UNIVERSITY OF SÃO PAULO
Institute of Biosciences
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The abundance-generalization dilemma explained by the Integrative Hypothesis of Specialization

O dilema abundância-generalização explicado pela Hipótese Integradora da Especialização

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Sebastián Montoya Bustamante

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Supervisor: Prof. Dr. Marco A. R. Mello

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To Oli, the future.

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SUMÁRIO – SUMMARY – SUMARIO

RESUMO

As espécies são abundantes porque possuem um alto grau de generalização? Ou apresentam um alto grau de generalização porque são abundantes? Por um lado, espécies com elevados graus de generalização poderiam tornar-se altamente abundantes porque a utilização de uma ampla variedade de recursos significaria uma vantagem seletiva sobre espécies menos generalizadas. Por outro lado, espécies altamente abundantes têm maior probabilidade de encontrar recursos, o que significaria que seu grau de generalização poderia ser maior devido à sua abundância. Essa relação causal entre a abundância de uma espécie e o seu grau de generalização, também conhecida como o "dilema abundância-generalização", tem assombrado as mentes dos ecólogos nas últimas décadas. Embora as primeiras evidências sugerissem que uma alta abundância levaria a altos graus de generalização, métodos mais refinados levaram à conclusão oposta. Contudo, ambos os processos por detrás das diferentes perspectivas desse dilema não são mutuamente exclusivos, indicando que defender uma perspectiva dominante pode nos impedir de entender a verdadeira relação causal. Nesta tese, empregamos a recentemente proposta Hipótese Integradora da Especialização (IHS, na sigla em inglês) para demonstrar uma conexão entre a heterogeneidade de recursos e a força da influência da abundância de uma espécie sobre o seu grau de generalização. Antes de nos aprofundarmos no estudo do dilema em questão, primeiro focamos em compreender a generalização nas interações consumidor-recurso e a melhor maneira de estimar o grau de generalização de uma espécie. Assim, esta tese está dividida em três capítulos. No primeiro capítulo, estudamos o desempenho de diferentes índices para estimar o grau de generalização de um consumidor. Descobrimos que nenhum índice publicado é plenamente adequado para esta tarefa, então propusemos um novo índice que supera os anteriores nas condições avaliadas. No segundo capítulo, baseamo-nos nas conclusões do primeiro para demonstrar que dois conceitos ecológicos –generalização e oportunismo do consumidor, muitas vezes considerados equivalentes– não são iguais. No terceiro capítulo, com uma compreensão mais acurada do que é a generalização e de como estimar o grau de generalização de um consumidor, aprofundamo-nos no dilema estudado, usando o novo índice proposto no primeiro capítulo, junto com as conclusões teóricas do segundo, a fim de compreender nossas descobertas à luz da IHS.

Palavras-chave

Abundância, especialização, generalização, interações entre espécies, oportunismo, uso de recursos.

ABSTRACT

Are species abundant because they have a high degree of generalization? Or do they present a high degree of generalization because they are abundant? On the one hand, species with high degrees of generalization could become highly abundant because the use of a wide variety of resources would mean a selective advantage over less generalized species. On the other hand, highly abundant species are more likely to find resources, which would mean that their degree of generalization could be greater due to their abundance. This causal relationship between the abundance of a species and its degree of generalization, also known as the "abundance-generalization dilemma", has haunted the minds of ecologists in recent decades. Although early evidence suggested that high abundance would lead to high degrees of generalization, more refined methods have led to the opposite conclusion. However, both processes behind the different perspectives of this dilemma are not mutually exclusive, indicating that defending a dominant perspective may prevent us from understanding the true causal relationship. In this thesis, we employ the recently proposed Integrative Hypothesis of Specialization (IHS) to demonstrate a connection between resource heterogeneity and the strength of the influence of a species' abundance on its degree of generalization. Before delving deeper into studying the dilemma at hand, we first focus on understanding generalization in consumer-resource interactions and the best way to estimate the degree of generalization of a species. Therefore, this thesis is divided into three chapters. In the first chapter, we studied the performance of different indices to estimate a consumer's degree of generalization. We discovered that no published index is fully suitable for this task, so we proposed a new index that outperforms the previous ones under the evaluated conditions. In the second chapter, we build on the conclusions of the first to demonstrate that two ecological concepts –generalization and opportunism, often considered equivalent– are not the same. In the third chapter, with a more accurate understanding of what generalization is and how to estimate a consumer's degree of generalization, we delve deeper into the dilemma studied, using the new index proposed in the first chapter, together with the theoretical conclusions from the second, in order to understand our findings in light of the IHS.

Keywords

Abundance, generalization, opportunism, resource use, specialization, species interactions.

RESUMEN

¿Las especies son abundantes porque presentan un alto grado de generalización? ¿O presentan un alto grado de generalización porque son abundantes? Por un lado, especies con elevados grados de generalización podrían volverse altamente abundantes porque el uso de una amplia variedad de recursos significaría una ventaja selectiva sobre especies menos generalizadas. Por otro lado, especies altamente abundantes tienen una mayor probabilidad de encontrar recursos, lo que significaría que su grado de generalización podría ser mayor debido a su abundancia. Esa relación causal entre la abundancia de una especie y su grado de generalización, también conocida como el "dilema abundancia-generalización" ha asombrado las mentes de los ecólogos en las últimas décadas. Aunque las primeras evidencias sugieren que una alta abundancia lleva a altos grados de generalización, métodos más refinados llevaron a la conclusión opuesta. Sin embargo, ambos procesos por detrás de las diferentes perspectivas del dilema no son mutuamente excluyentes, indicando que defender una perspectiva dominante nos puede impedir entender la verdadera relación causal. En esta tesis, empleamos la recientemente propuesta Hipótesis Integradora de la Especialización (IHS, en siglas en inglés) para demostrar una conexión entre la heterogeneidad de recursos y la fuerza de la influencia de la abundancia de una especie sobre su grado de generalización. Antes de profundizar en el estudio del dilema en cuestión, primero nos enfocamos en comprender la generalización en las interacciones consumidor-recurso y la mejor manera de estimar el grado de generalización de una especie. Así, esta tesis está dividida en tres capítulos. En el primer capítulo, estudiamos el desempeño de diferentes índices para estimar el grado de generalización. Descubrimos que ningún índice publicado es totalmente adecuado para esta tarea, y, por tanto, propusimos un nuevo índice que supera a los anteriores bajo las condiciones evaluadas. En el segundo capítulo, nos basamos en las conclusiones del primer capítulo para demostrar que dos conceptos ecológicos –generalización y oportunismo, muchas veces considerados como equivalentes– no son iguales. En el tercer capítulo, con una comprensión más adecuada de lo que es la generalización y de cómo estimar el grado de generalización de un consumidor, profundizamos en el dilema estudiado, usando el nuevo índice propuesto en el primer capítulo, junto con las conclusiones teóricas del segundo, con el fin de comprender nuestros descubrimientos a la luz de la IHS.

Palabras clave

Abundancia, especialización, generalización, interacciones entre especies, oportunismo, uso de recursos.

GENERAL INTRODUCTION

The origin of everything

It all started in Ancient Greece, as many other things in the Western World, with a not-so-simple question that haunted the minds of prominent philosophers: Which came first, the chicken or the egg? While this question may look easy, it is deeper than most people think. This question is not about the chickens and eggs from a farm, but about the origin of everyone and everything in the universe (Sorensen, 2003). After all, we have always wanted to understand how the universe came to be.

In fact, the chicken and the egg represent any two objects bound together by a causal relationship (Davidson, 1967; Mooij et al., 2016). Since both are believed to be the cause of one another, their relationship creates an infinite loop. For Aristotle, such a dilemma rested on a false presupposition, because both chickens and eggs were infinitely old, so neither could come first (Sorensen, 2003). However, his answer did not stop many others from trying to solve this dilemma by other means (Sorensen, 2003).

Since Charles Darwin was yet to be born, a thousand years had to pass before his groundbreaking work, *On the origin of species* (Darwin, 1859), could shed some light on this supposedly infinite loop. Then, after its publication, along with the growing evidence supporting the evolution of species by means of natural selection, evolutionary biologists suggested the egg came first (but see Pilpel & Rechavi, 2015).

Even so, the so-called chicken-and-egg dilemma, besides being a great way to keep children busy, has served as a good example for teaching causal relationships, creating metaphors in many fields such as Medicine (Borghi et al., 2012), Social Sciences (Triandafyllidou & Bartolini, 2020), and of course, Ecology (Blanchet et al., 2009; Fort et al., 2016).

Ecology's own chicken-and-egg dilemma

The abundance-generalization dilemma in consumer-resource interactions is one of Ecology's chicken-and-egg dilemmas (Benadi et al., 2022; Fort et al., 2016). Are species abundant because they exhibit a high degree of generalization? Or do they exhibit a high degree of generalization because they are abundant? There is no straightforward answer. On the one hand, species with a high degree of generalization could become highly abundant, because using a wide variety of resources could represent a selective advantage over less generalized species (Brown, 1984). On the other hand, highly abundant species have a higher probability of finding resources, which means their degree of generalization could be higher due to their abundance (Vázquez et al., 2007).

Since a species' abundance and its degree of generalization establish this apparent bilateral causalilty, ecologists have become obsessed in determining *which came first*, that is, the causal direction of the relationship (see Fort et al., 2016). Although early evidence suggested that abundance was the cause (Fort et al., 2016; Simmons et al., 2019), more refined methods have suggested the other way round (Song et al., 2022). However, the processes behind both perspectives are different and not mutually exclusive (Dormann et al., 2017). Therefore, this dichotomous view of the dilemma is likely concealing important ecological processes modulating the relationship between abundance and generalization.

Consequently, we might be getting more insight into the abundance-generalization causal relationship if we switch our view from *which came first* to *how* and *when*. Is it possible to determine under what conditions a species' abundance is causing its degree of generalization and vice versa? Probably yes, and there seems to be a working hypothesis that could help us approach this dilemma: The Integrative Hypothesis of Specialization (Pinheiro et al., 2019).

The Integrative Hypothesis of Specialization

The Integrative Hypothesis of Specialization (IHS), initially coined the Integrative Hypothesis of Parasite Specialization (Pinheiro et al., 2016), was also born from an ecological dilemma: the trade-off and resource breadth hypotheses as explanations for the relationship between performance and generalization. The IHS states that the intensity of constraints in consumer-resource interactions primarily depends on resource heterogeneity (Pinheiro et al., 2019). This happens, because consumer adaptations to use a resource help it use similar resources but represent maladaptations to use dissimilar resources. Such intensification or relaxation of constraints explains the different topologies observed in species interaction networks (Pinheiro et al., 2019). Evidence supporting this hypothesis is growing for both mutualistic (Mello et al., 2019) and antagonistic interactions (Felix et al., 2022), including single-taxon (Diniz et al., 2022) and mixed-taxon systems (Queiroz et al., 2021). Compound topologies, instead of nested topologies, seem to be the predominant structure in real-world networks (Pinheiro et al., 2022).

Assuming that no matter how abundant a species is, if it is not adapted to use a resource, it will not be able to use it, then resource heterogeneity imposes a limitation to what resources a species can use. Therefore, there are specific conditions under which a species abundance exerts stronger influence on its degree of generalization, and conditions under which the influence is weaker. Consequently, when resources are less heterogeneous, constraints are relaxed, and the influence of a consumer's abundance on its degree of generalization should be stronger. This implies that the Integrative Hypothesis of Specialization potentially explains the causal relationship between a species' abundance and its degree of generalization (Fig. 1).

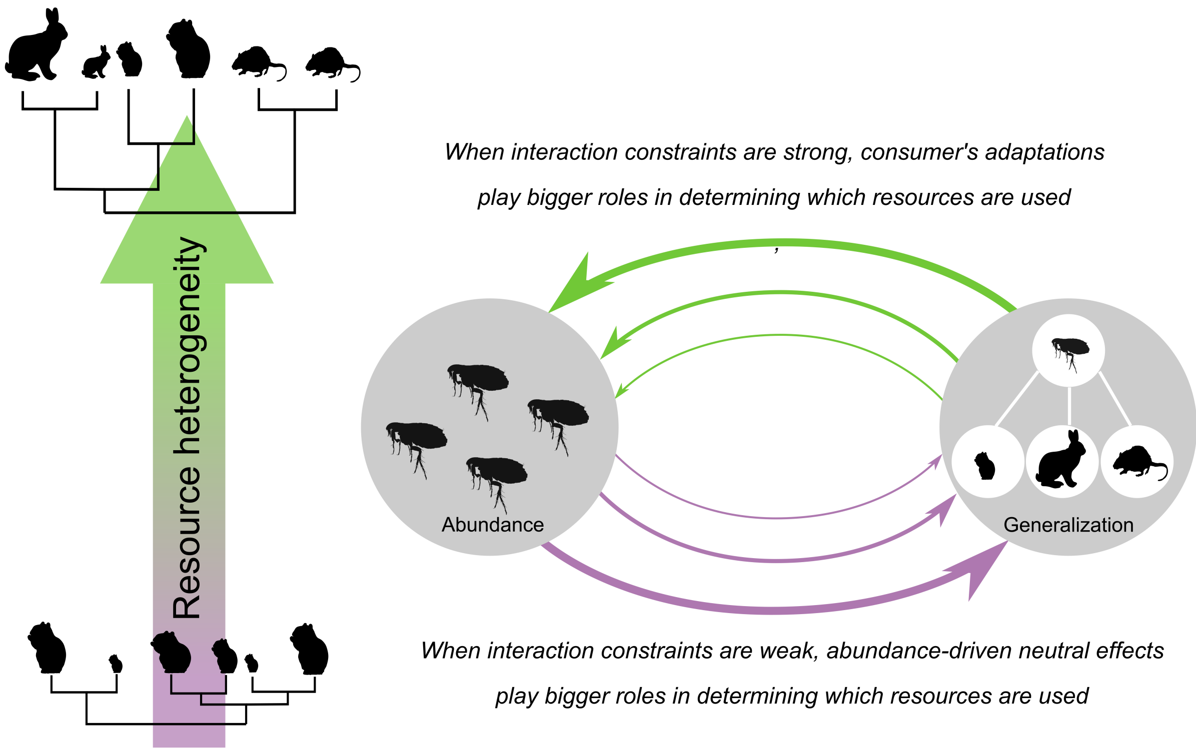


Figure 1. The Integrative Hypothesis of Specialization as a framework to study the abundance-generalization dilemma. A consumer's abundance exerts a stronger influence on its degree of generalization when resources are less heterogeneous (represented by the size of the purple arrow). When resources become more heterogeneous the consumer's degree of generalization will exert stronger influence on its abundance, because adaptations play bigger roles on which resources are used (represented by the size of the green arrow).

Understanding generalization and the structure of this thesis

Throughout this work, we aimed at understanding the abundance-generalization relationship in consumer-resource interactions by harnessing the Integrative Hypothesis of Specialization as a theoretical framework. However, before diving into the dilemma, it was necessary to take a step back and ask ourselves: do we really understand the objects of this dilemma? Do we know what *the egg* is?

This is how we got to the first and second chapters of this thesis, where we focused on understanding what generalization is, what it means to be a generalist, and how to estimate a consumer's degree of generalization. Specifically, in the first chapter, "*A new index to estimate ecological generalization in consumer-resource interactions"*, we assessed the performance of different indices to find an optimal way to estimate a consumer's degree of generalization. This chapter was published in *Methods in Ecology and Evolution*.

In the second chapter, "*A framework to describe resource use in consumer-resource interactions: disentangling generalization and opportunism"*, we harness the findings from the first chapter to demonstrate that two ecological concepts, generalization and opportunism, frequently seen as equivalent, are not the same. Then, having understood what generalization is, and how to estimate a consumer's degree of generalization, we were able to finally dive into the abundance-generalization dilemma.

Thus, in the third and final chapter, "*Unraveling the abundance-generalization dilemma: insights from the Integrative Hypothesis of Specialization"*, we employ the new index from the first chapter and the theoretical findings from the second to understand the abundance-generalization dilemma in the light of the IHS.

CONCLUDING REMARKS

Is a species abundant because it has a high degree of generalization or is it generalized because it has high abundance? Understanding such an intriguing chicken-and-egg dilemma was our aim throughout this thesis. However, during this journey, we came to the realization that we did not have a clear understanding of the characters involved in the story. Consequently, understanding *the egg* of the dilemma—that is, ecological generalization—became a crucial first step. Thus, the first and second chapters focused on theoretical and methodological approaches to understand this concept and the terms associated with it.

After all, what is *the egg*?

What is generalization? A simple way to define generalization is as a process that results in a consumer having similarly high preferences for using a broad range of potential resources. Similarly, specialization is a process that results in a consumer having high preferences for a reduced subset of the potential resources. Within our literature review, we found that the use these definitions (or similar ones) was relatively consistent. Conversely, the use of the term "generalist" and "specialist" was vaguer. To understand what it means to be a generalist (or a specialist), we had to first understand how to estimate a consumer's degree of generalization.

In the first chapter, we explored different ways for estimating a consumer's degree of generalization. In our exploration, we found that, for such a task, it is necessary to (1) determine a set of potential resources, (2) quantify the relative abundance of resources, and (3) quantify the relative use of resources (or the proportion of interactions with resources). However, we demonstrated that most of the available indices were not entirely adequate. Therefore, we proposed and assessed a new index, that unlike others, had optimal performance under the assessed conditions. With that new index it was possible to advance our understanding of what it means to be a generalist (or a specialist).

Let us classify consumers into discrete categories (generalists or specialists) based on their degree of generalization. For any given set of potential resources there is a generalization-specialization continuum where an *extreme* generalist and an *extreme* specialist can be easily identified. On the one hand, an *extreme* generalist went through a process of generalization that led to equal preferences for all potential resources. On the other hand, an *extreme* specialist went through a process of specialization that led to preferring a single resource. As shown in the first chapter, within that continuum, it is possible to establish a midpoint (or threshold) that separates generalists from specialists based on the number of potential resources.

Having established that midpoint, we can say that a generalist is a consumer that went through a process of generalization that placed it in the generalization-specialization continuum between the midpoint and an *extreme* generalist. Likewise, a specialist is a consumer that went through a process of specialization that placed it between the midpoint and an *extreme* specialist.

In the ecological literature it is common to find examples where consumers are classified as generalists (or specialists) under criteria that are not necessarily related to the process of generalization (or specialization). For instance, there is a tendency to name as a generalist those consumers with higher degree of generalization. However, such a definition disregards the possibility of finding communities where all consumers are generalists (or specialists). Additionally, it does not establish an unbiased midpoint between being a generalist and a specialist. Instead, these consumers should be referred to as consumers having a *higher* (or *lower*) degree of generalization.

Are *a chicken's* and *a duck's egg* the same?

After demonstrating that traditional indices were not entirely adequate for estimating a consumer's degree of generalization, we started wondering what they were meant to measure in the first place. We knew their scope was related to resource use, but what exactly did each index operationalize?

In our literature search, we noticed a very popular term: *opportunism*. However, this concept seemed to be so entangled with generalization, that most researchers use them as synonyms. But are they? Our second chapter shows they are not. Opportunism is a concept related to the process of foraging, and it can be defined as a foraging behavior where consumers tend to accept most available opportunities for using resources. Consequently, an *extreme* opportunistic consumer takes advantage of all opportunities, while an *extreme* selective consumer rejects most opportunities, using only the least abundant resource. These behaviors are the extremes of an opportunism-selectivity continuum that can be quantified using the traditional indices of generalization.

Our findings allowed us to establish a clear differentiation between a consumer's degree of opportunism and its degree of generalization. For a given set of potential resources, on the one hand, the degree of opportunism quantifies the proportion of opportunities that are being used by the consumer, revealing the extent to which resource selection is influenced by abundance-driven neutral effects. On the one hand, the degree of generalization quantifies how similarly high are the preferences for a set of potential resources, which might provide insights into how constrained resource use is.

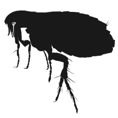
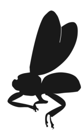
Should we keep referring to the abundance-generalization relationship as a chicken-and-egg dilemma?

Fort et al. (2016) introduced the use of the chicken-and-egg dilemma as a metaphor to explain the abundance-generalization relationship. Although metaphors are useful ways to communicate science, they tend to highlight some aspects of ecological phenomenon, but hide other important details (Olson et al., 2019). This is probably why most research on the abundance-generalization relationship ended up focusing on determining *which came first*.

In our third chapter, we used the Integrative Hypothesis of Specialization (IHS) to understand the abundance-generalization relationship. In concordance with our expectations, we found that resource heterogeneity modulates the abundance-generalization relationship, meaning that there are specific conditions where the influence of a consumer's abundance on its degree of generalization is stronger, and vice versa.

Our findings showcase how switching our view of the abundance-generalization relationship from a chicken-and-egg-like dilemma to understanding the underlying mechanisms led to a deeper understanding of the ecological pattern in question. Yet there is still ground to cover as much of the variance in our models was not explained by the predictors used. Future studies could explore the role of individual specialization and sampling effects in the abundance-generalization relationship.

As shown by Olson et al. (2019), metaphors are essential in Ecology, and there is nothing wrong with comparing the abundance-generalization relationship to the chicken-and-egg dilemma. However, we should not let the metaphor blur the focus of our research.

REFERENCES

Benadi, G., Dormann, C. F., Fründ, J., Stephan, R., & Vázquez, D. P. (2022). Quantitative Prediction of Interactions in Bipartite Networks Based on Traits, Abundances, and Phylogeny. The *American Naturalist, 199*(6), 841–854. https://doi.org/10.1086/714420

Blanchet, S., Méjean, L., Bourque, J.-F., Lek, S., Thomas, F., Marcogliese, D. J., Dodson, J. J., & Loot, G. (2009). Why do parasitized hosts look different? Resolving the "chicken-egg" dilemma. *Oecologia, 160*(1), 37–47. https://doi.org/10.1007/s00442-008-1272-y

Borghi, L., Nouvenne, A., & Meschi, T. (2012). Nephrolithiasis and urinary tract infections: 'The chicken or the egg' dilemma?. *Nephrology Dialysis Transplantation, 27*(11), 3982–3984. https://doi.org/10.1093/ndt/gfs395

Brown, J. H. (1984). On the Relationship between Abundance and Distribution of Species. *The American Naturalist, 124*(2), 255–279. https://doi.org/10.1086/284267

Darwin, C. (1859). *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. London: John Murray.

Davidson, D. (1967). Causal Relations. *The Journal of Philosophy, 64*(21), 691–703. https://doi.org/10.2307/2023853

Diniz, U. M., Nadia, T. L., Mello, M. A. R., & Machado, I. C. S. (2022). Few plants and one dominant fly shape a unique pollination network in a Neotropical mangrove. *Aquatic Botany, 180*, 103526. https://doi.org/10.1016/j.aquabot.2022.103526

Dormann, C. F., Fründ, J., & Schaefer, H. M. (2017). Identifying Causes of Patterns in Ecological Networks: Opportunities and Limitations. *Annual Review of Ecology, Evolution, and Systematics, 48*(1), 559–584. https://doi.org/10.1146/annurev-ecolsys-110316-022928

Felix, G. M., Pinheiro, R. B. P., Poulin, R., Krasnov, B. R., & Mello, M. A. R. (2022). The compound topology of host–parasite networks is explained by the integrative hypothesis of specialization. *Oikos, 2022*(1). https://doi.org/10.1111/oik.08462

Fort, H., Vázquez, D. P., & Lan, B. L. (2016). Abundance and generalisation in mutualistic networks: Solving the chicken-and-egg dilemma. *Ecology Letters, 19*(1), 4–11. https://doi.org/10.1111/ele.12535

Mello, M. A. R., Felix, G. M., Pinheiro, R. B. P., Muylaert, R. L., Geiselman, C., Santana, S. E., Tschapka, M., Lotfi, N., Rodrigues, F. A., & Stevens, R. D. (2019). Insights into the assembly rules of a continent-wide multilayer network. *Nature Ecology & Evolution, 3*(11), Article 11. https://doi.org/10.1038/s41559-019-1002-3

Mooij, J. M., Peters, J., Janzing, D., Zscheischler, J., & Schölkopf, B. (2016). Distinguishing cause from effect using observational data: Methods and benchmarks. *The Journal of Machine Learning Research, 17*(1), 1103–1204

Olson, M. E., Arroyo-Santos, A., & Vergara-Silva, F. (2019). A User's Guide to Metaphors in Ecology and Evolution. *Trends in Ecology & Evolution, 34*(7), 605–615. https://doi.org/10.1016/j.tree.2019.03.001

Pilpel, Y., & Rechavi, O. (2015). The Lamarckian chicken and the Darwinian egg. *Biology Direct, 10*(1), 34. https://doi.org/10.1186/s13062-015-0062-9

Pinheiro, R. B. P., Félix, G. M. F., Chaves, A. V., Lacorte, G. A., Santos, F. R., Braga, É. M., & Mello, M. A. R. (2016). Trade-offs and resource breadth processes as drivers of performance and specificity in a host-parasite system: A new integrative hypothesis. International Journal for *Parasitology, 46*(2), 115–121. https://doi.org/10.1016/j.ijpara.2015.10.002

Pinheiro, R. B. P., Felix, G. M. F., Dormann, C. F., & Mello, M. A. R. (2019). A new model explaining the origin of different topologies in interaction networks. *Ecology, 100*(9), e02796. https://doi.org/10.1002/ecy.2796

Pinheiro, R. B. P., Felix, G. M. F., & Lewinsohn, T. M. (2022). Hierarchical compound topology uncovers complex structure of species interaction networks. *Journal of Animal Ecology, 91*(11), 2248-2260. https://doi.org/10.1111/1365-2656.13806

Queiroz, J., Diniz, U., Mello, M.A.R., Machado, I.C.S. (2021). Bats and hawkmoths form mixed modules with flowering plants in a nocturnal interaction network. *Biotropica, 53*(2): 596-607. https://doi.org/10.1111/btp.12902

Simmons, B. I., Vizentin-Bugoni, J., Maruyama, P. K., Cotton, P. A., Marín-Gómez, O. H., Lara, C., Rosero-Lasprilla, L., Maglianesi, M. A., Ortiz-Pulido, R., Rocca, M. A., Rodrigues, L. C., Tinoco, B. A., Vasconcelos, M. F., Sazima, M., Martín González, A. M., Sonne, J., Rahbek, C., Dicks, L. V., Dalsgaard, B., & Sutherland, W. J. (2019). Abundance drives broad patterns of generalisation in plant–hummingbird pollination networks. *Oikos, 128*(9), 1287–1295. https://doi.org/10.1111/oik.06104

Song, C., Simmons, B. I., Fortin, M.-J., & Gonzalez, A. (2022). Generalism drives abundance: A computational causal discovery approach. *PLOS Computational Biology, 18*(9), e1010302. https://doi.org/10.1371/journal.pcbi.1010302

Sorensen, R. A. (2003). *A brief history of the paradox: Philosophy and the labyrinths of the mind.* Oxford Univ. Press.

Triandafyllidou, A., & Bartolini, L. (2020). Irregular Migration and Irregular Work: A Chicken and Egg Dilemma. In S. Spencer & A. Triandafyllidou (Eds.), *Migrants with Irregular Status in Europe: Evolving Conceptual and Policy Challenges* (pp. 139–163). Springer International Publishing. https://doi.org/10.1007/978-3-030-34324-8_8

Vázquez, D. P., Melián, C. J., Williams, N. M., Blüthgen, N., Krasnov, B. R., & Poulin, R. (2007). Species abundance and asymmetric interaction strength in ecological networks. *Oikos,* 116(7), 1120–1127. https://doi.org/10.1111/j.0030-1299.2007.15828.x