Research

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Species' roles in food webs show fidelity across a highly variable oak forest

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Ecological communities are composed of many species and an intricate network of interactions between them. Because of their overall complexity, an intriguing approach to understanding network structure is by breaking it down into the structural roles of its constituent species. The structural role of a species can be directly measured based on how it appears in network motifs – the basic building blocks of complex networks. Here, we study the distribution of species' roles at three distinct spatio-temporal scales (i.e. species, network, and temporal) in host–parasitoid networks collected across 22 sites over two years within a fragmented landscape of oaks in southern Finland. We found that species' roles for hosts and parasitoids were heterogeneously distributed across the study system but that roles are strongly conserved over spatial scales. In addition, we found that species' roles were remarkably consistent between years even in the presence of disturbances (e.g. species turnover). Overall, our results suggest that species' roles are an intrinsic property of species that may be predictable over spatial and temporal scales.

Global biodiversity is being threatened by a variety of anthropogenic drivers (Sala et al. 2000), and the biodiversity loss that can result from these drivers may in turn lead to the loss of beneficial ecosystem functions, such as pollination and decomposition (Dobson et al. 2006). Notably, the loss of just a single species can reverberate through a community, impacting the abundances of other species and the susceptibility of the community to further disturbance (Ives and Cardinale 2004). It has been shown, for example, that changes in herbivore abundances can induce trophic cascades that directly alter plant and predator abundances (Lewis 2009).

There are many potential drivers of biodiversity loss, including non-native species, climate change, and habitat loss and destruction (Sala et al. 2000) and these drivers can disrupt ecological communities in a variety of ways. For example, the introduction of non-native species can extirpate native species by out-competing or preying on them and can induce changes in local habitats (McGeoch et al. 2010). Similarly, shifts in the local climate can alter community composition (Koh et al. 2004) and have been shown to disrupt interactions between species (Gilman et al. 2010, Harley 2011). The loss or destruction of local habitat can lead to increased isolation, decreased dispersal efficiency (van der Putten et al. 2004), and changes to the competitive balance between organisms (Kareiva 1987), all of which which can have additional community-level consequences via changes in species–species interactions.

One holistic approach to understanding how disturbances influence species is to determine their impact on a community's network of interactions (Ings et al. 2009). This approach allows us to assess changes to interactions within a community, without making a priori decisions about the relative importance of any particular interaction (Tylianakis et al. 2008). Unfortunately, analyses at the network level are often challenging due to the inherent complexity of these systems (Memmott 2009). One way in particular that researchers have attempted to gain insight into ecological networks, despite their complexity, is through the concept of network motifs (Milo et al. 2002, 2004). Network motifs provide a way to simplify the characterization of large networks by breaking them down into meso-scale subnetworks made up of a limited number of species (Bascompte and Melián 2005, Camacho et al. 2007, Stouffer et al. 2007). The underlying principle is that any network can be decomposed into a unique set of motifs that act as the building blocks of the larger network and which, when reassembled, would form the original network (Milo et al. 2002). These smaller subnetworks can also represent sets of ecological interactions that are widely regarded as important, such as apparent and exploitative competition (Holt 1997).

In addition, this concept of motifs has been expanded to quantify the roles of individual species within a network (Stouffer et al. 2012). Just as motifs are the meso-scale building blocks of networks (Bascompte and Stouffer 2009), species' roles offer a species-centric perspective of network

structure by describing the configuration of a species' interactions in the network. Moreover, rather than having a single measure with which to quantify overall network structure, we can decompose a network into the complete distribution of roles of each of its constituent species, providing an enticing alternative to community- or network-level analyses.

We follow this species-centric approach here to study changes in species' roles through space and time within a fragmented host–parasitoid community. A previous study has demonstrated that this system is characterized by considerable spatial and temporal variability in species composition and diversity (Kaartinen and Roslin 2011). Moreover, the variation observed in species composition seems largely unpredictable. Paradoxically, the host–parasitoid network structure overall remained relatively consistent between years and across the landscape (Kaartinen and Roslin 2011, 2012). While the overall structure of the host–parasitoid networks remained consistent through space and time, previous research indicates that the changes in species composition and in immigration caused by the fragmentation could alter the interactions in such a way to still create an impact on species' roles (Vázquez et al. 2005).

In order to better understand the potential mechanisms underlying the interplay between species composition, species' roles, and the emergent property of whole-network structure, we systematically investigate the degree to which different predictors influence the distribution of species' roles between species, across space, and over time. Specifically, we first tested whether species' roles are an intrinsic species property, predicted by species identity, independent of the network in which they appear. Second, we analyzed variation in species' roles across a landscape by investigating whether the role of a species depends on the network in which it is found. Third, we explored whether species' roles are consistent over time despite the highly variable nature of our study system.

We then quantified whether and how potential drivers of role variation influenced species' roles and a community's role structure at each level of the analysis. These drivers were all selected because they represent intuitive biological factors that would be expected to contribute to natural variation in species' roles. At the species level, we hypothesized that feeding guild, abundance, number of interactions, or degree of specialization would explain variation in species' roles. At the network level, we hypothesized that related network-scale metrics would explain variation in species' roles across the landscape; these included proportion of species belonging to a particular feeding guild, species richness of the network, network connectance, and network specialization. Lastly, at the temporal level, we hypothesized that habitat fragmentation, changes in species composition between years, and interaction turnover would explain variation in species' roles through time.

Methods

Empirical data

The interaction networks studied here come from a fragmented range of European oaks *Quercus robur* in southern Finland with oaks scattered as large stands, small stands, and as isolated trees. As habitat islands, these oak trees sustain a high diversity of Hymenopteran and Lepidopteran species and their associated parasitoids (Kaartinen and Roslin 2011). The host–parasitoid communities were sampled from 22 individual oak trees (henceforth referred to as sites) spread over an area of approximately 5 km^2. They were sampled across two years (2006 and 2007), giving a total of 44 host–parasitoid networks (i.e. each site-year combination has a corresponding network). Across all networks, there were 28 leaf-miner and galler host species and 60 leaf-miner and galler parasitoid species (Supplementary material Appendix 1, Fig. A1 and A2). Interactions between species were documented following successful emergence of a parasitoid from a host species (Kaartinen and Roslin 2011).

Here we consider all events that indicate the existence of a host–parasitoid interaction as qualitative (binary), and therefore independent of the empirically-observed interaction strength. Reduction of quantitative networks to their qualitative equivalent may result in rare species or interactions contributing more than they otherwise would to any subsequent characterizations (Banašek-Richter et al. 2004). To determine if our results were indeed influenced by rare species or interactions, we compared the results for the qualitative networks to those expected if we had resampled the quantitative networks proportional to the observed interaction frequencies (Supplementary material Appendix 2). Overall, the resampling analysis indicated that none of our primary results were influenced by our use of qualitative networks.

Network motifs

Previous work in multitrophic food webs has focused primarily on three-species motifs within ecological networks (Bascompte and Melián 2005, Camacho et al. 2007, Stouffer et al. 2007, 2012). Unfortunately, there are only two possible three-species motifs in bipartite networks (Fig. 1) in contrast to the 13 possible in multitrophic networks (Stouffer et al. 2007). This distinction is driven by the fact that bipartite networks are two-mode networks made up of two distinct groups of species that may only interact between but not within groups. Therefore, to robustly explore species' roles in bipartite networks, we have expanded the previous methodology to include all of the bipartite motifs from two to six species, giving a total of 44 motifs (Supplementary material Appendix 3, Fig. A27). Though it reduced the meso-scale complexity, our results were consistent when only considering motifs up to size four or five.

Species' roles in bipartite networks

To measure the roles of all species in a network, we first calculated the frequency of each of the 44 bipartite motifs that appear in each bipartite network (Fig. 1). Though each motif of size s is, by definition, composed of s species, each species does not always appear in a unique position within that motif for reasons of symmetry (Kashtan et al. 2004, Milenković and Pržulj 2008, Stouffer et al. 2012). For example, in the two species motif $A \rightarrow B$, the positions of A and B are uniquely

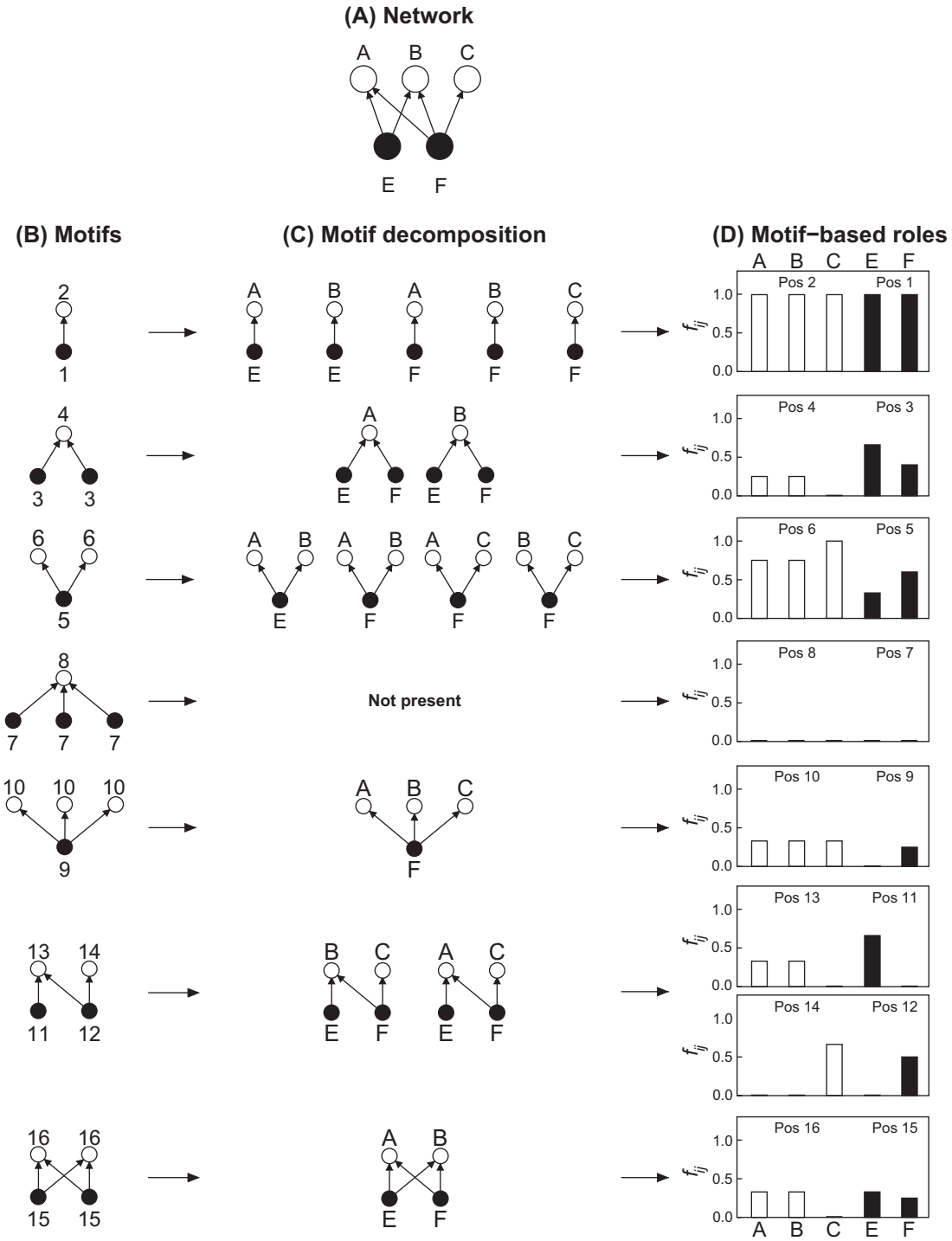

Figure 1. Quantifying species' roles from a hypothetical host–parasitoid food web. (A) The food web contains three parasitoid species (A, B, and C) and two host species (E and F). (B) In bipartite networks, there are one unique two-species motif, two unique three-species motifs, and four unique four-species motifs, with two, four, and ten unique positions respectively. (C) The food web can be decomposed into all species combinations whose interactions match the motif's configuration. Note that not all motifs must be observed. (D) The role of a species is defined as the relative frequency with which it appears across the structurally-unique positions in the different motifs. Importantly, the relative frequencies are normalized within each motif size class. Note that, some positions are not unique and can be occupied by multiple species simultaneously (e.g. position 3 is occupied by two host species).

defined by the direction of the interaction between them. Across the 44 bipartite motifs used in this study, there are a total of 148 unique positions (Supplementary material Appendix 3).

To quantify the role of species i in network n based on the observed motif frequencies, we enumerated the frequency $c_{ij|n}$ with which species i appears in each unique motif position j in network n. For all species i, this enumeration process creates a vector

$$\vec{c}_{i|n} = \{c_{i1}, c_{i2}, \ldots, c_{i148}\}_n \quad (1)$$

which is a multidimensional measure of how that species' interactions are arranged in its community's network: its role. Because some species have more interactions, they will naturally appear in more motifs than other species; as a result, some species will tend to have larger values of $c_{ij|n}$. To control for this effect, we normalize the vector $\vec{c}_{i|n}$ within each motif size class s (i.e. two, three, four, five, and six species). Each species in a network is then described by its normalized role $\vec{f}_{i|n}$ where all $f_{ij|n}$ are given by

$$f_{ij|n} = \frac{c_{ij|n}}{\sum_k c_{ik|n}\delta_{jk|s}} \quad (2)$$

where the sum is across all motif positions and $\delta_{jk|s}$ is Kronecker's delta ($\delta_{jk|s} = 1$ if positions j and k are in the same group s and $\delta_{jk|s} = 0$ otherwise; in this case the group is motif size class). The role, $\vec{f}_{i|n}$ of a species, therefore, describes its relative tendency to appear across the different motif positions throughout the network. More generally, we can consider the roles defined here as a quantitative representation of the shape of a species' 'interaction niche' since it describes how its host–parasitoid interactions are embedded within the larger space of the network (Fig. 1).

Fidelity of species' roles

Here, we aim to determine whether consistency of roles is maintained in the presence of disturbances. In order to first quantify consistency of roles, we introduce the concept of 'role fidelity' which can be thought of as the degree of predictability in the distribution of species' roles at a given scale of the data. Here, we specifically examined the strength of fidelity at the species, network, and temporal levels. The roles of host and parasitoid species were analyzed separately since they always represent orthogonal sets to each other (Fig. 1). This separation prevents the permutational analysis (described below) from assigning a role of a parasitoid to that of a host and vice versa. From this perspective, species fidelity would indicate that species' roles were significantly associated with species' identity across both sites and years. Similarly, network fidelity would indicate that the subset of roles observed in a network are a significantly non-random subset of all possible roles, and temporal fidelity would indicate that the subset of roles observed at a site in 2006 were not significantly different from those observed at that same site in 2007.

Our approach here is based on between- and within-group comparisons of role fidelity in a fashion analogous to a traditional analysis of variance. We note, however, that there are multiple ways in which fidelity could emerge and which could provide fruitful avenues for future study. One such way is via differences in species abundances, where it might be reasonable to expect more abundant species to show more consistent role fidelity than rare species. Though we have worked to control for the influence of rare species via the resampling analysis conducted here, this does not eliminate the possibility that underlying mechanics driving species abundance may also drive aspects of any observed role fidelity.

Species fidelity

We first tested whether or not species identity explained a significant amount of the total variation present in the observed species' roles. This is analogous to determining if there is significant clustering of species' roles on the basis of species identity. One approach to do this is to use permutational multivariate analysis of variance (PERMANOVA); the methods of a PERMANOVA are an extension of the traditional analysis of variance that generates a multivariate analogue to Fisher's F-ratio based on total dissimilarity relative to within-group dissimilarity (Anderson 2001). Note that, our method is not the same as a traditional PERMANOVA due to there being no true replication within this study. Instead, we are using the PERMANOVA as a way to test for the clustering of data at various levels of community organization via a permutational approach.

Within our PERMANOVA, the total dissimilarity D across all species and networks is given by

$$D = \frac{1}{N}\sum_{i=1}^{N-1}\sum_{j=i+1}^{N} b_{ij}^2 \quad (3)$$

where N is the total number of species' roles and b_{ij} is distance between role i and role j (we will describe the choice of a distance metric later). This measure of total dissimilarity treats roles as independent from networks. As a result, comparisons between species' roles are made within and between networks in the course of the analysis. For any group k, the within-group dissimilarity d_k is given by

$$d_k = \frac{1}{g_k}\sum_{i=1}^{N-1}\sum_{j=i+1}^{N} b_{ij}^2\,\delta_{ij|k} \quad (4)$$

where g_k is the number of roles in the group and $\delta_{ij|k}$ is Kronecker's delta (as before, $\delta_{ij|k} = 1$ if role i and role j are roles in the same group k and $\delta_{ij|k} = 0$ otherwise). Note that the grouping or clustering here can be done at a variety of levels. For example, grouping by species identity would give within-group dissimilarity d_k for all roles played by species k across the whole data set. Likewise, grouping by network would give within-group dissimilarity d_k for all roles played by species in network k. Total within-group dissimilarity across all species and networks is then given by $D_w = \sum_k d_k$, and the total dissimilarity and within-group dissimilarity are finally combined to give the test statistic $F = \frac{(D - D_w)/(g_k - 1)}{D_w/(N - g_k)}$ (Anderson 2001).

To test significance of any level of clustering, one can create a null distribution of the test statistic F by directly permuting the observed data (Anderson 2001). Specifically, we randomly shuffle the labels on the roles and recalculate F^*. After repeating this process to create a large ensemble of test statistics, the p-value is given by the proportion of random test statistics that are as or more extreme than the observed test statistic (Veech 2012).

A key step for using PERMANOVA is identifying an appropriate distance metric dependent on the data being analyzed. Recall that species' roles specify a set of relative frequencies with which a species appears across different

motif positions. We therefore chose the Bray–Curtis distance which is a robust measure of dissimilarity for multiple properties of ecological communities (Faith et al. 1987, Anderson 2001, Anderson and Robinson 2003).

To quantify overall species fidelity with a PERMANOVA, we followed the procedure outlined above with all roles $\vec{f}_{i|n}$ as the dependent variable and species identity as the grouping factor. We also restricted the randomizations for generation of the null distribution to the level of individual networks (i.e. a site-year combination) such that species identities were shuffled only within the network that they appear in (Anderson 2001) to account for non independence of species' roles within each network. We conducted the analysis using the adonis function from the vegan package (Oksanen et al. 2012) in R 2.15.1 (R Core Team), and we generated 4999 permuted values for the null distribution. Species that appeared in just one network were excluded from this analysis as we could not calculate their within-group distances.

In order to isolate species which contribute more or less to the overall variation of species' roles, we also calculated the fidelity of roles at the individual species level. Specifically, we use Eq. (4) to calculate the overall dissimilarity d_k of all empirically-observed roles for each species k. Here, we again conducted a permutation test where we randomized the species' identities within networks and calculated the test statistic d_k^*, and we repeated this process 4999 times to generate a null distribution of test statistics. We then used a direct test to compute $p_k = P(d_k^* \leq d_k)$, the proportion of randomizations that showed equivalent or greater similarity than that observed empirically (Veech 2012). When $p_k < 0.05$ (at $\alpha = 0.05$), there is significant species fidelity since the observed subset of roles for species k represent a tightly-clustered, non-random subset of all possible roles.

Network fidelity

To calculate network fidelity, we followed a similar procedure to that of the species-fidelity calculations. First, we ran a PERMANOVA to determine if network identity (i.e. site-year combinations), explained a significant amount of the total variation present in the species' roles; the roles $\vec{f}_{i|n}$ were once again the dependent variable with network identity as the grouping factor and unrestricted permutations.

We then decomposed the PERMANOVA results to the individual network level following Eq. (4), except that the grouping index k now indicates the network identity and Kronecker's delta $\delta_{ij|k} = 1$ when the roles i and j are both from network k and $\delta_{ij|k} = 0$ otherwise. As before, when $p_k < 0.05$ (at $\alpha = 0.05$), there is significant network fidelity since, across sites and years, the subset of roles observed in network k are a tightly-clustered, non-random subset of all possible roles.

Temporal fidelity

To quantify temporal fidelity, we first ran a PERMANOVA analysis with the roles $\vec{f}_{i|n}$ as the dependent variable and site identity and an interaction between site identity and year as the grouping factors. Year was not included as a separate grouping factor because we were only interested in the variation of roles at a site between years and not differences between years independent of site. To control for underlying variation across sites, we restricted the randomizations in this PERMANOVA to be within the same site. Note that, in contrast to species or network fidelity, we are interested here in the similarity of species' roles between sample years at each site when referring to temporal fidelity. Within our statistical framework, an indication of temporal fidelity is provided by a non-significant interaction between site identity and year in the PERMANOVA since such an interaction would imply that species' roles tended to differ between years at the different sites. Next, we obtained results at the individual site level by running analogous PERMANOVA analyses on a site-by-site basis following Eq. (4). The grouping index k now indicates the site identity and Kronecker's delta $\delta_{ij|k} = 1$ when the roles i and j are both from site k and $\delta_{ij|k} = 0$ otherwise. As before, when $p_k \geq 0.05$ (at $\alpha = 0.05$), there is temporal fidelity at site k since the subset of roles observed in 2006 were not statistically distinguishable from the subset of roles observed in 2007.

Potential drivers of species and network fidelity

In addition to quantifying levels of fidelity in our empirical networks, we also aimed to identify potential drivers of differences in fidelity across species and networks. At the species level, we hypothesized that species' feeding guild, abundance, number of interactions, or degree of specialization could help explain why some species showed fidelity as opposed to others. Abundance was measured as the rank abundance for each species in their network (the least abundant species was given the lowest rank), number of interactions was given by the ranked number of interactions for each species in the qualitative network (the species with the fewest interactions was given the lowest rank), and specialization was calculated using the dfun function in the bipartite package (Dormann et al. 2008) in R 2.15.1 (R Core Team). We performed a χ^2 test to determine if the proportion of species belonging to a particular feeding guild was related to observed species fidelity. In addition, we quantified the relationship between each of the other drivers and and whether or not the species showed significant fidelity with a generalized linear mixed model with species identity as the random effect (to control for additional variation between species), binomial errors, and logit link function using the lme4 package (Bates et al. 2013) in R 2.15.1 (R Core Team). We simplified this full multivariate model by removing predictors until no significant reduction in AIC occurred (Crawley 2007).

We also explored the effect of the corresponding metrics at the network level (i.e. each network in the data set), where we tested the influence of the proportion of host species that belonged to the leaf-miner feeding guild, the proportion of parasitoid species that belonged to the leaf-miner parasitoid feeding guild, species richness, connectance, and specialization on network fidelity. Species richness was equal to the total number of host and parasitoid species in a given network, connectance was given by $L/(H*P)$, where L is the number of links, H is the number of host species and P is the number of parasitoid species. Specialization was calculated using the H2fun function in the bipartite package (Dormann et al. 2008) in R 2.15.1 (R Core Team). We quantified the

relationship between each driver and and whether or not the network showed significant fidelity with a generalized linear model, binomial errors, and a logit link function using the glm function in R 2.15.1 (R Core Team). We simplified this full multivariate model by removing predictors until no significant reduction in AIC occurred (Crawley 2007).

Potential drivers of temporal fidelity

We also aimed to identify potential drivers of differences in fidelity through time. Recall that the empirical data studied here was collected in a heavily fragmented ecosystem and there was considerable species turnover between years at each site (Kaartinen and Roslin 2011). Changes in the composition of species, as a result of natural turnover or from reduced immigration pathways due to habitat fragmentation, could also potentially alter how species interact across the sites (Tylianakis et al. 2008, Laliberté and Tylianakis 2010, Kaartinen and Roslin 2011). We therefore hypothesized that changes in any of fragmentation, species composition, or changes in interactions observed at a site would lead to increased variability in species' roles, thereby decreasing the fidelity of species' roles between years.

To quantify changes in species composition with time, we calculated the species turnover of the host and parasitoid communities at each site between 2006 and 2007 using the Whittaker index (Whittaker 1960) since it is a robust measure of beta diversity (Koleff et al. 2003); a value of zero indicates a community with no species turnover between years while a value of one indicates a community with complete species turnover. To quantify changes in species' interactions with time, we calculated interaction turnover (β_{WN}) at each site by measuring pairwise differences in the interactions observed between years (Poisot et al. 2012). Just like species turnover, a value of zero indicates a community with identical interactions between years while a value of one indicates a community with completely different interactions. Finally, we quantified the expected influence of habitat fragmentation via a modified measure of connectivity that describes expected insect immigration at each tree (Kaartinen and Roslin 2011). The values of habitat connectivity are rescaled here such that zero indicates a poorly-connected, highly-isolated site while the value of one indicates a site that is not isolated.

To assess whether species turnover, interaction turnover, and habitat connectivity act as drivers for increased or decreased temporal fidelity of host or parasitoid roles, we quantified the relationship between each measure and the measure of temporal fidelity for each site with a generalized linear model, binomial errors, and a logit link function using the glm function in R 2.15.1 (R Core Team). We simplified this full multivariate model by removing predictors until no significant reduction in AIC occurred (Crawley 2007).

Results

Species-level fidelity

The species-level PERMANOVA analysis indicate that species identity explained a significant amount of role variability of both hosts and parasitoids ($F_{21,313}$, $p < 0.001$ and $F_{48,487}$, $p < 0.001$, respectively; Table 1). When examining the way that individual species contributed to overall species fidelity, we observed that significantly more host and parasitoid species showed role fidelity than would be expected at random (8 out of 21 host species, $p < 0.001$; 16 out of 49 parasitoid species, $p < 0.001$). Overall, these analyses suggest that species identity is a significant predictor of the role of a given species in the network and that the roles of individual species tend to be conserved across the different sites and between the two years.

Drivers of species fidelity

We found that none of feeding guild, abundance, number of interactions, or degree of specialization were significantly related to the species fidelity of host or parasitoid roles.

Network fidelity

Results from the network-level PERMANOVA analysis indicate that network identity explained a significant amount of role variability for both hosts and parasitoids ($F_{43,291}$, $p < 0.001$ and $F_{43,492}$, $p < 0.001$, respectively; Table 2).

When examining the way that individual networks contribute to network fidelity, we found that significantly more networks showed fidelity of host and parasitoid roles than would be expected at random (9 out of 44 networks, $p < 0.001$; 15 out of 44 networks, $p < 0.001$, respectively). Overall, these analyses suggest that the roles within the different networks are significantly more similar to each other than they are to roles from other networks.

Drivers of network fidelity

We found that proportion of species belonging to a particular feeding guild, species richness, and connectance were not

Table 1. Summary of results from the species-level PERMANOVAs for host and parasitoid species. Permutations in the PERMANOVAs were restricted to only shuffle roles within each network to account for non independence of species' roles within an interaction network.

Species type	Source of variation	DF	SS	MS	*F*	R^2	p
Hosts							
	Species identity	21	10.019	0.477	4.098	0.216	<0.001
	Residuals	313	36.446	0.116		0.784	
Parasitoids							
	Species identity	48	15.679	0.327	3.371	0.249	<0.001
	Residuals	487	47.188	0.097		0.751	

Table 2. Summary of results from the network-level PERMANOVAs for host and parasitoid species. Permutations in each PERMANOVA were unrestricted.

Species type	Source of variation	DF	SS	MS	*F*	R^2	p
Hosts							
	Network	43	8.880	0.207	1.599	0.191	<0.001
	Residuals	291	37.586	0.129		0.809	
Parasitoids							
	Network	43	13.795	0.321	3.217	0.219	<0.001
	Residuals	492	49.072	0.099		0.781	

significantly related to the network fidelity of host or parasitoid roles (all removed from model). The specialization of the network was significantly related to the network fidelity of host roles ($z_{43} = -2.088$, $p = 0.037$) but not of parasitoid roles (removed from model; Fig. 2).

Temporal fidelity

For host and parasitoid species, our temporal PERMANOVA analysis indicates that site identity and a site-by-year interaction both explained a significant amount of role variability ($F_{21,297}$, $p = 0.026$, $F_{22,297}$, $p = 0.026$, and $F_{21,504}$, $p < 0.001$, $F_{22,504}$, $p < 0.001$, respectively; Table 3). This suggests that the roles in at least some of the sites were variable for both host and parasitoid species. When breaking down these results by site, we found that host roles were significantly different between years at only 3 out of 22 sites ($p = 0.095$) while parasitoid roles were significantly different between years at 9 out of 22 sites ($p < 0.001$).

Drivers of temporal fidelity

Of the hypothesized drivers of role variability at the temporal level, none of habitat fragmentation, parasitoid species turnover, or interaction turnover, were significantly related to the temporal fidelity of host or parasitoid roles (all removed from the model). Host species turnover, however, was significantly related to the temporal fidelity of parasitoid roles ($z_{21} = 1.991$, $p = 0.047$; Fig. 3).

Table 3. Summary of results from the temporal-level PERMANOVAs for host and parasitoid species. Permutations in the PERMANOVAs were restricted to only shuffle roles within each site (i.e. between years) to assess differences in the clustering of roles in 2006 and 2007.

Species type	Source of variation	DF	SS	MS	*F*	R^2	p
Hosts							
	Site	21	5.317	0.253	1.975	0.113	0.026
	Site:Year	22	3.817	0.173	1.353	0.081	0.026
	Residuals	297	38.078	0.128		0.806	
Parasitoids							
	Site	21	7.928	0.378	3.793	0.124	<0.001
	Site:Year	22	5.993	0.272	2.737	0.094	<0.001
	Residuals	504	50.168	0.099		0.782	

Discussion

Overall, we found that the roles for host and parasitoid species showed signs of fidelity at the level of species and networks, and at the level of sites examined through time. Of the hypothetical drivers of role fidelity, we first found a significant relationship between network specialization and network fidelity of host roles such that networks that showed fidelity were significantly more specialized than those that did not. This may suggest that there is less niche overlap in these networks (Poisot et al. 2013) resulting in increased role overlap, and that turnover in these networks is more predictable because there are fewer interaction niches that can be filled. In addition, we found that the temporal fidelity of parasitoid roles was significantly related to host turnover such that increased turnover was positively related to increased fidelity. This result is particularly counter intuitive since we would have expected that lower host species turnover between years would act as a stabilizing factor for parasitoid roles. What's

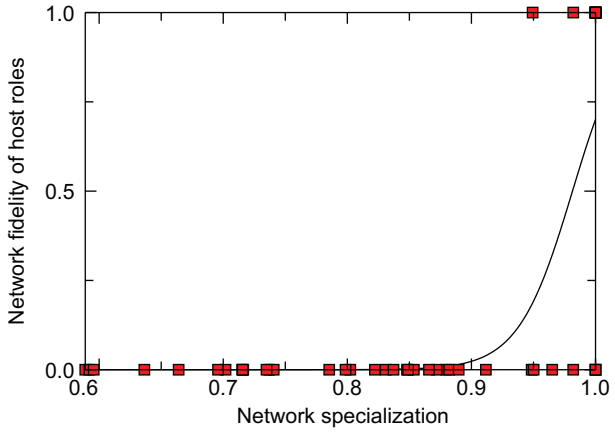

Figure 2. The relationship between network fidelity of host roles and the specialization of each network. We observed a significant relationship between the magnitude of network fidelity of host roles and host specialization with more specialized networks showing greater fidelity of host roles ($p = 0.037$).

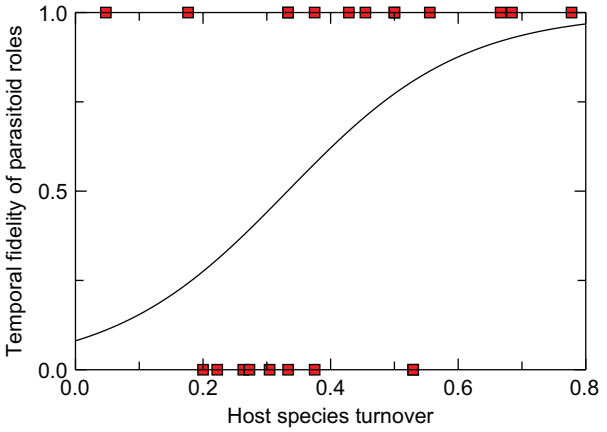

Figure 3. The relationship between temporal fidelity of parasitoid roles and host species turnover. We found that the temporal fidelity of parasitoid roles was significantly related to host turnover such that increased turnover was positively related to increased fidelity ($p = 0.047$).

more, high host turnover was correlated with high parasitoid turnover as well. Lastly, we found that our results are consistent when accounting for the potential influence of rare species in our networks. Beyond predicting the roles themselves, the predictable and unpredictable ways in which these communities vary across space and time imply that there is much to understand about the broader interplay between species, network, and temporal fidelity.

The implications of species fidelity

Despite hypotheses to the contrary (Lewinsohn and Cagnolo 2012), we found that hosts' and parasitoids' roles are significantly clustered by species identity. This conclusion is in general agreement with a previous study that concluded that phylogenetically-related species showed similar roles, independent of ecosystem type (Stouffer et al. 2012). Our study therefore provides additional evidence that species' roles may be an intrinsic species characteristic. Of potentially greater importance here, however, are the far-reaching implications of species fidelity in a community that experiences substantial turnover (Lewinsohn and Cagnolo 2012).

Though the roles we study here are quantified at the level of individual species, it is clear that the role of any particular species is a by-product both of that species' interactions and the interactions of the other species in the community (Luczkovich et al. 2003, Stouffer et al. 2012). To better illustrate this fact, consider a hypothetical community composed of two parasitoid species, both of which interact with two host species. If one host species leaves this community, the roles of all three remaining species will necessarily change. In such a situation, the only way in which we could observe significant role fidelity of the remaining species, as we observe here, would be for a new host species to enter the community and take on the exact same role that was lost and, what's more, participate in the same interactions.

It would therefore appear that species fidelity imposes multiple constraints on the roles observed within a community and, consequently, food-web structure. In fact, if we know that a specific species is observed in a community, species fidelity allows us to predict both the interaction niche of that same species and, by extension, the interactions of many other species. This interplay between species fidelity and the overall distribution of roles will also help us to better understand the mechanisms underlying the patterns observed at both the network and site levels.

The implications of network fidelity

Our exploration of network fidelity is fundamentally a test of how species' roles are distributed within a landscape context. Our analyses indicated that the roles in any given network were more similar to each other than to the roles found in the other networks. This result suggests that each network is characterized by considerable role 'overlap' and likely implies that our individual networks exhibit limited functional diversity (Petchey et al. 2008). A lack of functional diversity might be important particularly since species' interactions have been linked to various measures of ecosystem function, such as community persistence (Stouffer et al. 2012). Alternatively, the combination of low functional diversity and high role overlap seen here indicates the potential of increased redundancy and complementarity which can buffer communities from disturbances (Naeem and Wright 2003).

Previous research in this system found that, on the basis of whole-network comparisons, the networks themselves maintained their structure across the landscape (Kaartinen and Roslin 2011). To be fully consistent with our results about network fidelity of species' roles, there must be multiple ways in which distinct species' roles can be combined to produce equivalent network structure overall. This may have important implications for studies focusing strictly on whole-network measures as the basis for comparisons over time or through space, as they may be overlooking important meso-scale structural changes.

Comparisons on the basis of species' roles, such as those explored here, can therefore provide a more comprehensive view of ecological networks by disentangling the contributions of individual species to network structure. Since trophic roles and network structure are both thought to relate to overall ecosystem function (Thompson et al. 2012), an open question is whether species-level or network-level predictions are equally informative or whether they provide complementary perspectives (Lewis 2009).

The implications of temporal fidelity

Though the temporal signal was slightly weaker, we found that the distribution of species' roles across many sites was more consistent between the two years than expected. This result aligns well with previous work that found that the quantitative structure of the food webs in this system changed very little between years (Kaartinen and Roslin 2012). One of the key differences within our study was that parasitoids' roles showed greater within-site variation between years than did hosts' roles. In contrast to our initial hypotheses, our study allows us to rule out multiple possible explanations for this difference, including interaction turnover and habitat fragmentation. The most parsimonious explanation might then simply be that increased variation of parasitoid roles is attributable to the fundamental ecological asymmetry between the two groups of species: hosts can be observed in a site without parasitoids whereas parasitoids cannot be present without their hosts (Russell 1989).

Interestingly, we still observed role fidelity even though there was, on average, 50% species turnover and 70% interaction turnover between years. If we return to the hypothetical community that we used when discussing species fidelity, temporal fidelity provides the expectation that nearly all species that depart are replaced by a new species with a comparable role, but at close to a community scale. Given that species' roles are also strongly related to species identity, consistency in network structure should also mean that changes in species composition are imminently predictable. Precisely how to quantify this 'predictability' remains an open question for future research since the brief temporal scale of our study does not allow much extrapolation.

Predictable species turnover, in a way that also maintains both the role distribution and network structure of a

community, might simply be a demonstration of the inherent resilience of host–parasitoid communities (Laliberté and Tylianakis 2010). It might similarly provide an intriguing mechanism with which to maintain ecosystem function when confronted by internal and external disturbances (Walker 1995). The interplay then between species, network, and temporal fidelity might allow us to make better predictions of overall changes in ecosystem function (Tomimatsu et al. 2013).

Conclusions

Understanding and predicting the importance of individual species to ecological communities is an ongoing challenge in ecological research (Lewinsohn and Cagnolo 2012). Here, we found that species' roles appear to be an intrinsic species property, that they are broadly conserved across a landscape, and may be conserved over time despite changes in species composition. It will be interesting to determine how easily our results can be extrapolated to other communities, as they might provide a meso-scale platform from which to develop predictions about changes in ecological community structure.

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Supplementary material (Appendix ECOG-00913 at <www.ecography.org/readers/appendix>). Appendix 1–3.