The compound topology of a continent-wide interaction network explained by an integrative hypothesis of specialization.

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ABSTRACT

Is there a prevalent pattern among interaction networks: nestedness or modularity? Must

consumers always trade-off generalism for average performance in resource

exploitation? These two questions have been addressed in various systems, with

contradictory results. A recent integrative hypothesis combines both questions within a

common theoretical framework, proposing that ecological specialization is structured by

different prevailing processes in smaller and larger network units. This should produce

both a compound interaction network, formed by internally nested modules, and a scale-

dependence on the relationship between consumer performance and generalism. Here,

we confirm both predictions in a large dataset on host-parasite interactions. We show

that modules indeed constrain nestedness at the whole network level, and that the

relationship between parasite generalism and performance on their hosts changed from

negative at large to positive at small scales. Our results shed light on both debates, and

provide some clues to their integration and solution.

INTRODUCTION

Darwin's "tangled bank" of species interactions is one of the most complex phenomena in nature. In the past decades, ecologists have imported analytical tools from network science (Barabási 2016) to disentangle this complexity (Bascompte & Jordano 2013). Despite the progress made in describing pervasive patterns and underlying mechanisms (Vazquez *et al.* 2009), some aspects of the architecture of ecological networks remain controversial, begging for further investigation (Dormann *et al.* 2017). One of those unanswered questions concerns what should be the predominant topology among ecological networks: nestedness or modularity (Thebault & Fontaine 2010).

By adapting the biogeographic concept of nestedness (Atmar & Patterson 1993) to interaction matrices, Bascompte *et al.* (2003) showed that several plant-animal networks have a nested topology, with the interactions of specialists tending to be subsets of the interactions of generalists. Later studies also found nestedness in many other mutualistic (Ollerton *et al.* 2003, 2007; Guimaraes *et al.* 2006) and antagonistic networks (Vázquez *et al.* 2007; Graham *et al.* 2009). Meanwhile, another topology, modularity, has also been widely reported (Olesen *et al.* 2007; Dupont & Olesen 2009; Mello *et al.* 2011; Krasnov *et al.* 2012). Since a modular network is one composed of modules of species that interact more frequently with one another than with other species of the same network, forbidden interactions between modules should constrain nestedness. Therefore, the two topologies seem to be mutually exclusive. Nevertheless, some ecological networks present high scores of both nestedness and modularity, and a positive relationship between these two topologies has even been reported (Fortuna *et al.* 2010).

Thus, a new question arose: how can a network be both modular and nested at the same time? A possible answer states that a dual nested-modular structure would arise if each

topology predominates at different structural scales of the network (Lewinsohn *et al.* 2006). Specifically, the authors suggested that some plant-animal networks are modular at the scale of the entire network, but their modules are internally nested. This kind of multi-scale architecture was named a compound (or combined) topology. Later, some empirical studies found evidence of compound topologies in pollination (Bezerra *et al.* 2009), seed dispersal (Sarmento *et al.* 2014), and phage-bacteria networks (Flores *et al.* 2013). In addition, theoretical studies confirmed this topology in simulated host-parasite networks (Beckett & Williams 2013; Leung & Weitz 2016).

Recently, an "integrative hypothesis of specialization" (IHS) was advanced, which proposed a mechanism by which a compound topology might emerge in ecological networks (Pinheiro *et al.* 2016). If its logic is correct, this hypothesis would also help to solve another important ecological controversy: what is the expected relationship between the resource range (generalism) of a given consumer and its average performance in exploring these resources (Futuyma & Moreno 1988)? The IHS states that this relationship should change with scale, from negative across the network as a whole to positive within each module, which should lead to the emergence of an interaction network formed by internally nested modules. The rationale of the IHS is briefly described in Box 1 and Fig. 1.

Despite their potential to help solve two important ecological debates, and to improve our understanding of the structure of ecological communities, neither the compound topology nor the IHS has been widely tested. Here, we address these two issues in an extensive host-parasite data set composed of flea-mammal interactions in 15 Palearctic regions. Since this data set was collected at large phylogenetic and geographic scales, it is a good model to test the relationship between generalism and performance, and also the existence of a compound topology.

Figure 1: The integrative hypothesis of specialization. Explanations are given in Box1.

First, we adapted the method described by Flores *et al.* (2013) and developed a general

framework to test nestedness at different network scales. Then, we tested whether the

flea-mammal networks have a compound topology. This question was addressed in both

the global network (formed by pooling together interactions reported in different

regions) and the local networks (formed by interactions reported for each region).

Second, we tested whether the relationship between host range (generalism) and

performance in fleas is scale-dependent, changing from positive within clusters of

similar resources (within each module) to negative between clusters (between modules).

This second question was addressed using only the local networks, since constraints in

the global network are mainly geographic (two species need to co-occur in the same site

to interact with one another) and would not reflect trade-offs in specialization. Our

results shed light on both debates, and provide some clues to their integration and

solution.

METHODS

Data set

We used an extensive host-parasite data set that has been analyzed in several studies on

ecological interactions (*e.g*, Krasnov *et al.* 2004, 2008; Vázquez *et al.* 2007; Fortuna *et*

al. 2010). It is composed of dozens of flea-mammal interaction matrices sampled all

around the world, from which we selected 15 Palearctic regions (see Table S1 in

Appendix S2) to maximize two parameters: the size of the matrix (at least 10 parasite

species and 10 host species per region), and the number of hosts sampled (more than

1,000 individual mammals per region).

The global matrix with all 15 regions pooled has a size of 263 species (nodes: 161 fleas

and 102 mammals), and contains 1,200 interaction records (links). The local networks

have an average size of 45.06 ± 12.64 species (mean ± standard deviation), with 26.26 ±

9.42 fleas and 18.8 ± 4.79 mammals, and contain on average 129.6 ± 57.22 interaction

records (Appendix S2: Table S1).

Furthermore, the global matrix and some local matrices produced networks with more

than one component, *i.e*., a cluster of species totally separated from the other nodes of

the network. In most of these networks, there is a giant component comprising most of

the network nodes and one or few minor components, each one including a small

number of nodes. The analyses below, at global and local scales, were carried out by

using only the respective binary version of the largest component of each matrix.

Network topology

Modularity

The first step to test for a compound topology is to unfold the modular structure of the

network. We did this computing the Barber modularity (Q) (Barber 2007) optimized by

the DIRTLPAwb+ algorithm (Beckett 2016), through the *computeModules* function of

the *bipartite* package (Dormann *et al.* 2008) for R (R Development Core Team 2017).

Modularity (Q) varies from 0 to 1, and the algorithm reveals also the number and

composition of the modules found in the network.

Nestedness

A nested matrix has its interactions arranged in a particular way: the interactions of the

least connected species are proper subsets of the interactions of the more connected

species (Ulrich *et al.* 2009). NODF is a metric that aims to synthesize this pattern in a

single number (Almeida-Neto *et al.* 2008). In its default procedure, a NODF score is

computed for each pair of species (independently for consumers and resources, i.e.,

rows and columns of the interaction matrix) and, then, averaged to calculate the NODF

score of the whole matrix. This procedure implicitly assumes that nestedness is evenly

distributed in the matrix. However, as pointed out by the authors of NODF themselves,

it is important to "*explore whether nestedness is a general pattern of the community or*

derives from some particular species subsets" (Almeida-Neto *et al.* 2008). If different

species subsets of the matrix have different degrees of nestedness, an overall NODF is

not an appropriate summary of the matrix structure (Gotelli & Ulrich 2012). It turns out

that this is exactly the case if the network has a compound topology, where nestedness

between pairs of species of the same module should be much higher than nestedness

between pairs of species of different modules.

In order to solve this problem, we adapted the method described in Flores *et al.* (2013),

and averaged nestedness independently between pairs of species of the same module

(NODF$_{SM}$), and between pairs of species of different modules (NODF$_{DM}$), and

compared those values with those expected by species degrees under two scenarios (null

models): in the absence of a modular structure (free null model) and in the presence of a

modular structure (restricted null model). The rationale behind using these two null

models is explained below, while the detailed instructions for performing both null

models are presented in Appendix S1.

Predictions

If nestedness and modularity coexist at large network scales as two sides of the same

coin, we expected nestedness between species of different modules (NODF$_{DM}$) to be

equal to or higher than expected by their degrees (*i.e.*, the free null model). Otherwise, if

modularity constrains nestedness between pairs of species of different modules, we

expect NODF$_{DM}$ to be smaller than expected by their degrees.

Notice, however, that NODF between pairs of species of the same module (NODF$_{SM}$)

will be higher than expected by species degrees whether or not modules are internally

nested. This would happen since, by definition, species of the same module share more

interactions with one another than expected by their degrees, regardless of those

interactions being nested or not. Hence, a $NODF_{SM}$ value higher than expected by the

free null model is a necessary, but not sufficient condition, for a network to have a

compound topology. This is the reason why we need the restricted null model – which

also conserves the modular structure of the original matrix when generating the null

matrices (Additional Information 1) –, to test whether $NODF_{SM}$ is higher than expected

given the modular structure. On the one hand, if the network is formed by modules that

are not internally nested, $NODF_{SM}$ should be higher than expected by the free null

model, but lower than expected by the restricted null model. On the other hand, if the

network is formed by internally nested modules (*i.e.*, a compound topology), $NODF_{SM}$

should be higher than expected by both the free and restricted null models.

But why did we not individualize each module and, then, test its nestedness

independently? Although this would be a valid procedure to test $NODF_{SM}$, it would not

allow to test whether interactions between pairs of species of different modules

($NODF_{DM}$) are more nested than expected *given* the constraints imposed by the

modules. This can be done by comparing the observed $NODF_{DM}$ with that expected by

the restricted null model.

Z-Score

For each main component of the 16 networks (the global network and 15 local

networks), we generated 1,000 random matrices using the free null model and another

1,000 matrices using the restricted null model. Next, for each random matrix, we

computed its overall NODF and decomposed it into $NODF_{SM}$ and $NODF_{DM}$ using the

observed partitions of their corresponding real network.

Finally, for all combination of matrices (16 in total: 1 global and 15 local), null models

(2: free and restricted), and NODF metrics (3: NODF, $NODF_{SM}$ and $NODF_{DM}$), a Z-

score was calculated as $Z = [Value_{obs} - mean(Value_{sim})] / \sigma(Value_{sim})$, where $Value_{obs}$ is

the observed value of the metric and $Value_{sim}$ represents the values of the metric in the

randomized matrices. Observed and expected modularity values were also compared

using Z-scores, but only for the free null model, as it does not make sense to compare

observed and expected modularities with a null model that fixes the modules.

Nestedness and modularity standardized by null models will be called relative

nestedness and relative modularity, respectively. For simplicity, they will be represented

here as Z_F or Z_R, depending on the null model, followed by the metric name (*e.g*, $Z_F Q$

and $Z_F NODF_{SM}$ represent, respectively, relative modularity and relative nestedness

between pairs of species of the same module, when standardized by the free null model).

Our goal was to see how modularity and nestedness interact with each other in a

continuous way. Therefore, in all analyses we used the original Z-scores, without

classifying them as significant and non-significant.

Matrix plotting

The interaction matrices were reorganized to maximize between- and within-module

nestedness as done in previous studies (Flores *et al.* 2013, 2016). Briefly, we first

reordered the matrix rows and columns by degree without disrupting its modular

structure and, then, permuted the modules in order to find the arrangement of modules

which maximizes the overall NODF of the matrix. This procedure facilitates the

visualization of a compound topology, if one exists.

Specialization versus performance at different scales

Performance index

In the host-parasite literature, the performance of a parasite in a host is usually

quantified indirectly through some metric assumed to reflect it: *e.g*, prevalence,

intensity, or abundance (Poulin 2007). We chose abundance: the average number of

individual fleas per individual mammal (calculated including infected and uninfected

hosts). This choice is justified as abundance is considered a good measure of

performance in host-parasite systems (Krasnov *et al.* 2006), since it integrates intensity

of infestation and prevalence in a single metric (abundance = intensity of infestation

times prevalence), measuring different aspects of parasite performance. While intensity

of infestation is the average number of individual parasites per infected individual host,

prevalence is the proportion of infected individuals in the host population.

Generalism within modules and between modules

For each flea species, specialization within and between modules was measured through

its cartographic position in the network: its within-module degree (Z, which should not

be confused with the Z-score of the null models) and participation coefficient (P)

(Guimerà & Amaral 2005).

These two metrics define the functional role of a species in a network, and they are

respectively related to the number of interactions a species makes with other species of

its own module and with species of other modules. Z and P values were calculated

independently for each local network.

Mixed models

We used mixed models (Bolker *et al.* 2009) to test whether flea performances are

positively correlated with their within-module degrees (Z) and negatively correlated

with their participation coefficients (P). Linear mixed models (LMMs) were built by the

lmer function of the *lme4* package (Bates *et al.* 2015), and fitted by restricted maximum

likelihood (REML).

We used the log-transformed abundance of each parasite species in each host species in

248 each region as the response variable, Z and P values for each flea species in each region

249 as the explanatory variables, and host species, parasite species and region as crossed

250 random factors. We decided to use parasite abundances per host species, rather than

251 average it between all hosts exploited by a flea, to control for host characteristics known

252 to affect abundance (e.g., carrying capacity, susceptibility, and richness of parasite

253 fauna) (Krasnov *et al.* 2005). Averaging would also decrease the power of the analysis

254 (Hopkins 1982; Schank & Koehnle 2009).

255 In addition, as pointed out in Box1 (see also Fig. 4 in Pinheiro *et al.* (2016)), in local

256 networks composed of very similar resources, we should not expect to find either a

257 negative relationship between abundance and P or modules. In those networks, the

258 modules recovered by the DIRTLPAwb+ algorithm will be spurious, not imposing

259 constraints to interactions, and the measured $NODF_{DM}$ should be higher than expected

260 by species degrees (the free null model). To test this prediction, we included an

261 interaction between $Z_F NODF_{DM}$ and the fixed factors of the model (P and Z). We expect

262 $Z_F NODF_{DM}$ not to have an influence on the effect of Z on abundance, but to influence

263 the effect of P. Specifically, we expected that the effect of P on abundance should be

264 negative only in local networks in which the modular structure constrains nestedness

265 between pairs of species of different modules, that is, in local networks with negative

266 values of $Z_F NODF_{DM}$.

267 We used backward stepwise regression to select fixed and random effects, following the

268 procedure suggested by Bolker *et al.* (2009). We used the *anova* function of the *stats*

269 package to perform a likelihood ratio (LR) test on the random effects (to which the

270 models are refitted with maximum likelihood) and, then, used the *Anova* function of the

271 *car* package to perform Wald X^2 tests on the fixed effects. To tell apart the variance

272 explained by either the fixed or random factors in the minimal selected model, we used

the *r.squaredGLMM* function of the *MuMIn* package for R to compute both marginal

and conditional R squared (Nakagawa & Schielzeth 2013). The confidence intervals of

the parameters were obtained by bootstraping using the *confint.merMod* function of

lme4 package. The confidence interval of the conditional effect of P given $Z_F NODF_{DM}$

was also computed by simulation using the *interplot* function of *interplot* package.

RESULTS

Topology

Global network

The global network presented higher modularity ($Z_F Q = 51.13$) and overall nestedness

equal ($Z_F NODF = 0.39$) to that expected by the free null model. However, the observed

scores of nestedness were much higher between pairs of species of the same module

than between pairs of species of different modules ($NODF_{SM} = 45.47$, $NODF_{DM} = 9.85$).

In addition, as expected if the modules constrain nestedness between species of different

modules, $NODF_{DM}$ was smaller than expected by the free null model ($Z_F NODF_{DM} = -$

13.46) (Fig. 2a), but equal to expected by the restricted null model ($Z_R NODF_{DM} = 0.22$)

(Fig. 2b). Finally, nestedness between pairs of species at the same module was higher

than expected by both null models ($Z_F NODF_{SM} = 53.89$, $Z_R NODF_{SM} = 22.08$) (Fig. 2a-

b).

Those results strongly support the hypothesis that the global flea-mammal network has

a compound topology, which can be easily seen when we plot the interaction matrix

maximizing nestedness without disrupting its modular structure (Fig 3).

Local networks

Nestedness and modularity varied widely among local networks, which, in general,

were more nested ($Z_F NODF = 2.03 \pm 1.94$) than modular ($Z_F Q = 0.36 \pm 1.31$) (Fig. 4a).

Figure 2: Observed values (dots) of NODF, NODF$_{SM}$, and NODF$_{DM}$ in the global network contrasted with the values expected by species degrees (distributions) in the absence (a: free null model) or presence (b: restricted null model) of a modular structure. NODF: overall nestedness. NODF$_{SM}$: nestedness between pairs of species of the same module. NODF$_{DM}$: nestedness between pairs of species of different modules. As expected if the global network has a compound topology, NODF$_{SM}$ is higher than expected by both null models, and NODF$_{DM}$ is smaller than expected by the free null model and equal to that expected by the restricted null model.

However, some relationships between these two topologies were evident. First, both observed and relative overall nestedness (NODF) (Fig. 4a, c and e; and Appendix S2: Table S2) decreased as modularity increased. Second, the same pattern was true for nestedness between pairs of species of different modules (NODF$_{DM}$) (Fig. 4a,c and e; and Appendix S2: Table S2). Third, although nestedness between pairs of species of the same module (NODF$_{SM}$) was not significantly related to modularity in any case (Appendix S2: Table S2), the Z$_F$NODF$_{SM}$ showed a trend to increase with Z$_F$Q (Fig. 4c).

In addition, as for the global networks, observed and relative values of NODF$_{SM}$ were higher than those of NODF$_{DM}$ (Fig. 4b,d and f), and the difference between them increased with modularity. Finally, NODF$_{SM}$ values were higher than expected by both null models, while NODF$_{DM}$ values were smaller than expected by the free null model

but equal to that expected by the restricted null model (Fig. 4b,d and f).

Fig. 3: Interaction matrix reorganized to maximize between- and within-module nestedness

without disrupting the modular structure of the network. Interactions within modules (delimited

by boxes) are showed in black, while those outside modules are showed in gray. Flea species

are represented in rows and mammals in columns. The compound topology of the global

network is evident.

Specialization versus performance

Random factors explained a significant portion of the variance in flea abundance

(Appendix S2: Table S3). In addition, as expected, only the within module degree (Z),

participation coefficient (P), and the interaction between P and $Z_F NODF_{DM}$ significantly

affects flea abundances. Neither $Z_F NODF_{DM}$ nor its interaction with Z was retained in

the minimum selected model (Appendix S2: Table S4 and Table S5).

Figure 4: Relationship between observed and relative (Z_F and Z_R) scores of nestedness components (NODF, $NODF_{SM}$ and $NODF_{DM}$) and modularity in local networks. Z_F and Z_R represent the relative score of a metric (nestedness or modularity) standardized by the score expected in the absence (the free null model) or in the presence (restricted null model) of the modular structure, respectively. NODF (green): overall nestedness. $NODF_{SM}$ (purple): nestedness between pairs of species of the same module. $NODF_{DM}$ (orange): nestedness between

pairs of species of different modules. Left panels (a, c and e): relationship between observed and

relative nestedness and modularity scores. Right panels (b, d and f): box plots of observed and

relative nestedness scores. Notice that relative modularity is always standardized by modularity

expected by the free null model, both in c and e. Lines show significant relationships (p<0.05).

On the one hand, flea abundances were always positively correlated with within-module

degree (Z) (Fig. 5). On the other hand, as expected, the relationship between flea

abundance and participation coefficient (P) changed from positive to negative as the

$NODF_{DM}$ becomes smaller than expected by the free null model, crossing zero at

$Z_F NODF_{DM} \approx -2$ (Fig. 5). In addition, the predicted positive effect of participation

coefficient (P) on flea performance was higher than that of within-module degree (Z)

when $NODF_{DM}$ becomes equal to or higher than expected by the free null model.

Finally, although the complete models explained a large amount of data variance, the

fixed factors were responsible for only a very small fraction of the explanation ($R^2_{(m)}$ =

0.086, $R^2_{(c)}$ = 0.53).

DISCUSSION

In the present study, we provide strong support for the integrative hypothesis of

specialization (Pinheiro *et al.* 2016) using a continent-wide host-parasite network. We

confirmed both (i) the emergence of a compound topology in the local and global

networks (Fig. 2, 3 and 4); and (ii) the scale-dependence of the relationship between

specialization and performance (Fig. 5). Our results unite two long-standing debates in

the ecological literature within the same theoretical framework and provide clues to

their solution.

Nestedness versus modularity

What is the predominant topology in ecological networks: nestedness or modularity? In

the past decades, conflicting results have been reported, leaving us with three possible

scenarios. First, different systems, taxa, and interaction types lead to networks with

different topologies. For instance, it has already been suggested that antagonistic

networks tend to be modular, while mutualistic networks tend to be nested (Thebault &

Fontaine 2010). Second, both topologies coexist as two sides of the same coin (Fortuna

et al. 2010), with the nested structure superimposed over the modular structure. Third,

alternative topologies should become manifest at different network scales, resulting in a

compound topology (Lewinsohn *et al.* 2006). Our results provide strong support for the

third scenario.

At first glance – considering only that the global and some local flea-mammal networks

presented scores of nestedness and modularity higher than or equal to those expected by

their species degrees (free null model) (Fig. 2a and Fig. 4c-d) – one could conclude that

those two topologies coexist in the flea-mammal networks as two emergent properties

of the same underlying phenomenon. However, the observed and relative values of

modularity and overall nestedness were negatively correlated in the local networks (Fig.

4a,c and e). And while nestedness between pairs of species of the same module was

higher than expected by the species degrees ($NODF_{SM}$), the opposite was true for

nestedness between pairs of species of different modules ($NODF_{DM}$) (Fig. 4d). In

addition, the difference between these two sets of nestedness increased with modularity

(Fig. 4a,c and e). Together, those results strongly suggest that modularity constrains

nestedness at large topological scales of this host-parasite system.

Figure 5: The predicted effects of within-module degree (Z) and participation coefficient (P) on

flea performances (abundance) for different values of $Z_F NODF_{DM}$ (relative nestedness between

pairs of species at different modules in a given local network when compared to that expected

by the restricted null model). Lines show the predicted effects of P and Z on abundance (and its

95% confidence intervals), while dots indicate the fifteen local networks. As expected by the

IHS, the effect of P changes from negative to positive (becoming higher than the positive effect

of Z) as nestedness between species in different modules increases. The effect of Z on

abundance in a given local network is independent of $Z_F NODF_{DM}$.

However, as pointed out in the Methods section, to say that the modules constrain

nestedness between species of different modules and increase nestedness between

species of the same module is a truism, a logical consequence of the definition of

modules itself. In ecological terms, it is like saying that species preferences

(specialization) constrain resource breadth processes (Brown 1984), which is trivial. A

much more interesting issue would be to evaluate if interactions are more nested than

expected *given* the species preferences, which are reflected in the network modular

structure. This raises two questions.

First, is nestedness between pairs of species of the same module higher than expected

given that they have similar dietary preferences, *i.e*, that they belong to the same

module? By comparing the observed $NODF_{SM}$ to that expected by the species degrees in

the presence of a modular structure (the restricted null model), we showed that this is

true for the flea-mammal network, which is formed by internally nested modules (Fig.

3).

Second, is nestedness between pairs of species of different modules higher than

expected given that they have dissimilar dietary preferences, *i.e*, that they belong to

different modules? That is, when a consumer c_i of module *A* pervades the modular

structure and consumes resources from module *B*, will c_i consume the most consumed

resources of module *B*? By comparing $NODF_{DM}$ to that expected by the restricted null

model, we show that this is also the case in the studied host-parasite system, since both

in the global (Fig. 2b) and the local networks (Fig. 4f) the interactions between species

of different modules were equally nested as expected by the restricted null model.

This scenario ($NODF_{SM}$ and $NODF_{DM}$ equal to or higher than expected given the

modular structure) suggests that, once the constraints imposed by modules are

overcome, the same processes that structure interactions within modules also structure

the few interactions outside them. This does not necessarily need to be true, since

competitive exclusion would predominate over resource availabilities outside the

modules. For example, if parasites have poor performances in hosts that do not belong

to their modules, diffused competition would prohibit parasites of module *B* to

successfully establish themselves in the most exploited hosts of module *A*. If this

happened, parasites would become supertramps (Diamond 1975) when exploiting hosts

of other modules, and an antinested pattern of interactions would emerge between pairs

of species of different modules (Poulin & Guégan 2000). Although it is not true in the

flea-mammal network, it is an interesting question to be addressed in other systems.

Understanding the processes governing the spillover of species interactions between

modules has important practical implications. It may help, for example, to predict

which species are the most likely to invade new habitats or which parasite species are

most likely to emerge in new hosts (Pimm 1991).

The hypotheses of trade-offs and resource breadth

What is the expected relationship between the resource range of a species and its

average performance at exploiting these resources (Futuyma & Moreno 1988)? As in

the case of network topology, conflicting results have been reported, and two scenarios

are possible. First, the relationship between resource breadth and average performance

varies among systems, taxa, places, and interaction types. Second, this relationship

should change at different community scales, from negative at larger scales to positive

at smaller scales, as predicted by the IHS (Pinheiro *et al.* 2016).

Our results provide strong support for the second scenario (Fig 5). In local networks

where modules represent a significant restriction to interactions, the relationship

between flea abundance and generalism changed from positive within to negative

among modules, as predicted by the IHS. In addition, the effect of P on abundance

became more negative as the modular structure imposed more constraints on the

interactions. Therefore, if the community (or, at least, the part we sampled) is composed

of more than one module, a multi-scale relationship between specialization and

performance should emerge. Otherwise, if the community is composed of very similar

resources (*i.e.*, just one internally nested module), we expect a simple positive

relationship between generalism and performance. A further step would be to test if the

contradictory results reported by previous studies which addressed the relationship

between performance and generalism would also be explained by differences in the

scale of each community studied. While some of them focused on different populations

of the same resource species (e.g, Szollõsi *et al.* 2011) others sampled entire resource

communities (Poulin 1998; Hellgren *et al.* 2009).

Fort *et al.* (2016) showed that higher abundance implies greater generalism in

ecological networks, and not the contrary (but see Dorman *et al.* (2017)). That is,

abundant species (the most available ones) are generalist because they have higher

probability of finding potential interaction partners. This makes sense in the context of

the IHS: the species with higher performances in exploiting a given set of similar

resources reach higher abundances and, then, interact freely with a large number of that

resources in the absence of trade-offs. Alternatively, although the nestedness between

pairs of species of different modules was equal to the expected one *given* the modular

structure in most of the local networks, the negative relationship between P and

abundance suggests that generalism between modules has a negative effect on

abundance, due to trade-offs. Therefore, although a species that is a hub in its own

module would eventually spill over on the most connected species of other modules, if

this species evolves adaptations to interact with a broad spectrum of dissimilar species,

which makes it a hub in the entire network, this would have a negative impact on its

performance.

Concluding remarks

Some authors have pointed out that discontinuities are much more common in nature

than previously thought. In addition, recent theoretical models (Holt 2006; Scheffer &

van Nes 2006) suggest that, contrary to the principle of limiting similarity (Macarthur &

Levins 1967), a balance between neutral and niche processes might generate self-

organized clusters of similar species, which have been called emergent groups (Hérault

2007). The IHS and the compound topology are in complete agreement with this view.

In fact, the idea that trade-offs generate modules, while a coupling between the

availabilities of resources and consumers determines the dynamics inside each module,

generating nestedness, suggests that there is a balance between niche processes at large

scales and neutral processes at small scales.

Finally, we are not proposing that every ecological network should, necessarily, have a

compound topology. Although it is likely that all nested matrices are modular at a larger

scale, because any interactions should be constrained at some point, not all modules

need to be internally nested. Several other patterns might be observed within a module,

each resulting from different underlying mechanisms (Presley *et al.* 2010). The methods

and the conceptual framework developed in our study provide tools to investigate these

patterns.

BOX 1 - The integrative hypothesis of specialization

Earlier coined the "integrative hypothesis of parasite specialization" (IHPS) (Pinheiro *et*

al. 2016), the hypothesis was proposed in the context of host-parasite interactions as a

solution to an old controversy in the parasitological literature: what is the expected

relationship between generalism and performance of parasites (Poulin 2007)?

However, since its assumptions are broad enough to apply to other interactions systems,

we describe it here as valid for any consumer-resource system and call it "the

integrative hypothesis of specialization" (IHS). The IHS states that consumer-resource

interactions are structured by a balance between resource breadth processes (Brown

1984) at small and trade-offs at large community scales.

On the one hand, at small community scales, resources should be very similar to one

another and an adaptation (the arrow in Fig. 1a) that increases the intrinsic performance

of a consumer in exploiting a specific resource type should also be an adaptation to all

other resource types (the "+" in Fig 1a). Therefore, we do not expect to find preferences

(*e.g*, phylogenetic, phenetic, or geographic signals) in consumer-resource interactions at

small scales. Instead, a coupling between resource availabilities and intrinsic consumer

performances should produce a nested pattern of realized performances: the resources

with highest availability should be more strongly exploited by all consumers, in

proportion to the intrinsic performances of the consumers on those resources (Fig. 1b).

Consequently, by sampling small scales of a community, one should find both a nested

pattern of interactions (Fig. 1c), and a positive relationship between generalism and

performance (Fig. 1d). This last pattern (Fig. 1d) is similar to the positive occupancy-

abundance relationships widely reported for biogeographic data (Gaston & Blackburn

2000), normally explained by Brown's resource breadth hypothesis (Brown 1984).

Since the mechanisms described above are very similar to that proposed by Brown, but

adapted to a context of interactions, we summarize them as resource breadth processes.

On the other hand, at larger community scales, the IHS states that there are trade-offs in

the capacity to exploit resources of different clusters. Specifically, adaptations to a

specific resource type (the arrow in Fig. 1e) should also be adaptations to other similar

resource types of the same cluster (the "+" in Fig. 1e), but maladaptations to dissimilar

resources of other clusters (the "-" in Fig. 1e). Thus, the pattern of realized

performances described above (Fig. 1 b) should be restricted to within each resource

cluster (Fig. 1f). In this context, the different clusters of resources are the real units of

specialization and the true generalist consumers are those that can exploit resources at

several clusters (blue species in figure 1). Consequently, by sampling large scales of a

community, we do not expect to find a completely nested network, but rather a modular

network with internally nested modules (i.e., a *compound topology*) (Lewinsohn *et al.*

2006) (Fig. 1g). In addition, although we expect a positive relationship between

performance and generalism within each cluster of similar resources, we also expect

trade-offs to result in a negative relationship between performance and capacity to

exploit resources of different clusters (modules in the network) (Fig. 1h).

Krasnov *et al.* (2004) have already suggested that the relationship between performance

and generalism should be negative in communities composed of dissimilar resources,

but positive in communities composed of similar resources. Indeed, Krasnov et al's

suggestion and the IHS have the same underlying rationale: the probability of an

adaptation to a given resource of being also an adaptation to other resources (*i.e*, the

resource breadth hypothesis) is higher the more similar the resources are. The IHS is

just a more inclusive hypothesis that also predicts the relationship between

specialization and performance in communities in which resource dissimilarity is not

gradually structured, that is, in communities with clusters of similar resources separated

from one another by gaps of dissimilarity (Allen 2006).

SUPPLEMENTARY FILES

Appendix S1

Details of both free and restricted null models computations.

Appendix S2

Supplementary Tables S1-S5

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