Report

Evolutionary History and Ecological Processes Shape a Local Multilevel Antagonistic Network

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Summary

Uncovering the processes that shape the architecture of
interaction networks is a major challenge in ecology.
Studies have consistently revealed that more closely related
taxa tend to show greater overlap in interaction partners,
fuelling the idea that interactions are phylogenetically
conserved [1–8]. However, local ecological processes such
as exploitative or apparent competition (indirect interactions) might instead cause a decrease in overlap in interacting partners. Because of the taxonomic and geographic
coarseness of existing studies [2–5, 7], the structuring effect
of such processes has been overlooked. Here, we assess the
relative importance of phylogeny and ecological processes
in a local, highly resolved, four-level antagonistic network.
Across all network levels we consistently find that phylogenetic relatedness among resource species is correlated with
consumer overlap but that phylogenetic relatedness among
consumer species is not or negatively correlated with
resource overlap. This pervasive pattern indicates that the
antagonistic network has been shaped by both phylogeny
on resource range and by exploitative competition limiting
resource overlap among closely related consumer species.
Intriguingly, the strength of phylogenetic signal varies in a
consistent way across the network levels. We discuss
the generality of our findings and their implications in a
changing world.

Results

Revisiting Indirect Interactions in Food Webs

Species interact with each other within complex networks of
trophic interactions called food webs [9]. Effects that species
have on each other are therefore not restricted to pairs of
species that interact directly, but can be distributed widely
through the network of trophic links. Such cascading effects,
or indirect effects, play a major role in determining the
dynamics of populations and the persistence of species in
communities [10–13]. The network structure of food webs
determines the routes by which indirect effects are transmitted
and therefore which species have the most strongly coupled
dynamics. Considering invasions of alien species and
climate-driven range expansions, it is important to be able to
predict where the effects of novel species in communities
will be strongest. This requires an understanding of the organizing principles shaping food web structure [14–17]. Body
size was found to be a major determinant of the distribution
of feeding links within predator-prey webs [18]. However, in
host-parasitoid communities, which comprise a large proportion of the earth's animal species [19], traits related to host
defenses and host detection are likely to play an important
role not captured by body size [20]. While these traits are difficult to measure or describe, one can generally expect that
more closely related species will show greater similarity in
these traits, a property called phylogenetic signal [21–23].
Therefore, closely related parasitoid or herbivore species
should share a larger number of host species; in other words,
they should show greater overlap in the set of hosts they
consume. Similarly, closely related host species should
show higher overlap in their natural enemies (hereafter referred
to as consumers). However, sharing many interaction partners
is also expected to increase the potential for first-order indirect interactions, mediated by common resource species
(exploitative competition [24, 25]) or by shared consumers
(apparent competition [10, 26, 27]). These ecological processes negatively affect populations' growth and survival
[28–31] and might therefore select for a decrease in the number of shared resources or consumers among related species,
either through adaptive shifts in interacting partner (ultimately
via displacement of traits involved in interaction with resource
or consumer species) or through contingent mutual exclusion
within local communities. Ultimately, both processes might
thus negatively affect the relationship between phylogenetic
relatedness and overlap in interacting partners (i.e., phylogenetic signal).

Depending on the relative strengths of phylogeny and indirect interactions, three main phylogenetic patterns linked to
three main hypotheses can be expected: (H1) Positive phylogenetic signal in partner overlap indicates that phylogeny
outweighs indirect interactions in determining the identity of
interacting partners; (H2) No or negative phylogenetic signal
in consumer overlap among related resource species is the
signature of stronger effect of apparent competition; and
(H3) No or negative phylogenetic signal in resource overlap
among related consumers indicates stronger effect of exploitative competition. The latter is expected because closely
related species tend to interact with their shared resource
species in a similar way and are therefore more likely to
exclude each other or to be under strong selection to shift
partners. Alternatively, an absence of phylogenetic signal in
interaction at either level could also be due to a lack of phylogenetic signal in traits underlying interactions with partners,
unlinked with competition.

Presence and Sign of Phylogenetic Signal in Interactions

Positive phylogenetic signal in ecological interactions has
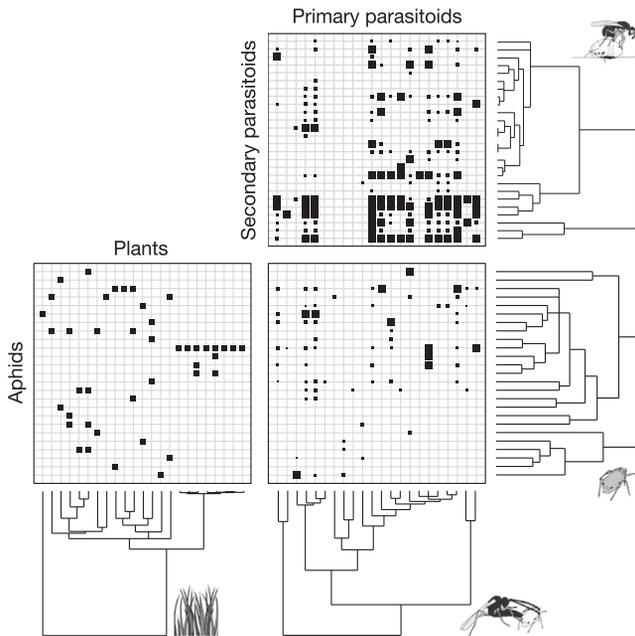been shown repeatedly at coarse taxonomical resolutions

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Figure 1. Phylogenies of Resource and Consumer Species for the Four Trophic Levels and Quantified Interactions between These Species

Size of square is proportional to the strength of interaction. Plant-aphid interactions were not quantified.

and geographical scales [1–8]. However, detecting the effect of the interplay between phylogeny and current ecological processes on community structure requires well-sampled interaction networks and detailed phylogenies of local communities that are resolved down to species. Here, we assess the relative importance of phylogeny and ecological processes in determining the identity of interacting species within a local four-level network of interactions between plants, aphids, primary parasitoids, and secondary parasitoids (koinobiont endoparasitoids and idiobiont ectoparasitoids), in Rush Meadow, UK (Figure 1).

We tested for the presence, strength, and sign of phylogenetic signal in indirect interactions in the network by correlating phylogenetic distances and ecological distances

(differences in interaction partners) among species at each trophic level (plants, aphids, primary parasitoids, and secondary parasitoids) by using Mantel tests. We found a consistent pattern of phylogenetic signal across trophic levels and years, with generally positive phylogenetic signal in consumer overlap for the resources and no or negative phylogenetic signal in resource overlap for the consumers (Figure 2). Specifically, we found a positive correlation between species' phylogenetic relatedness and their consumer overlap for each trophic level of the network (plants, aphids, and primary parasitoids, all considered as resources, Figures 2A–2C, respectively), no correlation between aphid phylogenetic relatedness and overlap in their host plants (Figure 2D), and negative correlation between parasitoid phylogenetic relatedness and their resource overlap for the two upper trophic levels (Figures 2E and 2F). Binary (presence/absence) and quantified interactions produced the same patterns, but the effect was stronger for binary interactions (see Figure S1 available online for results on quantified interactions). Although phylogenetic signal was not significant every year (Figure 2), trends across years were significant (Table 1).

Variation of Phylogenetic Signal among and within Trophic Levels

The strength of the positive phylogenetic signal at the resource level (i.e., overlap in consumers among related resource species) decreased with increasing trophic levels, whereas for overlap in resources the strength of the negative phylogenetic signal increased with increasing trophic levels (Figure 3). A similar pattern was found with quantified interactions but the significance and strength of the phylogenetic signals were weaker (Figure S2).

In the primary parasitoid/secondary parasitoid part of the network, phylogenetic signal in consumer overlap among primary parasitoids was stronger when considering interactions with koinobiont endoparasitoids than with idiobiont ectoparasitoids (Z score endo = 2.86 ± 0.07, Z score ecto = 1.64 ± 0.34, t = −6.4, p = 0.0048 for binary data and Z score endo = 2.56 ± 0.21, Z score ecto = 1.12 ± 0.49, t = −3.05, p = 0.0077 for quantified data). Phylogenetic signal in resource overlap among secondary parasitoids was stronger for endoparasitoids than for ectoparasitoids although the difference was not significant (Z score endo = −0.42 ± 0.25, Z score
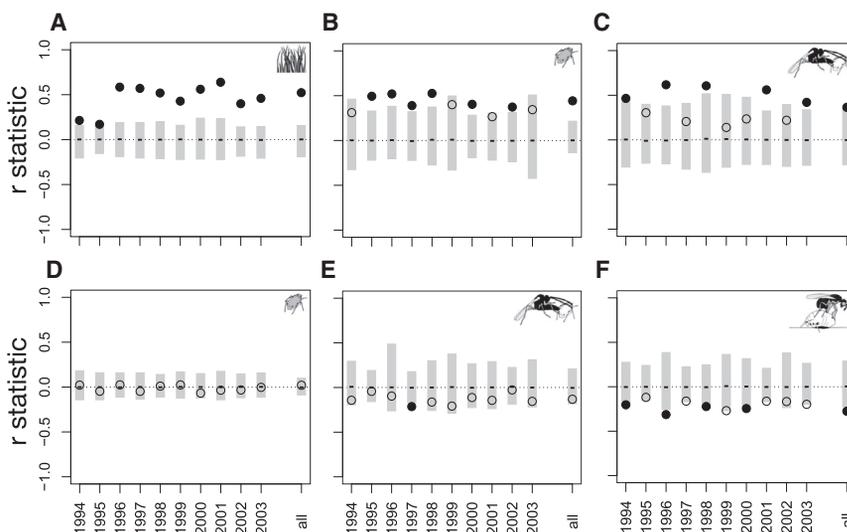

Figure 2. R Statistic of Mantel Tests between Phylogenetic and Ecological Distances for Binary Interactions

(A) Plants as resource.
(B) Aphids as resource.
(C) Primary parasitoids as resource.
(D) Aphids as consumers.
(E) Primary parasitoids as consumers.
(F) Secondary parasitoids as consumers.
Circles represent observed values. Grey bars represent 95% confidence intervals of the Mantel randomization. Filled circles represent values that are significantly different from the randomization. Data are shown for each year and for pooled years (all). Jost's combined p values are reported in Table 1. See Figure S1 for quantified interactions.

Table 1. p Values for Jost's Combined Significance Level Test of Overall Significant Positive or Negative Phylogenetic Signal for All Network Levels, for Both Resources and Consumers

Network Level	Interactions	Resource	Consumer
Plant – Aphid	Binary	(+) < 0.0001	0.6513
Aphid – primary parasitoid	Binary	(+) < 0.0001	(−) 0.0082
	Quantified	(+) < 0.0001	(−) 0.0285
Primary – secondary parasitoid	Binary	(+) < 0.0001	(−) < 0.0001
	Quantified	(+) 0.0210	(−) 0.0003

The sign of the observed phylogenetic signal is shown in brackets.

ecto = −0.28 ± 0.42, t = 2.5, p = 0.77 for binary data and Z score endo = −0.43 ± 0.35, Z score ecto = 0.51 ± 0.44, t = 1.89, p = 0.0749 for quantified data).

Discussion

Phylogenetic patterns are remarkably similar across the network, with pervasive, positive phylogenetic signal in consumer overlap among resources and no signal or negative signal in resource overlap among consumers. The positive phylogenetic signal detected at the resource levels (plants, aphids, and primary parasitoids considered as resources) means that resource species tend to have a greater proportion of their consumer species in common the more closely related they are (H1 supported for resources, H2 rejected). By contrast, the pattern of no or negative phylogenetic signal detected at the consumer level means that the overlap in resource species between any pair of consumer species is either independent of their relatedness or smaller, the more closely related the consumers are (H3 supported). Although the absence of phylogenetic signal found for aphids as consumers could also be caused by a lack of phylogenetic signal in underlying traits unrelated to indirect interactions, overall the asymmetry in the sign of phylogenetic signal in interactions between resource and consumer levels is consistent with the phylogenetic signature expected under a scenario where exploitative competition for limited resources has a stronger structuring effect than apparent competition.

Two nonexclusive mechanisms can explain this structuring effect of exploitative competition. First, exploitative competition can generate strong selection for related consumers to shift resource. Second, because related consumers tend to interact with their shared resource species in a more similar way than distantly related species, closely related species are more likely to locally exclude each other (competitive exclusion). Both factors ultimately lead to a lower overlap of resources among related consumer species (negative phylogenetic signal) within local communities, as observed in our data, but in different ways. Whereas an adaptive shift in resource, which requires changes in foraging traits, has a long-term effect, the outcome of competitive exclusion can vary in space and time depending on local conditions or just by chance. Our results suggest that, in our study system, the balance between adaptive shift in foraging traits and local competitive exclusion is in favor of the former process. First, the pattern of negative signal is clearly apparent when all years are pooled (Figure 2). If local competitive exclusion had a predominant role, the signal would be erased across years, because related species would be recorded on the same host in different years. Second, the effects detected in our study were stronger with binary than with
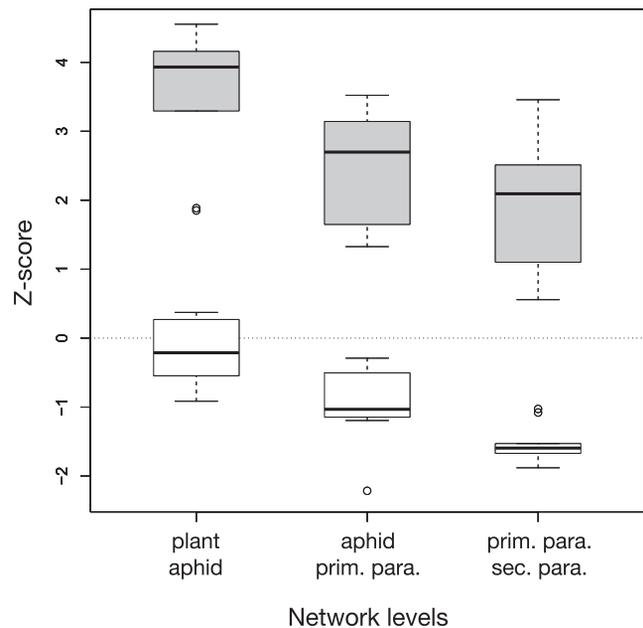

Figure 3. Boxplots showing the Distribution of Z Scores of Phylogenetic Signal of Binary Interactions for Each Network Level

Z score = (x − μ)/σ, where x is the observed Mantel's statistic value and μ and σ are the mean and SD of Mantel's statistic of the 1,000 permutations, respectively. Error bars represent the 95% confidence interval of the median. Grey boxes represent the resource level and white boxes represent the consumer level. Network levels and interaction type (resource, consumer) both had a significant effect on Z score values (respectively: $F_{2,56}$ = 19.2, p < 0.0001 and $F_{1,56}$ = 382.7, p < 0.0001). Interaction between factors was not significant. See Figure S2 for quantified interactions.

quantified interactions (Figure 2; Figure S1), suggesting that competition results in host shift rather than in differential frequencies on shared hosts.

Phylogenetic signal also showed more subtle variation within trophic levels. For secondary parasitoids, koinobiont endoparasitoid species each feed on more closely related species than do idiobiont ectoparasitoid species, and closely related endoparasitoids diverge more on resource species than ectoparasitoids, supporting stronger effect of evolutionary history on resource range and stronger effect of exploitative competition for endoparasitoids. Such an effect might be explained by differences in the characteristics of the ecological interactions studied; in particular, differences in the level of interaction intimacy between endo- and ectoparasitoids [32]. Endoparasitoids develop inside their host species and usually include a period of arrested development. During this time, they need to counter host immune defenses, which are likely to be phylogenetically conserved. Ectoparasitoid larvae, by contrast, feed externally with much less scope for specialist defenses. The stronger effect of phylogeny with increased interaction intimacy is probably a general pattern. High-interaction intimacy, mediated by high physical dependence and/or physiological integration between interacting species, involves matching of multiple traits that are likely to show a degree of phylogenetic conservatism.

Our results also show that as network level increases (i.e., from plant-aphids to aphid-primary parasitoids and to primary-secondary parasitoids), the positive phylogenetic signal at the resource levels becomes weaker, whereas the negative phylogenetic signal at the consumer levels becomes

stronger (Figure 3). This may be explained by differences in life history between parasitoids, herbivores, and plants. Resources of parasitoids are generally more limiting than those of herbivores [33], and this incurs stronger exploitative competition (more negative phylogenetic signal). In addition, resource choice can be determined partly by the resource species' own resources [34], which decreases the magnitude of the positive phylogenetic signal in the interaction [14]. More phylogenetic studies of highly resolved multitrophic antagonistic networks are needed to assess the generality of the pattern detected.

Despite these variations in signal strength, phylogenetic signal asymmetry between resources and consumers is consistent across the network. This raises the question of the generality of asymmetric phylogenetic signal across various types of interaction networks. A stronger phylogenetic signal at the resource than the consumer level has been observed in various antagonistic networks, but the causes of such pattern have hardly been discussed [3, 6, 7, 14, 35]. Our study not only extends these findings but also brings about a new dimension by highlighting a negative phylogenetic signal in interactions at the consumer levels. We propose the interplay between ecological and evolutionary processes as an explanation, with the outcome of exploitative competition being strong enough to counteract evolutionary constraints. Taken together, these results suggest that although antagonistic networks are strongly shaped by evolutionary history, exploitative competition is also an important structuring factor of their architecture. Interestingly, an opposite pattern has been found in mutualistic networks with stronger phylogenetic signal at the consumer than at the resource levels [2]. Such a discrepancy could be explained by the fact that mutualistic interactions may generate positive within-guild indirect interaction, or facilitation, in addition to potential competition for the shared mutualistic partner [36]. Such facilitation among within-guild species may promote stronger partner overlap. However, more species-level studies are clearly needed before attempting a generalization to all mutualistic networks.

Finally, our work has implications for predicting interactions in a changing world. As environmental changes affect species range distribution [37], producing "nonanalog" communities [38], interactions between species can be lost and gained [39], in this context, phylogenetic signal in ecological interactions has been proposed as a way to predict interactions in these new communities [14]. Our results highlight that communities are assemblages of coevolved species under local ecological processes, sometimes resulting in dramatic variation of strength of phylogenetic signal. There is clearly scope to predict potential consumer-mediated indirect effects of invasive species based on phylogenetic position. However, resource-mediated effects cannot be predicted this way because of host shift or competitive exclusion among close relatives.

Experimental Procedures

Interaction Network
Data were sampled monthly over 10 years in Rush Meadow, Silwood Park, UK. Interactions were fully quantified, except for the interactions between plants and aphids, and resolved to species level. Full details of data collection are shown in [40].

A total of 23 host plants, 25 aphid, 22 primary parasitoid, 18 secondary endoparasitoid, and 8 ectoparasitoid species, were included in this analysis (Figure 1, Supplemental Experimental Procedures).

Ecological and Phylogenetic Distances
We calculated the ecological distances between pairs of species of the Rush Meadows network, in terms of the overlap of their interacting partners (resource and consumer species). Two metrics were used: the Bray Curtis index, which takes into account interaction strengths, and the Jaccard index, which does not.

Phylogenetic distances among species within trophic levels were calculated from published phylogenies for plants [41] and from phylogenies constructed from field samples for aphids and primary and secondary parasitoids (see details on Supplemental Experimental Procedures).

Presence and Sign of Phylogenetic Signal
Presence and sign of phylogenetic signal in the overlap of interacting partners was tested by using Mantel tests between the phylogenetic and the ecological distances by using 1,000 permutations. Mantel test is appropriate here because data can be expressed as pairwise distances among taxa [42], it is commonly used in interaction network phylogenetic analyses [2, 3, 7, 43–45], and it allows testing for both positive and negative correlations. Mantel tests were performed for each sampling year and trophic level and for resource and consumer levels separately. Significance over all years was tested by using Jost's combined significance level test [46], a generalization of Fisher's combined probability test [47].

Strength of Phylogenetic Signal
To assess and compare the strength of phylogenetic signal, we quantified deviation of the observed correlations from the null expectations of the Mantel test by calculating Z scores. Z score = $(x – \mu)/\sigma$, where x is the observed Mantel's statistic value and μ and σ are its mean and SD across the 1,000 permutations. Z scores from different years and from different trophic levels were considered as independent (Supplemental Experimental Procedures). We analyzed Z scores with a linear model that included two factors and their interaction: network (three levels: 1. plant, aphid; 2. aphid, primary parasitoid; and 3. primary parasitoid, secondary parasitoid), and type of interaction (two levels: resource and consumer). A model simplification procedure was done to select the minimal adequate model.

The effect of type of secondary parasitoid was investigated by comparing the strengths of phylogenetic signals between subnetworks involving only endoparasitoids and only ectoparasitoids. Z scores were compared between types of parasitoids by using Welch t-tests for unequal variance.

Accession Numbers

The GenBank accession numbers for the 131 sequences reported in this paper are JX507365–JX507495.

Supplemental Information

Supplemental Information includes two figures, one table, and Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2013.05.066.

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