CHAPTER 2

Spatial structure and dynamics in a marine food web

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Introduction

The role of space in population and community dynamics has been recently emphasized (e.g. Hanski and Gilpin 1997; Tilman and Kareiva 1997; Bascompte and Solé 1998). Several models for the coexistence of interacting species in heterogeneous environments have been formulated. These include the energy and material transfer across ecosystem boundaries and its implication for succession and diversity (Margalef 1963; Polis et al. 1997), the geographic mosaic of coevolution (Thompson 1994), the regional coexistence of competitors via a competition–colonization trade-off (Tilman 1994), the random assembly of communities via recruitment limitation (Hubbell 2001), and metacommunities (Wilson 1992). As a general conclusion of these approaches, succession, dispersal, local interactions, and spatial heterogeneity have appeared strongly linked to the persistence of diversity. However, the underlying pattern of ecological interactions in a spatially structured ecosystem and its implications for the persistence of biodiversity remains elusive by the lack of synthetic data (Loreau et al. 2003).

Introducing space and multiple species in a single framework is a complicated task. As Caswell and Cohen (1993) argued, it is difficult to analyze patch-occupancy models with a large number of species because the number of possible patch states increases exponentially with species richness. Therefore, most spatial studies have dealt with a few number of species (Hanski 1983), predator–prey systems (Kareiva 1987), or n-competing species (Caswell and Cohen 1993; Tilman 1994; Mouquet and Loreau 2003). On the other hand, the bulk of studies in food-web structure and dynamics have dealt with either large (but see Hori and Noda 2001) or small (but see Caldarelli et al. 1998) number of species, but make no explicit reference to space (Caswell and Cohen 1993; Holt 1996, 1997). Only a few studies have explored the role of space on a small subset of trophic interacting species (Holt 1997; Melián and Bascompte 2002).

The present study is an attempt to link structure and dynamics in a spatially structured large marine food web. We use data on the diet of 5526 specimens belonging to 208 fish species (Randall 1967) in a Caribbean community in five different habitats (Opitz 1996; Bascompte et al., submitted). First, we analyze structure by addressing how simple trophic modules (i.e. tri-trophic food chains (FCs) and chains with omnivory (OMN) with the same set of species are shared among the five habitats. Second, we extend a previous meta-community model (Mouquet and Loreau 2002) by incorporating the dynamics of trophic modules in a set of connected communities. Specifically, the following questions are addressed:

1. How are simple trophic modules composed by the same set of species represented among habitats?
2. How does the interplay between dispersal and food-web structure affect species dynamics at both local and regional scales?

Data collection: peculiarities and limitations

The Caribbean fish community here studied covers the geographic area of Puerto Rico–Virgin Islands.

Data were obtained in an area over more than 1000 km^2 covering the US Virgin Islands of St Thomas, St John, and St Croix (200 km^2), the British Virgin Islands (343 km^2), and Puerto Rico (554 km^2). The fish species analyzed and associated data were obtained mainly from the study by Randall (1967), synthesized by Opitz (1996).

Spatially explicit presence/absence community matrices were created by considering the presence of each species in a specific habitat only when that particular species was recorded foraging or breeding in that area (Opitz 1996; Froese and Pauly 2003). Community matrices include both the trophic links and the spatial distribution of 208 fish taxa identified to the species level. Randall's list of shark species was completed by Opitz (1996), which included more sharks with affinities to coral reefs of the Puerto Rico–Virgin islands area, based on accounts in Fischer (1978). Note that our trophic modules are composed only by fishes, and that all fish taxa is identified to the species level, which implies that results presented here are not affected by trophic aggregation.

The final spatially explicit community matrix includes 3,138 interactions, representing five food webs in five habitat types. Specifically, the habitat types here studied are mangrove/estuaries (m hereafter; 40 species and 94 interactions), coral reefs (c hereafter; 170 species and 1,569 interactions), seagrass beds/algal mats (a hereafter; 98 species and 651 interactions), sand (s hereafter; 89 species and 750 interactions), and offshore reefs (r hereafter; 22 species and 74 interactions). To a single habitat 85 species are restricted while 46, 63, 12, and 2 species occupy 2, 3, 4, and 5 habitats, respectively. Global connectivity values (C) within each habitat are similar to previously reported values for food webs (Dunne et al. 2002). Specifically, $C_m = 0.06$, $C_c = 0.054$, $C_a = 0.07$, $C_s = 0.095$, and $C_r = 0.15$.

Food-web structure and null model

We consider tri-trophic FCs (Figure 2.1(a)) and FCs with OMN (Figure 2.1(c)). We count the number and species composition of such trophic modules within the food web at each community. We then make pair-wise comparisons among communities ($n = 10$ pair-wise comparisons) and count the number of chains (with identical species at all trophic levels) shared by each pair of communities. To assess whether this shared number is higher or lower than expected by chance we develop a null model. This algorithm randomizes the empirical data at each community, yet strictly preserves the ingoing and outgoing links for each species. In this algorithm, a pair of directed links A–B and C–D are randomly selected. They are rewired in such a way that A becomes connected to D, and C to B, provided that none of these links already existed in the network, in which case the rewiring stops, and a new pair of links is selected.

We randomized each food web habitat 200 times. For each pair of habitats we compare each successive pair of replicates and count the shared number of simple tri-trophic FCs and chains with OMN containing exactly the same set of species. Then we estimated the probability that a pair-wise comparison of a random replicate has a shared number of such modules equal or higher than the observed value. Recent algorithm analysis suggest that this null model represents a conservative test for presence–absence matrices (Miklós and Podani 2004).

We calculated the number of tri-trophic FCs, and OMN chains common to all pairs of communities, and compared this number with that predicted by our null model (Figure 2.1(b) and (d)). The coral reef habitat shares with all other habitats a number of FCs and OMN larger than expected by chance ($P < 0.0001$ in all pair-wise comparisons except for the mangrove comparison, where $P < 0.002$ and $P < 0.01$ for FCs and OMN, respectively). Similarly, seagrass beds/algal mats and sand (a/s contrasts) share a significant number of FCs and OMN ($P < 0.0001$). Globally, from the 10 possible intercommunity comparisons, five share a number of modules higher than expected by chance (Figure 2.1(a) and (c) where arrows are thick when the pair-wise comparison is statistically significant, and thin otherwise). This suggests that habitats sharing a significant proportion of trophic modules are mainly composed by a regional pool of individuals.

The average fraction of shared FCs and OMN between habitat pairs is 38%±24.5% and 41%±25%, respectively, which still leaves more than 50% of

(a)

(b)

(c)

(d)
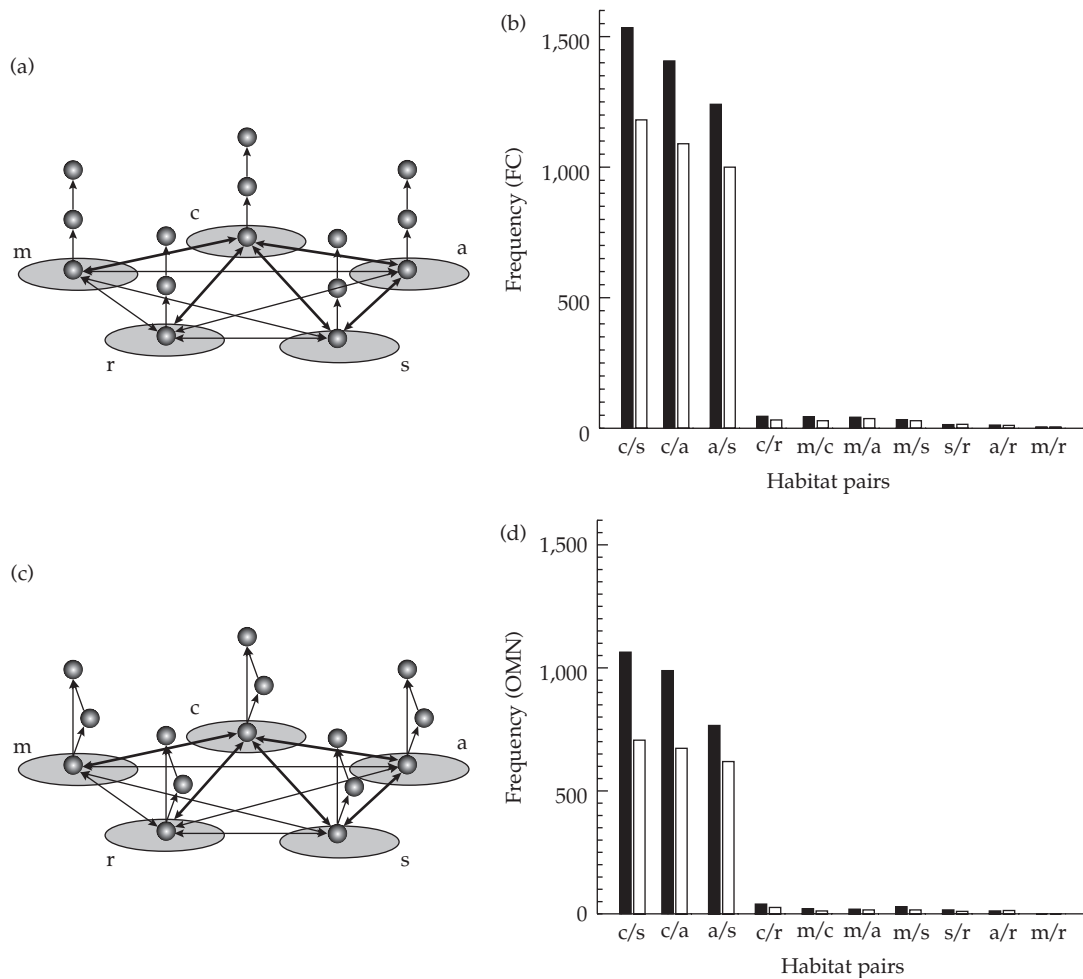
Figure 2.1 The food-web modules studied here are (a) tri-trophic FCs, and (c) OMN chains. Circles represent the five different habitat types. For each habitat pair, the link connecting the two habitats is thick if the number of shared trophic modules is significant, and thin otherwise; (b) and (d) represent the frequency of shared tri-trophic FCs and OMN chains, respectively in all pair-wise community comparisons. Black and white histograms represent the observed and the average expected value, respectively. Habitat types are mangrove/estuaries (m), coral reefs (c), seagrass beds/algal mats (a), sand (s), and offshore reefs (r). As noted, coral reefs (c), share with the rest of the habitats a number of FCs and OMN larger than expected by chance, which suggest a high degree of connectance promoted by dispersal.

different species composition trophic modules between habitats. However, it is interesting to note that 15 species (specifically, herbivorous species from *Blenniidae* and *Scaridae* families, and top species from *Carcharhinidae* and *Sphyrnidae* families) are embedded in more than 75% of trophic modules, which suggests that a small number of species are playing an important role in connecting through dispersal local community dynamics. Note that these highly connected species link

trophic modules across space in larger structures, which suggest a cohesive spatial structure (Melián and Bascompte 2004).

Dynamic metacommunity model

In order to assess the local and regional dynamics of the structure studied, we extend a previous metacommunity model (Mouquet and Loreau 2002, 2003) by incorporating trophic modules

(tri-trophic FCs and FCs with OMN) in a set of interacting communities. The model follows the formalism of previous metapopulation models (Levins 1969) applied to the scale of the individual (Hastings 1980; Tilman 1994). At the local scale (within communities), we consider a collection of identical discrete sites given that no site is ever occupied by more than one individual. The regional dynamics is modeled as in mainland–island models with immigration (Gotelli 1991), but with an explicit origin of immigration that is a function of emigration from other communities in the metacommunity (Mouquet and Loreau 2003). Therefore, the model includes three hierarchical levels (individual, community, and metacommunity). The model reads as follows:

$$\frac{\mathrm{d}P_{ik}}{\mathrm{d}t} = \theta I_{ik} V_k + (1-d) c_{ik} P_{ik} V_k - m_{ik} P_{ik} \\ + R_{ik} P_{ik} - C_{ik} P_{ik}. \tag{2.1}$$

At the local scale, P_{ik} is the proportion of sites occupied by species i in community k. Each community consists of S species that indirectly compete within each trophic level for a limited proportion of vacant sites, V_k, defined as:

$$V_k = 1 - \sum_{j=1}^{S} P_{jk}, \tag{2.2}$$

where P_{jk} represents the proportion of sites occupied by species j within the same trophic level in community k. The metacommunity is constituted by N communities. d is the fraction of individuals dispersing to other habitats, and dispersal success, θ, is the probability that a migrant will find a new community, c_{ik} is the local reproductive rate of species i in community k, and m_{ik} is the mortality rate of species i in community k.

For each species in the community, we considered an explicit immigration function I_{ik}. Emigrants were combined in a regional pool of dispersers that was equally redistributed to all other communities, except that no individual returned to the community it came from (Mouquet and Loreau 2003). After immigration, individuals were associated to the parameters corresponding to the community they immigrated to. I_{ik} reads as:

$$I_{ik} = \frac{d}{N-1} \sum_{l \neq k}^{N} c_{il} P_{il}, \tag{2.3}$$

where the sum stands for all the other communities l. R_{ik} represents the amount of resources available to species i in community k

$$R_{ik} = \sum_{j=1}^{S} a_{ijk} P_{jk}, \tag{2.4}$$

where a_{ijk} is the predation rate of species i on species j in community k, and the sum is for all prey species. Similarly, C_{ik} represents the amount of consumption exerted on species i by all its predators in community k, and can be written as follows:

$$C_{ik} = \sum_{j=1}^{S} a_{jik} P_{jk}, \tag{2.5}$$

where a_{jik} is the predation rate of species j on species i in community k, and the sum is for all predator species.

We have numerically simulated a metacommunity consisting of six species in six communities. In each community, either two simple tri-trophic FCs, or two OMN chains are assembled with the six species. The two trophic modules within each community are linked only by indirect competition between species within the same trophic level. We assumed a species was locally extinct when its proportion of occupied sites was lower than 0.01. Mortality rates (m_{ik}) are constant and equal for all species. Dispersal success (θ) was set to 1.

We considered potential reproductive rates to fit the constraint of strict regional similarity, SRS (Mouquet and Loreau 2003). That is, species within each trophic level have the same regional basic reproductive rates, but these change locally among communities. Under SRS, each species within each trophic level is the best competitor in one community. Similarly, we introduce the constraint of strict regional trophic similarity (SRTS). That is, each consumer has the same set of local energy requirements but distributed differently among communities. Additionally, we assumed a direct relationship between the resource's local reproductive rate and the intensity it is predated with (Jennings and Mackinson 2003).

Under the SRS and SRTS scenarios, regional species abundance and intercommunity variance are equal for each of the two species within the same trophic level. Regional abundance in OMN is

higher, equal, and lower for top, intermediate, and basal species, respectively. Local abundances differ significantly between the two modules explored. Specifically, when there is no dispersal ($d = 0$) there is local exclusion by the competitively superior species (Mouquet and Loreau 2002). This occurs for the basal and top species in the simple trophic chain. The variance in the abundance of the basal and top species between local communities is thus higher without dispersal for tri-trophic FCs (Figure 2.2(a)).

However, the situation is completely different for OMN. Now, intercommunity variance is very low for both the basal and top species in the absence of dispersal, and dramatically increases with d in the case of the top species. When the communities are extremely interconnected, the top species disappears from the two communities ($P_{ik} < 0.01$), and is extremely abundant in the remaining communities. For intermediate species, increasing dispersal frequency decreases the intercommunity variance, except when d ranges between 0 and 0.1 in FCs (Figures 2.2(a) and (b)).

Finally, we can see in Figure 2.2(b) (as compared with Figure 2.2(a)) that intercommunity variance for high d-values is higher in a metacommunity with OMN. Thus, the interplay between dispersal among spatially structured communities and food-web structure greatly affects local species abundances. The results presented here were obtained with a single set of species parameters. Under the SRS and SRTS scenarios, results are qualitatively robust to deviations from these parameter values.

Summary and discussion

It is well known that local communities can be structured by both local and regional interactions (Ricklefs 1987). However, it still remains unknown what trophic structures are shared by a set of interacting communities and its dynamical implications for the persistence of biodiversity. The present study is an attempt to link local and regional food-web structure and dynamics in a spatially structured marine food web.

Communities in five habitats of the Caribbean have shown significantly similar trophic structures which suggest that these communities are open to
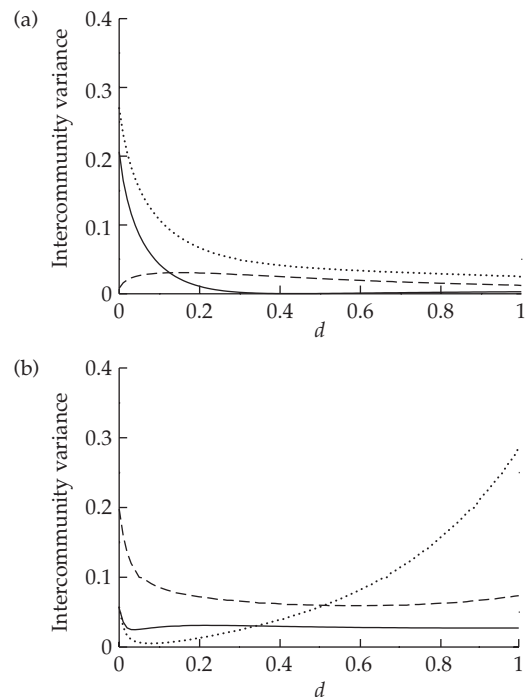
Figure 2.2 Intercommunity variance in local species abundance for the basal (continuous line), intermediate (broken line), and top (dotted) species as a function of the proportion of dispersal between communities (d). (a) Represents tri-trophic FCs and (b) OMN chains. Parameter values are $m_{ik} = 0.2$, c_{ik} for basal species is 3, 2.8, 2.6, 2.4, 2.2, and 2 from the first to the sixth community, respectively. For intermediate species c_{ik} is 1.5, 1.4, 1.3, 1.2, 1.1, and 1, respectively from the first to the sixth community. Top species reproductive values are 0.8, 0.75, 0.7, 0.65, 0.6, and 0.55, respectively. Predation rates of intermediate and top species j on species i in community k are 0.6, 0.5, 0.4, 0.3, 0.2, and 0.1, respectively. The initial proportion of sites occupied by species i in community k, (P_{ik}) is set to 0.05. As noted, in closed metacommunities, tri-trophic FCs show an extreme variation in local abundances for both the basal and top species ($P_{ik} < 0.01$) in two and three communities, respectively. On the other hand, OMN shows the highest intercommunity variance for high dispersal rates ($d = 1$). The top species becomes unstable, and goes extinct in two local communities ($P_{ik} < 0.01$).

immigration (Karlson and Cornell 2002). It has been recently shown that mangroves in the Caribbean strongly influence the local community structure of fish on neighboring coral reefs (Mumby et al. 2004). Additionally, empirical studies have shown that dispersal among habitats and local species interactions are key factors for

metacommunity structure (Shurin 2001; Cottenie et al. 2003; Kneitel and Miller 2003; Cottenie and De Meester 2004), and the persistence of local and regional diversity (Mouquet and Loreau 2003). However, it still remains unclear how the interplay between dispersal and more complex trophic structures affects species persistence in local communities (Carr et al. 2002; Kneitel and Miller 2003).

In the present work, closed communities ($d = 0$) with tri-trophic FCs showed an extreme variation in local abundances for both the basal and top species (Figure 2.2(a)). On the other hand, OMN shows the highest intercommunity variance for high dispersal rates ($d = 1$). The top species becomes unstable, and goes extinct in two local communities (Figure 2.2(b)). Recent empirical studies have shown that increasing dispersal frequency in intermediate species decreases the variance among local communities (Kneitel and Miller 2003), a pattern consistent with theoretical results presented here (see dotted line in Figure 2.2(a) and (b)). Further data synthesis and theoretical work is needed here to integrate the functional links between habitats and the local dynamics of species embedded in food webs.

In summary, the similarity in the trophic modules reported here suggests a strong link among the spatially structured communities. The level of connectivity among these local communities and the type of trophic modules alter local abundance of species and promote local changes in diversity. It still remains unexplored how the results here presented change by the introduction of a larger number of interacting modules in a set of spatially structured communities. Our result predicts a relative stability in the composition of basal species, and a dramatic influence in the abundance of top species depending on the connectivity (i.e. dispersal) among distinct habitats.

Acknowledgments