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Review

Towards the Integration of Niche and Network Theories

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The quest for understanding how species interactions modulate diversity has progressed by theoretical and empirical advances following niche and network theories. Yet, niche studies have been limited to describe coexistence within tropic levels despite incorporating information about multi-trophic interactions. Network approaches could address this limitation, but they have ignored the structure of species interactions within trophic levels. Here we call for the integration of niche and network theories to reach new frontiers of knowledge exploring how interactions within and across trophic levels promote species coexistence. This integration is possible due to the strong parallelisms in the historical development, ecological concepts, and associated mathematical tools of both theories. We provide a guideline to integrate this framework with observational and experimental studies.

Highlights

We propose to integrate niche and network theories into a single framework.

This integration is possible through the strong parallelisms of concepts and methodologies of both theories.

Feasibility and stability conditions are the key concepts that can allow the integration.

How species interactions across trophic levels fulfill feasibility and stability conditions is yet to be discovered.

Niche Theory Meets Network Theory

One central aim in ecology is understanding how species interactions modulate biodiversity. At the origin of this interest is Darwin's legacy; he reasoned that species coexistence is less likely among closely related species as they tend to compete for similar resources for surviving and reproducing [1]. Given this reasoning, ecologists built the concept of the **niche** (see Glossary) to assess the degree of resource overlap among species [2,3], and early work explored the consequences of competition for a single-resource niche dimension [4,5]. However, researchers soon recognized that a species' niche is composed of multiple dimensions [6,7]. For instance, plants compete directly and indirectly for abiotic resources such as water, nutrients, and light [8–10], as well as for biotic resources in the form of mutualistic interactions (e.g., pollinators, disperses, and mycorrhizae) [11–14]. In addition to resource competition, parallel work has shown that antagonist interactions within a **trophic level** (i.e., intraguild predation) [15] as well as those coming from other trophic levels (e.g., predation, herbivory, and parasitism) are also part of a species' niche [16–19]. Moreover, positive interactions such as facilitation can be as important as competitive interactions for structuring ecological communities [20,21]. This body of knowledge has revealed that species coexistence is a much more complex process than originally thought.

Parallel to describing the multidimensional nature of species' niche, ecologists have obtained critical progress by revealing general principles of the consequences of multiple species interactions for species coexistence. For example, the concept of apparent competition [22,23] has been particularly key to understanding the role of indirect multi-trophic interactions in coexistence by describing how competition within a guild of species is modulated by shared enemies (e.g., predators and pathogens). This concept recently set the path to recognize that competition for resources and predation can be of equal importance for limiting or promoting diversity within a guild of primary producers or consumers (e.g., plants or herbivores) [24,25].

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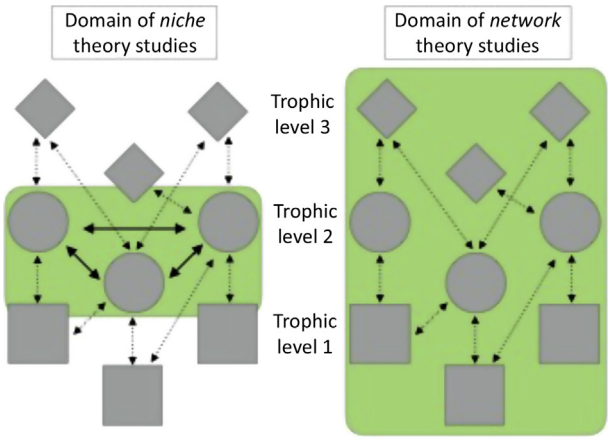

Trends in Ecology & Evolution

Figure 1. Research Domains of Niche and Network Theories. Niche theory (left side) has been successful in incorporating the effect of direct and indirect interactions within and between trophic levels (denoted by black arrows) on determining species coexistence within a single trophic level (light green rectangle) [7,16,22,24]. However, niche studies have not addressed how these direct and indirect trophic interactions modulate coexistence across trophic levels. By contrast, this task has been addressed by network research (right side). While the area of study is bigger (green rectangle), network studies have not considered the structure of interactions within trophic levels (no unbroken lines present). By integrating niche and network theories we can start considering explicitly and simultaneously species interactions across trophic levels and their role (feedbacks) in modulating species coexistence. Note that arrows are double-headed, indicating the existence of such feedbacks. Unbroken and broken arrows indicate whether the interaction is within or between trophic levels, respectively.

However, these advances together with niche studies are limited in their approach, as their goal is to understand the role of species interactions in shaping species coexistence within one single trophic level [26]. The rest of the species within a community that do not belong to the focal trophic level is considered to be always present and static. This critical limitation of niche studies clashes with the increasing interest of ecologists in disentangling the mechanisms maintaining species coexistence in more than one trophic level (see Figure 1 for a schematic representation). Indeed, part of this motivation is due to having multi-trophic information readily available [27,28], but the fundamental question is how to extend niche theory to study the effects of species interactions on determining diversity across multiple trophic levels simultaneously.

To address this limitation, we call for the integration of niche theory with network theory. Network theory has already partially addressed the challenge of how to consider the role of species interactions in shaping species coexistence across several trophic levels [29,30], but it has missed the information within trophic levels that niche theory incorporates. In particular, network studies have focused on the association of the structure of species interactions with community dynamics in mutualistic (e.g., plant–pollinator and plant–disperser) [31–35] and antagonistic systems (e.g., host–parasite, prey–predator, and plant–herbivore) [34,36–38] Yet, because network studies emphasize species interactions between trophic levels, they consider that species within the same trophic level do not directly interact, or they all interact with the same strength [33,35].

Because niche studies lack the ability to describe species coexistence for more than one trophic level, and network studies ignore the structure of species interactions within trophic levels (Figure 1), it is surprising that both theories have not spoken fluently to each other despite

Glossary

Equilibrium point: a fixed state at which species abundances are constant over time.
Dynamical stability: the property of an ecological system to return to an original equilibrium point after a pulse perturbation.
Intrinsic growth rate: the rate at which a population increases in size in the absence of density-dependent regulation.
Feasibility: the property of an ecological system to hold an equilibrium point with positive abundances in all its constituent species.
Feasibility domain: the range of conditions (e.g., demographic parameters) compatible with all species having positive abundance.
Feedback: the process by which the output of a system is routed back as an input of another system forming a loop.
Fitness: the species ability to mature and produce offspring.
Fitness differences: according to Chesson (2000) [48], average fitness differences between species are an equalizing mechanism of species coexistence that reduce competitive imbalance between competitors. In the absence of niche differences, determine the superior competitor in a community.
Multi-trophic network: a network representing patterns of multiple interaction types between species, including competition, mutualistic, or antagonistic relationships. Also known as multiplex networks.
Niche: the environmental conditions and resources a species requires for living and reproducing.
Niche differences: according to Chesson (2000) [48], niche differences are a stabilizing mechanism of species coexistence by causing intraspecific competition to exceed interspecific competition.
Per capita growth rate: the relative contribution to the population increases in size per individual.
Species dynamics: changes in species' population over space and time.
Trophic level: a level of organization within the food chain of an ecosystem, the organisms of which obtain resources in a similar way.

their complementarities; doing so can provide new research avenues and understanding of how species diversity is maintained. Our aim here is to show a direct integration of both theories as they share strong similitudes in their theoretical motivations, ecological concepts, and mathematical tools. This path of mutual understanding paves the road to combine theoretical concepts and associated toolboxes from both theories into a common methodological framework. We believe the emerging framework is particularly useful for investigating species coexistence in **multi-trophic networks**, which include competitive, mutualistic, and antagonistic interactions simultaneously. Additionally, we provide a road map that accommodates this new framework to experimental and observational studies.

Conceptual Parallelisms Between Niche and Network Theories

Obtaining a common theoretical framework from the integration of both niche and network theories is straightforward as these studies have started from similar conceptual constructs, and after decades of research have independently converged on equivalent conclusions about the conditions leading to species coexistence. To reach the maximum audience, we verbally detail this historical convergence and explain here why both theories speak the same language despite using different technical terms. We also aim to present a rigorous mathematical explanation of this conceptual parallelism. This is possible because both theories use similar population dynamics models to build ecological theory rooted in the Lotka-Volterra form [4,24,25,35,38–41] (Box 1). We are aware that the direct application of Lotka-Volterra models to describe natural systems might be limited assuming species linear responses, and do not take into account meta-community dynamics. Part of these limitations will be solved later when we present more mechanistic models that capture additional nonlinear species responses in order to explain how to apply this emerging framework to experimental and observational approximations [42,43].

As we previously mentioned, the niche concept was a fundamental construct to understand patterns of species distribution and co-occurrence within a trophic level based on how species interact with the habitat they experience (Grinnellian niche), how they modify the habitat (Eltonian niche) and how interact with other species in the community (Hutchinsonian niche) [44]. Under classic niche theory, the only condition modulating species coexistence was the amount of niche overlap between species [4,45], which ecologists assumed to arise, for instance, from differences in phenology, bill size, shade tolerance, or feeding preferences. The rationale was that the smaller the niche overlap, the larger the chances of species coexistence [7,46,47].

However, subsequent work [25,41,48] showed that **niche differences** alone are not enough to determine species coexistence. Under recent advances of niche theory (also known as 'modern coexistence theory'), niche differences are only a stabilizing mechanism that tends to promote coexistence when species limit themselves more than they limit others [48]. Modern coexistence theory has provided techniques to directly measure niche differences as the relative ratio between intra- and interspecific competition [25], and consider that neutral dynamics occur when species do not differ in their niches but have equivalent **fitness** [49]. The estimation of niche differences using coexistence theory techniques remains phenomenological (i.e., the source of variation is unknown), and recent studies are, for instance, mapping how species functional trait differences relate to niche differences [50].

Conversely, species can also differ in their fitness. **Fitness differences** are related to species' ability to capture and transform resources into offspring, which is generally a combination of demographic parameters (e.g., fecundity, survival, and recruitment) and the species' sensitivity

Box 1. Conceptual Parallelism between Conditions Leading Species Coexistence for Niche and Network Theory

For a pair of species in competition, the coexistence conditions according to niche theory are defined by:

$$\underbrace{\sqrt{\frac{\alpha_{11}\alpha_{22}}{\alpha_{12}\alpha_{21}}}}_{(1-\text{Niche difference})^{-1}} > \underbrace{\frac{r_1}{r_2}\sqrt{\frac{\alpha_{22}\alpha_{21}}{\alpha_{11}\alpha_{12}}}}_{\text{Fitness difference}} > \underbrace{\sqrt{\frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}}}_{1-\text{Niche difference}} \quad \text{[I]}$$

where $r_1 > 0$ corresponds to the **intrinsic growth rate** (demographic parameter) of species 1, and $\alpha_{12} > 0$ represents the competitive per capita effect of species 2 on the per capita growth rate of species 1. This equation states that the fitness difference (i.e., the ratio between intrinsic growth rates modulated by what is known as the competitive response ratio) of the two species has to fall between a lower and an upper bound, computed from the niche difference (i.e., range of values defined by the ratio between inter- and intraspecific competition). Note that these inequalities can be also simply written as $\alpha_{11}/\alpha_{21} > r_1/r_2 > \alpha_{12}/\alpha_{22}$. Moreover, such inequalities have also to assume that the niche difference is smaller than one, i.e.,

$$\alpha_{12}\alpha_{21} < \alpha_{11}\alpha_{22} \quad \text{[II]}$$

which guarantees that the equilibrium point is dynamically stable (the system returns to its original equilibrium point after a pulse perturbation) in a Lotka-Volterra competition model of the form:

$$\begin{cases} \dfrac{dN_1}{dt} = N_1(r_1 - \alpha_{11}N_1 - \alpha_{12}N_2) \\ \dfrac{dN_2}{dt} = N_2(r_2 - \alpha_{21}N_1 - \alpha_{22}N_2) \end{cases} \quad \text{[III]}$$

where N_1 and N_2 correspond to the abundance of species 1 and 2, respectively. Note that the inequalities in Equation I correspond to an equilibrium point called feasible because all species have positive abundances (i.e., $N_1^* > 0$ and $N_2^* > 0$) [35,52–54,99]. By contrast, the inequality of Equation II only grants the dynamical stability (in fact, in that specific case the global stability) by having intraspecific competition stronger than interspecific competition. Note that feasibility is a necessary condition for species persistence in a Lotka-Volterra model [54].

Let us explain how dynamical stability and feasibility conditions arise in multi-trophic systems by taking as an example a two-trophic level system describing the mutualistic interactions between a set of plants (P) and a set of pollinators (A). Note that similar conclusions are obtained by considering antagonist interactions such as a prey–predator system. This mutualistic system can be described by the following set of dynamical equations:

$$\begin{cases} \dfrac{dP_i}{dt} = P_i\left(r_i^{(P)} - \sum_j \alpha_{ij}^{(P)}P_j + \sum_j \gamma_{ij}^{(P)}A_j\right) \\ \dfrac{dA_i}{dt} = A_i\left(r_i^{(A)} - \sum_j \alpha_{ij}^{(A)}A_j + \sum_j \gamma_{ij}^{(A)}P_j\right) \end{cases} \quad \text{[IV]}$$

where the variables P_i and A_i denote the abundance of plant and animal species i, respectively. The parameters of this mutualistic model correspond to the values describing intrinsic growth rates (r_i), within-guild competition ($\alpha_{ij} > 0$), and the benefit received via mutualistic interactions between trophic levels ($\gamma_{ij} > 0$). All these interaction strengths can, in turn, be embedded in a two-by-two block matrix;

$$\boldsymbol{\beta} = \begin{bmatrix} \boldsymbol{\alpha}^{(P)} & -\boldsymbol{\gamma}^{(P)} \\ -\boldsymbol{\gamma}^{(A)} & \boldsymbol{\alpha}^{(A)} \end{bmatrix} \quad \text{[V]}$$

The conditions for feasibility depend on both the species interactions defined by $\boldsymbol{\beta}$ and the demographic parameters of species r (analogous to Equation I above) [71]. Note that the conditions for dynamical stability are more complex [40]. Indeed, several meaningful notions of stability have been defined in ecology, such as Volterra-dissipative, D-stability, sign-stability, and local stability. Sign-stability, Volterra-dissipative, and D-stability are only determined by the interaction matrix $\boldsymbol{\beta}$. Sign-stability has the property of granting global stability only on the description of who eats whom and not on the strength of the trophic interactions. Volterra-dissipative implies the global stability of a feasible equilibrium, while D-stability grants only local stability. Finally, local stability involves also the equilibrium densities and therefore the intrinsic growth rates. The relations among these notions of stability (and more) are well represented by Logofet's flower [53].

to reduce these demographic parameters in the presence of neighbors [25,43,49]. Fitness differences in essence determine the superior competitor within a species pair in the absence of niche differences. It has been well recognized that coexistence is the result of a balance between the relative strength of niche versus fitness differences. That is, two species will stably coexist when their niche differences overcome their fitness differences [48,49] (see Table 1 for examples of both species differences across a wide range of organisms). This condition has

Table 1. Examples of Niche and Fitness Differences for Different Organisms and Trophic Levels[a]

Trophic level	Evidences of niche and fitness differences		Refs
	Niche	Fitness	
Plant–plant	Spatial segregation, phenology, or plant morphology differences reduce niche overlap.	Species ability to draw down common limiting resources determines species fitness.	[4,8,48]
Plant–insect	Fragmented evidences suggest that differences in pollinators can stabilize plant coexistence.	Herbivorous insects and their network of hyperparasitoids can significantly affect plant fitness.	[11,70,83]
Plant–vertebrate	Interactive effects between abiotic stress, tolerance to herbivory, and herbivore body size determine plant abundances and richness.		[84,85]
Plant–fungi	Fungal pathogens mediate coexistence through trade-offs between competitive ability and resistance to pathogens and through pathogen specialization.	Low specificity of fungal pathogens determines local abundance of plant species in a tropical forest.	[19,86]
Insect–insect	Plant species, stem size, and location within stem determine niche differences within a guild of herbivorous insects.	Searching ability, female fecundity, and resource degradation and preemption determine fitness differences among parasitoids, phytophagous insects, and arachnids.	[87,88]
Insect–plant	Wild bees specialize in their floral reward including nectar, pollen, pollen resins, volatiles, lipids, and waxes.	Foraging rates and food storage determine fitness differences (i.e., drone production, winter survival) among genetically diverse honey-bee colonies.	[11,89]
Insect–vertebrate	Tick habitat differs greatly among species from rodent burrows to caves and bird nests.	The timing and duration of aquatic insect emergence is regulated by temporal variation in salmon density.	[90,91]
Vertebrate–vertebrate	Differences in bill shape and body size stabilize coexistence between birds by the use of different resources.	Intraguild predation of large carnivores on African wild dogs reduces their population size.	[92,93]
Vertebrate–plant	Strong overlap of dietary requirements between wild and domestic herbivores.		[94,95]
Insect–vertebrate	Vertebrates differ in the number and specificity of their parasitic insects.	Ticks reduce offspring and increase mortality in a wide variety of animals including birds, lizards, and mammals.	[90,96]
Trematode–mollusk	Spatial heterogeneity stabilizes coexistence of a guild of salt marsh trematodes.	Competition-colonization trade-offs determine trematode fitness.	[72]
Alga–alga	Niche and fitness: Phylogenetic relatedness does not predict competitive outcomes between freshwater algae.		[58]
Bacteria–vertebrate	Specific immunity of *Streptococcus pneumoniae* serotypes stabilizes coexistence.	Acquired immunity to noncapsular antigens determines serotype fitness.	[97]
Protist–bacteria	Niche and fitness: Differences in mouth size of bacterivorous protist species reduces competitive exclusion.		[46]

[a]Some examples explicitly separate the study of the species' niche from the species' fitness, while in other examples researchers have only studied one component, or both niche and fitness differences have been considered together. Note that for many trophic levels, information of niche and fitness differences is asymmetric, these differences are better known for one trophic level than for the other (e.g., plants–fungi or insects–vertebrate).

also been reinterpreted as the larger the niche difference between two species, the larger the combination of their fitness differences compatible with their coexistence [49,51] (Box 1). This reinterpretation is critical as it provides the main bridge of common understanding between niche and network theories, explaining how species coexistence is possible.

Network research on species coexistence started by studying the stabilizing mechanisms for entire communities [5], rather than focusing on pairwise interactions. This stability was defined in a dynamical rather than a static way. **Dynamical stability** is the property of a system to return to an original **equilibrium point** (if it exists) after a pulse perturbation (e.g., a change in species abundances) coming from demographic stochasticity, which includes migration and random changes in birth and death processes. Early network studies showed that this dynamical stability depends on species interactions (analogous to niche differences) within

and between trophic level compartments (contained in $\boldsymbol{\beta}$ matrix, Box 1). Importantly, a number of interesting questions emerged from these concepts, such as whether the observed structure of large multi-trophic systems necessarily leads to more dynamically stable communities [5]. However, extensive research showed that dynamical stability alone (as niche differences alone) is not enough to guarantee stable coexistence of all species in a community. This means that it can be possible to have a dynamically stable community where the equilibrium point will always lead to one or more species with zero abundance ($Ni^* = 0$), even if reintroduced into the community [35,52,53]. In other words, the system is dynamically stable but contains only a subset of species from the original pool.

As it has happened with the historical development of niche theory, subsequent work on network theory has shown that it is also necessary to account for the species' fitness in order to evaluate the condition of whether species can attain positive abundances at equilibrium [54]. Network studies called this condition **feasibility**, which also depends on the species interactions contained in the matrix ($\boldsymbol{\beta}$) and the species' demographic parameters (r) [35,52,55] (Box 1). Importantly, these recent advances have shown that the structure of species interactions between trophic levels can modulate the range of combinations of demographic parameters leading to feasible systems [35,55]. Therefore, in line with niche theory, network studies also found that species coexistence within communities depends on how the demography of species match the constraints imposed by species interactions.

This historical convergence shows the existence of a common theoretical framework for understanding how species interactions modulate diversity, which has two key ingredients: (i) species' demography and (ii) the structure of species interactions. This structure is contained in the $\boldsymbol{\beta}$ matrix described in Box 1. The take-home message of this framework is that a community of species can coexist when both ingredients are combined in the following way:

Box 2. Emerging Properties of the Integration of Niche and Network Theory

For multi-trophic dynamical systems of the general form $dN_i/dt = N_i\, f_i(\boldsymbol{N})$, an $n \times n$ block matrix emerges for describing species interaction across n trophic levels:

$$\beta = \begin{bmatrix} \alpha_1 & \gamma_{12} & \cdots & \gamma_{1n} \\ \gamma_{21} & \alpha_2 & \cdots & \gamma_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ \gamma_{n1} & \gamma_{n2} & \cdots & \alpha_n \end{bmatrix}, \qquad [I]$$

where the diagonal blocks (α_i) correspond to the within-trophic level (i) interactions (i.e., competition, intraguild predation, facilitation) and the other blocks (γ_{ij}) represent the between-trophic level interactions (effect of trophic level j on i in the form of mutualism or antagonism interactions). As $\boldsymbol{\beta}$ is a block matrix, each element of the matrix represents a submatrix of species interaction. For instance, α_1 is a matrix describing all species interaction within the trophic level 1, and $\boldsymbol{\gamma}_{12}$ is another matrix describing all interactive effects of species from the trophic level 2 on species from the trophic level 1.

Stable coexistence of all species ($N_i^* > 0$) across trophic levels depends on whether this interaction matrix $\boldsymbol{\beta}$ and the demographic parameters r_i satisfies together both the stability and feasibility conditions [53,54,71]. There are different classes of dynamical stability. For instance, local stability is the property of the system to return to the equilibrium point after a small pulse perturbation (changes in species abundances), whereas global stability is concerned with external perturbations of any given magnitude converging to the same equilibrium point. Each class demands specific properties to be fulfilled by the interaction matrix $\boldsymbol{\beta}$ in combination with the species demographic parameters r_i [53,71], and which class of stability should be studied depends on both the research question and knowledge about the system. The feasibility of a multi-trophic system corresponds to the conditions allowing all species to have positive abundances, which also depends on both the interaction matrix $\boldsymbol{\beta}$ and the demographic parameters r_i [35,52–54,71]. The figure below illustrates the conditions of feasibility in a three-species system. The green area on the sphere represents the range of demographic parameters leading to feasibility given the interaction strengths matrix. To some extent, Figure I of the extension of modern coexistence theory to multispecies coexistence; the border of the green area is the multispecies analogous of the fitness and niche difference inequality (see Equation I in Box 1) that applies to species pairs only.

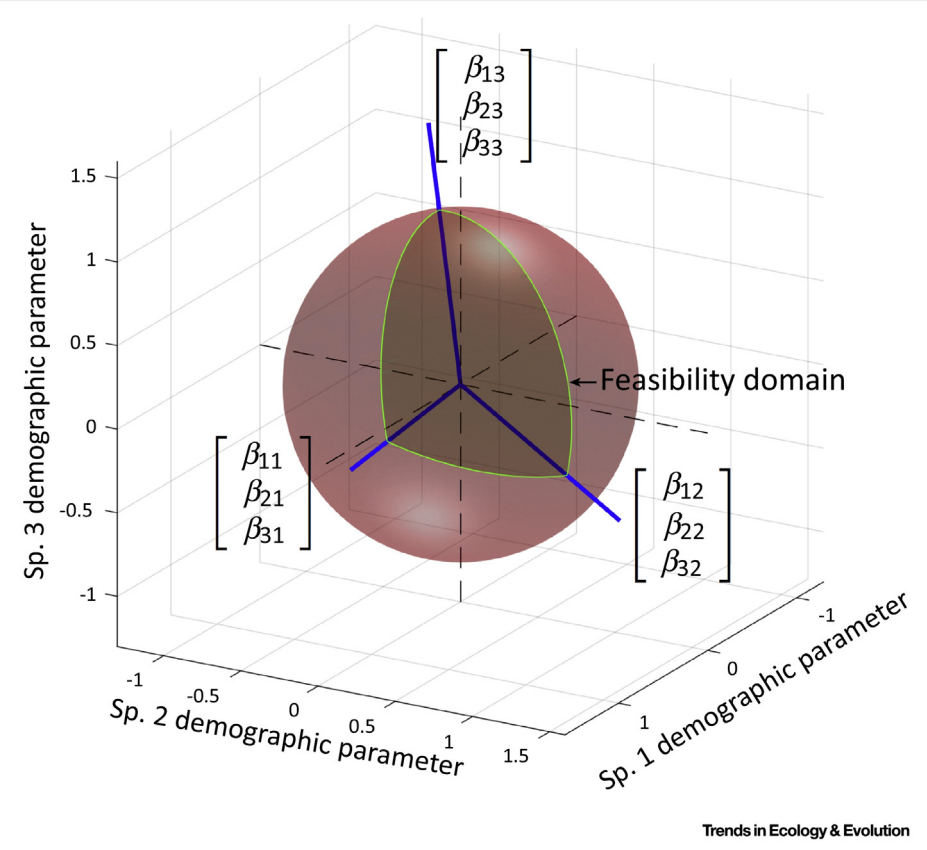

Figure I. Illustration of the Feasibility Domain for a Multi-Trophic System. The figure shows the normalized domain of demographic parameters (feasibility domain relative to the unit sphere) that a two-trophic system (e.g., two pollinators and one plant) can theoretically have to be compatible with all species having positive abundances. This normalized feasibility domain (green spherical triangle) is constrained by the intra- and interspecific interaction matrix (**β**). The columns of the interaction matrix (e.g. [β_{11}, β_{12}, β_{13}]) give the boundaries of the feasibility domain (three blue lines). The larger this volume is, the larger the set of demographic values compatible with feasibility, and the larger the likelihood of species coexistence across trophic levels [55,71].

species interactions define the coexistence space (i.e. the feasibility region) and species coexist when the combination of their demographic parameters (i.e. fitness) falls within this space (Box 2 and Figure 2). One crucial advantage of this framework is that it is not limited to any particular type of multi-trophic interactions, and can be therefore accommodated to both mutualistic and antagonistic interactions, such as a plant–pollinator or a predator–prey community. Another key important advantage is that this framework is not limited to two trophic levels. It can be extended to multi-trophic structures, where three or more trophic levels are considered simultaneously. Indeed, these multi-trophic structures are simply the combination of competitive/facilitative interactions within trophic levels, as well as antagonistic and mutualistic interactions between trophic levels [56] (Box 2).

Coupling the Integration of Niche and Network Theories With Experimental and Observational Work

We acknowledge that one critical step to consider in full is that this integrative framework depends on how easily researchers can adapt it to their particular systems. The basic task is to

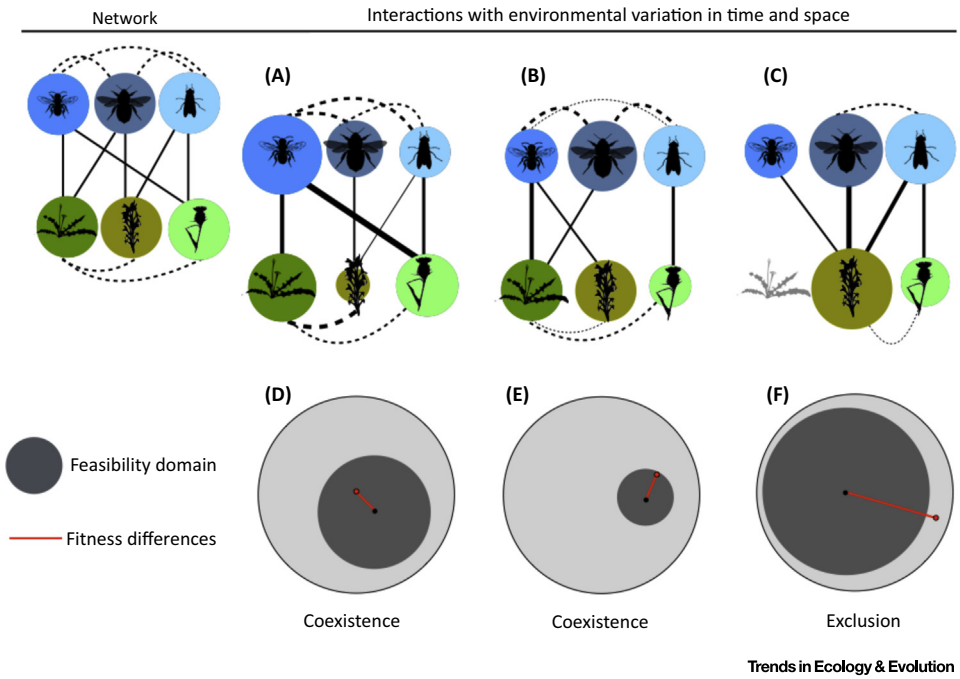

Figure 2. Effects of Species' Intrinsic Properties and Network Structure on Species Coexistence
For a Figure360 author presentation of Figure 2, see the figure legend at https://doi.org/10.1016/j.tree.2018.01.007

Species traits such as body size, phenological timing, or feeding preferences interact with environmental variations in space and time to determine (i) network structure and (ii) species' fitness. Broken lines represent the strength of species interactions within trophic levels and unbroken lines represent the same across trophic levels. Obtaining information on how such trait–environment interactions modified these two elements in ecological communities remains fundamental to predict the consequences of species interactions for the maintenance of diversity [98]. Consider a hypothetical case of a plant–pollinator system in which environmental variation modifies these two elements in three different ways (Panels A–C). The size of the circles denotes the realized species' fitness, which arises as a combination of species interactions and their demographic parameters (plants in green and insects in blue). Additionally, we have learned from the integration of niche and network theories that the structure of species interactions within and between trophic levels renders the feasibility domain (here represented in two dimensions for simplicity; dark gray area in Panels D–F). Note that each network structure gives a different size of feasibility domain. In principle, the larger the feasibility domain, the more likely species coexist as it allows for a larger combination of fitness differences (see F feasibility domain compared with D and E). However, it is paramount to point out that even with a large feasibility domain, species may not coexist if the position of the vector containing species' fitness (red line) falls outside the feasibility domain (i.e., falls within the light gray area) [71]. This is the case of F where one plant species is excluded. Conversely, the system can be maintained despite showing a smaller feasibility region if the vector of species' fitness falls within the feasibility domain (cases D and E). Therefore, the take-home message is that coexistence occurs when species interactions create a feasibility domain compatible with the observed fitness differences. Recall that fitness differences are measured as the distance between the center of the feasibility domain and the position of the vector containing species fitness (red line). Importantly, systems with low fitness differences may face larger perturbations. For instance, species can coexist in case E but can be less resistant to perturbations compared with case D, given that the position of the vector of species' fitness is close to the exclusion region.

obtain information of demographic parameters as well as species interaction coefficients within and between trophic levels. However, it is not so obvious how this information can be obtained and related to theory. We can start learning from the ability of recent advances in niche theory to couple theory with field and lab experiments [42,57–60].

These studies suggest that the most rigorous way to proceed would be to conduct experiments in order to parameterize and validate a system of equations containing a model of population dynamics for each trophic level. Technically, this parameterization is easier to obtain when the

life-span between organisms is similar. In particular, population models describing **species dynamics** with an annual life cycle seem among the best approximations to choose for several reasons. They define the network structure and species fitness in the exact same way as the original definition using the Lotka-Volterra framework [25,43], yet they are complex enough to include nonlinear mechanisms of species coexistence such as the storage effect, and saturating functional responses to competitive, mutualistic, and antagonistic interactions (Box 3). They can also take into account the effect of environmental variation in space and time on modifying diversity maintenance due to changes in intransitive competition [59], intraspecific trait variation [61], or phenotypic plasticity [62]. Moreover, annual species are relatively easy to manipulate, models describing population dynamics have been successfully used for plants [43,57], and can be extended to other annual organisms including pollinators (e.g., wild bees), herbivores (e.g., snails, grasshoppers), or pathogens (e.g., fungal seed pathogens).

An alternative to experiments is the use of observational data (e.g., [63,64]). Observational approaches are justified when organisms differ in their life-span, or when their manipulation is not feasible for technical or conservation issues. The traditional limitation of observational studies is that the structure of species interactions between trophic levels is often easier to describe, at least at the species level, than the structure of species interactions within trophic levels. This limitation can be solved by using mathematical models fed with spatially explicit and/or temporal series data. These methodologies allow inferring species demographic parameters and species interactions from changes in species fitness due to both natural variations in the community density and species relative abundances [65,66]. For example, recent work [64] combined statistical models for survival, growth, and recruitment with individual-based models to describe temporal patterns in plant species co-occurrences. These model-generated population abundances were then integrated into projection models to estimate the structure of competitive interactions within plant species.

Regardless of the approach selected, we stress the urgency of linking theory and empirical work. We are at the dawn of understanding whether species characteristics, commonly reported in the niche and network literature, are more strongly related to differences in species demography or to the strength and sign of species interactions [50,67,68]. Moreover, we are not aware of a single study that has attempted to empirically estimate in a quantitative way the matrix of species interactions within and between trophic levels simultaneously. We believe that taking such an approach is crucial for answering an outstanding research question that emerges with the integration of both theories, namely, how species interactions between trophic levels drive niche and fitness regions within trophic levels and vice versa. Therefore, this is the topic of our next section.

How Do Species Interactions Between Trophic Levels Drive Niche and Fitness Differences Within Trophic Levels?

By coupling recent conceptual advances of niche and network theory, we are ready to understand how the species differences that determine coexistence within trophic levels (niche and fitness differences) **feedback** with the structure of species interactions that determine coexistence between trophic levels and vice versa. To illustrate these ideas, let us consider a mutualistic plant–pollinator system (see graphical example in Figure 2). What we have learned from prior work is that differences in feeding behavior, body mass, or insect phenology can contribute to the niche differences that tend to stabilize coexistence between plants (see Table 1) [69,70]. However, pollinators also contribute to the fitness differences promoting plant competitive dominance. For instance, changes in the abundance of pollinators can, in turn, modify the competitive hierarchy of a plant guild by increasing the number and the quality of seeds produced by pollinator-dependent

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Box 3. An Example of How To Integrate Niche and Network Theories with Experimental and Observational Data

Our approach to evaluate how between-trophic interactions drive niche and fitness differences within trophic levels and vice versa involves three steps.

Step 1: Depart from a relatively simple system of equations. Here it is composed of two annual population models describing changes in population size with time in plants (seeds, $P_{i,t+1}$) and pollinators (eggs, $A_{i,t+1}$). Both models are mirror images including an equal number of parameters with the same biological meaning,

$$\begin{cases} P_{i,t+1} = P_{i,t}\left((1-g_i)s_i + \dfrac{\lambda_i g_i(1+\sum_k \gamma_{ik}A_{k,t})}{1+\sum_j \alpha_{ij}g_jP_{j,t}}\right) \\ A_{i,t+1} = A_{i,t}\left((1-e_i)t_i + \dfrac{\nu_i e_i(1+\sum_k \delta_{ik}P_{k,t})}{1+\sum_j \theta_{ij}e_jA_{j,t}}\right) \end{cases}, \quad [I]$$

where each model is the summation of two components. The first component describes the possibility of a storage effect process, and the second component describes per capita fecundity. Specifically, this second component describes how mutualisms enhance the species intrinsic ability to produce offspring, reduced by the competitive effects exerted by other species within the same guild.

Step 2: Estimates species vital rates. Estimate per capita growth rate in the absence of species interaction [plants ($\boldsymbol{\lambda}$), pollinators ($\boldsymbol{\nu}$)], is best described as the intercept of the statistical models built for Step 3 (see below). Additional efforts are needed to estimate rates of seed germination ($\boldsymbol{g}$) or larva survival ($\boldsymbol{e}$), and the storage effect as the survival of the species' life stages that do not produce offspring within a year [e.g., soil seed bank in plants ($\boldsymbol{s}$) and nonreproductive adult mortality in some pollinators ($\boldsymbol{t}$)].

Step 3: Estimate species interaction matrix. To estimate species intra- and interspecific competitive interactions within trophic levels [plants ($\boldsymbol{\alpha}$), pollinators ($\boldsymbol{\theta}$)], the best approach is to fit a series of statistical models describing for each species its per capita growth rate as a function of competitor's relative abundance. For mutualistic interactions [pollinator's effect on plants ($\boldsymbol{\gamma}$), plants' effect on pollinators ($\boldsymbol{\delta}$)], do the same but describe species' per capita growth rate as a function of the mutualistic relative abundances (Figure I).

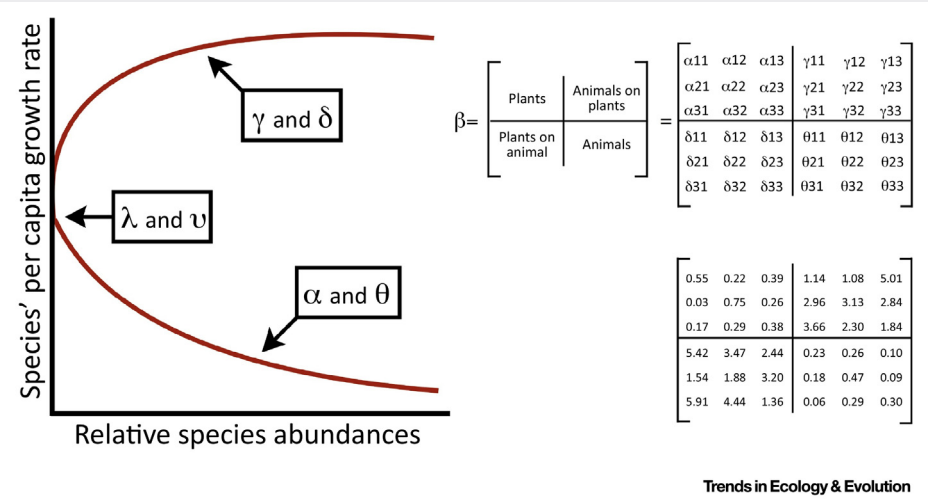

Figure I. Competitive relationship between species including itself are expected to take a negative exponential form [59,66], whereas mutualistic relationship are expected to be functionally saturating best described by non-inflicted curves [100]. With this information is possible to then build the β matrix summarizing species interactions across trophic levels.

plants. Differentiating between these alternatives is crucial because if pollinators primarily drive niche differences over fitness differences between plant competitors, then we can expect a more diverse plant community (e.g., [11,70]). A completely different outcome would occur if pollinators primarily drive fitness differences among plants. In that case, a dominant plant species favored by pollinators can dominate the community.

Similarly, considering pollinators beyond being a resource for plants implies that we have to assess simultaneously their population dynamics. For instance, plant characteristics such as floral morphology or plant phenological timing can contribute to the different pollinator requirements (i.e., niche differences) that stabilize their coexistence. But some plant species can also contribute to the dominance of a few pollinators (i.e., fitness differences) if those can particularly benefit from them, as occurs with pollinator specialists. All in all, this could lead us to rethink whether mutualistic interactions between trophic levels always increase the likelihood of species coexistence. Traditionally, mutualisms have been considered a positive interaction that enhance coexistence because the individuals involved obtain a certain benefit that can be translated to their population growth rates (but see [16] in a general context). However, to what extent these beneficial effects between particular species across trophic levels can reduce the likelihood of species coexistence in the entire system (i.e., within and among trophic levels) is not known yet (Figure 2).

Note that we need to use a geometrical rather than an algebraic approach to study fitness and niche differences for more than two species (see Figure I in Box 2). This approach informs us whether species coexistence is possible when the fitness differences between species fall within the **feasibility domain** (Figure 2). Moreover, this approach allows us to quantify how environmental variation modulates the extent of the feasibility domain and the differences in fitness between species. Estimating these environmentally dependent relationships is important as they determine how strongly an ecological community can be perturbed without pushing species towards extinction. As a rule of thumb, the closer the fitness differences to the edge of the feasibility domain, the lower the ability of the community to face perturbations (Figure 2) [71]. It is also important to note that this approach can be applied to other network types, such as food webs, parasitoid webs [24,72], and multi-trophic networks combining antagonistic and mutualistic interactions [56,73].

Answering this question using empirical approaches involves three steps (Box 3). First, we need a framework for describing species population dynamics as a function of species demographic parameters and species interactions within and between trophic levels. For example, for a plant–pollinator system, this framework can be a system of two annual population models (one for each trophic level) that can include a storage effect component if desired (Box 3). Second, in order to parameterize the models, we need information on species demography. For species, demographic parameters such as **per capita growth rate** in the absence of competition, germination rate, or larval survival, can be inferred relatively easily from experimental or observational data [43,57,64,66]. Third, we need to estimate the matrix $\boldsymbol{\beta}$ that summarizes species interactions across trophic levels.

This third step is by far the most challenging aspect as the number of parameters that need to be estimated grows exponentially with the number of species in the community. In principle, these estimates can be obtained from statistical models fitting empirical or observational data [27,59,74]. For intra- and interspecific competitive coefficients within plants and within pollinators, these parameters can be obtained by describing how species per capita growth rates depend on each competitor's relative abundance [50,59] (see Figure I in Box 3). For the case of

mutualistic effects of plants on pollinators and vice versa, the procedure is similar to the one previously described, but this time per capita growth rates should be described as a function of the relative abundance of each mutualistic species. In the likely case that this option is not feasible, one possibility is to group species by functional groups, and estimate interaction coefficients (at that resolution) via changes in population size of both trophic levels through time [75]. While the functional group approach assumes uniformity of responses within functional groups, it might be a requirement when scaling up to higher dimensions. Another possibility is to use novel techniques that combine ecological, phylogenetic, and geographic information to predict forbidden links and define a realized rather than a potential matrix of species interactions for large communities [76]. This latter possibility infers the strength of species interaction (e.g., competition, mutualism, etc.) without the necessity of measuring fitness directly. In sum, obtaining information for estimating the matrix $\boldsymbol{\beta}$ is challenging, but there are techniques available to solve that limitation [75–77].

This three-step approach can also be combined with variation in species' functional traits, phylogenetic relatedness, or intraspecific variation to test a myriad of ecological questions regarding the functional and phylogenetic assembly of communities (e.g. limiting similarity hypothesis, Darwin's naturalization hypothesis) [4,78]. Moreover, measuring emergent properties of the community, such as biomass or food production, would allow linking the mechanisms of biodiversity maintenance to ecosystem functioning (e.g. biodiversity insurance hypothesis, biodiversity-complementarity hypothesis) [79,80]. For instance, experimental assemblages varying plant and flower morphology and pollinators' body size can allow testing the role of species traits in providing higher food production yields [81] by the effects of plant and animal traits on niche and fitness differences (see [82] for details).

Concluding Remarks

The integration of niche and network theories provides a natural pathway to obtain a deeper understanding of the role of species interactions in modulating species coexistence. Here, we show that this integration is straightforward thanks to the strong parallelism of ecological concepts, complementary approaches, and associated mathematical tools found across these two research areas. The emergent property of this integration is the consideration that diversity within ecological communities is maintained when species interactions create a coexistence space that accommodates the differences in fitness between species. Importantly, we have provided a methodological framework readily available to investigate how the strength of mutualistic, antagonistic, and competitive interactions across trophic levels promote species coexistence in multi-trophic networks and variable environments. The key limitation we face now is the empirical parameterization of the interaction matrix, which summarizes the structure of species interactions across trophic levels. It should be no surprise that applying the integration of niche and network theory to experimental and observational approaches can be challenging, but we have provided a guideline to accomplish this aim. While this is not an easy task, the benefits can be unlimited.

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Outstanding Questions

Are species interactions between trophic levels more related to the stabilizing niche differences that promote species coexistence or to the average fitness differences that promote competitive exclusion?

How do network structure and species intrinsic properties interact with environmental variation in space and time to determine species coexistence?

Do species coexist because their interactions create large feasibility domains that accommodate a wide range of fitness differences?

Or in contrast, do species coexist because their interactions create small opportunities for coexistence but species barely differ in their fitness?

How does the feasibility domain change with the spatial scale?

How does the feasibility domain change as we include a wider range of species interactions?

How can we combine field and observational experiments to properly measure the matrix of species interactions within and between trophic levels?

Can the theoretical integration of niche and network theories inform a new set of experiments centered on testing hypotheses of community assembly and functioning?

What is the relative contribution of the mechanisms stabilizing species coexistence within and between trophic levels to the functioning of ecosystems?

How do global change drivers and their associated perturbations modify species interactions and the realized fitness of species?

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Supplemental Information

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