High temporal variability in the occurrence of consumer–resource interactions in ecological networks

Daniela N. Lopez, Patricio A. Camus, Nelson Valdivia and Sergio A. Estay

Ecological networks have been used to represent interactions between species as fixed linkages despite that populations naturally oscillate over time and space. As such, the influence of the persistence of linkages between species in communities has been overlooked. Unfortunately, empirical analysis of the temporal variation of trophic networks is constrained by the lack of data with high spatial, temporal and taxonomic resolution. Here, we evaluate the spatiotemporal variability of multiple consumer–resource interactions to quantify the relative dominance of highly persistent versus poorly persistent interactions, the commonness of the interaction persistence patterns, and the effect of biotic and abiotic conditions on these patterns. We took advantage of a dataset from four large marine intertidal rocky-shore networks monitored seasonally for three years along 1000 km of the coast of northern Chile. Our results showed that the communities were characterized by few persistent interactions and a large number of transient trophic interactions, which was well described by a common exponential decay in the rank-frequency relationship of consumer–resource interactions despite dissimilarities in environmental conditions among sites. These results were independent of the degree of consumer–resource co-occurrence. Our results stress the need for more long-term studies that evaluate the temporal variability of ecological networks.

Ecological networks where species are represented by nodes and interactions are represented by links between nodes, have been a useful theoretical tool for understanding the structural properties of ecological communities (Mitchell 2009). Currently, there are many studies analyzing the topological and statistical properties of ecological networks in order to link these network features to biological characteristics such as species richness, functional diversity, or productivity (Poisot et al. 2015). However, most ecological networks, and therefore biological communities, are recognized and analyzed as static or quasi-static structures of interacting species. Subsequently, this view considers that all observed species and links are present simultaneously, and the variability of interactions is seldom considered despite that the presence and strength of species interactions vary in space and time (Winemiller 1990, Schoenly and Cohen 1991, Poisot et al. 2012, Thompson et al. 2012, Rasmussen et al. 2013).

During the last decade, the study of dynamic networks has focused on improving internal structural features, identifying heterogeneity, and providing temporal and spatial resolution with the specific goal of detecting consistent patterns of network structure over time. Consumer–resource interactions (C–R) are one of the most important forces determining the structure and stability of ecological communities (McCann 2011). The presence and strength of C–R interactions tends to oscillate over time and space, influencing the structure and organization of the community and in some cases generating complex dynamics (Pascual and Dunne 2005). Thus, ecological networks sampled at a specific time period or inferred from spatiotemporally heterogeneous data will not accurately reflect the long-term structure of the ecological community (Thompson and Townsend 1999, Poisot et al. 2012, Hiltunen et al. 2013).

The ecological mechanisms that promote this variability can encompass different scales and ecological hierarchies from animal behavior to population dynamics and predator–prey cycles (reviewed by Berlow et al. 2004). Specifically, some of these potential mechanisms include, but are not limited to, predator functional responses, interference competition, prey switching, variation in prey abundance, changes in encounter probability, variation in productivity, and fluctuating environmental conditions (Pascual and Dunne 2005, Berlow et al. 2004, Van der Putten et al. 2004, Zook et al. 2011, Kaartinen and Roslin 2012, Poisot et al. 2012). The exact way in which these mechanisms interactively influence
the spatiotemporal fluctuations of C-R interactions is still a matter of discussion.

For example, at the population level, population dynamic theory predicts that, within a population, environmental variation can strengthen or weaken existing internal feedback processes and so boost or dampen the oscillations of resource consumption (Ings et al. 2009, Gilbert 2009, Amarasekare 2015). At larger scales, such as at the community level, these changes in resource exploitation generate dynamic scenarios in which the interactions between multiple prey species are redistributed, generating a high frequency of transient links that stabilize the ecological networks (Ings et al. 2009, Louelle 2010). Unfortunately, despite these theoretical insights, the dynamics and persistence of C-R interactions within whole network are not completely understood.

Evaluations of the temporal dynamics of ecological networks have been carried out particularly for plant-pollinator networks. However, these studies have examined short temporal scales, usually no longer than a couple of months (Carstensen et al. 2014, Fahimipour and Hein 2014, Simononok and Burke 2014, Trojelsgaard et al. 2015), with the most extensive studies covering few months in a row or two-three separate growing seasons (Basilio et al. 2006, Alarcón et al. 2008, Rasmussen et al. 2013). To date, these studies of the temporal dynamics of ecological networks have provided compelling evidence for the significant influence of environmental variability on the dynamics of mutualistic networks, but because of the short time scales evaluated, they cannot capture the influence of demographic processes and population dynamics that occur at longer temporal scales (inter-seasonal or inter-annual).

Additionally, food webs, mutualistic networks, and host–parasitoid networks are characterized by different types of interactions, where food webs and host–parasitoid networks describe antagonistic interactions, and mutualistic networks include those that are beneficial (Ings et al. 2009). In this sense, some studies have detected strong variation in the architecture and stability of communities depending on the type of interaction analyzed (Bascompte and Jordano 2007, Thébault and Fontaine 2010). This expected high variability has been observed in several networks, which differ in the number of species involved (nodes), interactions (links), the number of species at each trophic level, and changes in the complexity (i.e. connectance) of the network (Winemiller 1990, Martinez 1991, Moore and de Ruiter 1991, Martinez et al. 1999, Akin and Winemiller 2006, Camus et al. 2013). However, continuous tracking of all network interactions over time and at different environmental conditions is still lacking, and therefore the quantification of the persistence of trophic interactions in the long-term has been difficult.

Another aspect of network variability that is of interest is the relationship between network variability and spatial heterogeneity (Bonsall et al. 2002). Few studies have analyzed the effect of spatial variation or gradients on the structure of complex networks (Martinez 1991, Closs and Lake 1994, Martinez et al. 1999, Woodward et al. 2010, Trojelsgaard et al. 2015). Some of these studies have detected that spatial differences in C-R interactions are indistinguishable, where a vast majority of links occur in all local communities (Martinez et al. 1999). In other cases, such as pollination networks, species and interaction similarities decrease with geographical distance (Trojelsgaard et al. 2015). This variation may be due to differences in the quality and availability of resources, which in the long term impacts C-R dynamics (Polis and Strong 1996). Considering the spatial and temporal sources of variation and the different ecological mechanisms that promote variability of consumer–resource interactions, we predict that most C-R interactions would have low temporal persistence in the long term.

Until now it has been difficult to empirically evaluate the variability and persistence of ecological interactions in real networks due to the lack of data with high spatial, temporal and taxonomic resolution. This in turn has hampered the testing of ecological hypotheses concerning the relative frequency of the occurrence of C-R interactions. Here we explored the structure of several large marine trophic networks sampled at high spatial, temporal, and taxonomic resolution in order to answer three main questions: Are the temporal dynamics of these networks dominated by highly persistent interactions or are they dominated by interactions of low temporal persistence? Is there a common pattern in the temporal persistence of the trophic interactions among these communities located along an environmental gradient of 1000 km of coastline? The results presented here provide new insights on the nature, structure and dynamics of ecological communities.

Material and methods

Biological and environmental oceanographic data

We analyzed a long-term dataset of consumer–resource interactions of macrobenthic (i.e. >5 cm) intertidal rocky-shore communities in northern Chile. Four sites were sampled every three months between austral spring 2004 and summer 2007 (10 sampling times in total) along ca1000 km of the northern coast of Chile: Río Seco (RS, 21.00°S, 70.17°W), Caleta Constitución (CC, 23.42°S, 70.59°W), Caleta Angosta (CA, 28.26°S, 71.38°W), and Lagunillas (LA, 30.10°S, 71.38°W). Minimum distance between sites is ∼200 km. Environmental conditions of each site were assessed through sea surface satellite data: mean values of sea surface temperature, dissolved oxygen, salinity, and chlorophyll-a concentration were obtained for the pixels nearest to the coast; these data were collected from WorldClim Global Climate Data (Hijmans et al. 2005) and MARSPEC (Sbrocco and Barber 2013) (Table 1).

In each site, macroalgal coverages were estimated and at least ten individuals of each carnivorous and herbivorous species were collected, following the protocol of Camus et al. (2013). After collection, samples were subsequently fixed in 10% formalin. In the laboratory, the prey items of each consumer individual were identified to the lowest possible taxonomic level by means of gut content examination (Camus and Daroch 2008, Camus et al. 2013). Across the four sites we recorded more than 1000 interactions, and nearly 80% of the samples were identified to the species level (Camus and Daroch 2008, Camus et al. 2013). For each site, we constructed a C-R matrix with the number
of times that each C-R interaction was observed in the 10 sample events (the ‘persistence matrix’). This was done using the sum of the ten original presence/absence matrices of each site. The final persistence matrix contained values from 0 to 10, where 0 means that the interaction was not observed, and 10 means that the interaction was present in all sample events (high persistence). In this analysis we ignored the specific sequences of presences of each interaction following the conceptual framework of the Average Topological Overlap (Nicosia et al. 2013). In addition, we determined species richness as the number of taxonomic identities (number of prey and consumers, Table 1). Finally, we computed a dissimilarity matrix (1 – Jaccard index) from the presence/absence data in order to determine the degree to which community composition varied between sampling sites (Dornelas et al. 2013).

**Statistical analysis**

We fitted a rank-ordered function to the observed distribution of persistence (ranging from 1 to 10) of C-R interactions. As the basis for parameter estimation, we used a discrete version of the generalized beta distribution (DGBD) (Martínez-Mekler et al. 2009, Zhang and Feng 2014). The DGBD has the form:

$$f(r) = \frac{A(N + 1 - r)^{a} / (r)^{b}}{\int_{0}^{N} \frac{A(N + 1 - r)^{a} / (r)^{b}}{\int_{0}^{N}}}$$

where \(r\) is the ranked value of persistence of the C-R interactions, \(N\) is the maximum possible value of the rank (10), \(A\) is a normalization constant, and \(a\) and \(b\) are power law exponents. The exponent \(a\) is related to the ‘left to right’ tail and the exponent \(b\) is related to the ‘right to left’ tail of the dataset (Sornette 2006, Martínez-Mekler et al. 2009, Finley and Kilikki 2014). Different combinations of values of \(a\) and \(b\) correspond to different shapes of the curve. If \(a < b\), the curve shows a smooth exponential decay because the frequencies of occurrence are similar across ranks. If \(a > b\), the curve shows a strong exponential decay because the left tail of the curve is significantly larger than the right tail.

**Relationship between C-R interaction persistence and C-R co-occurrence**

In order to distinguish between interactions of low persistence driven by behavioral changes and those driven by low co-occurrence, we estimated the co-occurrence of predators and prey for each sampling time and site. For that, we firstly calculated the marginal sums of the rows and columns of the consumer–resource matrix for each sampling event. Then, the resulting matrix was transformed to presence–absence data. These co-occurrence matrices contained therefore binary values of 0 to 1, where 1 indicated that the predator and prey were both observed (i.e. ‘co-occurred’) in a given site and sampling time, and 0 indicated otherwise. We constructed a final co-occurrence matrix, summing all of the co-occurrences from the ten seasonal samplings at each site. The final co-occurrence matrix contained values from 1 to 10, where 1 indicated that predator and prey were observed simultaneously once, and 10 meant that the predator and prey were observed simultaneously in all sample events. By definition, the persistence C-R interaction is always equal or lower than the C-R co-occurrence (0 was excluded because it meant that species did not interact at all). We looked at the relationship between the co-occurrence and persistence matrices and calculated the correlation between them. However, due to the number of co-occurrences sets an upper limit to the number of interactions, the expected correlation under independence is not zero. To obtained the expected correlation under independence we develop a null model by conserving the number of co-occurrence at each level and randomly assign them to all possible level of persistence (Gotelli and Graves 1996). We performed this randomization 1000 times for each site to estimate the 95% confidence interval of the expected value under the hypothesis of independence between persistence and co-occurrence.

**C-R interaction persistence across communities**

To evaluate the degree to which C-R interaction persistence was similar between communities, we computed pairwise Spearman rank correlations for the persistence matrices of each community. All matrices were sorted in the same way and contained the same C-R interactions. Interactions that were absent in a given site scored zero for persistence. A high correlation coefficient would be expected if the persistence of each interaction was similar between sites. After the analysis, we sequentially recalculated the correlation coefficient after consecutively removing the least frequent and most persistent interactions. We recalculated the correlation coefficient in order to capture the level at which interactions more or less persistent contribute to the similarity of the persistence of trophic interactions between sites.

**Data deposition**

Results

Persistence in the occurrence of C-R interactions

Our results showed that more than 1000 trophic interactions were detected during the study at each site (Fig. 1). Pairwise comparisons of species composition between sites (Jaccard disimilarities) ranged from 0.23 to 0.32 of dissimilarity (Supplementary material Appendix 1 Fig. A2). Less than 1% of the C-R interactions were consistently observed over time in all four communities, and more than 40% of the interactions occurred only once (Fig. 2). In addition, ≤16% of the interactions were detected more than the five sampling events (or >80% of the interactions occurred less than five times, Fig. 1). Additionally, at each site the maximum percentage of common links between sampling times was 39%, reflecting the low temporal persistence of the trophic interactions (Supplementary material Appendix 1 Fig. A1). Accordingly, we observed a strong exponential decay in the rank-frequency distribution of interaction persistence for all sites, and the goodness-of-fit for the DGBD function was high (Fig. 2). From north to south, the coefficients of the DGBD were as follows: Río Seco $a = 1.15$, $b = 0.62$, $R^2 = 0.97$; Caleta Constitución $a = 0.99$, $b = 0.92$, $R^2 = 0.99$; Caleta Angosta $a = 0.99$, $b = 1.05$, $R^2 = 0.99$, and Lagunillas $a = 1.3$, $b = 0.65$, $R^2 = 0.99$. The exponential decay of the rank-frequency distribution of interaction persistence was similar for all communities (Fig. 2) despite the relatively large environmental differences in temperature, chlorophyll-a, and biotic aggregate properties such as species richness (Table 1). Moreover, our results showed that the co-occurrence of predators and prey did not directly explain the persistence of the trophic interactions (Fig. 4). In all sites the observed correlations were inside or slightly below the 95% confidence interval expected under the hypothesis of complete independence. For each site results (observed, [Null 95% CI]) were: Río Seco: 0.606 [0.573, 0.643]; Caleta Angosta: 0.586 [0.582, 0.644]; Caleta Constitución 0.549 [0.555, 0.625]; Lagunillas 0.589 [0.60, 0.669]. These result shows that while prey and predator species could be present simultaneously in the field, consumption did not necessarily occur, or in other words, co-occurrence did not drive predator–prey interactions.

Correlation of trophic interactions between communities

The between-site Spearman rank correlations ranged from $r = 0.59$ to $r = 0.73$, suggesting that the persistence of C-R interactions was quite similar between sites. After removing the interactions observed <5 times, however, the between-site correlations decreased to values between $r = 0.38$ and $r = 0.65$ (Fig. 3). This result indicates that the large number of less persistent interactions accounted for the high between-site correlations of persistence.

Discussion

Our results showed a common decay in the rank-frequency distribution of interaction persistence for intertidal rocky-shore assemblages spanning more than 1000 km of the
of interactions with low persistence could be explained by several factors.

Regarding the temporal scale of this study, the results found here agree with those of previous short-term studies of (ca 10 weeks) plant–pollinator networks in which few links are repeated over time and space (Rasmussen et al. 2013, Carstensen et al. 2014, Simanonok and Burkle 2014). However, in other networks of different types of interactions, the pattern of low temporal persistence is not as common. For example, a long-term study (ca six years) of mammal-parasite networks (Pilosof et al. 2013) has shown that host temporal persistence is high in host–parasite interactions. Also showing high temporal persistence of trophic interactions, a recent study of a forest predator–prey network in Białowieża found that 70% of trophic interactions are shared between summer and winter (Saavedra et al. 2016). Our results clearly show a pattern of persistence that is more similar to that of mutualistic networks than that reported for consumer–resource networks. However, the dissimilarity between the results found here and those of other networks could be caused by differences in design rather than intrinsic structural differences among systems. In this study we analyzed interactions on networks several times larger than those involved in the previously named studies. This fact could explain the observed differences with prior studies. For example, a small network could be a representation of the core species and interactions in the community, which actually could be the more persistent interactions on those networks (Saavedra et al. 2016). However, by ignoring the large pool of satellite species that are probably less abundant, we are probably overestimating the average persistence of the network and overlooking the important role that those species and interactions play in structuring the community. In this sense, future studies should pay attention to the large number of ‘transient’, low-persistent interactions that could be a key component in the structure and dynamics of large complex networks.

The co-occurrence of predator and prey could explain the differences of the persistence of trophic interactions. High species turnover could generate seasonal asynchrony between consumer and prey populations, thus reducing the
probability of encounters or co-occurrence. In this vein, Camus et al. (2013) and Camus (2008) has pointed out that the same communities studied here have high seasonal turnover in terms of species composition (resources and prey). Despite this, our results show that the link between co-occurrence and persistence is weak. We analyzed only the pairs of species than interacted trophically at least once. From this set we observed that there was no relationship between persistence and co-occurrence (Fig. 4), even for species that coexisted throughout the entire sampling period. This pattern is closely linked to the type of interaction between species. For example, several so-called grazers have been demonstrated to actually be generalist predators (Camus et al. 2013), which leads to a relatively a low dependency between a consumer and a specific resource; that is a low degree of “intimacy” (Guimarães et al. 2007). So, it could be expected that a generalist trophic strategy implies a higher chance of prey switch over time and space, which should lead to low C-R interaction persistence. Therefore, the dominance of generalist predators, coupled with a significant spatiotemporal variation in prey abundances, could be part of a mechanism determining the transient nature of large trophic networks. However, we did not found a relationship between density and the number of dietary items per species using the data published by Camus et al. (2013), thus, generalist predators were not necessarily the most abundant.

Following with the type of interaction and intimacy, other studies have shown clear differences in the structural properties of networks due to factors such as type of interaction and degree of interaction intimacy (Guimarães et al. 2007, Fontaine et al. 2011, Pires and Guimarães 2012). Most trophic interactions embedded in large food webs are labile, less specialized, and have lower intimacy values (Sinclair et al. 2003) than mutualistic and host–parasite networks, unless the predators present in the systems are specialists. Therefore, in networks where most predators are not specialized, we would expect that the persistence of trophic interactions is low. On the other hand, pollinator specialization in mutualistic networks has been positively correlated with the interaction frequency of plant–animal (Blüthgen et al. 2007). Therefore, the interactions of networks constituted of specialist species should be more persistent. Likewise, similar results have been found in host–parasite networks where organisms show high

Figure 4. Relationship between the persistence and co-occurrence of consumer–resource (C-R) interactions of four large marine intertidal rocky-shore networks. The matrices show that, across sites, low values of persistence (i.e. C-R interactions occurring once over 10 sampling times) can be observed across different levels of species co-occurrences, particularly for pairs of species occurring between two and seven times.
levels of physical and trophic dependence and where parasites commonly use one or few host species (Poulin 1992, Vázquez et al. 2005b).

In a spatial context, the frequency of occurrence of interactions was highly correlated (Fig. 3) between communities, but there was a decrease in correlation coefficients after the least persistent interactions were removed from the analysis. Firstly, this result indicates that the trophic interactions persistence was similar among communities due to the large number of minimally persistent interactions. Secondly, the most persistent interactions had different frequencies of occurrence among sites. For example, the trophic interaction between the gastropod *Tegula atra* and a encrusting Corallinaceae alga was observed in all sampling events but only in three of the four sites. Consumer behavioral responses to local environmental conditions could well explain the geographical variation in the frequency of occurrence of given interactions (Moore and de Ruiter 1991, Pool et al. 2016). In our study, local environmental conditions varied among sites: Caleta Constitución and Lagunillas are characterized by the persistent influence of an upwelling event, while Río Seco and Caleta Angosta are less influenced by this source of nutrient-rich, cold water (Camus and Andrade 1999, Thiel et al. 2007). In central Chile and the Pacific coast of North America, upwelling activity has been shown to significantly affect foraging rates of intertidal limpets and snails, respectively (Sanford et al. 2003, Nielsen and Navarrete 2004). Moreover, regional-scale analyses demonstrate that predation on adult prey and recruits peaks at intermediate levels of upwelling (Menge and Menge 2013). Therefore, local environmental conditions might mediate the significant spatial variation observed in this study.

Finally, a comment about a potential link between interaction persistence and interaction strength. Community stability has been generally linked with interaction strength; weaker interactions increase stability (Zhang and Small 2006). To our best knowledge, however, interaction persistence has seldom been included into the community stability theory. Recently, Saavedra et al. (2016) attempt to link interaction persistence with community stability. That study determined that the interactions among the species that remain in the network between seasons could be a proxy of the persistence of interactions and community persistence (Saavedra et al. 2016). So this approach could be used as a measure of community stability. In this way, the importance of persistence to network stability depends on the relationship between interaction persistence and interaction strength. The low-frequency interactions observed in our study could play a role in maintaining community stability, only if the persistence of interactions is a surrogate of interaction strength (Vázquez et al. 2005a, 2007). For example, transient interactions can result from behavioral prey shifts that occur over short time scales; these can dampen the destabilizing effects of temporal mismatches between consumers and resources (McCann et al. 1998). If this is true, the presence of a high number of low-persistence trophic interactions might imply that the network is robust to random disturbances (i.e. random removal or addition of species) but susceptible to non-random eliminations of highly connected or constantly dominant species. In this way, the energy path would remain almost unchanged in the network if a low-persistent interaction is eliminated, given the high probability that species use other resources in the future. On the other hand, the non-random elimination of highly persistent interactions could result in drastic changes in the network energy paths.

In this study, we describe the general patterns of trophic networks comprised of a low number of persistent interactions and a large number of transient species interactions. The spatiotemporal coverage of our study allows us to infer some generality of our results. Further theoretical and empirical work is still needed to determine how, when, and where the persistence of C-R interactions affects community-wide stability. Our results, along with other recent studies, challenge the analysis of ecological communities as static and persistent natural entities – where all species and links are present simultaneously – and stress the role of temporal variation and persistence of species interactions in structuring local communities.

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**References**


Supplementarey material (available online as Appendix oik-04285 at <www.oikosjournal.org/appendix/oik-04285>).
Appendix 1.