average, have proportionately more trophic links in larger food-webs. There was no correlation between C and island size or distance from the nearest colonization source.

Observed food-webs had a mean C of 0.209, but the simulated mean C was 0.226. Although one hundred of 102 observed food-webs (pre- and post-defaunation) fell within two standard deviations of the randomly assembled food-web mean C ($n = 98$ 010; Fig. 2), more observed food-webs fell below the simulation mean than expected by chance ($G = 18.82$, $n = 102$, $DF = 1$, $p < 0.001$). These differences between observed and simulated C were not significantly correlated with island size or distance from the nearest colonization source as noted above, suggesting that these important island biogeographic variables had little effect on C .

The “realized metaweb” which incorporated all 102 food-webs contained 250 distinct taxa and 3908 distinct food-web links ($C = 0.251$, $L/S = 64$, SD = 24). Between the realized and speculative metawebs, species shared a mean of 62% (SD = 38%) of their links. Specialists shared 83% of links (SD = 31%, $n = 149$), compared to only 29% for generalists (SD = 22%, $n = 101$). The speculative metaweb C (0.21) fell within the range of pre-defaunation



*Surveys with low species richness were sampled less than 1000 times due to software constraints. These survey numbers (Species richness (S), Number of simulations (N)) are: A2 (S = 2, N = 107), A3 (S = 3, N = 145), A19 (S = 7, N = 400), A70 (S = 3, N = 179), A88 (S = 3, N = 179).

Fig. 2. Connectance (C) for all observed and null food-webs vs species richness (S) (The standard deviation calculations are from Monte Carlo simulations.)

C of individual food-webs ($C = 0.21$ to 0.27 , $n = 6$, $SD = 0.026$; Fig. 2).

Discussion

We detected differences in colonization patterns for trophic specialists and generalist species, using mangrove arthropod data (Simberloff and Wilson 1969). We found strong community-level support for trophic specialists typically colonizing later than trophic generalists, suggesting that those arthropods that recolonized the mangroves were not merely a random subset of the regional species pool (Simberloff 1981). This finding was also supported by Monte Carlo simulations of randomly assembled food-webs. Trophic structure complexity (C) was negatively correlated with time but not with species richness during reassembly. Although we assume that species cannot colonize successfully without their prey already present (Holt et al. 1999), our evidence strongly suggests that colonists' trophic breadth and arrival time, rather than undifferentiated species richness establishes observed community complexity and trophic structure.

Role of trophic breadth during re-colonization

Trophic breadth may influence species colonization order because generalists are more likely able to consume early-colonizing prey, while specialists' success depends on the (prior) presence of particular species, particularly on species-poor islands (Holt et al. 1999). While there are likely multiple reasons why generalists colonized before specialists, we suggest some reasons which could be fruitful if tested in the context of community assembly. While generalists appeared to be good early colonizers, later-arriving specialists might be more successful than generalists (Fig. 1). This observation is consistent with specialists being relatively more efficient foragers and thus superior competitors for trophic resources, while late arrival helps ensure that specialist's prey are present (MacArthur and Levins 1964, Hicks and Tahvanainen 1974, but see Fox and Morrow 1981, Kalcounis-Ruppell and Millar 2002). Why generalists colonize earlier could also be explained by body size effects (Gotelli and Ellison 2002); physiological tolerance differences between generalists and specialists (Jenkins and Buikema 1998); reproductive strategies (e.g. r - vs K - selection) (MacArthur and Wilson 1967, Parsons 1983); predictability of resources (Jaenike 1978); differences in relative rates of mobility or even systematic differences in abundance. Generalists may be more effective dispersers than specialists (Spiller et al. 1998), may be less sensitive to effects of habitat size, and may persist longer when conditions are less favorable (Parsons 1983). As a result, generalist numbers may build up during the initial stages of recolonization and thereby increase community complexity (i.e. increased connectance, $C > 0.18$; Fig. 1). However, these results are somewhat surprising given that specialists primarily consumed the assumed omnipresent basal resources: mangrove, detritus, algae, lichens, and fungi. Mangrove specialist arrival may be linked to flower, fruit, or seed

production. Generalized predators like spiders, lacewings, and some parasitic hymenoptera were the early colonists and their prey were commonly present.

Super-generalists colonized some islands later than did specialists and generalists. This challenges the claim that early colonization success is based largely on having broad trophic habits. Assuming that trophic breadth is a primary factor for successful early colonization and that all species densities are equal, super-generalists might be expected to be among the first successful colonists. However 51% of their colonization events occurred after day 150 of 360, though undetected colonization events for this group are possible (i.e. due to death or emigration). It is evident that although super-generalists have a very broad diet, they may be constrained by other life-history traits other than diet (Siepel 1994). For example, ant colonies produce reproductives only after long intervals. For this group of super-generalists microhabitat quality may be a better predictor of colonizing success than area and distance from the mainland (Simberloff 1976). Population estimates would help explore these possibilities by determining relative immigration and extinction rates for testing these and other explanations and alternative hypotheses.

Community complexity

The average community complexity, among all food-webs in terms of C (0.20) is near the middle of the range of most published food-webs ($0.05 \leq C \leq 0.3$, Dunne et al. 2005). Typically, C does not vary with species richness when considering food-webs with more than 15 species (Martinez 1992), however these results suggest that connectance is more variable and can be greater in primary successional communities. Our observed trend of connectance decreasing with time in the initial sampling periods primarily indicates early colonization of small food-webs ($S < 10$) by generalists resulting in high C ($0.3 \leq C \leq 0.47$; Fig. 1). C was much more stable ($C \cong 0.20$) among older and more species-rich food-webs (from period 3 to 5, $S \geq 15$) because the later colonists varied more in trophic breadth and comprised smaller fractions of the existing communities. Constant connectance was unlikely an artifact of food-web size, or substantial increases in generalists' prey numbers with increasing S . High species turnover suggests that generalists' prey species were more likely "exchanged" between sample dates experiencing small rather than substantial gains in prey species (Simberloff and Wilson 1969). Moreover, proportionally fewer generalist species were colonizing in later surveys (i.e. GF must decrease if SF increases). Thus the variation in later colonists' trophic breadths maintained complexity as species richness increased, despite the positive correlation between species richness and time since defaunation (Simberloff and Wilson 1969). This finding corroborates the constant connectance hypothesis (Martinez 1992) that C is roughly independent of S above the threshold of $S > 10-15$, and is also consistent with microcosm studies demonstrating that species are lost from initial communities with highly variable C in a way that reduces the variation of C among more persistent communities (Fox and McGrady-Steed 2002). Alternatively, a diet breadth model also explains how community

complexity becomes constrained when species richness increases (Beckerman et al. 2006). Combining foraging theory with food-web theory, the diet breadth model assesses how community complexity is constrained by the interplay between species' optimal foraging behavior and physiology. More analyses using the community assembly approach and the diet breadth model are needed to resolve and specify under what conditions increasing species richness constrains community complexity (Murtaugh and Kolath 1997).

Simulated food-webs

The *C* values of simulated food-webs differ significantly from those of observed food-webs (Fig. 2) indicating that biotic interactions may constrain trophic links in real food-webs. Biotic effects in the observed food-webs or sampling effects in the null food-webs may explain these differences. Fox and McGrady-Steed (2002) demonstrated similar nonrandom effects of the assembly process on connectance. In our findings, lower *C* could mean decreased predation and competition for some species, thereby increasing colonization success and quite possibly persistence time (May 1973). This interpretation is congruent with the recognition by Holt et al. (1999) that trophic resources present during colonization are key biotic factors affecting community structure. There is little evidence to support an alternative explanation of statistical sampling effect accounting for the differences between simulated and observed food-webs.

Simberloff and Wilson (1969) observed that island size and degree of isolation affected arthropod recolonization on defaunated mangrove islands. This finding supported Island biogeography theory's core principle that island size and isolation profoundly influence the interplay of species' immigration and extinction rates affecting colonization, persistence, and coexistence (MacArthur and Wilson 1967). Although the Equilibrium theory of island biogeography presents a robust framework for investigating maintenance of species diversity, Pielou (1979) cogently observed that species are referenced as propagules and lacked species-specific biologies. Using Simberloff and Wilson's study, Heatwole and Levins (1972) discovered that communities do return to their previous equilibrium state when colonists are assigned to eight trophic groups. Although Simberloff (1976) demonstrated problems with their approach and methods, Glasser's reanalysis of Simberloff and Wilson's study also found that trophic position and available energetic resources affected colonization order and community structure during recolonization (Glasser 1982). These findings may help explain the discrepancies between Simberloff and Wilson's (1969) observed similarities in species richness and differences in species composition between the pre-defaunation and one-year surveys. That is, compositional differences may obfuscate functional similarities.

Limitations

Our study eliminated the 10% of species with no connection to the speculative metaweb and also excluded species

lacking trophic connections from individual food-webs (mean <1 species per food-web). Such small changes appear unlikely to qualitatively alter our conclusions, especially about connectance in larger food-webs ($S > 10$ species; Martinez 1991, 1992, Martinez et al. 1999). For example, Martinez et al. (1999) described how highly incomplete sampling of food-webs can still provide relatively accurate measures of *C*. Although our species' diets are somewhat uncertain, it seems unlikely for such uncertainty to result in the patterns highlighted here. The consistency of our results at different SF thresholds further suggests that the patterns are fairly robust.

Variations were eliminated in the first trophic level and among non-arthropod consumers by assuming a constant number of basal species and only considering arthropod consumers in each food-web. This suggests that our findings may be applicable only to higher trophic levels and arthropods. However, this limitation may not be extremely restrictive. Arthropods are one of the most speciose taxa on the planet and exhibit a full range of trophic consumption habits (e.g. herbivore, carnivore, omnivore, parasite, parasitoid, etc.).

Our analysis used more highly resolved trophic information for constructing links between species within each food-web, which widely differs from Heatwole and Levins' approach of pooling species into eight broad trophic categories. In addition, our analysis compared responses of individual islands to each other. Our simulated colonizations revealed few instances of trophic specialists increasing with time, even when specialist/generalist criteria were altered (Table 3). However, some of the parasitoid links in the speculative metaweb were less-specific because they were described within the literature at the family level. This resulted in the undesired outcome of some parasitoids being designated as super-generalists. This suggests some parasitoid trophic links could be systematically over-estimated within the speculative metaweb. However, this over-estimation likely did not bias the result of super-generalists colonizing later. Ants were the most apparent taxa and were the primary group responsible for the result of super-generalists arriving later. They typically arrived during or before the third sampling period and persisted until the last. Alternatively late-arriving parasitoids were typically found in two or fewer sampling periods for each island, were infrequently observed in consecutive sampling periods, and colonized less-frequently than the ants. Our result of super-generalists colonizing later was not an artifact of overly-broad diet descriptions within the speculative metaweb, but due to the late arrival of ants which are the most apparent and common super-generalists. Like many other published food-webs, this speculative metaweb could be improved with more taxonomic and life-history work (Cohen et al. 1993).

Finally, our analyses did not incorporate interaction strength into the complexity of food-web structure. Were abundance data available and detailed biologies known for all 250 taxa, additional biological mechanisms might have given us further insight about the colonization process of these islands.

In conclusion, we found trophic breadth to be associated with colonization order in the mangrove arthropod system. With different colonization order of different trophic

breadths, we found that overall community trophic structure can be altered and helps explain regularly observed food-web patterns such as constant connectance (Martinez 1992). That is, we provide additional evidence that community dynamics of colonization and extinction constrain connectance to be less variable and independent of species richness over time (Fox and McGrady-Stead 2002). The pattern of specialists colonizing after generalists was non-random and not likely an artifact of specialist-generalist threshold or poor diet descriptions, as such errors would be systematic. Although our results of species richness (S) and specialists fractions (SF) increasing with time combined with independence of connectance (C) with species richness (S) appear to be contradictory, it was the significant increases in the super-generalist fraction (SGF) that helped resolve the apparent contradiction by counterbalancing the increase of specialist fractions (SF) with time. This in turn eliminated more significant changes of connectance (C) with species richness (S) and time. Thus, we suggest that the fractions of both specialists and super-generalists may increase as communities gain and lose species over time. While apparently robust in the arthropod-dominated mangrove system, such patterns should be tested in other systems to explore their generality in community assembly. These and other hypotheses may be more effectively tested as improved data and analytical techniques become available.

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Supplementary material Appendix 1–3 can be found online as appendix O15915 at www.oikos.ekol.lu.se/appendix.