Network structure beyond food webs: mapping non-trophic and trophic interactions on Chilean rocky shores

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Abstract. How multiple types of non-trophic interactions map onto trophic networks in real communities remains largely unknown. We present the first effort, to our knowledge, describing a comprehensive ecological network that includes all known trophic and diverse non-trophic links among >100 coexisting species for the marine rocky intertidal community of the central Chilean coast. Our results suggest that non-trophic interactions exhibit highly nonrandom structures both alone and with respect to food web structure. The occurrence of different types of interactions, relative to all possible links, was well predicted by trophic structure and simple traits of the source and target species. In this community, competition for space and positive interactions related to habitat/refuge provisioning by sessile and/or basal species were by far the most abundant non-trophic interactions. If these patterns are corroborated in other ecosystems, they may suggest potentially important dynamic constraints on the combined architecture of trophic and non-trophic interactions. The nonrandom patterning of non-trophic interactions suggests a path forward for developing a more comprehensive ecological network theory to predict the functioning and resilience of ecological communities.

Key words: competition; ecological communities; ecological networks; facilitation; food webs; multiplex networks; mutualism; negative interaction; positive interaction; rocky intertidal.

Introduction

Food webs, the relationships of who eats whom in ecological communities, are traditionally used to study the complex interdependencies of species and their response to changes such as species extinctions. Undoubtedly, great theoretical advances and many practical applications have been developed from studies of the structure, intensity, and dynamics of trophic interactions within natural communities. Yet, ecological interactions among coexisting species involve much more than just feeding (Bascompte et al. 2003, Berlow et al. 2004, Ings et al. 2009, Kéfi et al. 2012, Pocock et al. 2012). Decades of empirical and theoretical studies demonstrate that specific non-trophic interactions, such as habitat modification, stress amelioration, interference competition, ecosystem engineering, and behavioral modifications,

may play important roles for community structure and ecosystem functioning (Jones et al. 1997, Lortie et al. 2004, Callaway 2007, Mougi and Kondoh 2012, Pocock et al. 2012). Recognition of this importance has led to studies that focus on isolated networks of non-trophic interactions (e.g., pollination webs; Ings et al. 2009), and more recently, on mixed interaction networks including different types of interactions (Vasas and Jordan 2006, Melián et al. 2009, Kéfi et al. 2012, Mougi and Kondoh 2012, Pocock et al. 2012, Lin and Sutherland 2013). Together these studies challenge the idea that a full understanding of the dynamics and stability of ecological communities can be achieved by knowledge of trophic interactions alone.

Improving our understanding and predictive capacity of the way complex ecological systems respond to disturbances may rely critically on how non-trophic interactions explain variations not explained by feeding interactions alone (Berlow et al. 2009). Toward this end, Kéfi et al. (2012) proposed a framework for incorporating diverse types of non-trophic interactions into dynamic food web models. However, since the possibil-

ities of non-trophic interactions seem endless, a critical challenge to theory development is knowing where to assign different types of non-trophic interactions across a food web. For example, the discovery of simple models that can mimic the nonrandom structure of real food webs (e.g., Williams and Martinez 2000) was a critical step in enabling theoretical explorations of random webs with plausible trophic structures. At this point, a similar conceptual development to model non-trophic relationships is unthinkable because of the absence of an empirical foundation. It remains largely unknown how multiple types of diverse non-trophic interactions map onto trophic networks in real communities, whether their combined structure is predictably constrained, or how the interplay of different interactions influences community stability. To start integrating non-trophic and trophic interactions in a meaningful way in community and ecosystem studies, particularly in ecological network theory, we must first gain insight into basic patterns of non-trophic interactions, such as how prevalent they are and if they have a structure; for example, whether they vary consistently with trophic levels.

Only a handful of data sets including different interaction types have been published to date. In 2006, Vasas and Jordan published a methodological paper in which they constructed an interaction web as a combination of a published food web and a selection of published non-trophic effects. Melián et al. (2009) assembled plant–pollinators and plant–herbivores bipartite data sets, thereby obtaining a two-interaction type network. More recently, Pocock et al. (2012) and Evans et al. (2013) studied bipartite and tripartite networks in an agro-ecosystem and investigated their robustness.

Here, we studied a community-wide, integrated trophic and non-trophic unipartite network. This interaction web includes all known trophic and non-trophic links among >100 coexisting species of diverse taxa for a marine rocky intertidal community from the central Chilean coast. Knowledge of all consumer interactions in a food web is a challenge all by itself (Martinez 1991). Also including the non-trophic interactions, many of which are restricted to particular life stage of the species, represents a daunting challenge in most natural systems. Since non-trophic interactions can be continuous rather than binary (Kéfi et al. 2012), in many cases, careful examination of system dynamics, sometimes accompanied by experimental manipulations, are necessary to determine even the presence of an interaction. We took advantage of the rich knowledge derived from a long tradition of natural history and manipulative experiments to identify the wide variety of non-trophic interactions known to play potentially important roles in community structure and dynamics in this ecosystem. We acknowledge that completeness of all non-trophic interactions will be unlikely for any real community, especially those rich in rare species.

Therefore, constructing "real ecological networks" is probably a perpetual work-in-progress as more experimental information becomes available. We argue that the moderate species diversity and the rich ecological information accumulated about the Chilean rocky shore have reached a level of resolution that allowed us to make meaningful exploration about the structure of these complex networks.

Here we describe how trophic and non-trophic interactions map onto each other and quantify the structural regularities of the trophic and non-trophic webs. More specifically, we address the following simple questions: How many direct non-trophic interactions are there and how are they distributed among species? Do the topological properties of trophic and non-trophic networks differ? Can simple species attributes help predict the type of interaction between two species? Can trophic characteristics help predict the non-trophic webs? Our goal is to provide a description and quantification of a comprehensive ecological network as a first step in the integration of non-trophic interactions in ecological theory and our mechanistic understanding of how complex ecological communities function.

METHODS

Data collection

We assembled an integrated trophic and non-trophic network for 104 species that inhabit the marine rocky intertidal zone of the wave-exposed central Chilean coast in the Humboldt upwelling ecosystem of the southeastern Pacific Ocean. Construction of the interaction web was based on expert knowledge derived both from the rich literature on species interactions and from our own experience of years of observation and experimentation along the central Chilean coast. Our plausible web is a time-integrated representation of direct interactions among co-occurring taxa. An interaction was included if the focal species plausibly had a direct measurable effect on the growth, survival, or feeding rates of a target species over an ecologically relevant time period (1–2 years). We did not explicitly include interactions with the abiotic environment, but did include those non-trophic interactions that occur when one species modifies environmental conditions (e.g., desiccation, temperature, and so on) to directly affect metabolism, growth, or survival of another species (e.g., habitat modification). Here, competition for space is considered a direct link between species because space is not included as a node in the network. In contrast, competition for prey is implicit in the food web.

Our web included all species found to co-occur as a community during intensive and spatially extensive community structure surveys carried out at multiple, similarly wave-exposed rocky intertidal sites separated by tens to hundreds of kilometers and spread across ~700 km along the central Chilean coast (see Broitman et al. 2001, Blanchette et al. 2009, Wieters et al. 2009 for

sampling details and species list). These surveys, repeated over multiple years, consisted of identifying and estimating the abundance of all species found within replicated 0.25-m^2 quadrats placed in high, mid, low, and low fringe tidal heights across one to three benches at each site. Thus, our web presents a bias to common macroscopic species found on open, wave-exposed rocky platforms and does not include cryptic species and those restricted to specific microhabitats, such as boulder fields, sand–rock transitions, and rock pools (see Appendix A). Organisms currently absent from the data set include parasites, amphipods, isopods, mobile polychaetes (e.g., *Nereis* sp.), porcellanid crabs, urchins, mites, insects, filter-feeding limpets, and fish.

Trophic interactions among species inhabiting the rocky shore of Chile have been well documented in published observational and experimental studies conducted in this system over the past 40 years (see Castilla and Paine 1987, Santelices 1990, Fernández et al. 2000, Thiel et al. 2007 for reviews). Non-trophic interactions between intertidal species are also relatively well known across the phyletically diverse community, which encompasses a broad range of body sizes, life forms, and evolutionary histories. Many non-trophic interactions in this system have been the focus of experimental studies, such as the facilitation of mussel settlement and provision of refuge for mobile crabs by algal turfs (Wieters 2005, Wieters et al. 2008), the positive effects of mussel beds and kelp holdfasts on many other invertebrate species seeking shelter (Navarrete and Castilla 1990*a*, Prado and Castilla 2006), the symbiotic relationship between a porcellanid crab and anemones (Baeza and Thiel 2002), the use of barnacle wall structures as settlement substrate by mussels (Navarrete and Castilla 1990*b*), negative interactions due to interference for refuges between intertidal crabs (Navarrete and Castilla 1990*a*) or between macro-algae competing for space (Santelices 1990), and the whiplash effect of the large kelp *Lessonia nigrescens* on other algae and grazers (Ojeda and Santelices 1984). Other non-trophic interactions are less often reported in the literature, but widespread nonetheless, such as the behavioral avoidance between some mollusk grazer species (Aguilera and Navarrete 2011) and between them and carnivore consumers (Espoz and Castilla 2000). For space restrictions, we have kept references to a minimum. Lists of the types of organisms and common types of non-trophic links present in the data set are included in Appendix A.

Non-trophic interactions present several unique challenges that make them more difficult to incorporate into webs than trophic interactions. First, many non-trophic interactions are often not directly observable, and thus empiricists must rely on good knowledge of natural history and sometimes labor-intensive experiments to demonstrate their existence. For instance, whether a species ameliorates the environmental stress perceived by another species (a positive habitat modification effect) cannot be inferred solely from the observation that individuals co-occur over space or time. In contrast, trophic interactions can often be observed in the field, either directly or using simple methods such as the examination of gut contents. Second, unlike the binary nature of trophic interactions (e.g., a predator either eats the prey species or does not), the net outcome of most non-trophic interactions occur along a continuum of strength and direction (positive or negative). For example, the architectural complexity, size, or density of a plant can determine how much it modifies the environment of other species. Notably, some non-trophic interactions, such as pollination by flower-visiting insects, are binary and directly observable, which has facilitated the assembly of several non-trophic "visitation webs" (Bascompte et al. 2006). Thirdly, the sign/direction of some non-trophic interactions may vary over space and time. For example, turf algae can facilitate mussel recruitment, while at the same time compete strongly for space once mussels become established. Likewise, whether turf algae facilitate mussel recruitment depends on the morphology and height of the alga, which is, in turn, controlled by local oceanographic conditions that drive nutrient supply and algal growth rates (Wieters 2005). These realities make the sign and strength of non-trophic interactions difficult to measure empirically, especially since positive and negative effects can cancel each other and produce empirical results indicating zero combined effect (Wood et al. 2010). Thus, we acknowledge that there are enormous empirical and logistical challenges to assembling a comprehensive network including both trophic plus non-trophic interactions for a natural community. Yet, we urge ecologists to start facing this challenge and embrace the complexity of real biological systems. Here we have tried to be as comprehensive as possible by including all available information within the defined region, and at the same time, be rigorous in not including interactions when information was lacking or when we could not find a consensus among experts. Possible biases in the construction of the web are listed and discussed in Appendix A.

As a first step, we created separate species-by-species matrices for trophic and non-trophic interactions. While trophic interactions were coded as 0 or 1 (species *i* either eats species *j* or not), non-trophic interactions of one species on another were categorized into one of four groups: no interaction (0), a negative interaction (1), a positive/facilitative interaction (2), or both negative and positive interactions (3). Note that these are the unidirectional effects of a species on another (i.e., the effect of species *i* on species *j*, and the effect of species *j* on species *i* are coded separately). In the rest of the text, when we mention a positive or a negative interaction, we refer to the unidirectional effect. We used published information and expert knowledge to assign these categories to species that had either a measurable increase, decrease, or no change in growth, survival, or

feeding rates of another. The last group (3) applied to cases where there are two different types of non-trophic interactions of different sign occurring between two species (e.g., turf algae and mussels), and to those interactions that often change sign over time (e.g., barnacles/turf algae and mussels). We did not include here intraspecific non-trophic interactions, since density dependence is plausible at some level for almost all species. The final matrices of trophic, positive non-trophic, and negative non-trophic interactions provide the most comprehensive description of plausible ecological interactions among all 104 species of the central Chilean intertidal ecosystem. The data set is available in an editable, annotatable, and shareable cloud-based network visualization software (*available online*).[9]

Data analysis

Distribution of links.—We explored how the structure of trophic and non-trophic links was distributed among species by computing the degree and prey-averaged trophic level of each node. *Degree* was calculated as the sum of incoming and outgoing links (e.g., all the prey and predators of a species for trophic interactions; Appendix B). The *prey-averaged trophic level* of each species was calculated as one plus the mean trophic level of all of the species resources, where the trophic level of a resource was the chain length from the resource to a basal species (Williams and Martinez 2004). To determine if the distribution of non-trophic interactions throughout the trophic network (i.e., number of non-trophic interactions by trophic level) was different than expected by chance, we compared the observed distributions to those obtained in 1000 randomized networks using two different null models. First, we only randomized the non-trophic links while keeping the trophic network structure fixed (i.e., identical to the one observed in the empirical network). Second, we randomized the location of both the trophic and the non-trophic interactions. See Appendix C for more details.

Other network properties.—We quantified network-level properties that have been suggested to have implications for the dynamics and stability of ecological communities (e.g., Krause et al. 2003, Memmott et al. 2004, Fortuna and Bascompte 2006, Bastolla et al. 2009, Fortuna et al. 2010). One way of characterizing a network structure is to identify *modules*, i.e., groups of species that are highly interconnected and that are poorly connected to species of other groups (Guimera and Amaral 2005; Appendix D). The approach of Guimera and Amaral (2005) investigates whether there is a particular division of the network into a number of modules of varying sizes that maximizes a function called *modularity* (Newman and Girvan 2004). Modularity measures the fraction of links falling within modules minus the expected value in an equivalent

network where links are placed at random (see Guimera and Amaral 2005 for methods). Modularity has a value between 0 and 1, with 1 corresponding to a perfectly modular matrix.

Another functionally important network-level property is *nestedness*, or the extent to which species with few connections share their interaction partners with more highly connected species (Bascompte et al. 2003), although care should be taken in interpreting this metric given its sensitivity to sampling effort (Blüthgen 2010). We used a nestedness metric termed NODF (Almeida-Neto et al. 2008). We limited analyses to those species that interacted with at least one other in the network (this included all species in the trophic network but less in the non-trophic networks). The NODF algorithm scales between 0 and 100, with a value of 100 indicating perfect nestedness. Note that these two metrics (nestedness and modularity) are known to be correlated and that this correlation is mediated by network connectance (Fortuna et al. 2010, Fontaine et al. 2011).

To test the significance of the observed structures of modularity and nestedness, we compared the observed statistics against randomized networks keeping only the connectance and the number of species fixed. This allowed us to confirm that the structure observed was not just a consequence of the connectance. We used 100 randomizations for modularity and 10 000 for nestedness (the difference in replicates is explained by the difference in computation time).

After identifying the modules, we sought ecological attributes describing the type of species or interaction that characterized the different modules. Although the modules were determined by the topology of the web, and not based on ecological criteria, species that are in the same module interact preferentially with each other and could play similar and complementary roles in the network (Guimera and Amaral 2005), or belong to the same type of habitat (Krause et al. 2003). For each link, we gathered information about the focal species (i.e., the predator or species performing the non-trophic interaction) and about the target species (i.e., the prey or species experiencing the non-trophic interaction). We used two types of information: (1) simple species traits (the average body mass of an individual of the species, ratio of the body mass of the source to the target species [body mass data from Riede et al. (2010); body mass of algae in g/cm^2], and mobility of the species [mobile vs. sessile, where a sessile taxon is one in which the adult stage is permanently or semipermanently attached to the substrate]) and (2) species trophic characteristics deduced from the knowledge of the trophic web (the trophic level, trophic generality [i.e., number of prey], and trophic vulnerability [i.e., number of predators]). We investigated whether these characteristics were related to the presence of a link between two species. We performed two types of analyses: a regression tree on species traits (not using information related to the trophic web) and a principal component analysis (PCA)

A) Trophic   B) Positive non-trophic   C) Negative non-trophic
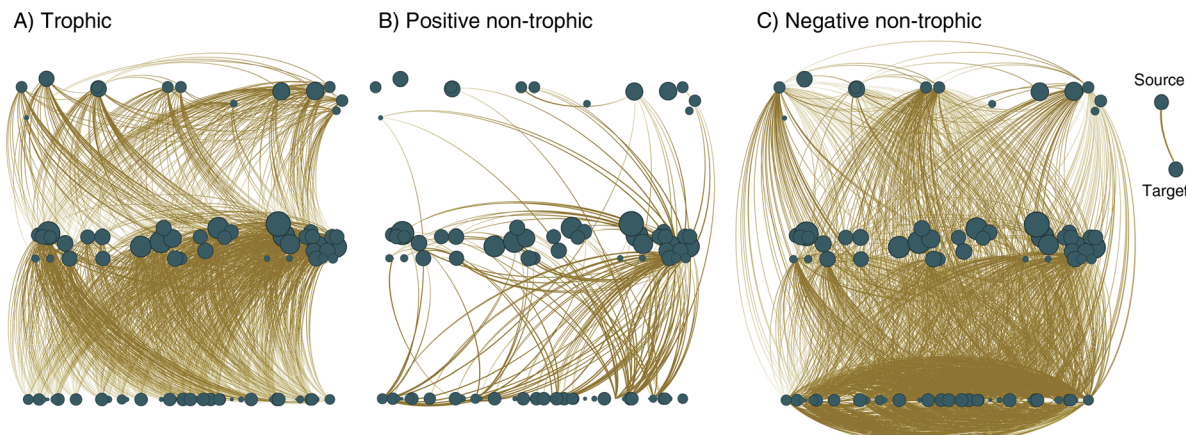

FIG. 1. Networks of trophic and non-trophic interactions between the 104 species of the Chilean intertidal ecosystem: (A) trophic network, (B) network of positive non-trophic interactions, and (C) network of negative non-trophic interactions. Each node indicates a species. The vertical position is the trophic level (basal species at the bottom and top predators at the top). The horizontal position within each level is random. The curvature of lines between the nodes indicates directionality of influence, with lines arcing counterclockwise from source to target species (as shown on the key on the right of panel C). The networks were plotted with Mappr, Vibrant Data's cloud-based visualization software (*available online*: http://vibrantdata.is). Among the 99 species that had at least one non-trophic interaction, 66 species had at least one positive non-trophic interaction, and 77 had at least one negative non-trophic interaction. The non-trophic connectance was 0.34, and the trophic connectance 0.13.

using species traits and their trophic characteristics based on the trophic web. None of the predictor variables used for the PCA had a Pearson pairwise correlation $|r| > 0.8$. Regression tree analysis is a nonparametric approach that recursively partitions the data into the most homogeneous subgroups. The threshold value at each split is determined computationally as the point of maximum discrimination between the two resulting subgroups.

RESULTS

How abundant are non-trophic interactions, and do they have a (nonrandom) structure?

In the rocky shore community of central Chile, there were more than twice as many non-trophic as trophic interactions, with 3296 non-trophic interactions and 1458 trophic interactions (Fig. 1). Among non-trophic interactions, negative ones (3176) were 20 times more abundant than positive ones (155; Fig. 1B, C).

The vast majority of the non-trophic links in the Chilean rocky shore web occurred among taxa at the basal trophic level, with five times more non-trophic than trophic interactions at the base of the web (Fig. 2; Appendix B: Table B1). Because species richness was higher at the basal level (Appendix B: Table B1), we investigated whether or not there were more non-trophic interactions at the base of the web than expected by chance or would be explained by the disproportionate basal species richness alone. The results showed that non-trophic interactions were overrepresented at the base of the web, i.e., there was a higher probability that any single basal species would be involved in a non-trophic interaction than would any single species at higher trophic levels (Appendix C).

Do the topological properties of trophic and non-trophic networks differ?

We present the results of the negative and positive non-trophic webs separately, but not of the total non-trophic interaction web, whose structure is almost identical to the negative non-trophic interaction web. The reason for this similarity is because the non-trophic interaction web is largely dominated by the negative interactions.

While the distribution of trophic interactions increased approximately linearly across taxa ranked by degree (Fig. 2A), the distribution of positive non-trophic degree was skewed, with 10% of the species accounting for 54% of the interactions (Fig. 2B). Most negative non-trophic interactions were concentrated among a core group of species (Fig. 2C): 52% of species had >100 non-trophic interactions, whereas 39% had <10 non-trophic interactions.

The clump of negative non-trophic interactions was composed of sessile species of two types: (1) basal, primary producer species (e.g., macroalgae) and (2) sessile invertebrate species (11 species; Fig. 2C). This highlights the importance of competition for space among sessile species in this ecosystem (Fig. 2C). Only one sessile species had a non-trophic degree of less than 20: the mussel *Brachidontes granulata*, which, for unknown reasons, is largely restricted to crevasses, does not form beds, and thus, competes little with other sessile species, nor does it provide habitat for other mobile species.

In the Chilean web, the species that have many trophic interactions tended to have few non-trophic interactions and vice versa (Appendix B: Fig. B1). We compared the identity of the species that have many non-trophic interactions to those that have many trophic interactions. Only one of the species with the most (upper 20%) trophic interactions overlapped with the species with the most
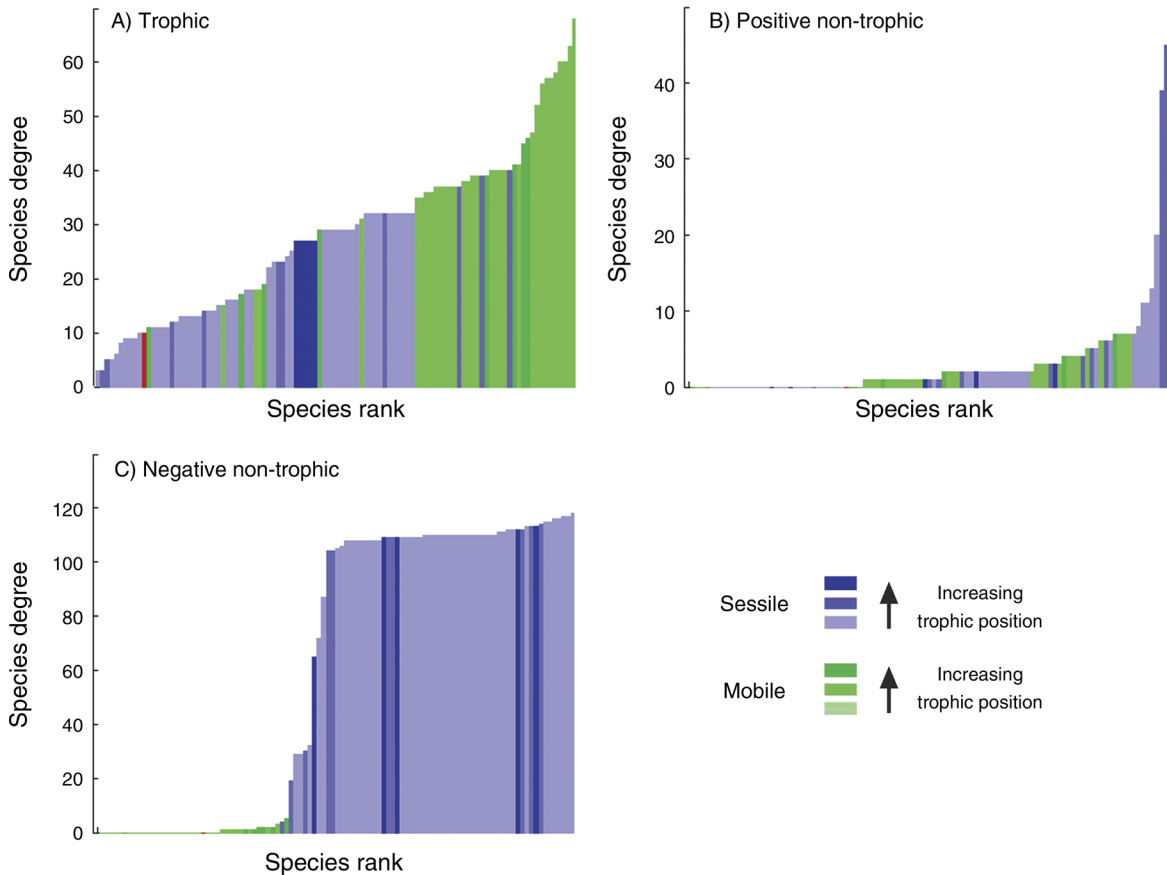
Fig. 2. Distribution of the species degree for (A) trophic, (B) positive non-trophic, and (C) negative non-trophic interactions. The degree is calculated as the sum of incoming and outgoing links for each species. In each panel, the *x*-axis corresponds to the 104 species ranked by their degree. The color of the bar includes information on the trophic level of sessile (blue) and mobile species (green). Darker blue and green reflect higher trophic levels in the web (e.g., light colors correspond to basal species, and dark ones to top predators). The only sessile species that are carnivorous are anemones (dark blue bars). Plankton (including particulate matter) is shown in red. Note that plankton has an artificially low trophic degree because all planktonic predators and their prey (also plankton) are lumped into this same taxon.

(upper 20%) non-trophic interactions (the barnacle *Notobalanus flosculus*); and only one of the species with the fewest (bottom 20%) trophic interactions overlapped with the group with the fewest (bottom 20%) non-trophic interactions (the trophic group of plankton species), which is statistically significantly less than expected by chance. Comparing species degree, rather than species identity, revealed that the 20% of species with the fewest trophic interactions contributed to 0.07% of the trophic degree, but 31% of the non-trophic degree (Appendix B: Fig. B1). Conversely, the 20% species with the most trophic interactions contributed to 35% of the trophic degree,

but only to 0.04% of the non-trophic degree (Appendix B: Fig. B1).

How are these networks structured at the scale of the entire web?

Modularity of the negative non-trophic interaction web was very low, although significantly different from random, suggesting a poor division of this network into constituent modules. Indeed, the negative non-trophic web was composed of one large block of interactions (Fig. 3E; Appendix D: Table D1). The positive non-trophic and trophic interaction webs had modularity values signifi-

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Fig. 3. Visualization of the web structures. The left column shows (A) trophic and (B) positive non-trophic interaction webs. Nodes are colored by compartment, and their size is proportional to their degree. The layout is "force-directed," where nodes that are more interconnected cluster together, and ones that are less connected to one another push apart. Negative non-trophic compartments are not displayed because of the very low level of modularity (Appendix D). The right column shows interaction matrices in which rows and columns were sorted by degree for the (C) trophic, (D) positive non-trophic, and (E) negative non-trophic webs. Interaction matrices are such that columns affect rows. Black squares represent a realized link from column to row. Light green squares are the diagonal terms of the original (unsorted) matrix that are not realized, while red squares (only in panel [C]) represent realized diagonal terms (i.e., self-interactions).
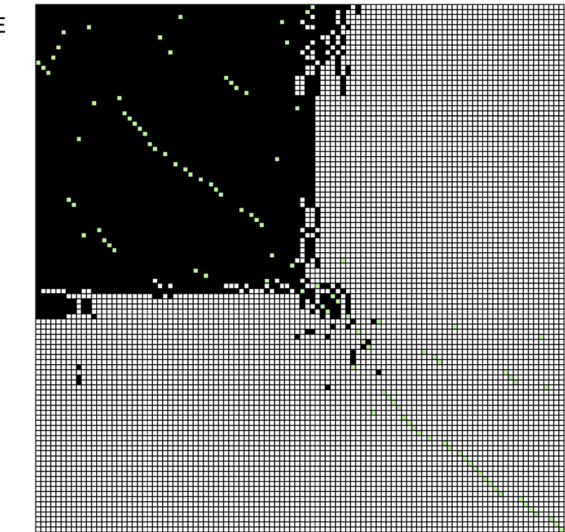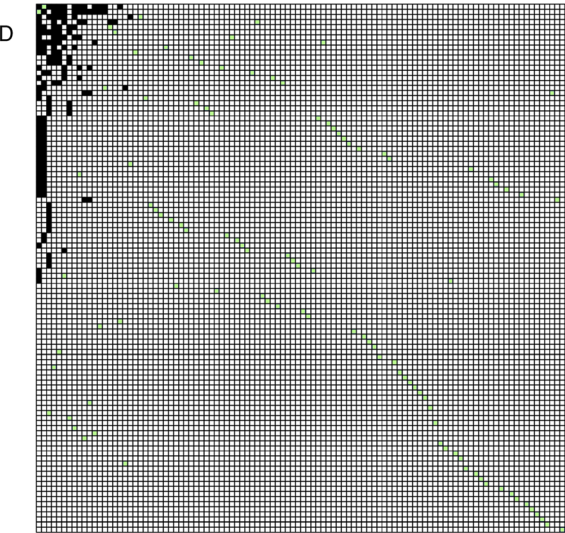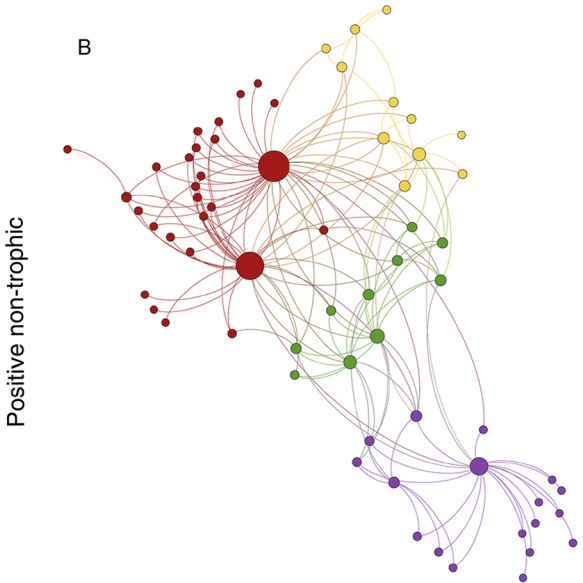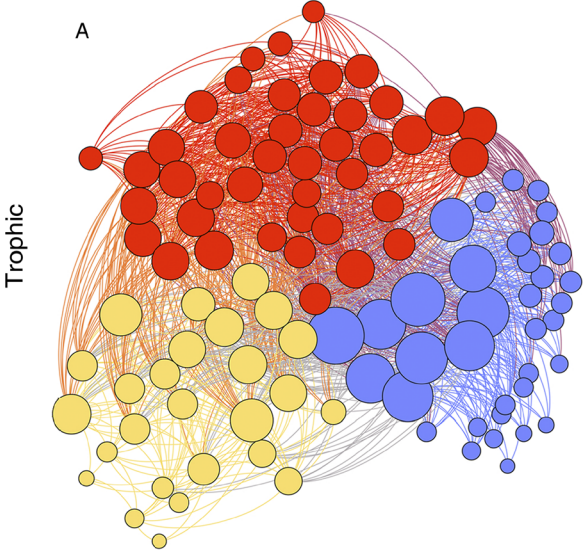
cantly higher than those expected in a random web with the same connectance (Appendix D: Table D1).

Fig. 3A, B shows the webs with nodes colored by compartments as identified by the algorithm of Guimera and Amaral (2005). Three compartments were identified in the trophic web (Fig. 3A; Appendix D). The red compartment is predominantly composed of grazers, ephemeral and crustose algae, as well as a passerine bird that consumes small limpet grazers. In contrast, the yellow compartment corresponds mostly to sessile invertebrates (mussels and barnacles) and their predators. The blue compartment corresponds to large-bodied grazers and browsers, corticated macroalgae and kelp.

In the case of the positive non-trophic interaction web, the relatively high degree of compartmentalization appears to reflect differential connectivity of various habitat-modifying sessile species that separate across shore height (Fig. 3B; Appendix D). In the lowest intertidal fringe (purple), the kelp *Lessonia nigrescens* provides critical shelter or habitat to diverse consumers and facilitates colonization of crustose algae. On the low shore (green), key turf algae (Gelidium, Corallina) facilitate recruitment and/or provide refuge to diverse species. Along the mid intertidal zone (red), the provisioning of habitat and substrate by dominant mussels species (Perumytilus and Semimytilus) is highlighted. Higher on the upper shore (yellow), canopies of foliose macroalgae (Mazaella, Porphyra) and beds of barnacles (Jehlius and Notochthamalus) provide habitat to small snails and limpets.

Comparing the observed nestedness values to random webs with fixed connectance showed that the networks were more nested than expected by chance. Nestedness occurs when a species' degree is a subset of others, i.e., when species with few links share their interaction partners with more highly connected species. Interestingly, the trophic and positive non-trophic webs showed lower levels of nestedness than the negative non-trophic web (Appendix D). The high nestedness of the negative non-trophic web was due to the degree distribution of species, characterized by a core group of species densely interacting (Fig. 3E).

Can simple species attributes help predict the type of interaction between two species?

Regression tree analysis shows that the best predictor of link type is the mobility of the source species. In this web, most non-trophic interactions are initiated by sessile species, while trophic interactions are generally initiated by mobile species in this web (Fig. 4). The negative non-trophic interactions usually involved a sessile species impacting another sessile species (Fig. 4), while positive non-trophic interactions usually corresponded to physical structure provided by a sessile species to a mobile species (Fig. 4). These general patterns are also visible in the direction of curvature of links in Fig. 1C: Most of the positive interactions go "from" a lower trophic level species "to" a higher trophic level species.

Can trophic characteristics help predict the non-trophic webs?

When considering all possible links between species, the subset of realized non-trophic links is nonrandomly distributed (Fig. 3). Since trophic links have been more commonly reported in the literature dealing with complex systems than non-trophic links, and species body mass is known to predict trophic links (Kalinkat et al. 2013), we explored the extent to which non-trophic interactions could be explained by trophic web structure and species body masses. We performed a principal component analysis (PCA) on the trophic and body mass attributes of the source and target species for all possible links. When all possible interactions are plotted in this "trophic attribute space," the different types of realized links (trophic, positive non-trophic, and negative non-trophic) visibly occupy different areas (Fig. 5). The first two PCA axes explain about 65% of the variation in link type. As expected in aquatic food webs, trophic links occur for high biomass ratios, i.e., for predators larger than their prey (Brose et al. 2005). Positive non-trophic interactions are initiated by small species from low trophic levels with high vulnerability and a low generality (i.e., which do not eat many species, but are eaten by many consumers). Negative non-trophic interactions are initiated by small species from low trophic levels on target species with similar characteristics.

DISCUSSION

In the marine rocky intertidal community of central Chile, we found that: (1) non-trophic interactions were more than twice as abundant as trophic ones, (2) the structure of those non-trophic links was nonrandom both alone and with respect to trophic structure, (3) the link degree distribution differed systematically between positive vs. negative non-trophic interactions, and (4) the occurrence of positive and negative non-trophic interactions was relatively well predicted by trophic link structure and simple species attributes. We focused on an ecosystem for which there exists ecological knowledge for the great majority of co-occurring taxa on wave-exposed platforms and their diverse ecological interactions. We acknowledge this is a "best of our knowledge" work-in-progress that we hope will spark further research and contributions to an online, open-access, interactive, and annotatable version of these data (see footnote 9). Future observations and experiments will likely result in additions and modifications of the trophic and non-trophic links identified so far in this community. Nevertheless, we argue in the following paragraph that these four main conclusions are likely to be robust to known uncertainties or sampling biases in the data.
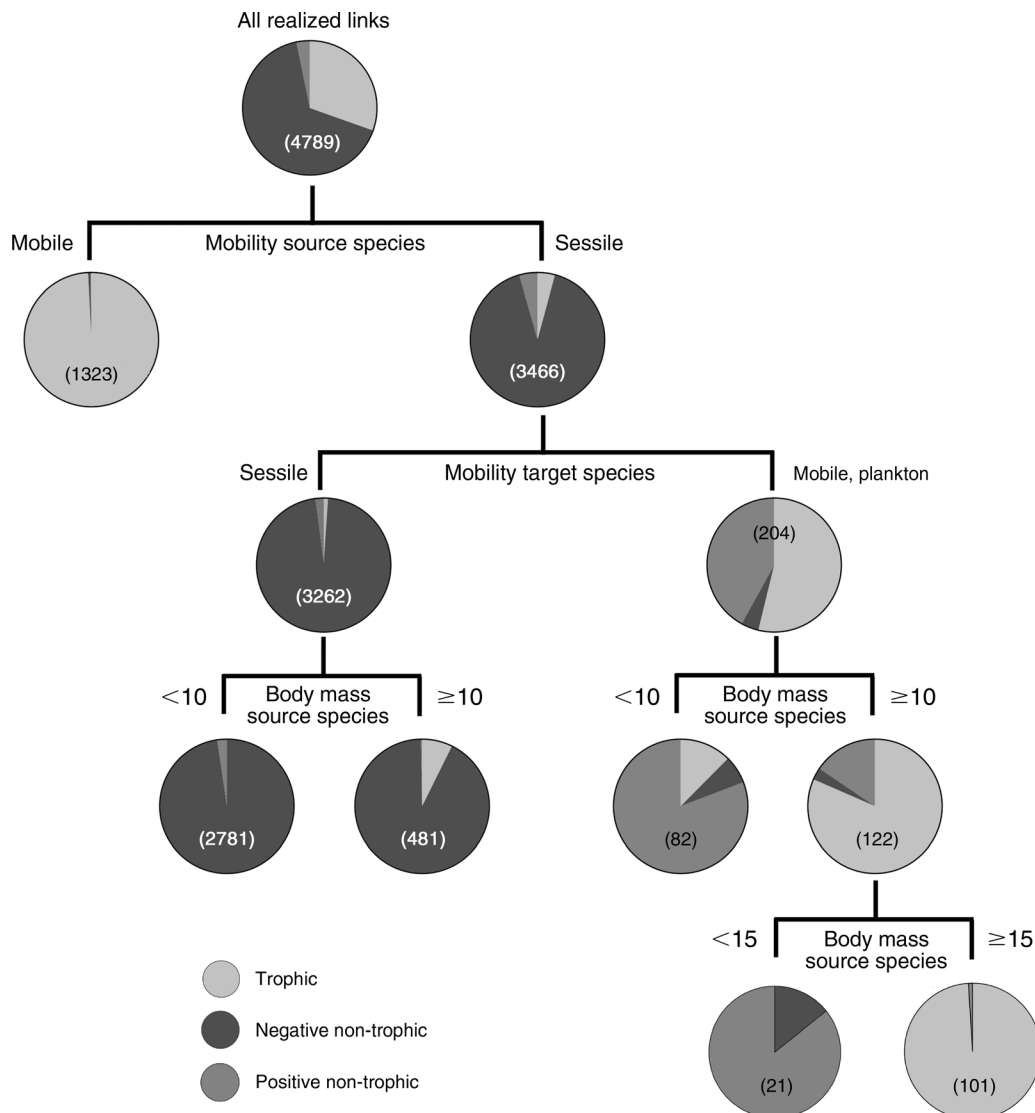
Fig. 4. Regression tree of all the realized links, including trophic interactions (light grey), negative non-trophic interactions (dark gray), and positive non-trophic interactions (intermediate gray; $R^2 = 0.84$). For each "leaf" in the tree, the pie chart shows the proportion of each link type, and the number in parentheses is the total number of links. The variable selected for each split is directly under the parent, and the threshold value for the split is listed on either side.

We made an effort to identify the main factors that could introduce bias in the salient patterns of the intertidal web and describe them in some detail in the Appendix A. While all these factors could alter some statistics of the web, most of them would either have no effect on our main conclusions due to effect size of the pattern relative to the anticipated error, and/or there is no obvious systematic direction in which they would bias the results. The link degree distribution of negative non-trophic interactions are the one result that could be altered by a biased overestimation of interference competition for space among basal species for which there have been no direct experimental manipulations (see Appendix A). As in most other systems, experimen-

tal manipulations or correlational information have centered on abundant species and, therefore, uncertainty lies lopsidedly on species rare in abundance. Evaluating whether these negative–negative interactions should instead be classified as amensalism, or perhaps even facilitation, will require some methodological advances to conduct "realistic manipulations" with rare species that are found surrounded by more abundant species.

The location and structure of non-trophic interactions in the Chilean web were highly nonrandom, with many more non-trophic interactions at the base of the food web than expected by chance (77% of the non-trophic interactions involved taxa at the base of the web with trophic position 1). These basal non-trophic interactions

consisted primarily of negative interactions due to competition for space among sessile species. These interactions were not species specific, and almost all the links were concentrated among approximately half of the species that interacted with each other, forming one large compartment. This result supports our knowledge that competition for space is a very common interaction in rocky intertidal communities (e.g., Connell 1961, Santelices 1990). It does not necessarily speak to the "importance" of this interaction in controlling the abundance of these species, but it indicates that these species frequently engage in competitive interactions. Most of the positive non-trophic interactions were also primarily associated with sessile and basal species that provide habitat, refuges, or stress amelioration to other species. We speculate that this pattern could be common across many ecosystems such as coral reefs and arctic tundra that are rich with basal and/or sessile species that provide habitat and structure.

Differences in the degree distribution of negative and positive non-trophic interactions were striking. Different mechanisms operated to generate the degree distributions of negative and positive non-trophic interactions. While negative non-trophic interactions such as competition for space connect a broad range of sessile species, positive interactions seemed to be restricted within different functional groups of species that had similar requirements within the group (e.g., settlement habitat or stress amelioration). Thus, the positive non-trophic interactions showed a skewed distribution where a few species had many interactions while many species had a few. These patterns suggest that pervasive negative interactions at the base of the web may have strong system-wide functional consequences, while the influence of positive interactions may be restricted to specific modules of species within the web.

In our interaction web, the trophic and positive webs were compartmentalized, while the non-trophic negative web was essentially composed of one large module. This can be intuitively understood by looking at the underlying ecological mechanisms: competition for space is not species specific, while many positive non-trophic interactions are restricted within specific groups of species. Recent work on the structure of trophic vs. non-trophic webs suggests that trophic networks tend to be more compartmented, while non-trophic mutualistic webs are more nested (Bascompte et al. 2003, Thébault and Fontaine 2010). Differences in web structure have been shown to have implications for how disturbances propagate and how species persist and co-evolve. Theoretical studies have suggested that, in mutualistic networks, nested structure minimizes competition and increases the number of coexisting species (Bastolla et al. 2009), and makes the community more robust to random extinctions (Memmott et al. 2004) and habitat loss (Fortuna and Bascompte 2006). In food webs, modular patterns are thought to increase network stability by retaining the impacts of perturbations within

modules and minimizing the impacts on other modules (Krause et al. 2003). Variation in modularity and nestedness across the different types of interactions observed in the rocky shore web means that disturbances will propagate very differently through the web depending on the non-trophic and trophic degrees of the species affected by the disturbance. Once we start compiling multi-interaction networks for more ecological systems, we can begin to leverage approaches developed in other disciplines for finding multi-dimensional patterns in multiplex networks (e.g., Mucha et al. 2010, Cardillo et al. 2013).

The study of multi-interaction networks may answer questions about the factors driving the structure of empirical networks such as: What determines whether a trophic or non-trophic interaction exists between two species? Studies have shown that species abundance (e.g., Vázquez et al. 2009) and phylogeny (e.g., Bersier and Kehrli 2008) are good predictors of network structure. In food webs, information on species traits, such as body size or trophic level, can explain some of the structure of empirical networks (e.g., Williams and Martinez 2000). Knowledge about which traits determine whether species engage in trophic and non-trophic interactions could allow predictions of ecological network structure, given a more easily measured set of traits. In a recent analysis of empirical ecological networks, including antagonistic and mutualistic networks, Eklöf et al. (2013) showed that the structure of ecological networks can be explained using only a few traits. In the Chilean web, very simple attributes of the species (the average biomass of the source and the target species of a link, the ratio of biomass of the source to the target species, and whether species are sessile or mobile) can classify the observed links as trophic, non-trophic negative, and non-trophic positive. Indeed, in the rocky intertidal, many non-trophic interactions come from physical structure provided by sessile species. Pursuing such analyses is both important for our fundamental understanding of what determines species interactions, and thereby the structure of ecological networks, as well as for constructing realistic and reliable models of ecological systems.

Understanding the functional consequences of the differences in structure between the different sub-webs of our interaction web will require a modeling framework that explicitly incorporates positive and negative non-trophic interactions into dynamic food web models (Kéfi et al. 2012). Describing and quantifying the structure of non-trophic interactions in a trophic network is a first, critical step towards their integration into ecological theory and our understanding of how complex ecological communities form, maintain themselves, and respond to perturbations. Our results from the Chilean intertidal ecosystem suggest that non-trophic interactions exhibit highly nonrandom structures both alone and with respect to food web structure. If these patterns are corroborated in other ecosystems,
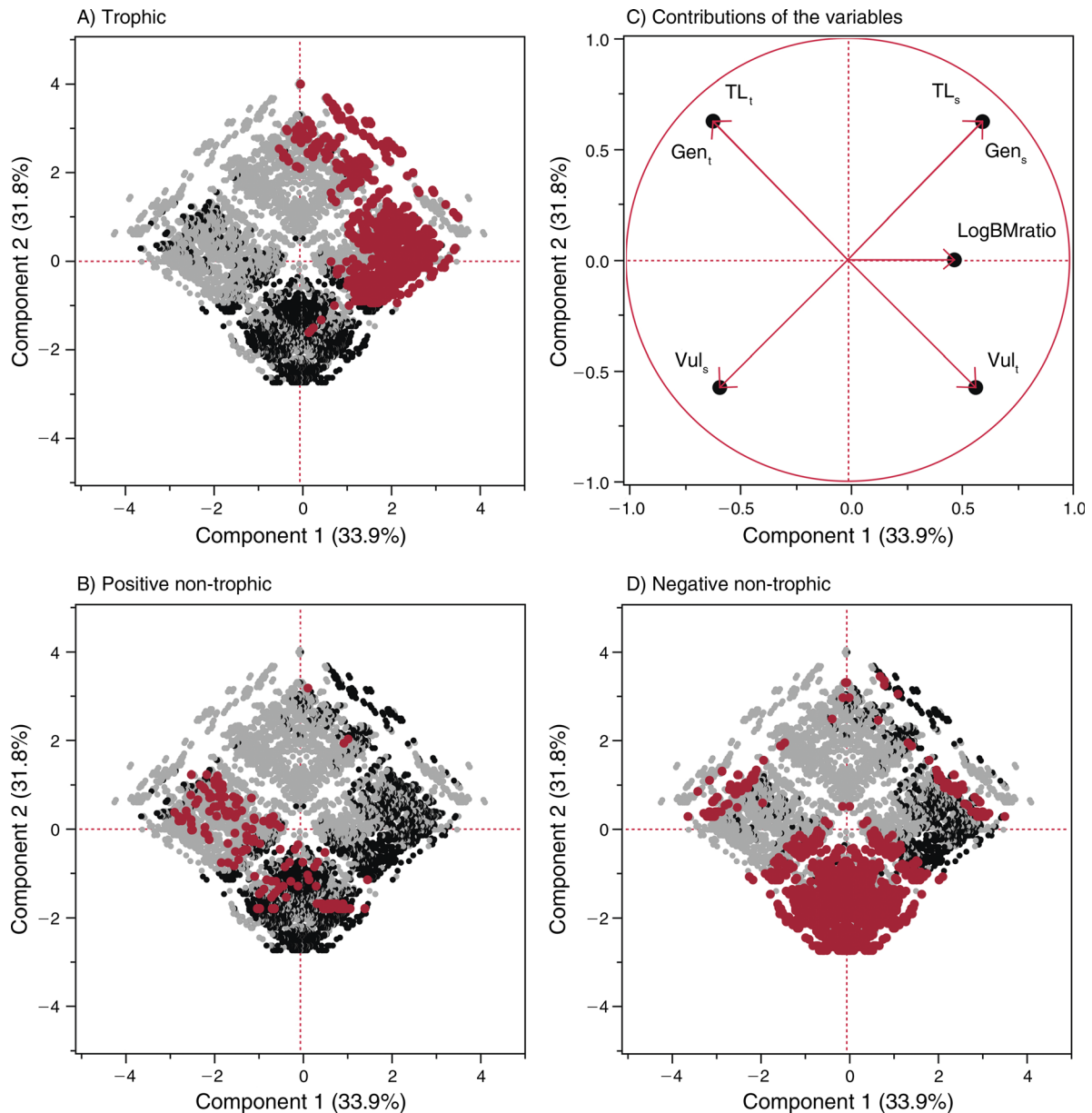
FIG. 5. Principal component analysis (PCA) on characteristics of the sources and target species of all the possible links (i.e., all the possible pairs of species), showing all the possible links in the network (gray) and all realized interactions (black). Trophic, positive non-trophic, and negative non-trophic interactions are shown in red in panels (A), (B), and (D), respectively. All variables were standardized to have a mean of zero and standard deviation of one. LogBMratio is the log of the ratio of source vs. target species biomass; TL_t and TL_s are the trophic levels of the target and source species, respectively; Gen_t and Gen_s are the trophic generality of the target and the source species; and Vul_t and Vul_s are the trophic vulnerability of the target and of the source species (note that the Gen and TL arrows are superimposed). The two first axes of the PCA explain 65.7% of the variance in links. Panel (C) shows the contribution of the variables to the first two axes of the PCA.

they may suggest potentially important dynamic constraints on the combined architecture of trophic and non-trophic interactions. Our analysis shows that competition for space and habitat/refuge provisioning by sessile and/or basal species were by far the most abundant non-trophic interactions in this interaction web. Thus, of all the diverse types of possible species interactions that could occur throughout the entire web,

efforts to incorporate non-trophic interactions into dynamic food web models might make significant progress by starting with these. Incorporation of competition among basal species for a common resource has shown to have strongly stabilizing effects on the persistence of complex food webs (Brose 2008), but this approach may need to be modified in order to consider space as a resource. Modeling approaches may not only

help understanding the functional consequences of these integrated webs of interactions, but also help exploring the consequences of our uncertainty at different geographical locations of the web.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–D are available online: http://dx.doi.org/10.1890/13-1424.1.sm