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Food webs are built up with nested subwebs

MICHIO KONDOH,^{1,2,3} SATOSHI KATO,¹ AND YOSHIKUNI SAKATO¹

¹*Ryukoku University, 1-5 Yokoya, Seta Oe-cho, Otsu, Japan*

²*PRESTO, Japanese Science and Technology Agency, 4-1-8 Honcho, Kawaguchi, Japan*

Abstract. Nested structure, in which specialists interact with subsets of species with which generalists interact, has been repeatedly found in networks of mutualistic interactions and thus is considered a general feature of mutualistic communities. However, it is uncertain how exclusive nested structure is for mutualistic communities since few studies have evaluated nestedness in other types of networks. Here, we show that 31 published food webs consist of bipartite subwebs that are as highly nested as mutualistic networks, contradicting the hypothesis that antagonistic interactions disfavor nested structure. Our findings suggest that nested networks may be a common pattern of communities that include resource–consumer interactions. In contrast to the hypothesis that nested structure enhances biodiversity in mutualistic communities, we also suggest that nested food webs increase niche overlap among consumers and thus prevent their coexistence. We discuss potential mechanisms for the emergence of nested structure in food webs and other types of ecological networks.

Key words: *antagonistic network; bipartite food web; complementarity hypothesis; complex network; food web; mutualism; mutualistic network; nestedness; null model analysis; trophic interaction.*

INTRODUCTION

Within ecosystems, a number of species are connected by interspecific interactions such as trophic, mutualistic, and parasitic interactions, forming a complex network of biological communities. Since the structure of interaction networks strongly affects community and population dynamics, identifying the structural patterns of those networks enhances our understanding of the mechanisms that shape or maintain communities (Pimm 1991, de Ruiter et al. 2005). Ecological network studies comparing, for example, mutualism vs. antagonism or different habitat types promote identification of the fundamental structural relationship between communities, and the key determinants of community structure and its relevance to community dynamics (Bascompte et al. 2003, Guimarães et al. 2006).

Nestedness (Atmar and Patterson 1983), defined in the context of community network research as “a pattern of interaction in which specialists interact with species that form perfect subsets of the species with which generalists interact” (Bascompte and Jordano 2007), has been found in bipartite community networks

of interspecific interactions (i.e., networks formed by two interacting functional groups, within each of which no interaction occurs). A nested interaction network has two characterizing features: (1) a generalist (i.e., a species interacting with more species) in a group interacts with generalists in the other group to form a core of densely interacting species; (2) a specialist in one group tends to interact with a few generalists in the other group.

Bascompte et al. (2003) reported that animal–plant mutualistic networks, such as plant–seed disperser and plant–pollinator communities, are highly nested. Subsequently, the same structure has been repeatedly found in other types of mutualistic networks, such as between ants and extrafloral nectary-bearing plants (Guimarães et al. 2006), anemone fish and sea anemone (Ollerton et al. 2007), and marine cleaning mutualism (Guimarães et al. 2007). These findings led to a hypothesis that nested structure is a general pattern of mutualistic networks (Bascompte et al. 2003, Thompson 2005, Guimarães et al. 2006) and initiated studies that aimed to identify the cause (Thompson 2005, Guimarães et al. 2006, Lewinsohn et al. 2006, Rezende et al. 2007a, Santamaría and Rodríguez-Gironés 2007, Krishna et al. 2008) and ecological consequence (Memmott et al. 2004, Bastolla et al. 2009) of nested structure in mutualistic communities.

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³ E-mail: mkondoh@rins.ryukoku.ac.jp

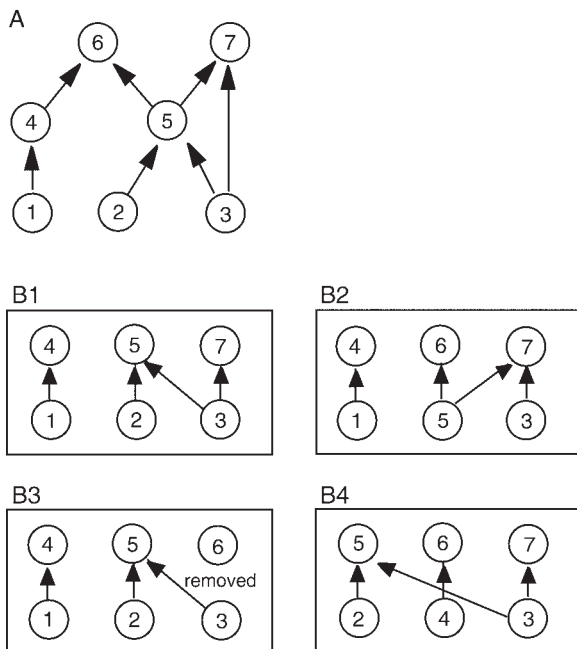


FIG. 1. The method used to extract bipartite subwebs from a complex food web. When three consumer species ($n = 3$) from complex food web (A), four bipartite subwebs (B1–B4) are extracted. In subweb B3, species 6, which has no resource in the subweb, is deleted, leading to a five-species subweb.

Given the important implications of nested structure in community ecology, its evaluation in other types of networks would be of particular importance, especially when nested structure is predicted to be disfavored by antagonistic interactions (Bascompte et al. 2003, Guimarães et al. 2006). However, most reported nested networks are of mutualistic interactions (Guimarães et al. 2006, 2007, Bascompte and Jordano 2007, Ollerton et al. 2007, Vázquez et al. 2009), except for a few studies (fish parasites [Poulin and Valtonen 2001]; scavenger communities [Selva and Fortuna 2007]; hosts and parasitoids [Joppa et al. 2010]). Thus, it is unclear whether nested structure is an exclusive feature of mutualistic networks.

Despite the rich body of research showing the importance of trophic network (food web) structure in determining a wide range of ecological processes such as population dynamics, biodiversity maintenance and ecosystem functioning (Pimm 1991, Worm and Duffy 2003, de Ruiter et al. 2005), only one study has examined nestedness in food webs. Bascompte et al. (2003) compared nestedness of 14 subsets of food webs with that of 52 mutualistic networks and concluded that food webs are significantly less nested than mutualistic networks. However, the 14 subwebs analyzed were extracted from only seven independent food webs with relatively small sizes. More comprehensive evaluation of nested structure in food webs would determine if nested structure is rare in these typical antagonistic networks

(Bascompte et al. 2003, Thompson 2005), and would provide further insights into the cause and consequence of nested interaction networks.

Here, we compare nestedness of bipartite trophic networks extracted from 31 community food webs and 59 mutualistic networks and show that (1) bipartite trophic networks with sufficient number of species or links are significantly nested and (2) the level of nestedness of trophic networks is comparative to that of mutualistic networks. These results show that a nested bipartite network is a major “building block” of complex food webs, contrary to the previous view that trophic interactions disfavor a nested community structure. In addition, the believed hypotheses that the coevolutionary process in mutualistic interactions generates a nested network or that nested structures enhance species coexistence are shown to have limited applicability to nested food webs.

MATERIALS AND METHODS

While nestedness is defined only for bipartite networks, food webs often consist of ambiguously defined trophic levels connected by a number of links of intraguild predation and thus cannot be viewed as a set of multilayered bipartite graphs. We therefore evaluated nestedness of food webs by extracting and analyzing the bipartite subwebs embedded in food webs. Two approaches, guild and random sampling, were used to evaluate nestedness in guild food webs and complex food webs, respectively. In the guild approach, we collected and analyzed published data of bipartite food webs representing a trophic guild (guild food webs), which consist of consumers that do not eat each other, and their resources (e.g., hosts and parasitoids; plants and herbivores). A similar approach was used by Bascompte et al. (2003), who analyzed resource–consumer bipartite networks (e.g., plants–herbivores, herbivores–carnivores) extracted from several detailed food webs. Non-bipartite complex food webs were analyzed by the random sampling approach, in which bipartite trophic modules (sub-webs embedded in a complex food web) are extracted from complex webs by a random sampling. The procedure to extract a bipartite web from a complex food web was as follows. First, n consumer species ($1 \leq n \leq$ [the number of consumer species of the system]) were randomly sampled from an original complex web and grouped into the “consumer part” (see Fig. 1 for case of $n = 3$). Next, the resource species utilized by those consumers were identified and added to the web as the “resource part.” Then, species that appeared in the web as both consumer and resource were removed from the resource part of the web. Consumer species that had no resource species in the web after this procedure were also removed. Two hundred bipartite subwebs were extracted from a complex food web, among which the most conservatively extracted bipartite subweb (produced by minimum deletion of species and trophic links) was regarded

TABLE 1. Nestedness (NODF) of the 31 representative food webs.

| Food webs | Species number (<i>S</i>) | Link number (<i>L</i>) | Nestedness | | <i>S</i> -NODF correlation | | | Reference |
|-----------------------|-----------------------------|--------------------------|------------|----------|----------------------------|----------|----------|-----------------------------------|
| | | | NODF | <i>P</i> | τ | <i>z</i> | <i>P</i> | |
| Guild | | | | | | | | |
| Altuda grassland | 74 | 184 | 30.41** | <0.001 | -0.083 | -1.729 | 0.084 | Joern (1979) |
| Marathon grassland | 78 | 173 | 31.17** | <0.001 | 0.06 | 1.251 | 0.211 | Joern (1979) |
| British <i>Prunus</i> | 94 | 116 | 36.87* | 0.03 | -0.045 | -0.935 | 0.350 | Leather (1991) |
| Finnish <i>Prunus</i> | 69 | 95 | 46.88* | 0.03 | -0.062 | -1.263 | 0.207 | Leather (1991) |
| Cabana | 75 | 176 | 32.04** | <0.001 | -0.024 | -0.510 | 0.610 | Valladares et al. (2001) |
| Córdoba zoo | 67 | 147 | 31.81** | <0.001 | 0.035 | 0.730 | 0.466 | Valladares et al. (2001) |
| Silwood 1 | 38 | 130 | 62.27** | <0.001 | 0.209** | 4.310 | <0.001 | Rott and Godrray (2000) |
| Belize | 134 | 183 | 10.23** | <0.001 | 0.047 | 0.986 | 0.324 | Lewis et al. (2002) |
| Hokkaido forest | 74 | 374 | 55.99** | <0.001 | 0.391** | 8.030 | <0.001 | Hirao and Murakami (2008) |
| Silwood 2 | 32 | 38 | 25.03 | 0.15 | 0.104* | 2.142 | 0.032 | Müller et al. (1999) |
| Complex | | | | | | | | |
| Benguela | 29 (29) | 72 (203) | 36.60 | 0.97 | 0.038 | 0.782 | 0.434 | Yodzis (1998) |
| Bridge Brook Lake | 70 (75) | 116 (553) | 12.25 | 1 | -0.071 | -1.480 | 0.139 | Havens (1992) |
| Canton Creek | 100 (108) | 397 (708) | 38.33** | <0.001 | 0.086 | 1.795 | 0.073 | Townsend et al. (1998) |
| Caribbean Reef 1 | 50 (50) | 196 (556) | 52.28** | <0.001 | 0.139* | 2.860 | 0.004 | Opitz (1996) |
| Caribbean Reef 2 | 250 (250) | 1028 (3355) | 36.65** | <0.001 | 0.564** | 11.750 | <0.001 | Opitz (1996) |
| Chesapeake Bay | 33 (33) | 36 (72) | 13.65 | 0.79 | 0.083 | 1.683 | 0.092 | Baird and Ulanowicz (1989) |
| Coachella Valley | 30 (30) | 101 (290) | 52.44 | 0.6 | 0.142* | 2.875 | 0.004 | Polis (1991) |
| El Verde | 146 (156) | 491 (1510) | 22.75** | <0.001 | -0.208** | -4.319 | <0.001 | Waide and Reagen (1996) |
| Little Rock Lake | 170 (181) | 724 (2375) | 24.51** | <0.001 | 0.059 | 1.237 | 0.216 | Martinez (1991) |
| Northeast U.S. Shelf | 81 (81) | 522 (1483) | 50.53** | <0.001 | -0.123* | -2.530 | 0.011 | Link (2002) |
| Scotch Broom | 153 (154) | 292 (370) | 11.44 | 0.33 | -0.179** | -3.732 | <0.001 | Memmott et al. (2000) |
| Skipwith Pond | 35 (35) | 141 (380) | 58.95 | 0.55 | -0.263** | -5.376 | <0.001 | Warren (1989) |
| St. Marks Estuary | 50 (51) | 99 (270) | 42.36** | <0.001 | 0.11* | 2.261 | 0.024 | Christian and Luczkovich (1999) |
| St. Martin Island | 43 (44) | 94 (218) | 27.42 | 0.58 | -0.129** | -2.648 | 0.008 | Goldwasser and Roughgarden (1993) |
| Stony Stream | 98 (112) | 397 (832) | 36.61** | <0.001 | -0.288** | -5.993 | <0.001 | Townsend et al. (1998) |
| Ythan Estuary 1 | 92 (93) | 172 (421) | 21.42** | <0.001 | -0.09 | -1.879 | 0.060 | Hall and Raffaelli (1991) |
| Ythan Estuary 2 | 129 (134) | 298 (598) | 16.93** | <0.001 | -0.256** | -5.335 | <0.001 | Huxham et al. (1996) |
| Maspalomas Lagoon 1 | 17 (17) | 19 (25) | 23.96 | 0.82 | 0.176** | 3.437 | 0.001 | Almunia et al. (1999) |
| Maspalomas Lagoon 2 | 17 (17) | 23 (29) | 27.27 | 0.89 | -0.113* | -2.230 | 0.026 | Almunia et al. (1999) |
| Maspalomas Lagoon 3 | 14 (14) | 15 (21) | 23.26 | 0.88 | 0.014 | 0.277 | 0.782 | Almunia et al. (1999) |
| UK grass | 66 (75) | 71 (113) | 14.38* | 0.01 | 0.251** | 5.201 | <0.001 | Martinez et al. (1999) |

Note: Species numbers and link numbers without and with brackets are of representative and original webs (where isolated species are excluded), respectively.

* $P < 0.05$; ** $P < 0.01$.

as a “representative” web of a complex food web. Thirty-one published food webs were analyzed, of which 10 and 21 webs are of guild and complex webs (see Table 1 for the list of food webs analyzed). We have confirmed that an alternative procedure of starting with n resource species and their consumers and removing the species from the consumer part does not alter the result qualitatively. Fifty-nine mutualistic webs (Rezende et al. 2007b), comprising 36 plant–pollinator and 23 plant–frugivore webs, were also analyzed.

We examined the dependence of nestedness on species richness using both intra-community and inter-community comparisons. In the former, we measured nestedness of 200 subwebs with varying number of species extracted from the same web. Subwebs were generated by using randomly sampled n consumer species (n from uniform distribution between 1 and the number of consumer species in the original web). In the inter-

community comparison, the representative bipartite web of each web was used, which is the subweb with the maximum number of species among the 200 subwebs. When there were more than two subwebs with the maximum species number, the web with the largest numbers of interaction was used. The representative web is the original web in guild food webs. The relationship between species richness and nestedness was analyzed by Kendall's rank correlation (τ) test.

The dependence of nestedness on link number was also examined. A strong correlation was expected between link number and species richness. To isolate the effect of link number from that of species richness, we calculated the residuals of a log-log least squares linear regression of link number against species number. Thus, the food webs were classified into ones with positive residuals and the others with negative residuals. We compared the average relative nestedness, defined as

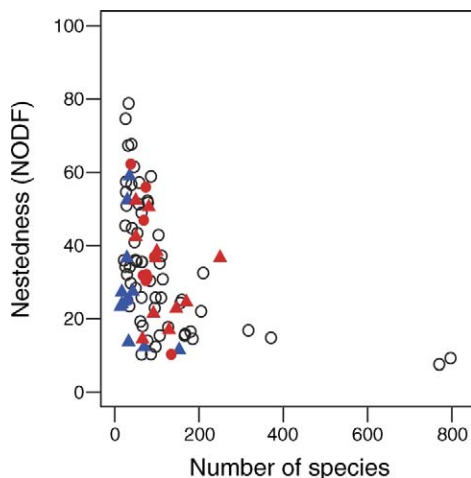


FIG. 2. Species richness and nestedness (NODF) of 31 representative food webs (triangles and circles in red or blue) and 59 mutualistic networks (open circles). Red and blue circles are for guild webs with significant and nonsignificant nestedness, respectively. Red and blue triangles represent complex webs with significant and nonsignificant nestedness, respectively.

$(\text{nestedness} - \text{nestedness}_{\text{avr}}) / \text{nestedness}_{\text{avr}}$ where $\text{nestedness}_{\text{avr}}$ is the average nestedness of the random replicates (null models; see the next paragraph for details), for both groups as Bascompte et al. (2003) did for mutualistic networks.

Since we were to compare nestedness of extracted webs with varying sizes, the level of nestedness was measured mainly by using NODF (Almeida-Neto et al. 2008), which is proved to be less affected by species number than other metrics (Almeida-Neto et al. 2008). NODF accounts for paired overlap and decreasing fill of the matrix representing an interaction network and takes values between 0 (perfectly non-nested) and 100 (perfectly nested). An alternative metric, N , was also used to allow a direct comparison between the earlier study (Bascompte et al. 2003) and ours, although N tends to be positively correlated with matrix size (Almeida-Neto et al. 2008). N is defined as $(100 - T) / 100$, where T is the matrix temperature (Atmar and Patterson 1993) representing the ratio of sum of squared deviations from the boundary line of unexpected presence or absence and the maximum value possible for the matrix, multiplied by 100. N values were between 0 (perfectly non-nested) and 1 (perfectly nested). NODF and T were calculated by ANINHADO software (Guimarães and Guimarães 2006), where evaluation of T is based on the algorithms identical to that of the nestedness temperature calculator (Atmar and Patterson 1993) used by Bascompte et al. (2003).

The significance of nestedness was tested by using null model analysis (Gotelli 2001). We used the incidence proportional model (Ulrich et al. 2009; identical to null model 2 in Bascompte et al. 2003) as a null model, where

probability that a consumer and a resource interact is given by the arithmetic mean of the interacting probabilities of the focal consumer and resource species. This model was chosen because (1) the same constraint should be applied to both consumers and resources, (2) a sufficient number of models are generated even if a network has only a few links, and (3) difference and variability in the number of interactions among species are assumed (Ulrich et al. 2009). We used t test to test the significance of difference in nestedness between different types of networks.

RESULTS

There was no qualitative difference between the main results based on NODF (Table 1) and T (Appendix A: Table A1), except their dependence on species number (Fig. 2; Appendix B: Fig. B1). Hereafter, we mainly present our result based on NODF metric.

The average nestedness (NODF) of all the representative food webs, which consist of the 10 original guild webs and the 21 largest bipartite webs extracted from complex webs, was 32.47 ± 2.64 (mean \pm SE). There was no significant difference between the nestedness of these 31 food webs and the nestedness of the 59 mutualistic networks (34.44 ± 2.33 ; $df = 72.11$, $t = -0.560$, $P = 0.58$). Among the 31 food webs, 20 food webs (64.5%; 9 out of 10 guild webs and 11 out of 21 complex webs) were significantly nested (Table 1), which is slightly smaller than the proportion of nested webs in mutualistic webs (74.6%; 44 out of 59). The webs that were not significantly nested were Silwood 2, Benguela, Bridge Brook Lake, Chesapeake Bay, Coachella Valley, Scotch Broom, Skipwith Pond, St. Martin Island, and Maspalomass Lagoon 1–3. The average nestedness of guild food webs and complex food webs were 36.27 ± 4.81 and 30.67 ± 3.16 , respectively. There was no significant difference between them ($df = 17.03$, $t = -0.974$, $P = 0.34$).

In intercommunity comparisons, while there was no significant correlation between species richness and nestedness among the 31 representative webs ($\tau = -0.108$, $z = -0.850$, $P = 0.40$; Fig. 2), the fraction of significantly nested food webs tended to increase with increasing species richness (Fig. 2). In guild webs, only Silwood 2 web was not significantly nested ($P = 0.15$), and it had the smallest number of species (32 species). In complex webs, all the 13 webs with ≥ 50 species except Bridge Brook Lake ($P > 0.999$) and Scotch Broom ($P = 0.33$) were significantly nested, while all the 8 webs with < 50 species were not significantly nested. No significant difference was detected between the relative nestedness of the representative webs with more links (webs with positive residuals of a log-log least squares linear regression of link number against species number) and those with negative residuals ($df = 25.99$, $t = 0.633$, $P = 0.53$; Appendix B: Figs. B2, B3).

In intra-community comparisons, no clear correlation was detected between species richness and nestedness.

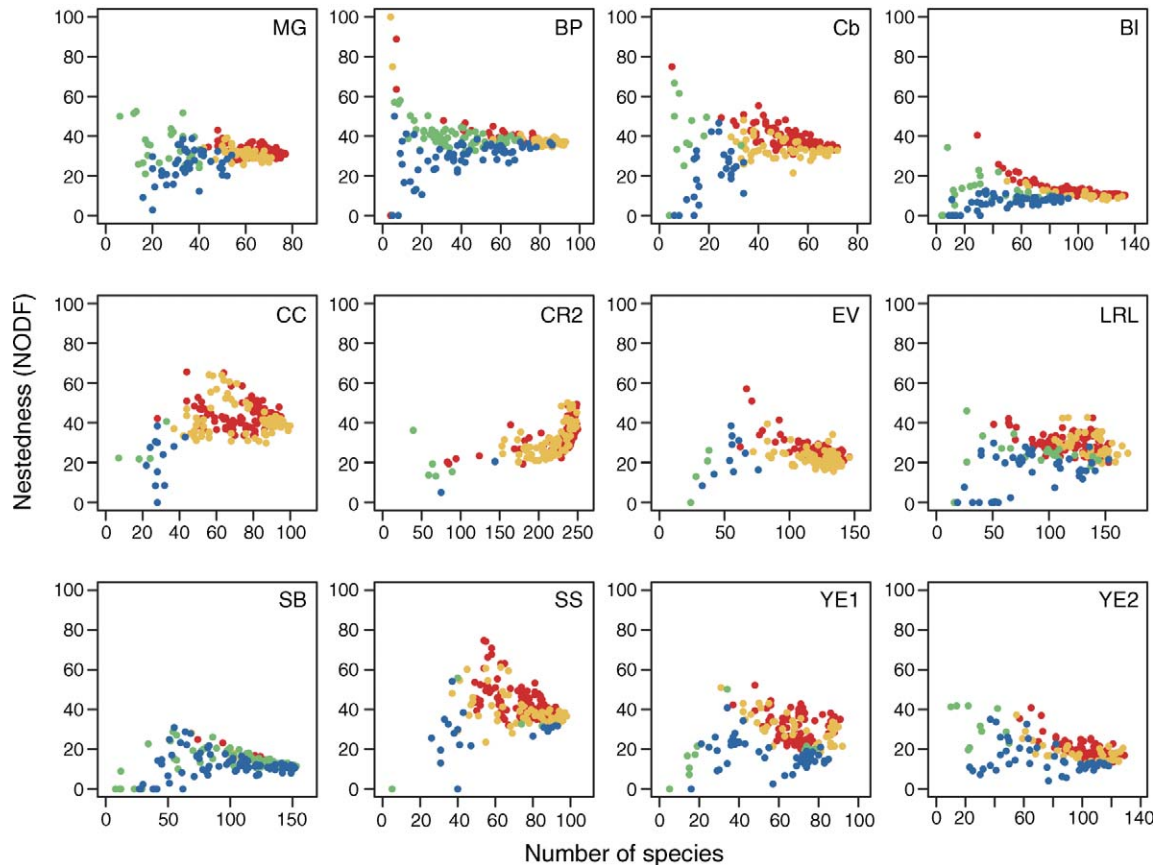


FIG. 3. Species richness and nestedness (NODF) of subwebs extracted from the 12 largest food webs. Guild webs are: Marathon Grassland (MG), British *Prunus* (BP), Cabana (Cb), and Belize (BI). Complex food webs are: Canton Creek (CC), Caribbean Reef 2 (CR2), El Verde (EV), Little Rock Lake (LRL), Scotch Broom (SB), Stony Stream (SS), Ythan Estuary 1 (YE1), and Ythan Estuary 2 (YE2). Red and yellow circles represent significantly nested subwebs with positive and negative residuals of a log-log least-squares linear regression of link number against species number, respectively; green and blue circles represent non-significantly nested subwebs with positive and negative residuals, respectively.

While a significantly positive correlation was observed in 8 out of 31 webs (25.8%), a significantly negative correlation was also observed in other 8 webs (Table 1, Fig. 3; Appendix B: Figs. B2, B3). The proportion of significantly nested food webs tended to increase with increasing species number in intra-community comparisons in both guild and complex food webs (Fig. 3; Appendix B: Figs. B2, B3).

DISCUSSION

Food webs generally seemed to consist of nested subwebs, contrary to the earlier view that nested structure is uncommon among groups of antagonistic interactions (Bascompte et al. 2003, Thompson 2005, Guimarães et al. 2006, Selva and Fortuna 2007). Bipartite trophic networks, such as guild food webs and webs extracted from complex webs, were nested to a level comparable to that of mutualistic networks. In addition, the majority of subwebs extracted from the original webs were significantly nested, if the total

species number was sufficiently large, showing a pattern similar to that of mutualistic webs (Bascompte et al. 2003). These results represent a structural similarity between trophic and mutualistic communities.

Contrary to our results, Bascompte et al. (2003) found less nestedness in food webs. This seems to be explained by the sensitivity of temperature metric to species number (Almeida-Neto et al. 2008). Almeida-Neto et al. (2008) reported that temperature (T) tends to be lower (N being higher) when species richness is higher, implying that a larger web is more likely to be judged more nested. Indeed, the positive relationship between species richness and N observed in both trophic and mutualistic networks (Fig. B1) vanished when NODF is used as a nestedness metric (Fig. 2). The higher nestedness in mutualistic webs in Bascompte et al. (2003) would be attributable to the sensitivity of N to species number (Almeida-Neto et al. 2008) and the fact that the mutualistic webs tended to be larger than the food webs in their study. In fact, food webs were as

highly nested as mutualistic networks when NODEF, a metric sufficiently insensitive to species number, was used.

There have been investigations as to the cause (Ollerton et al. 2003, Thompson 2005, Guimarães et al. 2006, Lewinsohn et al. 2006, Rezende et al. 2007a, Santamaría and Rodríguez-Gironés 2007, Krishna et al. 2008) and ecological consequence of nested structure observed in community networks (Memmott et al. 2004, Bastolla et al. 2009). Those studies are in most cases based on the believed pattern that nested structure is a characterizing feature of mutualistic networks. Our finding that both trophic and mutualistic networks (and others) are similarly nested allowed us to gain interesting insights into these issues.

The present study has implications about what generates nested networks. It has been hypothesized that nested mutualistic networks are jointly produced by two evolutionary processes: (1) coevolutionary complementarity (e.g., pollinator's long tongue and plant's long corolla) initiating the pairwise mutualistic interaction and (2) coevolutionary convergence allowing other species to be connected to the network (Thompson 2005). In this view, the core of generalists is evolutionarily associated by specialists (complementarity hypothesis; Guimarães et al. 2006, Bascompte and Jordano 2007, Rezende et al. 2007a). However, the fact that food webs are also nested clearly contradicts the prediction of complementarity hypothesis that antagonistic interactions, such as prey-predator interactions, should disfavor complementarity and thus lead to fewer nested networks with greater specificity (Guimarães et al. 2006, Selva and Fortuna 2007). Hence although the complementarity hypothesis may explain the nestedness of mutualistic networks, it does not explain nestedness in ecological networks including food webs.

Mutualistic interactions are often accompanied by consumer resource utilization provided by the interacting species. Nested structure may be a general feature of consumer-resource interactions since most communities in which nested networks have been observed are variants of consumer-resource networks (e.g., pollinator-plant, seed disperser-plant, prey-predator, host-parasitoid, host-parasite, and scavenger-resource webs). There are three possible mechanisms through which resource-consumer interactions generate nested networks. First, optimal diet choice can give rise to nested structure. This theory predicts that an adaptive consumer utilizes all the resources above a specific threshold quality (MacArthur and Pianka 1966), implying that interspecific hierarchy in resource quality combined with consumers with varying threshold levels can produce a nested structure. A resource of higher value (in the context of optimal foraging theory) would be a more "generalist" resource, while a consumer with the lowest threshold level would be a more generalist consumer. Second, interspecific hierarchy that determines prey-predator roles (see cascade model in Cohen et al. 1990),

such as body size, can also create a nested food web, where the highest and lowest species in the hierarchy act as "generalist" consumer and resource, respectively. Third, but not exclusive, hypothesis is that the nested structure has emerged from random combination of two sets of nodes in proportion to their abundances (Poulin and Guégan 2000, Vázquez and Aizen 2003, Krishna et al. 2008). Of course nested structure in different communities may have arisen from different mechanisms, which remain to be determined.

The nested structure of food webs has implications for biodiversity maintenance. Noting the definition of nestedness in food webs (the resources utilized by species i is a subset of resources utilized by species j [$>i$]), it is clear that the nested assignment of resources to consumers maximizes resource overlap among consumers. The established theory that competing species cannot exist if the overlap of their resource usage is large (MacArthur and Levins 1967) suggests that the nested network of resource-consumer interactions should inhibit biodiversity maintenance. This is in contrast with the prediction that nested mutualistic networks should minimize effective interspecific competition and thus enhance multispecies coexistence (Bastolla et al. 2009). Given that nested architecture has been widely observed in biological communities, we suggest that there should be a nonrandom pattern or mechanism (e.g., niche differentiation in behavior, life history, or timing of resource use) that compensates this negative effect on species coexistence for those communities to persist. A potential compensating mechanism may arise from links and species not described in the bipartite trophic networks. Although it is no doubt that analyses of isolated and simple "modules" have been a standard method and contributed to the development of community ecology (Holt 1997), module dynamics is often altered by taking into account the effect of surrounding community where the focal module is embedded (Kondoh 2008). Since nested structure has the opposite consequence to species coexistence in trophic and mutualistic networks, it would be interesting to study how those different types of network are combined together to form the whole community (Melián et al. 2009). Future research is needed to identify the mechanism of how nested food webs can persist in nature.

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APPENDIX A

Nestedness (*N*) of the 31 representative food webs (*Ecological Archives* E091-217-A1).

APPENDIX B

Species richness and nestedness of ecological networks (*Ecological Archives* E091-217-A2).