

Universidade Federal de Minas Gerais

Programa de Pós-graduação em Ecologia, Conservação e Manejo  
da vida Silvestre

# Uma hipótese integradora da especialização ecológica

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*Two come about because of One,  
but don't cling to the One either!  
So long as the mind does not stir,  
the ten thousand things stay blameless;  
no blame, no phenomena,  
no stirring, no mind.*

Zen master Seng-ts'an., 600 d.c

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Agradeço aos meus pais pelos meus genes e por alguns dos meus melhores memes.

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Por fim, agradeço a Deus por não existir e, não existindo, tornar possível a existência de um universo fechado em si mesmo, compreensível à ciência.

*Sentimos que, mesmo que todas as questões científicas possíveis tenham obtido resposta, nossos problemas da vida não terão sido sequer tocados. É certo que não restará, nesse caso, mais nenhuma questão; e a resposta é precisamente essa.*

Ludwig Wittgenstein

Dedico esta dissertação à memória do meu avô, Manuel Félix de Souza (08/09/1932 – 03/10/2015), e do meu sogro, Telmo Vilela (08/12/46 – 30/10/2016), pessoas que me mostraram um pouco daquilo que eu não apreenderia de nenhum livro.

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# INTRODUÇÃO GERAL

ESCRITA NO FORMATO ARTIGO DE DIVULGAÇÃO CIENTÍFICA A  
SER SUBMETIDO PARA A REVISTA *CIÊNCIA HOJE*.

*Quem já perguntou alguma vez à tese e à antítese se desejam se  
transformar em uma síntese?*

Stanislaw J. Lee

## INTRODUÇÃO GERAL – FORMATO CIÊNCIA HOJE

### 1 Especializar ou não especializar, eis a questão!

2 Você tem em suas mãos uma revista que cobre diversas áreas do conhecimento humano.  
3 Cada um dos artigos desta edição foi escrito por um especialista que precisou dedicar  
4 anos de estudo e trabalho árduo para dominar o conhecimento, a linguagem e o método  
5 da respectiva área de pesquisa. Por que isso é assim? Porque cientistas precisam se  
6 especializar, tornando-se, por exemplo, biólogos, físicos ou químicos? Seria possível a  
7 alguém extremamente curioso dominar e produzir conhecimento em várias áreas ao  
8 mesmo tempo?

9 Alexander von Humboldt (Figura 1), conhecido como “o último homem que sabia de  
10 tudo”, reclamou certa vez: “As pessoas sempre dizem que sou curioso sobre várias  
11 coisas... Porém, poderíamos realmente proibir um homem de abrigar um desejo de  
12 conhecer e abraçar tudo o que o rodeia?” Claro que não: a princípio, ninguém deveria  
13 ter o direito de cercear a curiosidade alheia. No entanto, na atual taxa em que  
14 acumulamos conhecimento, é muito difícil para qualquer ser humano tornar-se um  
15 cientista de ponta em mais de uma área. Um Humboldt moderno precisaria lidar com  
16 um volume assombroso de conhecimento, arrumar tempo para desenvolver habilidades  
17 específicas de cada disciplina e escrever artigos e livros para públicos muito diferentes.  
18 Porém, enquanto o conhecimento científico cresceu exponencialmente desde o século  
19 XIX, a expectativa de vida mudou pouco e o dia continuou tendo 24 horas. Disto resulta  
20 que um cientista tem hoje praticamente o mesmo tempo e energia disponíveis para um  
21 cientista vitoriano, porém muito mais informação para assimilar. Junte-se a isto o  
22 ambiente altamente competitivo da academia, que resulta em fenômenos como  
23 “publique ou morra”, e você tem a especialização do conhecimento.

24 Porém, a especialização não é um privilégio da  
25 selva acadêmica. Espécies na natureza enfrentam  
26 o mesmo dilema: especializar ou não especializar,  
27 eis a questão! Cada espécie biológica possui um  
28 nicho ecológico: um conjunto de condições (por  
29 exemplo, PH, temperatura e umidade) e recursos,  
30 os quais ela é capaz de tolerar e utilizar. Este  
31 nicho é continuamente ajustado ao longo do  
32 processo evolutivo, podendo expandir-se ou  
33 contrair-se com o tempo. Surge então um aparente  
34 paradoxo: se indivíduos que deixam um maior  
35 número de descendentes são selecionados, e este  
36 número será maior quão maior for a gama de  
37 condições e recursos que o indivíduo puder tolerar  
38 e utilizar, por que não observamos espécies cujas  
39 amplitudes de nichos abrangem todas as  
40 condições e recursos disponíveis no planeta? Se



Fig. 1) Alexander von Humboldt (14 de setembro de 1769 —6 de maio de 1859), conhecido como o último homem que sabia de tudo, foi explorador, geógrafo, naturalista e filósofo.



1   pudessem falar, tais espécies poderiam parafrasear Humboldt: “Poderia algo proibir-me  
2   de utilizar todos os recursos que me rodeiam?” Porém, neste caso a resposta é sim.

3   De fato, todo ser vivo é especializado em algum grau. Mesmo o ser humano que hoje  
4   habita todos os continentes do globo, não o faz sem ajuda tecnológica. Quais  
5   mecanismos levam a esta especialização é uma pergunta que os ecólogos tentam  
6   responder há décadas, e é um dos focos de pesquisa do Laboratório de Síntese  
7   Ecológica da Universidade Federal de Minas Gerais. Estamos interessados em  
8   desvendar quais processos ecológicos e evolutivos moldam o grau de especialização em  
9   interações de parasitismo e mutualismo. As respostas para estas questões têm  
10   implicações práticas bastante atuais. Primeiramente, entender o que leva uma espécie de  
11   abelha a polinizar poucas ou várias espécies de plantas poderia ajudar a solucionar a  
12   atual crise de polinizadores. Ao mesmo tempo, explicar porque determinado parasito é  
13   restrito a um pequeno grupo de hospedeiros, enquanto outro é capaz de infectar  
14   diferentes famílias ou ordens de organismos, teria implicações, por exemplo, para o  
15   estudo e controle de doenças emergentes, como a febre amarela e o zika, por exemplo.

## 16   **Hipóteses clássicas**

17   Historicamente uma das explicações mais aceitas para a ausência de generalistas  
18   extremos é a hipótese dos *trade-offs* (em português, demandas conflitantes). Segundo  
19   ela, qualquer mutação que aumente a eficiência com que um organismo explora um  
20   dado recurso (uma adaptação), deveria diminuir a eficiência com que este mesmo  
21   organismo explora outros recursos. Consequentemente, espécies generalistas  
22   enfrentariam mais demandas conflitantes do que espécies especialistas e acabariam por  
23   utilizar de forma menos eficiente cada item do seu amplo cardápio. Por outro lado, um  
24   especialista abriria mão de um grande leque de recursos em prol de utilizar com máxima  
25   eficiência cada um. As duas estratégias teriam suas vantagens e desvantagens, e ambas  
26   deveriam ser observadas na natureza. A partir de certo ponto, porém, os benefícios de  
27   ampliar ainda mais o nicho não compensariam os custos de fazê-lo, demarcando assim  
28   um limite para o generalismo e explicando por que espécies humboldtianas não são  
29   produzidas ao longo do processo evolutivo.

30   A linha de raciocínio por trás dessa hipótese é bem intuitiva e plausível, equivalente a  
31   dizer que o tempo e a energia que alguém dedica a aprender uma dada área do  
32   conhecimento não podem mais ser despendidos em outras áreas. Ela faz ainda algumas  
33   previsões facilmente testáveis. A mais simples delas, e que focaremos aqui, prevê que se  
34   desenhássemos um gráfico com a gama de recursos usados por várias espécies (no eixo  
35   x) versus a eficiência média com que estas espécies exploram estes recursos (no eixo y),  
36   deveríamos observar uma relação negativa entre estas duas variáveis (Figura 2). Quanto  
37   mais recursos uma espécie adicionasse ao seu cardápio, mais demandas conflitantes ela  
38   enfrentaria, levando assim a uma diminuição da eficiência média com que esta explora  
39   cada recurso (sua desempenho média). Esta previsão foi testada em diferentes grupos de  
40   organismos, para diferentes tipos de interação e nos mais variados biomas ao redor do  
41   globo. Porém, não passou em todos os testes. Algumas vezes a relação negativa

1 esperada pela hipótese foi observada, porém em vários outros casos essa relação não foi  
 2 detectada, ou mesmo mostrou-se positiva! Para algumas situações, quanto mais recursos  
 3 uma espécie adicionava ao seu cardápio, melhor ela se mostrava em utilizar cada um  
 4 desses itens. Seria como se a cada nova disciplina ou habilidade aprendida, você se  
 5 tornasse melhor nas habilidades que já dominava anteriormente.

6 Porém, este resultado não é tão inesperado quanto parece. Todos que já tentaram  
 7 aprender mais de uma língua estrangeira sabem que quanto mais línguas você domina,  
 8 mais fácil se torna dominar a próxima. O ponto é que algumas atividades requerem  
 9 habilidades semelhantes, e o desenvolvimento de uma habilidade ajuda no  
 10 desenvolvimento das demais. Será que o mesmo não poderia acontecer na natureza?  
 11 Alguns ecólogos acreditam que sim e cunharam uma hipótese alternativa à hipótese das  
 12 demandas conflitantes: a hipótese da amplitude de nicho. Essa alternativa supõe que  
 13 uma adaptação para determinado recurso também seria uma adaptação para outros  
 14 recursos e, logo, quanto mais amplo fosse o nicho de um organismo, maior seria sua  
 15 desempenho média ao longo desse nicho (Figura 2).

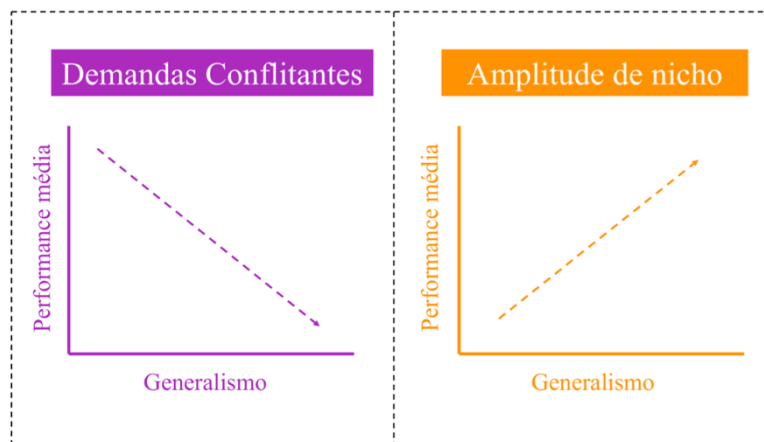


Figura 2: Predições opostas feitas pelas hipóteses clássicas de especialização. Enquanto a hipótese de demandas conflitantes diz que especialistas tem maior desempenho que generalistas, a hipótese de amplitude de nicho diz o contrário. Ambas foram confirmadas em diferentes estudos, e o debate permanece.

28 O que fazer quando temos duas hipóteses igualmente plausíveis, aparentemente opostas,  
 29 ambas bem sustentadas por evidências contraditórias? Deveríamos dizer que os sistemas  
 30 biológicos são complexos demais para serem previstos, devendo ser analisados caso a  
 31 caso, e, portanto, o certo seria buscar uma explicação para cada sistema estudado?  
 32 Talvez este não seja o melhor caminho. Como dizia Albert Einstein: “o grande objetivo  
 33 da ciência é cobrir o maior número de fatos por dedução lógica a partir do menor  
 34 número de hipóteses ou axiomas”, ou seja, a ciência busca formular teorias gerais  
 35 capazes de explicar um grande número de situações e não somente uma situação  
 36 específica. Em 2016, publicamos um artigo na revista *International Journal for*  
 37 *Parasitology* (v.46, n.3), em que analisamos interações entre parasitos causadores de  
 38 malária e aves, e propusemos o que pode ser uma solução para o debate. Essa proposta  
 39 considera que a chave para entender a especialização é a escala de observação. Antes de  
 40 entrar nos detalhes dessa nova hipótese, precisamos entender dois conceitos modernos  
 41 da teoria de redes - uma área da matemática que estuda como entidades interagem umas  
 42 com as outras e que tem nos ajudado a desemaranhar a teia da vida (ver  
 43 “Desemaranhando a colina de Darwin”, em *CH* 343).

## 1 Modularidade versus Aninhamento

2 Para entender melhor esses dois conceitos, pense no seu grupo de “amigos” do  
 3 facebook. É muito provável que esse conjunto de pessoas possa ser dividido em  
 4 subgrupos de alguma forma: colegas de trabalho, de faculdade, familiares, etc. Cada um  
 5 destes subgrupos é formado por pessoas com interesses similares que interagem muito  
 6 mais entre si do que com pessoas em outros subgrupos. Usando o jargão da teoria de  
 7 redes, estes subgrupos são chamados de módulos, e o grau de **modularidade** (Figura 3)  
 8 da sua rede de amigos fala sobre o quanto você transita por diferentes círculos sociais.

9 Perceba, porém, que a modularidade da sua rede social não tem necessariamente a ver  
 10 com a sua popularidade, seu número de amigos. Existem pessoas que são extremamente  
 11 populares, porém apenas dentro de certo círculo social. Ao mesmo tempo, outras  
 12 pessoas possuem poucas amizades, mas estas se encontram espalhadas por diversas  
 13 “tribos”. A forma como as interações entre pessoas populares e impopulares estão  
 14 distribuídas define o **aninhamento** (Figura 3) da sua rede social. Se pessoas com menos  
 15 amizades tendem a ser amigas das pessoas com mais amizades, a rede será aninhada.

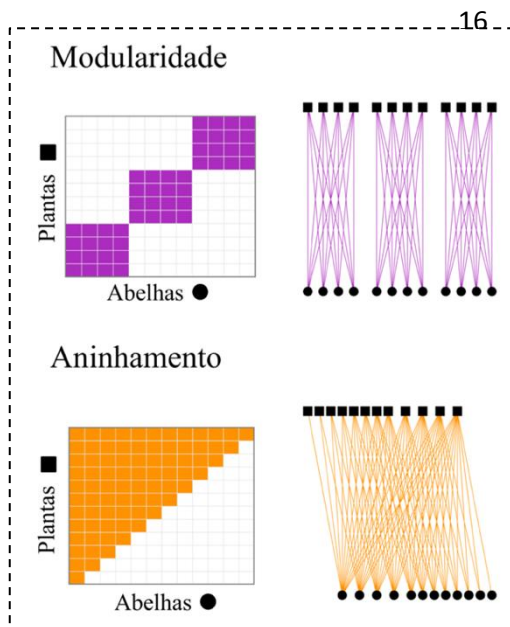


Figura 3: Modularidade versus Aninhamento em uma rede de polinização. As figuras à esquerda mostram o que os ecólogos chamam de matrizes de interação, nas quais cada coluna representa uma espécie de planta e cada linha representa uma espécie de abelha. Células coloridas nas matrizes representam interações observadas na natureza, ou seja, casos em que aquela espécie de planta foi observada polinizando aquela espécie de abelha. As figuras à direita mostram as redes de interação desenhadas a partir das matrizes. Nas redes as espécies de planta são representadas por quadrados e as abelha por círculos, enquanto as linhas conectando abelhas e plantas representam as interações observadas. Repare a diferença entre as estruturas modular e aninhada. Enquanto na primeira existem subgrupos que interagem muito mais entre si, na segunda esses subgrupos não existem e os especialistas interagem preferencialmente com os generalistas.

34 A mesma lógica se aplica para qualquer rede de interação. Uma rede ecológica será  
 35 modular caso existam subgrupos de espécies que interajam preferencialmente entre si,  
 36 como por exemplo, parasitos que exploram o mesmo grupo de hospedeiros. Já o  
 37 aninhamento surge quando as interações feitas pelos especialistas são subconjuntos das  
 38 interações feitas pelos generalistas, por exemplo, quando as plantas polinizadas por  
 39 poucas espécies são polinizadas pelos polinizadores que polinizam um grande número  
 40 de plantas. Sabe-se que o balanço entre modularidade e aninhamento tem relação direta  
 41 com a estabilidade de um ecossistema e, por isso, esse é um assunto tão estudado  
 42 atualmente.

43 Tradicionalmente, modularidade e aninhamento têm sido vistos como estruturas  
 44 mutuamente exclusivas em redes ecológicas. Segundo este ponto de vista as interações

1 entre espécies em uma comunidade deveriam ser ou aninhadas ou modulares, mas  
 2 nunca as duas coisas ao mesmo tempo. Por algum tempo, assim como no caso demanda  
 3 conflitante versus amplitude de nicho, nenhuma solução conciliadora foi encontrada, e o  
 4 debate entrou para o grupo do “cada caso é um caso”. Em 2006, o Prof. Thomas  
 5 Lewinsohn da Universidade Estadual de Campinas e colaboradores propuseram, em um  
 6 artigo na revista *Oikos* (v.113, n.1), uma estrutura combinada entre aninhamento e  
 7 modularidade que resolveria o dilema (ver também o artigo do professor Thomas e  
 8 colaboradores de 2006 na revista *Oecologia Brasiliensis* (v.10, n.1)). Segundo eles,  
 9 redes de interação poderiam apresentar uma estrutura modular em larga escala, porém  
 10 aninhada dentro dos módulos. Juntando essa estrutura com as ideias que apresentamos  
 11 no artigo da *International Journal for Parasitology*, acreditamos ter encontrado uma  
 12 solução para ambos os debates. Esta solução é o que chamamos de hipótese integradora  
 13 da especialização ecológica.

#### 14 **Hipótese Integradora da Especialização Ecológica**

15 Nossa hipótese conecta os pontos entre os dois debates por mostrar que os processos por  
 16 trás da modularidade e aninhamento são os mesmos usados para explicar as hipóteses de  
 17 demanda conflitante e amplitude de nicho. Por um lado, a modularidade seria uma  
 18 consequência direta das demandas conflitantes: uma adaptação para melhor explorar um  
 19 dado recurso impede a utilização de recursos muito diferentes, levando à formação de  
 20 módulos na rede. Por outro lado, o aninhamento resultaria dos processos de amplitude  
 21 de nicho: uma adaptação para um tipo de recurso facilitaria a utilização de recursos  
 22 semelhantes, levando a uma hierarquia na utilização dos recursos (os recursos menos  
 23 utilizados sendo explorados pelas espécies mais generalistas) (Figura 4).

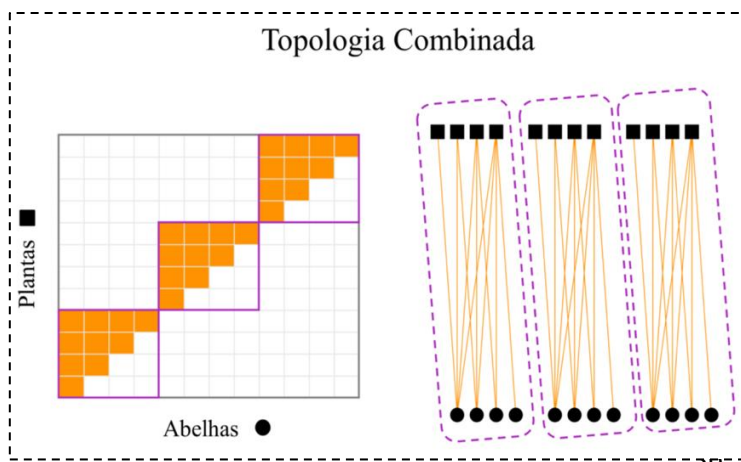


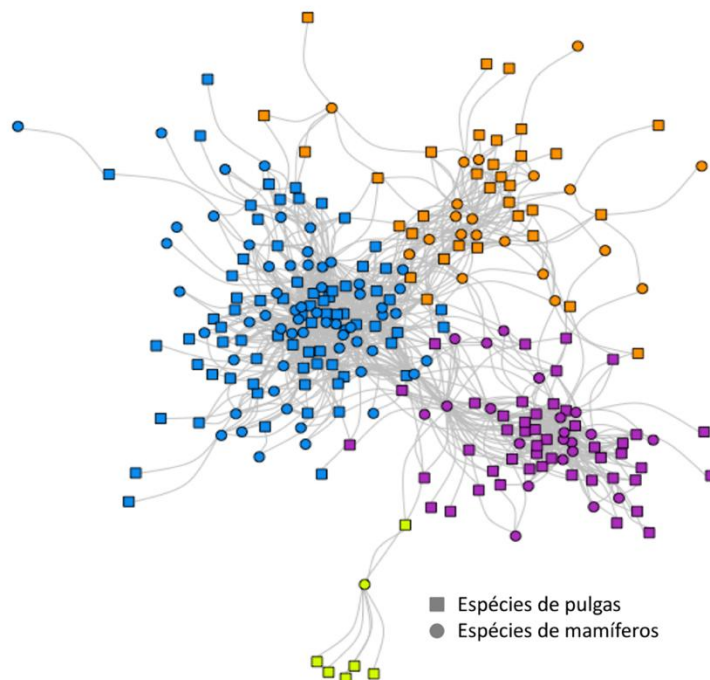
Figura 4: Topologia Combinada. As demandas conflitantes de lidar com recursos muito diferentes definem os limites dos módulos (em roxo). Dentro destes, porém, os recursos são muito parecidos e as interações se encontram aninhadas (em laranja). Uma espécie que utilize muito bem um recurso, também será boa em usar outros recursos do mesmo módulo, porém não se dará tão bem com os recursos de outros módulos.

37 Segundo a Hipótese Integradora da Especialização Ecológica, ambos os processos  
 38 ocorrem ao mesmo tempo em qualquer sistema ecológico, mas qual deles será mais  
 39 importante é uma questão de escala de observação. Uma adaptação que permita a um  
 40 parasito escapar do sistema imune de um dado hospedeiro, por exemplo, também  
 41 poderia ser uma adaptação a outros hospedeiros do mesmo gênero, mas atrapalharia o  
 42 desenvolvimento deste parasito em outras famílias ou ordens de hospedeiros. Como  
 43 consequência, um estudo feito em pequena escala, amostrando poucos grupos

1 taxonômicos ou poucas regiões, deveria encontrar evidências a favor das hipóteses de  
 2 amplitude de nicho e aninhamento. Isto por que nesta escala os recursos são tão  
 3 parecidos entre si que as demandas conflitantes não estariam presentes. Por outro lado,  
 4 ao amostrar várias regiões ou grupos taxonômicos muito distintos, as demandas  
 5 conflitantes ganhariam importância, levando à emergência de módulos na rede. Nesta  
 6 escala maior, o aninhamento estaria restrito às interações realizadas dentro dos módulos.

7 Voltemos agora à nossa analogia com as atividades humanas. Embora não esperemos  
 8 que um virtuose em violino ganhe uma medalha olímpica em salto com vara, podemos  
 9 esperar que ele ainda toque com maestria outros instrumentos musicais. Isto por que as  
 10 habilidades envolvidas em tocar violino são muito semelhantes àsquelas usadas, por  
 11 exemplo, para tocar violoncelo e viola, porém muito diferentes das usadas no atletismo.

12 Recentemente, confirmamos várias das previsões feitas pela Hipótese Integradora da  
 13 Especialização Ecológica em um artigo que está submetido à publicação, no qual  
 14 analisamos redes de parasitismo entre pulgas e pequenos mamíferos (Figura 5).  
 15 Demonstramos tanto a estrutura combinada quanto a dependência da escala de  
 16 observação nas hipóteses de amplitude de nicho e demandas conflitantes. Por fim, dado  
 17 seu potencial para resolver pelo menos dois grandes debates ecológicos, nosso próximo  
 18 passo é testá-la em outros tipos de interação e, por que não, em redes fora da ecologia.  
 19 Afinal, Humboldts seriam proibidos em qualquer tipo de rede? Ou será que existem  
 20 moléculas, neurônios e sites humboldtianos?



21

22 Fig. 5) Rede de interação entre espécies de pulga e pequenos mamíferos. As amostras foram coletadas em  
 23 vários países asiáticos. As cores representam módulos na rede.

# MANUSCRIPT

## THE INTEGRATIVE HYPOTHESIS OF ECOLOGICAL SPECIALIZATION EXPLAINS THE ARCHITECTURE OF INTERACTION NETWORKS\*

*Old ideas give way slowly, for they are more than abstract logical forms and categories. They are habits, predispositions, deeply engrained attitudes of aversions and preference. Moreover, the conviction persists – thought history shows it to be a hallucination – that all the questions that the human mind has asked are questions that can be answered in terms of the alternatives that the questions themselves present.*

John Dewey

\*This manuscript was written on Nature's format

# 1 **The integrative hypothesis of ecological specialization explains the** 2 **architecture of interaction networks**

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11 **ABSTRACT:** For a given species exploiting a range of resources, what is the best strategy:  
12 generalism or specialization? This is an old debate in the literature, which has remained  
13 unsolved for decades. Recently, we proposed a parsimonious hypothesis, “The integrative  
14 hypothesis of ecological specialization” (IHES), which helps solve this dilemma. Here we  
15 provide empirical support for this hypothesis and show how it can solve also another debate:  
16 nestedness *vs.* modularity in ecological networks. Using an extensive host-parasite database, we  
17 confirmed three major predictions of the IHES: (i) niche homogenization at small scales, (ii) a  
18 combined topology in interaction networks, and (iii) scale-dependence of trade-offs and  
19 resource breadth processes. By reconciling traditional hypotheses and connecting previously  
20 disjointed debates in parasitology and ecology, our hypothesis represents a significant step  
21 towards ecological synthesis. Moreover, the IHES is based on three elementary assumptions  
22 that also could be true in non-ecological complex systems.

## 23 **MAIN TEXT:**

24 Ecology is considered a “mess” by some scientists, as descriptions of patterns abound,  
25 while universal explanations are lacking<sup>1,2</sup>. This confusion hinders solving crucial

1 theoretical and real-world problems, from understanding the diversity of tropical forests  
2 to avoiding pollinator decline. Therefore, synthesis is urgently needed<sup>3,4</sup>. In fact, two  
3 major goals of any science are parsimony and theoretical unification<sup>5</sup>: in Einstein's  
4 words, "*to cover the greatest number of empirical facts by logical deduction from the*  
5 *smallest number of hypotheses or axioms*". We addressed this challenge in the field of  
6 ecological interactions, and propose a parsimonious explanation for pervasive patterns.  
7 Earlier, this synthesis was coined "The integrative hypothesis of parasite specialization"  
8 <sup>6</sup>. Our hypothesis unites and solves two important ecological debates: trade-off vs.  
9 resource breadth<sup>7</sup> and modularity vs. nestedness<sup>8</sup>.

10 The IHES was originally proposed to explain the relationship between resource range  
11 and consumer performance<sup>9</sup>. This relationship is traditionally explained by invoking  
12 either the trade-off<sup>10</sup> or the resource breadth<sup>11,12</sup> hypotheses. The former assumes that  
13 adaptations of a consumer for a more effective exploitation of resources evolve at the  
14 cost of the capacity to exploit a wide range of resources, and predicts a negative  
15 relationship between performance and resource range. The latter assumes that the same  
16 attributes that enable a consumer to exploit diverse resources allow it to exploit each  
17 resource more efficiently, and so predicts a positive relationship. Although they make  
18 opposite predictions, both have received empirical support and remain alive in the  
19 literature as competing explanations<sup>6,13,14</sup>. We advocate that the IHES might reconcile  
20 them as follows:

21 Assumption (1): Specialization involves trade-offs between performance in the use of  
22 different resource types, and those trade-offs are stronger when the dissimilarity  
23 between resource types is greater;



1 Assumption (2): The likelihood that a given attribute that enables a consumer to exploit  
2 diverse resources allows it to exploit each resource more efficiently (resource breadth  
3 processes); becomes smaller the greater the dissimilarity between resource types;

4 Assumption (3): In most ecological communities dissimilarity is not structured  
5 gradually. Those systems are commonly composed of clusters of related organisms  
6 separated from other clusters by discontinuous differences<sup>15</sup>.

7 Conclusion: Specialization is driven by a balance between the costs of trade-offs and the  
8 benefits of resource breadth processes. New adaptations that increase a consumer's  
9 performance in a given resource type generally increase its performance in resources of  
10 the same cluster, but decrease it in other clusters.

11 The IHES also resolves the nestedness vs. modularity debate<sup>8</sup>. While modularity is a  
12 direct consequence of trade-offs, nestedness arises from intra-module resource breadth  
13 processes. Within modules, after major trade-offs have been solved, interaction patterns  
14 should be driven mainly by abundance-dependent processes. From this balance between  
15 trade-offs and resource breadth processes at different scales emerges a network with a  
16 combined topology: a modular network with internally nested modules. This archetype  
17 was hypothesized some years ago<sup>16</sup> and was partially confirmed in pollination<sup>17</sup> and  
18 seed dispersal<sup>18</sup> networks, and fully confirmed in phage-bacteria networks<sup>19,20</sup>.

19 In conclusion, in the light of the IHES, scale is a major driver of network architecture.  
20 Figure 1 summarizes the rationale of the IHES and its main predictions, which we tested  
21 using an extensive database of flea-mammal interactions in 15 Palearctic regions.

## 22 **Niche homogenization at small scales**

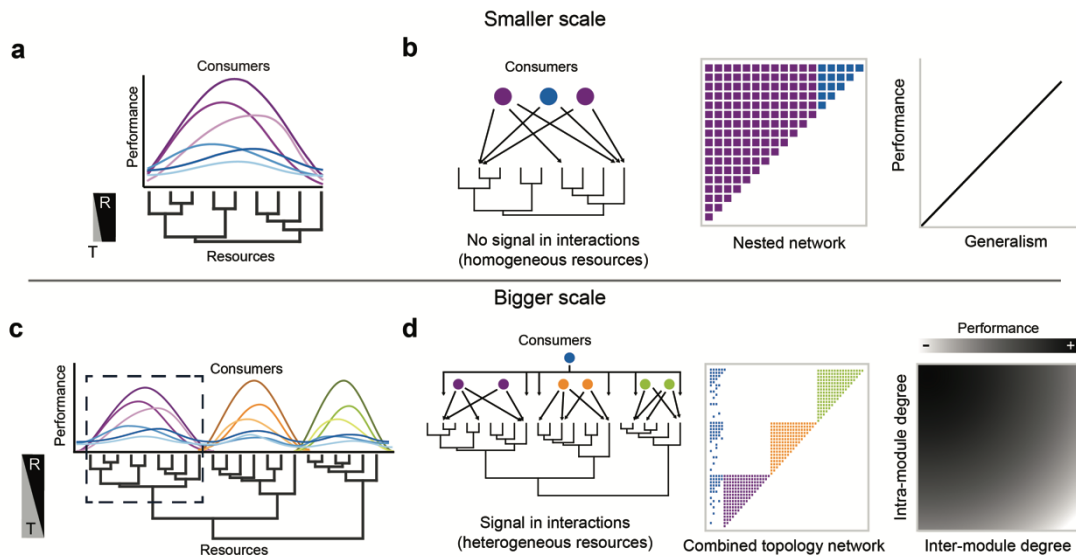
23 The most basic theoretical prediction resulting from the IHES is: from the decreasing  
24 importance of trade-offs at small phylogenetic and geographical scales should follow

1 the homogenization of consumer niches (Fig. 1). In other words, consumers should have  
2 more “freedom of choice” at smaller scales, as resources become equivalent from their  
3 perspective.

4 Our host-parasite community is highly diverse and was sampled over a broad  
5 geographic area, and so we expect both phylogeny and geography to drive the  
6 interaction patterns. This prediction was confirmed since mammals that are either  
7 phylogenetically close or occur in the same region had a higher likelihood of sharing  
8 fleas (Fig2). Considering this phylogenetic and geographical structure, the theoretical  
9 prediction above can be operationalized in a testable form: interaction signal should  
10 decrease from larger to smaller phylogenetic and geographical scales.

11 In order to test this prediction, we divided the mammal phylogenetic tree in all its  
12 possible monophyletic sub-trees, and then computed the phylogenetic signal of  
13 interactions in each sub-tree. We used a Mantel test to assess the signal in each sub-tree  
14 and standardized scores (see methods for details) to compare signals between sub-trees.  
15 As predicted, the strength of the phylogenetic signal of interactions decreases from  
16 larger to smaller phylogenetic scales in any given lineage (Fig 2a,b). To test for a  
17 geographical signal in parasite interaction patterns, we first analyzed co-occurrences  
18 among host species in the 15 sampling regions, and then built a dissimilarity matrix  
19 among hosts using cluster analysis. We made a similar analysis as in the case of  
20 phylogeny and obtained similar results: the smaller the geographical scale, the weaker  
21 the geographical signal of interactions (Fig 2c,d).

22



**Fig. 1: Predictions of the Integrative hypothesis of ecological specialization at different scales.** R: Resource breadth processes. T: Trade-offs. **a**, At small scales, the IHES predicts a hierarchy in the use of resources by consumers (e.g., parasites infecting hosts). Since resources are very similar, consumers with higher performance on a specific resource tend to have higher performance on all other resources. The dendrogram shows the dissimilarities between resources. **b**, Expected patterns generated by the hierarchy presented in (a). First, resources are very homogeneous from the consumer perspective. Thus, we do not expect to find signals (phylogenetic or geographical) in the interactions. Other factors, such as resource abundance, ecological drift, and competition, probably predominate as drivers of the interactions. Second, we expect that the set of resources exploited by a more specialized consumer is always a subset of the resources exploited by a more generalist consumer (i.e., a nested structure). Third, since the capacity to exploit a specific resource is positively related to the capacity to exploit other resources, generalists tend to reach higher performance than specialists, as previously predicted by the resource breadth hypothesis. **c**, At larger scales, the IHES predicts that the hierarchy showed in A occurs only within clusters of similar resources, and that there are trade-offs in the capacity to exploit resources of different clusters. The dashed rectangle delimits the scale presented in A. **d**, Expected patterns when considering many clusters of related resources. First, we expect a strong interaction signal, since resources of different clusters are very heterogeneous. Second, we do not expect that the entire network is nested, but rather modular with internally nested modules (i.e., a combined topology). Third, inside each cluster of similar resources we expect a positive relationship between performance and intra-module generalization. Nevertheless, we also expect that trade-offs result in a negative relationship between performance and capacity to exploit resources of different clusters.

These results support the prediction of homogenization of mammal resources and consequent increase in consumer “freedom of choice” at smaller scales. The more

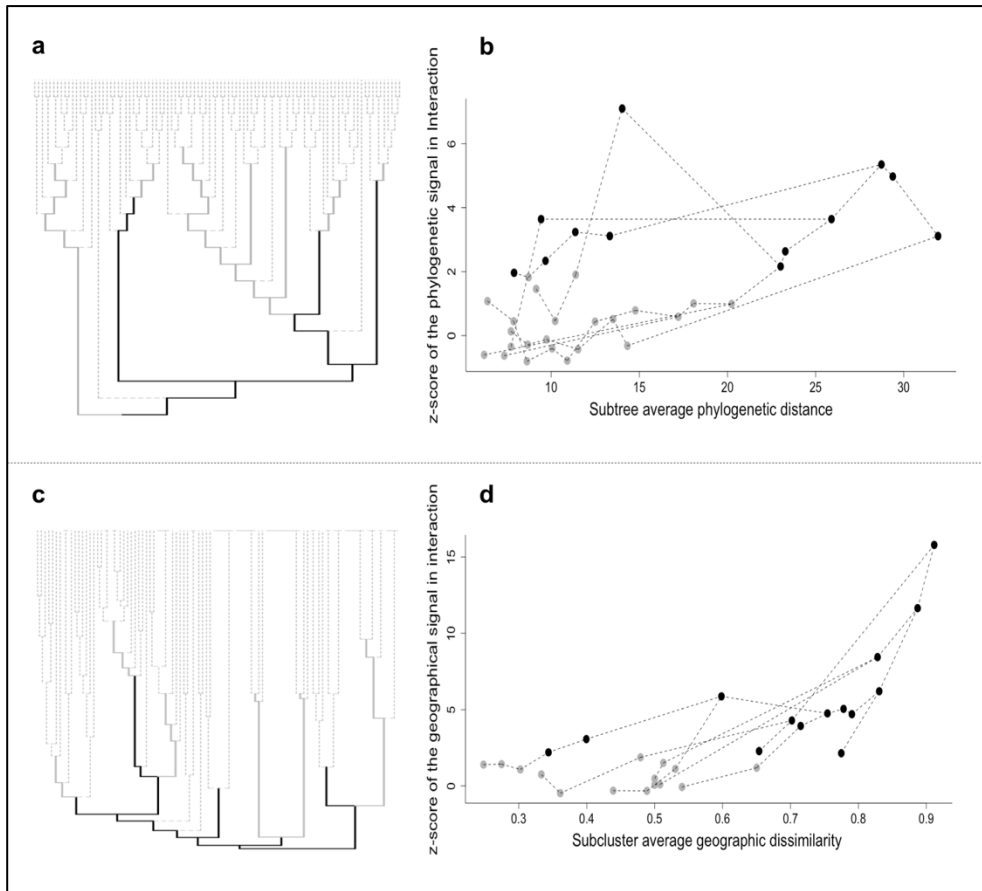
1 similar the resources become, the more the benefits of resource breadth processes are  
2 expected to predominate over the costs of trade-offs. Consequently, at small scales the  
3 network should change from a modular to a nested topology. In the next section, we  
4 address this duality in detail.

5 It is important to notice that, although the resource breadth hypothesis assumes  
6 homogenization of Hutchinsonian niches among consumers, it does not assume fitness  
7 equivalence. Different fleas would have the potential to infect the same set mammals,  
8 but with different performances. Why, then, does the fittest species not exclude the  
9 others at smaller scales? We suggest that stabilizing mechanisms (negative frequency-  
10 dependent processes) surpass the fitness differences within the modules, which allows  
11 coexistence<sup>21,22</sup>.

## 12 **Combined Topology**

13 From the balance between trade-offs and resource breadth processes predominating at  
14 different community scales, follows the second prediction of IHES: a combined  
15 topology (Fig. 1). This topology solves a paradox in the literature: some ecological  
16 networks present both significant modularity and nestedness<sup>8</sup>, which seems  
17 counterintuitive. A combined topology solves this paradox by proposing that almost all  
18 nestedness in the interaction matrix comes from niche overlap between species within  
19 modules. Recently, this prediction was partially confirmed by computer simulation<sup>23</sup>  
20 and confirmed more precisely in phage-bacteria systems<sup>19</sup> by decomposing the  
21 nestedness of the interaction matrix in its intra- and inter-module components. It was  
22 possible, then, to compute the nestedness of the entire matrix discounting the nestedness  
23 that comes from nested interactions within modules. We used the same approach,  
24 coined by the authors “constrained nestedness”<sup>19</sup>, for our flea-mammal network.

1



2

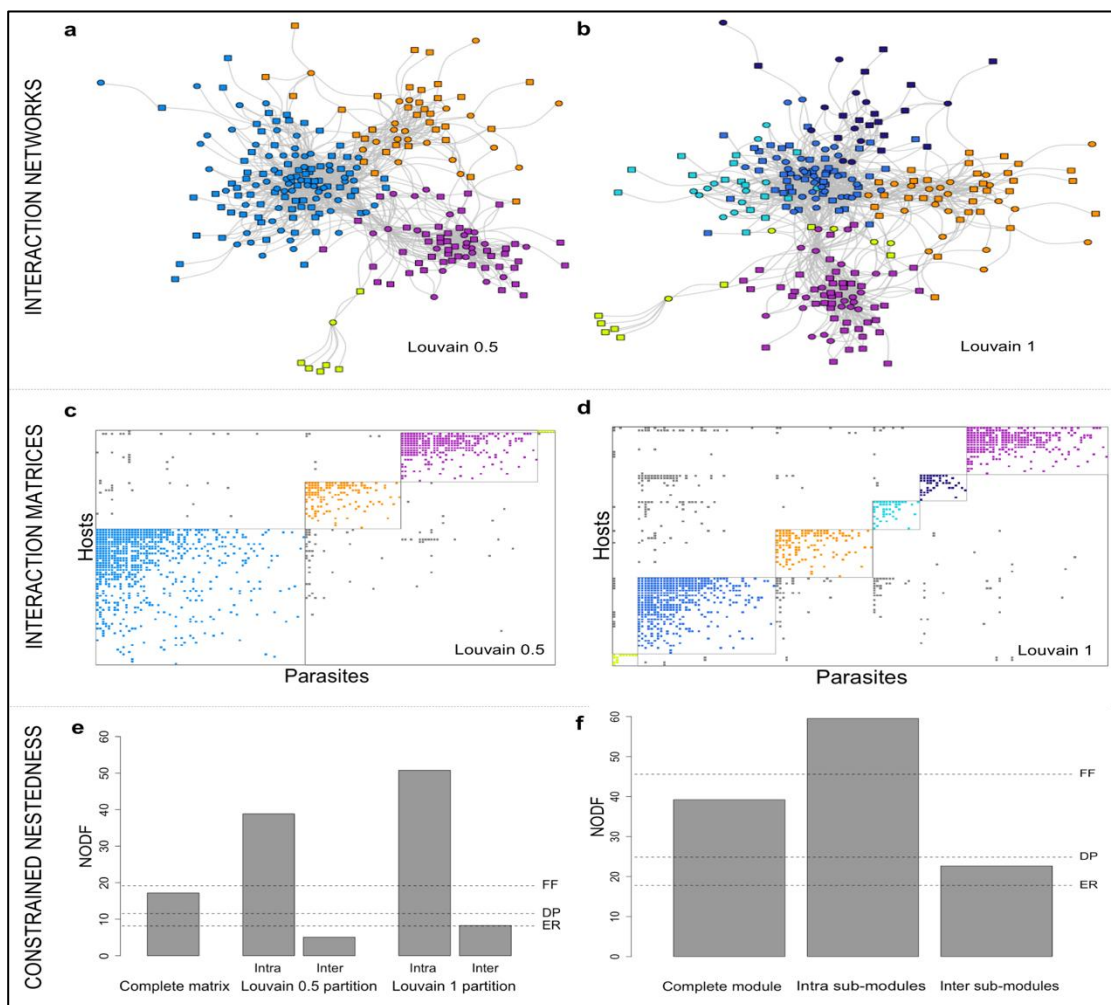
3 **Fig. 2: Niche homogenization at small network scales.** Gray and black (in lines and dots) represent,  
 4 respectively, non-significant and significant phylogenetic or geographic signals ( $p < 0.05$ ). **a**, Mammal  
 5 phylogenetic tree. Dashed branches represent sub-trees discarded for having less than seven species. **b**,  
 6 The z-score of the phylogenetic signal for each analyzed sub-tree plotted against the average phylogenetic  
 7 distance among mammal species in the sub-tree. Dashed lines connect subtrees in the same lineage. **c**,  
 8 Mammal dendrogram of geographic dissimilarity. Dashed branches represent sub-dendrograms discarded  
 9 for having less than seven mammal species. **d**, The z-score of the geographic signal for each sub-  
 10 dendrogram plotted against the average dissimilarity among mammal species in the sub-dendrogram.  
 11 Dashed lines connect sub-dendrograms in the same lineage.

12 The first step was to unfold the modular structure of the flea-mammal network.  
 13 However, it is known that networks have a hierarchical architecture<sup>24</sup> (the modules are  
 14 themselves composed of smaller modules), and different layers of this hierarchy would  
 15 reflect different levels of trade-offs<sup>25</sup>. In order to assess this hierarchical architecture, we

1 used the Louvain algorithm<sup>26</sup>, as it has a resolution parameter that allows partitions at  
2 hierarchical layers to be recovered. By adjusting the resolution parameter to two  
3 different values, 1 and 0.5, we found two hierarchical levels in the flea-mammal  
4 network (Fig 3a-d), which we will call here the Louvain 1 and Louvain 0.5 partitions,  
5 respectively. The smaller the resolution parameter, the greater the size of the modules  
6 recovered. Hence, the Louvain 0.5 partition belongs to a higher hierarchical level than  
7 the Louvain 1 partition. In other words, the modules of the Louvain 0.5 partition are  
8 formed by pooling the modules of the Louvain 1 partition. The two partitions are  
9 significantly modular (Extended Data Table 1) when contrasted with three different null  
10 models (Erdős-Rényi, Degree-probable and Fix-Fix; see details in methods), meaning  
11 that both represent true levels of organization of this system. Although the Louvain  
12 method is not commonly used in ecology, where other algorithms that search for  
13 partitions with highest values of the Barber<sup>27</sup> and Guimerà<sup>28</sup> indices are preferred<sup>29</sup>, the  
14 partitions recovered by these alternative methods were very similar to those recovered  
15 by Louvain 1 or Louvain 0.5. Whereas the optimization of the Barber metric recovered  
16 a partition like Louvain 1, the partition found by optimizing the Guimerà metric  
17 resembles Louvain 0.5 (Extended Data Table 2). This result is quite interesting, as those  
18 metrics do not unveil the same information. The Barber metric is good for recovering  
19 regions of the network with high density of connections, whereas the Guimerà metric is  
20 best for finding subgroups of species with similar interaction patterns<sup>29</sup>. With the  
21 modular structure of the network described, we performed the constrained nestedness  
22 analysis<sup>19</sup> (see methods for details). We decomposed nestedness, here measured as  
23 NODF<sup>30</sup>, into its intra- and inter-module components using the Louvain 1 and Louvain  
24 0.5 partitions. In both cases interaction overlap was much higher within than between  
25 modules (Fig. 3e). Most importantly, the intra-module interaction overlap was larger

1 than expected by all null models for both partitions, whereas the inter-module  
 2 interaction overlap was smaller than expected by all null models for the Louvain 0.5  
 3 partition and smaller to that expected by both Degree-probable and Fix-Fix null models  
 4 for the Louvain 1 (Fig 3e, Extended Data Table 1). On the one hand, NODF measures  
 5 average interaction overlap between all pairs of nodes<sup>30</sup>. On the other hand, our results  
 6 point out that these values follow different distributions within and between the  
 7 modules, which suggests that averaging the values might not make sense.

8



9

10 **Fig. 3) The combined topology of the flea-mammal network and its hierarchical structure at two**  
 11 **levels.** Colors represent modules. The blue module in the Louvain 0.5 partition is divided into three  
 12 modules in the Louvain 1 partition, represented by different shades of blue. **a,b** Modular structure of the

1 flea-mammal network to both Louvain 0.5 and Louvain 1 partitions. Circles represent mammal species,  
2 and squares represent flea species. **c,d** Interaction matrix reorganized to maximize inter- and intra-module  
3 nestedness without disrupting the modular structure of the network to both Louvain 0.5 and Louvain 1  
4 partitions. **e**, The NODF value of the entire matrix and its intra- and inter-module components, for both  
5 Louvain 0.5 and Louvain 1 partitions, vs. the NODF values expected from three null models (ER: Erdős-  
6 Rényi, DP: Degree-probable, and FF: Fix-Fix). **f**, The NODF value of the interactions inside the greater  
7 module of Louvain 0.5 partition (the blue module), and its intra- and inter-sub-module components,  
8 considering its sub-modules in Louvain 1 partition, vs. the NODF values expected from three null models  
9 (ER: Erdős-Rényi, DP: Degree-probable, and FF: Fix-Fix).

10 In summary, we confirmed the prediction of a combined topology (Fig 3) by showing  
11 that the network presents a dual structure: modular at larger scales and nested at smaller  
12 scales. This result is a second line of evidence in favor of the IHES and follows directly  
13 from the first one: the homogenization of flea niches (i.e., mammals) from larger to  
14 smaller network scales (geographical and phylogenetic) (Fig. 2). It is important to note  
15 that this flea-mammal network was analyzed before in studies on network  
16 architecture<sup>8,31,32</sup>. By disregarding the possibility of a combined topology, those studies  
17 reached the conclusion that this system was shaped by both nested and modular  
18 interactions at a large scale, which we show is not the case. Since the same erroneous  
19 conclusion may have been reached by other studies based on other interaction networks  
20 (a problem first pointed out some years ago<sup>33</sup>), it might be interesting to reanalyze those  
21 datasets considering the possibility that some of them might have a combined topology.

22 Until now we have been assuming a scale-dependence of trade-offs and resource  
23 breadth processes and testing its expected patterns. The next section puts this scale-  
24 dependence to the test.

25

26



## 1 **Scale-dependence of processes**

2 If a combined topology results from the balance of trade-offs and resource breadth  
3 processes, we should suppose scale-dependence of the expected relationship between  
4 consumer performance and resource breadth (Fig. 1). The underlying rationale is that,  
5 while the costs associated with trade-offs must prevail over the benefits of resource  
6 breadth processes in a hypothetical consumer expanding its niche between resources of  
7 different modules, the opposite should be true when this niche expansion occurs  
8 between resources of the same module<sup>6</sup>.

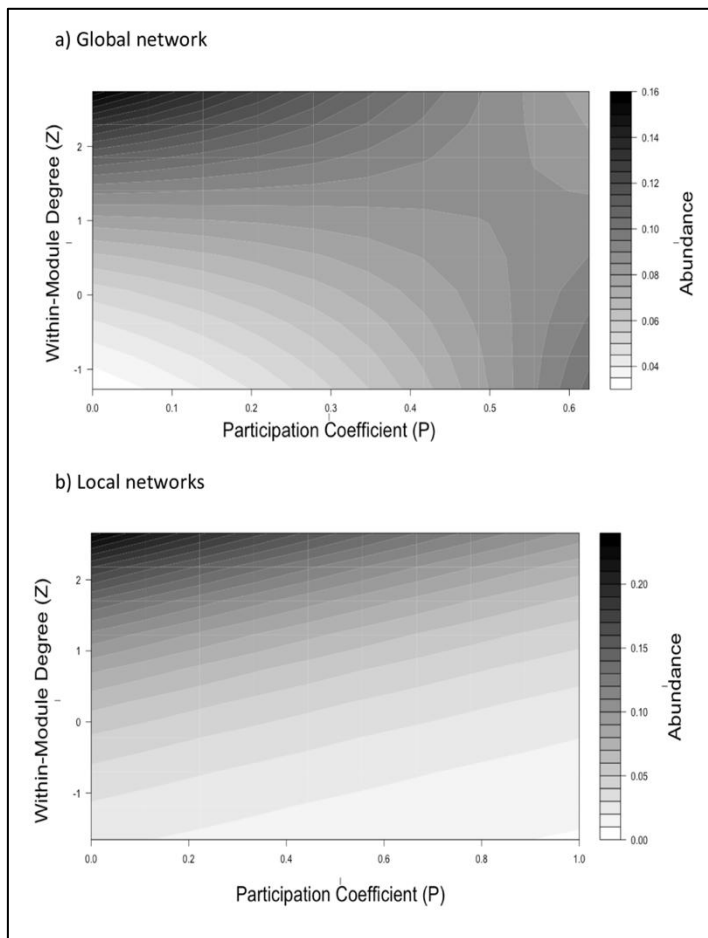
9 The simple way to operationalize this prediction is to correlate flea performances with  
10 their cartographic positions in the network, specified by two indices: within-module  
11 degree and participation coefficient<sup>34,35</sup>. These two measures define the functional role  
12 of a given species in a network, and are respectively related to the number of  
13 interactions a species has within its own module and with species that belong to other  
14 modules. Consistent with the IHES, flea performances should be positively correlated  
15 with their within-module degrees ( $Z$ ) and negatively with their participation coefficients  
16 ( $P$ ). We tested this prediction with generalized linear mixed models using flea  
17 abundance as a proxy for performance. Interestingly, the IHES was partially supported  
18 by the Louvain 0.5 partition - despite an unexpected increase in performance in the  
19 bottom-right corner (high  $P$  and low  $Z$  values) (Extended Data Table 3a, Fig. 4a) -,  
20 while in the Louvain 1 partition flea abundance was positively correlated with  $Z$ , but did  
21 not respond to  $P$  (Extended Data Table 3b). Those results suggest that the predicted  
22 pattern should only be expected in hierarchical levels of modularity in which module  
23 boundaries represent accurately the turning point in the balance between trade-offs and  
24 resource breadth processes. In support to this interpretation, when we decomposed the  
25 largest module of Louvain 0.5 in its corresponding sub-modules using Louvain 1, and

1 applied a constrained nestedness analysis to it, the inter-module component of  
2 nestedness was still high (Fig. 3f). Since Louvain 0.5 occupies a higher hierarchical  
3 level than Louvain 1, many interactions occur within modules when considering the  
4 former partition and between modules when considering the latter.

5 As explained above, our network has a strong geographic signal, which suggests that the  
6 modules are mainly geographically defined. However, the hosts, and not the regions, are  
7 the habitats of parasites<sup>36</sup>. The hosts' phenotypes (physiology, morphology, behavior  
8 and metabolism) represent, more than the external environment, the real conditions and  
9 resources explored by its parasites. Therefore, the phenotypic dissimilarities of hosts  
10 should impose stronger trade-offs than their geographical distribution. To discard the  
11 geographical constraints, we built local networks, which are phylogenetically structured  
12 (Extended Data Table 4), unfolded their modular structure, and computed the local  
13 values of  $Z$  and  $P$  for each flea species. However, only seven out of fifteen local  
14 networks were large enough for the analysis. In addition, only the Louvain 0.5 partition  
15 was recovered for local networks, since the modules recovered for Louvain 1 were so  
16 small that they did not allow calculating within-module degrees ( $Z$ ). We correlated  
17 these local  $P$  and  $Z$  values for each flea species with their local abundance, again using  
18 generalized linear mixed models, and found the relationship predicted by the IHES:  
19 local abundances correlated positively with  $Z$  but negatively with  $P$  values (Extended  
20 Data Table 3c, Fig. 4b).

21 In conclusion, the IHES was partially corroborated by the analysis of the global  
22 network, and fully corroborated by the analysis of local networks. In addition, parasite  
23 performances were better predicted by their functional roles in the local networks  
24 (Extended Data Table 3), as expected if host phylogeny imposes stronger trade-offs to  
25 fleas than host distribution. However, although the complete model explained a large

1 amount of data variance at both the local and global scales, the fixed factors were  
 2 responsible for only a small fraction of the explanation (Extended Data Table 3).



**Fig. 4: Relationship between parasite performance (abundance) and functional role in both the global network and the local networks.** The parasite functional roles are defined by their within-module degrees ( $Z$ ) and participation coefficients ( $P$ ). Since the random factors explain much of the variation in parasite abundance, we did not plot the original abundances, but the values predicted by the model. **a**, Global network and Louvain 0.5 partition. **b**, Local network and Louvain 0.5 partition.

18

## 19 **Concluding remarks**

20 The integrative hypothesis of ecological specialization (IHES)<sup>6</sup> presents a simple  
 21 process-based model linked to fundamental ecological theories, which explains  
 22 conflicting patterns observed in ecological interactions of several kinds, including  
 23 mutualisms and antagonisms, at the community scale. Here we present several lines of  
 24 evidence in support of IHES, confirming its main three predictions: niche  
 25 homogenization at smaller scales, a combined topology of interaction networks, and  
 26 scale-dependence of both trade-offs and resource breadth processes. Given its potential  
 27 to solve at least two important ecological debates, trade-off *vs.* resource breadth<sup>7</sup> and

1 modularity vs. nestedness<sup>8</sup>, the next step should be to test the IHES in other interaction  
2 types, such as seed dispersal, pollination, myrmecophytes, viral infection, herbivory and  
3 predation. There is no reason to suppose that the three assumptions of the IHES do not  
4 hold for those other interaction types.

5 The IHES is also consistent with recent studies on complex systems. Firstly, new  
6 theoretical models<sup>37</sup> suggest that competition might generate self-organized clusters of  
7 similar species separated by gaps from other clusters. Secondly, a growth model for  
8 bipartite networks based on conflicting attachment and trade-offs also predicts a  
9 combined topology<sup>38</sup>. Thirdly, modularity did not evolve in simulated neuronal  
10 networks in the absence of “costs of connections”<sup>39</sup>. Therefore, although the IHES was  
11 formalized using ecological concepts, its conclusions state general rules that do  
12 probably also hold for non-ecological systems.

13

#### 14 **MATERIAL AND METHODS:**

15 **Host-parasite database.** We used an extensive host-parasite database widely utilized in  
16 studies of ecological interactions<sup>40</sup>. This database is composed of dozens of flea-  
17 mammal interaction matrices sampled all around the world, from which we selected 15  
18 Palearctic regions to maximize two parameters: the size of the matrix (at least 10  
19 parasites and 10 host species), and the number of hosts sampled (more than 1,000  
20 individual mammals). On the one hand, the global matrix, composed of all 15 regions,  
21 has a size of 161 x 102 (161 flea and 102 mammal species), and contains 1,189  
22 interaction pairs. On the other hand, the local networks have an average richness of  
23  $26.26 \pm 9.42$  flea and  $18.8 \pm 4.79$  mammal species, and contain on average  $129.6 \pm$   
24  $57.22$  interaction pairs. Furthermore, the global matrix and some local matrices produce

1 networks with more than one component, i.e., a cluster of species totally separated from  
2 other vertices of the network. The analyses below, at global and local scales, were  
3 carried out only using the respective main components of each matrix.

4 **Phylogenetic Analyses.** As the backbone for the phylogenetic tree of fleas we used the  
5 most recent molecular phylogeny<sup>41</sup> that presented data on 205 species and 110 genera.  
6 The positions of genera and species that were not represented in Zhu *et al.*'s<sup>41</sup> tree were  
7 determined according to their morphologically based taxonomic affinities (see Krasnov  
8 *et al.*<sup>42</sup>). We used the global phylogenetic supertree of Bininda-Emonds *et al.*<sup>43</sup> as the  
9 backbone for the phylogenetic tree for mammals. The topology of branches within some  
10 clades was modified using various sources (see online Supplementary Materials in  
11 Krasnov *et al.*<sup>44</sup>).

12 **Niche homogenization analyses.** We tested whether host assemblages exploited by  
13 each parasite species, and vice-versa (parasite assemblages exploiting each mammal  
14 species), were composed of species both phylogenetically and geographically closer to  
15 one another than expected by chance. The Jaccard index<sup>45</sup> was used to measure  
16 composition dissimilarity in interactions and local co-occurrence, while the  
17 phylogenetic distance between species was calculated as the number of steps in the  
18 phylogeny necessary to connect them. The interaction dissimilarity matrices were  
19 correlated with both the geographic dissimilarity and phylogenetic distance matrices  
20 using a Mantel test. Mantel statistics were based on the Spearman rank correlation rho  
21 and for each test 10,000 permutations were performed. In addition, we computed the  
22 phylogenetic and geographic signals at different community scales. To define the  
23 phylogenetic scales we divided the mammal and flea phylogenetic trees into  
24 monophyletic sub-trees, selected the sub-trees with at least seven species, and tested the  
25 phylogenetic signal of interactions for each tree. To define the geographic scales we

1 built a dendrogram of dissimilarity based on co-occurrences in the 15 sampling regions  
2 using a cluster analysis, and used the same approach for the sub-clusters as we used for  
3 the subtrees. In order to compare the signals at different scales (sub-trees and sub-  
4 clusters) we computed the standardized z-score of the correlation coefficient  
5 (correlation on the observed matrix *minus* the average correlation of the permuted  
6 matrices *divided* by the standard deviation of the correlations of the permuted matrices).

7 **Combined topology analysis.** Network modularity was computed using three different  
8 methods: Louvain's method<sup>26</sup>, Barber modularity<sup>27</sup> optimized by the LPA<sub>b</sub>+  
9 algorithm<sup>46</sup>, and Guimerà's method<sup>28</sup>. For the Louvain algorithm we used two different  
10 values of the resolution parameter: 1 and 0.5. We compared the similarity between  
11 partitions using the adjusted Rand index<sup>47</sup>. Modularity computation is a heuristic  
12 procedure, so we ran 100 independent computations for each algorithm and chose the  
13 partition with the highest modularity value. Therefore, the modules of the Louvain 1  
14 partition are not exactly sub-modules of the Louvain 0.5 modules, as the partitions were  
15 computed independently. However, their incongruence is small. Network nestedness  
16 was measured using the NODF index<sup>30</sup>. This index is commonly used in the ecological  
17 literature and is based on interaction overlap and decreasing of fill. To assess the  
18 significance of the observed nestedness and modularity values, we compared those  
19 observed values with the values obtained from matrices permuted following three  
20 different null models: Erdős-Rényi, Degree-probable and Fix-Fix<sup>48</sup>. While the Erdős-  
21 Rényi null model only preserves the original connectance and size in the permuted  
22 matrices, the Fix-Fix null model keeps the original degrees of the species (number of  
23 interactions) constant. The choice between those two models is a compromise between  
24 type 1 and type 2 statistical errors<sup>49</sup>. Nevertheless, the degree-probable null model  
25 represents a middle ground, as it preserves the original connectance and size but keeps

1 degrees only probabilistically in both margins. Finally, the constrained nestedness  
2 analysis was performed as previously described<sup>19</sup>. In short, the only difference between  
3 it and the conventional NODF analysis is that constrained NODF takes into account  
4 whether a given pair of species is composed of two species of the same module, or of  
5 two species of different modules. It computes, then, the two components of NODF  
6 separately and disentangles interaction overlap within and between modules. All  
7 comparisons of observed vs. permuted null model values (for modularity, nestedness,  
8 and constrained nestedness), were made using direct two-tailed z-tests. The interaction  
9 matrices were reorganized to maximize inter- and intra-module nestedness without  
10 disrupting the modular structure of the network as previously described<sup>19</sup>.

11 **Trade-off vs. resource breadth analysis.** We chose parasite abundance, the average  
12 number of individual fleas per individual mammal (calculated including infected and  
13 uninfected hosts), as a proxy for the performance of a given parasite in a given host  
14 species. This choice is justified as abundance is considered a good measure of  
15 performance in this system<sup>50</sup> since it integrates intensity of infestation and prevalence as  
16 a single number (abundance = intensity of infestation *times* prevalence), measuring  
17 different aspects of parasite performance. While intensity of infestation is equal to the  
18 average number of individual parasites per infected individual host, prevalence is equal  
19 to the proportion of infected individuals in the host population. The within-module  
20 degree (Z) and participation coefficient (P) were calculated as proposed by Guimerà<sup>34</sup>,  
21 but with an algorithm adapted to bipartite networks<sup>27</sup>. To test the relationship between  
22 performance and generalization at different scales (i.e., Z and P values) we used  
23 generalized linear mixed models (GLMM)<sup>51</sup>. First, for the global network we built a  
24 GLMM with the abundances of parasites in each host species as the response variable, Z  
25 and P values as explanatory variables, and host species and parasite species as random

1 factors. We decided to use host species as random factors, rather than to work with the  
2 average abundance of each parasite in all of its hosts, to control for host characteristics  
3 known to affect parasite abundance (e.g., carrying capacity, susceptibility, and richness  
4 of parasite fauna)<sup>52</sup>. Nevertheless, parasite species were used as random factors in order  
5 to control for pseudoreplication, as the same parasite species appears several times (one  
6 for each host species), with different abundances but the same Z and P values. Finally,  
7 only hosts species infected by at least three parasite species were used. After that, we  
8 used a backwards stepwise approach with variance analysis based on the chi-squared  
9 test. Finally, the minimum model was tested against a null model to test its significance.  
10 To tell apart the variance explained by either the fixed and random factors, we  
11 computed both marginal and conditional R squared<sup>53</sup>. To analyze the local networks we  
12 used a similar approach, but the abundance of each parasite in each host species in each  
13 local network was used as a response variable, and we included site as a random  
14 variable. Only seven out of fifteen (Extended Data Table 4) local networks were large  
15 enough for the analysis.

16 **Software used.** Except for the computation of Louvain modularity, which was  
17 performed in Pajek software<sup>54</sup>, all other analyses were performed in R program<sup>55</sup>.



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## Supplementary Material:

**Table S1. Significance of the modularity values and nestedness, and its intra and inter components.**

Measure	Obs	Sig Erdős-Rényi	Sig Degreeprob	Sig Fix-Fix
Modularity - Louvain 0.5	0.48	0.002-	0.002-	0.002-
Modularity - Louvain 1	0.67	0.002-	0.002-	0.002-
Nestedness	17.18	0.002-	0.002-	0.002-
Intra Nestedness - Louvain 0.5	38.83	0.002-	0.002-	0.002-
Inter Nestedness - Louvain 0.5	5.05	0.002-	0.002-	0.002-
Intra Nestedness - Louvain 1	50.75	0.002-	0.002-	0.002-
Inter Nestedness - Louvain 1	8.25	0.040-	0.002-	0.002-

↩

The arrows indicate the direction of significance. ↑: the network is more modular/nested than expected by the null model. ↓: the network is less modular/nested than expected by the null model.

**Table S2. Similarity between partitions measured by the adjusted Rand index**

Partitions	Louvain 0.5	Louvain 1	Barber
Louvain 1	0.57		
Barber	0.59	<b>0.96</b>	
Guimerà	<b>0.70</b>	0.62	0.61

Bold-face values represent pairs of similar partitions.

**Table S3. Stepwise selection of mixed models calculated from the global and the local networks.**

a Global Network – Louvain 1 partition				b Global Network – Louvain 0.5 partition			
Model 1: $\ln(\text{Abundance}) \sim Z^*P + (1 \text{Host species}) + (1 \text{Parasite species})$				Model 1: $\ln(\text{Abundance}) \sim Z^*P + (1 \text{Host species}) + (1 \text{Parasite species})$			
Model 2: $\ln(\text{Abundance}) \sim Z+P + (1 \text{Host species}) + (1 \text{Parasite species})$				Model 2: $\ln(\text{Abundance}) \sim Z+P + (1 \text{Host species}) + (1 \text{Parasite species})$			
Model 3: $\ln(\text{Abundance}) \sim P + (1 \text{Host species}) + (1 \text{Parasite species})$				Model 3: $\ln(\text{Abundance}) \sim P + (1 \text{Host species}) + (1 \text{Parasite species})$			
Model 4: $\ln(\text{Abundance}) \sim Z + (1 \text{Host species}) + (1 \text{Parasite species})$				Model 4: $\ln(\text{Abundance}) \sim Z + (1 \text{Host species}) + (1 \text{Parasite species})$			
Null model: $\ln(\text{Abundance}) \sim 1 + (1 \text{Host species}) + (1 \text{Parasite species})$				Null model: $\ln(\text{Abundance}) \sim 1 + (1 \text{Host species}) + (1 \text{Parasite species})$			
Models	D.f.	Chisq	p-value	Models	D.f.	Chisq	p-value
Model 2	6			Model 2	6		
Model 1	7	0.32	0.5704	Model 1	7	5.2423	0.0220
Models	D.f.	Chisq	p-value	Models	D.f.	Chisq	p-value
Model 3	5			Null model	4		
Model 2	6	13.89	0.0001	Model 1	7	27.972	<0.0001
Models	D.f.	Chisq	p-value	[Selected: Model 1: $\ln(\text{Abundance}) \sim Z^*P + (1 \text{Host species}) + (1 \text{Parasite species})$ ]			
Model 4	5				Estimates	Std. Error	t value
Model 2	6	0.42	0.5138	(Intercept)	-2.96	0.16	-18.19
Models	D.f.	Chisq	p-value	Z	0.40	0.07	5.44
Model 4	5			P	0.94	0.36	2.57
Model 2	6			Z:P	-0.76	0.32	-2.35
Null model	4			[marginal R <sup>2</sup> : 0.02894829      conditional R <sup>2</sup> : 0.40999008]			
Model 4	5	15.77	<0.0001				
[Selected: Model 4: $\ln(\text{Abundance}) \sim Z + (1 \text{Host species}) + (1 \text{Parasite species})$ ]							
		Estimates	Std. Error				
(Intercept)		-2.80	0.15				
Z		0.27	0.06				
[marginal R <sup>2</sup> : 0.01661989      conditional R <sup>2</sup> : 0.41647875]							
c Local Networks – Louvain 0.5 partition							
Model 1: $\ln(\text{Abundance}) \sim Z^*P + (1 \text{Host species}) + (1 \text{Parasite species}) + (1 \text{Regions})$							
Model 2: $\ln(\text{Abundance}) \sim Z+P + (1 \text{Host species}) + (1 \text{Parasite species}) + (1 \text{Regions})$							
Model 3: $\ln(\text{Abundance}) \sim P + (1 \text{Host species}) + (1 \text{Parasite species}) + (1 \text{Regions})$							
Model 4: $\ln(\text{Abundance}) \sim Z + (1 \text{Host species}) + (1 \text{Parasite species}) + (1 \text{Regions})$							
Null model: $\ln(\text{Abundance}) \sim 1 + (1 \text{Host species}) + (1 \text{Parasite species}) + (1 \text{Regions})$							
Models	D.f.	Chisq	p-value				
Model 2	7						
Model 1	8	0.12	0.7251				
Models	D.f.	Chisq	p-value				
Model 3	6						
Model 2	7	45.68	<0.0001				
Models	D.f.	Chisq	p-value				
Model 4	6						
Model 2	7	4.18	0.0407				
Models	D.f.	Chisq	p-value				
Null model	4						
Model 2	7	201.31	<0.0001				
[Selected: Model 2: $\ln(\text{Abundance}) \sim Z+P + (1 \text{Host species}) + (1 \text{Parasite species}) + (1 \text{Regions})$ ]							
		Estimates	Std. Error				
(Intercept)		-2.90	0.31				
Z		0.54	0.07				
P		-0.88	0.41				
[marginal R <sup>2</sup> : 0.04845019      conditional R <sup>2</sup> : 0.45103884]							

**Table S4. Phylogenetic signal in the interactions recorded on seven local mammal-flea networks used on mixed models analysis.**

Region	Phylogenetic signal in mammal interactions	Phylogenetic signal in flea interactions
Adzharia	0.006*	0.758
Mongolia North West Khangay	0.284	0.294
Moyynkum	0.226	0.950
North Kyrgystan	0.005*	0.943
Slovakia	0.007*	0.002*
Turkmenistan	0.410	0.901
Volga Kama	0.050*	0.777

Asterisks indicate significant results detected in one-tailed mantel tests.