LETTER

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Trophic tug-of-war: Coexistence mechanisms within and across trophic levels

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Abstract

Ecological communities encompass rich diversity across multiple trophic levels. While modern coexistence theory has been widely applied to understand community assembly, its traditional formalism only allows assembly within a single trophic level. Here, using an expanded definition of niche and fitness differences applicable to multitrophic communities, we study how diversity within and across trophic levels affects species coexistence. If each trophic level is analysed separately, both lower- and higher trophic levels are governed by the same coexistence mechanisms. In contrast, if the multitrophic community is analysed as a whole, different trophic levels are governed by different coexistence mechanisms: coexistence at lower trophic levels is predominantly limited by fitness differences, whereas coexistence at higher trophic levels is predominantly limited by niche differences. This dichotomy in coexistence mechanisms is supported by theoretical derivations, simulations of phenomenological and trait-based models, and a case study of a primeval forest ecosystem. Our work provides a general and testable prediction of coexistence mechanism operating in multitrophic communities.

KEYWORDS

community assembly, fitness difference, food web, multitrophic, niche difference, predation

INTRODUCTION

A fundamental characteristic of ecological complexity is that species interact within and across trophic levels (Beckage et al., 2011; Godoy et al., 2018). The pattern of these trophic interactions is known as *multitrophic structure*. As they dictate energy flow and nutrient cycling in an ecosystem, multitrophic structures are fundamental in shaping the patterns of *community assembly*—the construction and maintenance of local communities with addition of new species (Fukami, 2015; Song et al., 2021). Indeed, the importance of multitrophic structure has been demonstrated with mounting empirical evidence across a wide range of life forms (Bartomeus et al., 2021; Drake, 1991; Olito & Fukami, 2009; Price & Morin, 2004; Pringle et al., 2019; Song, Altermatt, et al., 2018). Thus,

understanding how these multitrophic structures regulate community assembly is a central question in community ecology, with direct implications for conservation and restoration of natural ecosystems (Eisenhauer et al., 2019; Gossner et al., 2016; Wratten et al., 2000).

Yet, our current understanding of community assembly has been mostly shaped by (often implicit) separation of trophic levels (Figure 1; Seibold et al., 2018). To understand community assembly, the most frequent approach focuses on how a new invading species affects its competitors in the same trophic level (Chase & Leibold, 2003; Letten et al., 2017; Shoemaker et al., 2020). We denote this *traditional focus* (Figure 1). In contrast, another approach focuses on how this invader affects other species on the higher trophic level, or more generally an adjacent trophic level (Petry

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Chuliang Song and Jurg W. Spaak contributed equally to this work.

Community focus
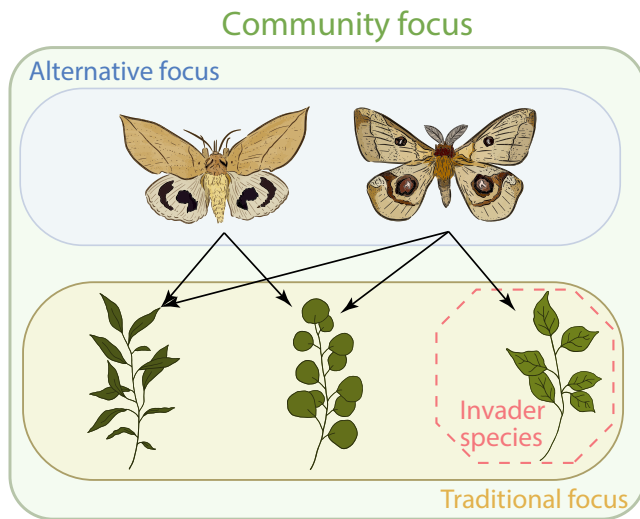
FIGURE 1 Different perspectives on multitrophic assembly. We consider a hypothetical, two-trophic community with 3 lower trophic species and 2 higher trophic species. Traditionally, we study the impact of an invader or increased species richness on the invaded trophic level (Traditional focus). This effect is usually negative due to heightened competition for resources or predator pressure. Alternatively, we may be interested in how an invader affects an adjacent trophic level (Alternative focus). However, it is yet unclear if the impact of invaders on the entire community (Community focus) can change our understanding of the assembly processes. The clip-arts are obtained from Adobe Stock.

et al., 2018; Terry et al., 2021). We denote this *alternative focus* (Figure 1). However, such separation of trophic levels is not always justified because understanding each trophic level alone might not be sufficient to understand the entire community (Godoy et al., 2018; Levine et al., 2017; Spaak, Godoy, & De Laender, 2021). The inclusion of multiple trophic levels strongly affects our view of community assembly. For example, if an invading species excludes another species from the same or different trophic level, this exclusion can further affect species throughout the entire network, known as *trophic cascade* (Brodie et al., 2014; Ripple et al., 2016). In addition, many ecological properties can only be studied for the community as a whole, such as link-species relationships (Carpentier et al., 2021), distribution of biomass across trophic levels (Galiana et al., 2021), or average food-chain length (Post, 2002). Thus, the focus on the multitrophic community as a whole is the most relevant scale for many ecological questions (Figure 1).

Despite an emergent line of theoretical frameworks on multitrophic structures (Barabás et al., 2014; Koffel et al., 2021; McPeek, 2022; Song, Rohr, & Saavedra, 2018; Wang & Brose, 2018), modern coexistence theory—a key theoretical framework widely adopted by empiricists—has been an exception (Barabás et al., 2018). The overarching aim of modern coexistence theory is to understand coexistence by decomposing it into two classes of *coexistence mechanisms* (Chesson, 2000; Song et al., 2019):

stabilizing mechanisms (increasing species' niche differences) and equalizing mechanisms (reducing species' fitness differences). The majority of empirical studies using modern coexistence theory have primarily focused on a single trophic level with competition (reviewed in Barabás et al., 2018 and Buche et al., 2022). This problem is partly because of the limitations in the theoretical framework: niche and fitness differences were not well-defined for multitrophic systems until recently (Spaak, Ke, et al., 2023). Specifically, in the canonical formalism of modern coexistence theory, niche differences measure the overlap in resource use between two competitors, while fitness differences measure the difference in total resource consumption as well as differences in mortality (Chesson, 1990; Chesson & Kuang, 2008). These definitions are restricted to competitive two-species communities (Spaak, Ke, et al., 2023). To address this limitation, Spaak and De Laender (2020) laid the theoretical foundation to extend the concepts of niche and fitness differences to facilitative interactions and multi-species communities. This was further expanded to multitrophic communities by Spaak, Godoy, and De Laender (2021). In these extended definitions, niche differences measure how similar the interspecific interactions are to the intraspecific interactions, while fitness differences measure how well a species would perform if all other species occupied exactly the same niche as the focal species (i.e., in the absence of niche differences). Box 1 traces the historical evolution of these definitions. These new measures of niche and fitness differences serve as a common currency to compare the direction and strength of coexistence mechanisms across different trophic levels.

Despite these theoretical advancements, these works did not specifically aim for a general understanding of the expected behaviour of niche and fitness differences in multitrophic assembly. We establish, for the first time, a null expectation of how multitrophic structures modulate ecological assembly within and across trophic levels in modern coexistence theory. We specifically investigate how community composition affects species coexistence and whether the coexistence mechanisms (stabilizing or equalizing) vary across different trophic levels. To answer these questions, we analyse different groupings of the same community: the subcommunity with species at the same level only (traditional focus), the subcommunity with species at an adjacent trophic level only (alternative focus), and the whole multitrophic community at once (community focus). By calculating and comparing the ranges of niche and fitness differences within each trophic level across these groupings, we aim to identify the primary drivers of diversity within trophic levels and whether they differ across trophic levels. For example, if niche differences of the lower trophic species fall within a narrow range, then the niche difference is not a primary constraint for coexistence, and vice versa, as niche differences explain only a small part of the variation in

BOX 1   A brief summary of modern coexistence theory for multitrophic communities.

The Competitive Exclusion Principle, as proposed by Gause, asserts that two species occupying the same niche cannot coexist (Gause, 1932; Hardin, 1960). However, many species are observed to coexist even when they appear to occupy very similar niches within restricted niche spaces (Hutchinson, 1959). The root of the apparent contradiction is that the precise definition and measurable characteristics of a 'niche' remain ambiguous (Godsoe, 2010; Pocheville, 2015; Sales et al., 2021; Vandermeer, 1972).

To address this fundamental challenge, modern coexistence theory does not attempt to directly measure the niche of a species. Instead, it emphasizes the degree to which the niches of two species differ, termed as the *niche difference*. In its original design, it only applied to two species competing for shared resources (Chesson, 1990) or to shared predators (Chesson & Kuang, 2008). As the overlap between resources or "predators" ranges from 0 to 1, niche difference also ranges from 0 to 1. In a similar spirit, *fitness differences* describes the proportionate consumption of resources by one species in relation to another. Over time, due to their intuitive nature and wide applicability, the concepts of niche and fitness differences are only interpreted *phenomenologically* and thus detached from their initial ties to resource competition (Carroll et al., 2011; Godoy & Levine, 2014).

In empirical research, ecologists stumbled upon natural communities where the original formulations of these concepts were inapplicable. For instance, negative niche differences or facilitation renders the computation of niche differences impossible. As a result, these communities were typically excluded from analysis (Germain et al., 2016; Godoy & Levine, 2014; Narwani et al., 2013). This theoretical limitation greatly reduced the applicability of modern coexistence theory in empirical studies. To address this gap, recent theoretical developments have reinterpreted negative niche differences as stronger interspecific than intraspecific competition (Ke & Letten, 2018) and facilitation as niche differences exceeding 1 (Spaak & De Laender, 2020). Consequently, niche differences ceased to be tied to specific niche dimensions (e.g., nitrogen availability, water usage, or root depth). Building upon that, recent theoretical work has developed a more abstract construct of niche difference, firmly grounded in mathematical rigour, to quantify the deviation of a focal species' niche from that of its competitors (Spaak & De Laender, 2020; Spaak, Godoy, & De Laender, 2021). These new theoretical advances are natural generalizations of the original formulations, as they produce identical results when applied to two species competing for resources. Yet, when applied to more complex communities, they can lead to new insight. For example, Spaak, Millet, et al. (2023) derived a null expectation for the effect of species richness, Spaak, Adler, and Ellner (2023a) and Spaak, Millet, et al. (2023) applied these methods to trait-based phytoplankton and zooplankton models with non-linear species interactions.

These new formulations allow us to understand how much niches differ, without the imperative to precisely define the niche or its specific dimensions. This is especially important given our current lack of understanding regarding the exact nature of relevant niche dimensions. It is unclear whether biodiversity in nature is driven by resource competition (Tilman, 1982), predator–prey interactions (Connell, 1971; Janzen, 1970), environmental fluctuations (Chesson, 1994), or even by stochasticity (Hubbell, 2001). For example, the limiting factor for the persistence of a predator might not be the strong resource overlap with another predator, but simply the low availability of its prey, which might be driven by competition at a lower trophic level.

While we have a mathematical framework for modern coexistence theory in multi-trophic communities (Spaak, Godoy, & De Laender, 2021), there remains a core challenge in its ecological interpretation. Predators and prey inhabit distinct niches, potentially spanning different niche dimensions. It is pertinent to question what niche and fitness differences truly represent in a multi-trophic community. For any focal species, the definition of niche difference compares the actual growth rate of the species to two hypothetical ones. These hypothetical rates are computed under the scenarios when all other species *on the same trophic level* as the focal species have either *no* or *complete* niche overlap with the focal species. Therefore, we do not compare the niche of a prey with that of a predator. Instead, we study how the niche of one predator differs from the niche space occupied by the rest of the community, i.e., the niche of a predator is compared to the niche of other predators while the niche of a prey is compared to the niche of other preys. Fitness differences are compared in the same vein. In sum, we sidestep comparisons of niche or fitness differences across trophic levels, and strictly restricted the comparison of niche differences among species in the same trophic level. With this nuanced interpretation, we build, for the first time, a null expectation for how trophic composition affects niche and fitness differences.

invasion growth rates, a measure of strength of persistence (Buche et al., 2022). Our findings reveal that while coexistence mechanisms are consistent for species within a trophic level (traditional and alternative focuses), a different pattern emerges when considering the whole community (community focus). Specifically, the diversity of lower trophic species is constrained by fitness differences, whereas the diversity of higher trophic species is constrained by niche differences. These findings are consistent in theoretical derivations, computer simulations, and empirically parameterized models. Our work provides testable theoretical expectations of coexistence mechanisms within and across trophic levels.

METHODS

Population dynamics of multitrophic communities

We consider communities with two trophic levels in the main text (see Appendix S4 for three trophic levels). We assume a Lotka-Volterra model,

$$
\frac{1}{N_i^{(1)}} \frac{dN_i^{(1)}}{dt} = \mu_i^{(1)} - \underbrace{\sum_j A_{ij}^{(11)} N_j^{(1)}}_{\substack{\text{Within-}\\\text{trophic}}} - \underbrace{\sum_k A_{ik}^{(12)} N_k^{(2)}}_{\substack{\text{Between-}\\\text{trophic}}},
$$

$$\text{(1)}$$

$$
\frac{1}{N_l^{(2)}} \frac{dN_l^{(2)}}{dt} = \underbrace{\mu_l^{(2)}}_{\substack{\text{intrinsic}\\\text{growth rate}}} - \underbrace{\sum_j A_{lj}^{(21)} N_j^{(1)}}_{\substack{\text{Between-}\\\text{trophic}}} - \underbrace{\sum_k A_{lk}^{(22)} N_k^{(2)}}_{\substack{\text{Within-}\\\text{trophic}}},
$$

$$\text{(2)}$$

where the superscripts (1) and (2) refer to the trophic level, the subscript i and j refer to the lower trophic species, while k and l refer to the higher trophic species. $N_i^{(1)}$ is the density of species i in the lower trophic level, $N_l^{(2)}$ is the density of species l from the higher trophic level, $\mu_i^{(1)}$ and $\mu_l^{(2)}$ denote the intrinsic growth rates in the lower- and intrinsic mortality rates in the higher trophic species. Similarly, $A^{(11)}$, $A^{(12)}$, $A^{(21)}$ and $A^{(22)}$ denote the interaction matrices between and within the respective trophic levels. $A^{(11)}$ and $A^{(22)}$ capture all interactions with other, not explicitly mentioned, trophic levels, e.g. resources (MacArthur, 1970), higher trophic levels (Chesson & Kuang, 2008) and generally all within-trophic interactions such as competition for space (Shoemaker et al., 2020), breeding opportunities, and other direct species interactions (Kawatsu et al., 2021). The results

from the Lotka-Volterra model can be translated to the Jacobian matrix approach (Allesina & Tang, 2012; May, 1972; Song & Saavedra, 2018b) or the more general non-parametric approach (Medeiros et al., 2023; Munch et al., 2023) under certain assumptions (Song & Saavedra, 2021).

Definition of niche and fitness differences

Niche and fitness differences measure how robust coexistence is (Box 1). Within the framework of modern coexistence theory, coexistence is commonly defined through the invasion criterion (Grainger et al., 2019), which states that if all species increase in abundance when they are rare, then species coexist. However, the invasion criteria do not always guarantee coexistence in multispecies communities (Barabás et al., 2018; Hofbauer & Schreiber, 2022; Pande et al., 2020). Thus, in addition to the invasion criterion, here we require stable coexistence to satisfy feasibility (i.e., equilibrium abundance of all species is positive) and dynamical stability (i.e., community returns to equilibrium after a small perturbation). In all of our analyses (theory, simulation, and empirically parameterized models), we have checked that the analysed communities satisfy both criteria of coexistence.

Niche and fitness differences have multiple definitions under the umbrella of modern coexistence theory (Adler et al., 2007; Bimler et al., 2018; Carmel et al., 2017; Carroll et al., 2011; Chesson, 2003; Godoy et al., 2014; Saavedra et al., 2017; Spaak & De Laender, 2020; Zhao et al., 2016) for a review see Spaak, Ke, et al. (2023). Here, we adopt the definition proposed by Spaak and De Laender (2020) with adjustments made by Spaak, Godoy, and De Laender (2021). This definition is currently the only one that can operate on multi-species and multitrophic communities and agrees with an intuitive understanding of facilitation or competition (Spaak, Ke, et al., 2023). While this definition is more general, we limit our focus to the Lotka-Volterra community model. As we focus on different groupings of the same community, we describe the computation of niche and fitness differences based on a Lotka-Volterra community model given by $\frac{1}{X_i} \frac{dX_i}{dt} = M_i - B_{ij} X_j$, where X_i denotes the species density, B is the interaction matrix, and M_i is the intrinsic growth rate. Depending on the current focal community, the interaction matrix B is given by $B = A^{(11)} - A^{(12)} \left(A^{(22)} \right)^{-1} A^{(21)}$ if the lower trophic level is considered, $B = A^{(22)} + A^{(21)} \left(A^{(11)} \right)^{-1} A^{(12)}$ if the higher trophic level is considered and $B = \begin{pmatrix} A^{(11)} & A^{(12)} \\ A^{(21)} & A^{(22)} \end{pmatrix}$ if the entire community is considered (Appendix S2).

The computation of niche and fitness differences is based on *invasion growth rates*—the species i growth rate while invading the resident community at equilibrium. We denote the equilibrium $X^{(-i,*)} = \left(B^{-i,-i} \right)^{-1} M^{-i}$, where $B^{-i,-i}$ and M^{-i} are the interaction matrix and intrinsic

growth rates with row and/or column i removed. With this notation the invasion growth rate r_i is given by $M_i - \sum_j B_{ij} X_j^{(-i,*)}$. To normalize niche and fitness differences, the invasion growth rate r_i is compared to two hypothetical invasion growth rates. The first one is the intrinsic growth rate M_i, which is the invasion growth rate if species i did not interact with other species (i.e., $B_{ij} = 0$ for all j). The second one is the no-niche growth rate η_i, which is the hypothetical invasion growth rate of species i if all other species occupied the same niche as species i, consequentially, they would also have the same trophic level. However, changing B_{ij} to B_{ii} does not only change the niche of species j, but also the fitness of species j (Chu & Adler, 2015). The no-niche growth rate η_i is therefore the growth rate if we set $B_{ij} = c_{ij} B_{ii}$, where $c_{ij} = \sqrt{\frac{B_{ij} B_{ii}}{B_{ii} B_{ji}}}$ is the conversion factor converting species i to species j (see Spaak & De Laender, 2021 for a detailed derivation).

Given these three invasion growth rates (μ_i, r_i and η_i), the niche difference $\mathcal{N}_i$ and fitness difference $\mathcal{F}_i$ are:

$$\mathcal{N}_i = \frac{\overbrace{r_i}^{\substack{\text{Invasion} \\ \text{growthrate}}} - \overbrace{\eta_i}^{\substack{\text{No-niche} \\ \text{growthrate}}}}{\underbrace{M_i}_{\substack{\text{Invasion} \\ \text{growthrate}}} - \eta_i}; \mathcal{F}_i = -\frac{\eta_i}{M_i - \eta_i}. \tag{3}$$

This definition is ecologically intuitive, as it maps three cases: Focusing on niche difference, $\mathcal{N}_i > 1$ implies that species i interspecific and intraspecific interactions differ in sign, i.e. benefits from the presence of other species (i.e. $M_i < r_i$; Spaak & De Laender, 2020), while $\mathcal{N}_i < 0$ implies that interspecific interactions are stronger (negative) than intraspecific interactions (i.e., $\eta_i > r_i$; Ke & Letten, 2018). Then focusing on fitness difference, $\mathcal{F}_i > 1$ implies that species depend on other species such as predation interactions (i.e., $M_i < 0$; Spaak, Godoy, & De Laender, 2021), while $\mathcal{F}_i < 1$ implies that a species can grow in the absence of other species (i.e., $M_i > 0$; Spaak, Godoy, & De Laender, 2021). Finally, a species has a positive invasion growth rate if its niche difference overcomes its fitness difference (i.e. $\mathcal{N}_i > \mathcal{F}_i$; Adler et al., 2007; Chesson, 2000) and without intra-specific facilitation (i.e., $M_i > \eta_i$; Spaak, Godoy, & De Laender, 2021). A conceptual diagram mapping these cases can be found in Spaak, Godoy, and De Laender (2021).

Importantly, niche or fitness differences are only comparable among species within the same trophic level, rather than across different levels. In all of our analyses, we have strictly restricted the comparison of niche or fitness differences among species in the same trophic level. Box 1 provides an in-depth explanation of this nuanced but fundamental issue.

Formalizing different perspectives on multitrophic assembly

We compute niche and fitness differences for different groupings of the same community: The traditional focus considers the trophic level in which a new species invades, the alternative focus looks at the adjacent trophic level, and the community focus examines all trophic levels simultaneously.

For the community focus, we can directly compute niche and fitness differences (Equation 3) of the community model (Equations 1 and 2). However, for the traditional and alternative focuses, we treat species of adjacent trophic levels as limiting factors, which are a generalization of resources (Chesson & Kuang, 2008; MacArthur, 1970). As niche and fitness differences are calculated from three growth rates evaluated at steady states, we solve these equations by setting the growth rates of the species in adjacent trophic levels to 0. This approach is mathematically equivalent to using times-scale separation from the MacArthur resource model (MacArthur, 1970; O'Dwyer, 2018). A key ecological difference, though, is that we do not assume that different trophic levels have different intrinsic time scales of ecological processes, rather we only compute growth rates after a steady state is reached.

To compute niche and fitness differences for only the lower trophic level (traditional focus), we apply the methods of niche and fitness differences to the effective Lotka-Volterra dynamics (Appendix S2, Equation S13):

$$\frac{1}{N^{(1)}} \frac{dN^{(1)}}{dt} = \underbrace{\left(\mu^{(1)} - A^{(12)} \left(A^{(22)} \right)^{-1} \mu^{(2)} \right)}_{\text{Effective intrinsic growth } \mu} - \underbrace{\left(A^{(11)} + A^{(12)} \left(A^{(22)} \right)^{-1} A^{(21)} \right)}_{\text{Effective interaction } B} N^{(1)} \tag{4}$$

where $A^{(12)}$, $A^{(22)}$, $A^{(21)}$ and $A^{(11)}$ are the interaction matrices between the corresponding trophic levels, $\mu^{(1)}$ and $\mu^{(2)}$ are the vectors of intrinsic growth rates for the lower and higher trophic level, and $N^{(1)}$ is the vector of densities of higher trophic species (see Appendix S2 for higher trophic level).

Theoretical predictions of how community assembly affects coexistence

For tractability of the theoretical derivations, we operate under the most simplifying assumption that the strength of all inter-specific interactions is identical (i.e., $A_{ij}^{(11)} = A_{ik}^{(12)} = A_{lj}^{(21)} = A_{lk}^{(22)} = a$ for $i \neq j$ and $l \neq k$) and the strength of all intra-specific interactions are set to be 1 (i.e., $A_{ii}^{(11)} = A_{ll}^{(22)} = 1$). Similarly, we assumed that all intrinsic growth rates of basal species are identical (i.e., $\mu_i^{(1)} = \mu^{(1)}$) and that all mortality rates of species in the higher trophic level are identical (i.e. $\mu_l^{(2)} = \mu^{(2)}$). Given these assumptions, we then analytically compute niche and fitness differences for all three focuses. To

verify these analytical derivations, we perform simulations using the slightly weakened assumptions where all inter-specific interaction strengths are drawn from some independent and identical distribution (i.e., $A_{ij}^{(11)}$, $A_{ik}^{(12)}$, $A_{lj}^{(21)}$, $A_{lk}^{(22)} \sim \mathcal{N}(0.3, 0.1)$).

Robustness of assembly patterns

To test the generality of our analytic arguments, we relax these assumptions with two approaches, corresponding to high- and low-dimensional niche spaces. The first approach, high-dimensional niche space, is based on random matrix theory, which posits that interspecific interaction strengths are drawn from some random distribution. The ecological justification of this approach is that species interactions emerge from a high-dimensional space of ecological traits (Barbier et al., 2021). In this approach, we explore a range of scenarios through a factorial combination of parameters. This includes considering various types of random distributions (e.g., uniform and normal), different mean interaction strengths (e.g., $\mathbb{E}\left[A_{ij}^{(11)}\right] = 0.1, 0.3, \ldots$), the possibility of decreasing mean interaction strengths with increased species richness (e.g., $\mathbb{E}\left[A_{ij}^{(11)}\right] \sim 1/\sqrt{S}$), different variations in interaction strength (e.g., $Var\left[A_{ij}^{(11)}\right] = 0.01, 0.02, \ldots$), and variations in trophic efficiency (i.e., $\mathbb{E}\left[A_{ik}^{(12)}\right] = e\mathbb{E}\left[A_{lj}^{(21)}\right]$ with $e < 1$). These assumptions are standard practice in parameterizing the Lotka-Volterra model (Akjouj et al., 2022; Bunin, 2017; Gibbs et al., 2022; Serván et al., 2018; Song et al., 2021). Detailed descriptions of our parameterization methods are provided in Appendix S2.

The second approach, low-dimensional niche space, is based on a trait-based mechanistic model. In this approach, we focused on communities characterized by a single trait, such as body size, encompassing both lower and higher trophic species. Then interaction strengths between species are derived mechanistically from the MacArthur model (Macarthur & Levins, 1967). This approach provides complementary information from the random matrix approach. The details of this model are provided in Appendix S2.

Assembly in empirical food webs

Finally, we compared our theoretical and simulation results to a vertebrate food web of the Bialowieza forest in northeast Poland (Jedrzejewska & Jedrzejewski, 1998). Białowieża is the last old-growth temperate primeval forest in Europe, characterized by a continental climate with Atlantic influence. Predator diets are investigated within two main periods: winter (October–March) and summer (April–September). The food web data were collected between 1985 and 1996. The food webs in summer and winter share 17 predators and 72 preys. Full details

about the study area and the food web can be found in Jedrzejewska and Jedrzejewski (1998).

Previous modelling work on these vertebrate food webs (Saavedra et al., 2016; Sauve & Barraquand, 2020) has adopted a special form of Lotka-Volterra dynamics,

$$\frac{1}{N_i^{(1)}}\frac{dN_i^{(1)}}{dt} = \mu_i^{(1)} - A_{ii}^{(11)}N_i^{(1)} - \sum_l \frac{\gamma_{il}}{m_l}N_l^{(2)}, \tag{5}$$

$$\frac{1}{N_l^{(2)}}\frac{dN_i^{(2)}}{dt} = -\mu_l^{(2)} - A_{ll}^{(22)}N_l^{(2)} + e\sum_i \frac{\gamma_{il}}{m_l}N_i^{(1)}, \tag{6}$$

where e denotes the conversion efficiency, and the predation rate is modelled as the ratio of the discovery rate (γ_{il}) to the body mass of the predator (m_l).

Sauve and Barraquand (2020) parameterized this food web using the rich empirical knowledge of the community, which we briefly summarize. The conversion efficiency e is set to be 0.1. The intrinsic growth rate ($\mu_i^{(1)}$) is estimated based on the metabolic scaling law ($\mu_i^{(1)} \propto m_i^{-1/4}$ where m_i is the body mass of prey i) (Savage et al., 2004), and the proportionality constant is dependent on the taxonomic group. The intraspecific competition rate of the prey ($A_{ii}^{(11)}$) is estimated using observed carrying capacities ($A_{ii}^{(11)} = \frac{\mu_i^{(1)}}{N_i^{(1)*}}$, where $N_i^{(1)*}$ is the observed carrying capacity). The predation strength γ_{il} is estimated from the intake of prey species i by an individual predator l over an average year (Baudrot et al., 2016; Rooney et al., 2006). The baseline mortality rate ($\mu_l^{(2)}$) is estimated as the inverse of their maximum longevity ($\mu_l^{(2)} = \left(L_l^{(2)}\right)^{-1}$, where $L_l^{(2)}$ is the maximum longevity of species l) (de Magalhaes et al., 2005). The density-dependent mortality ($A_{ll}^{(22)}$) is estimated based on natural history observations that the year-round average of predator biomass densities is a fair proxy of the number of individuals that the Białowieża Forest can sustain under pristine conditions (Jedrzejewska & Jedrzejewski, 1998). The empirically parameterized dynamics have successfully reproduced a quantitative match to the observed patterns. Full details can be found in Sauve and Barraquand (2020).

We simulate community dynamics using the parameterized food webs. Species without a positive invasion growth rate, as well as those that were excluded, were removed from the analysis. This simplification was necessary because computing niche and fitness differences in such complex communities is challenging (Spaak & Schreiber, 2023a). Specifically, 4 out of 115 species were removed in the summer community, and 3 out of 93 were removed in the winter community. We then compute niche and fitness differences for the remaining species. By determining the range of these values within each trophic level, we could identify whether niche or fitness differences were the primary limiting factors for diversity within that level. For example, a narrow range of niche

differences among lower trophic species would suggest that niche difference is not a major constraint on their coexistence.

RESULTS

Theoretical predictions of how community assembly affects coexistence

Here we establish theoretical expectations on how community assembly affects its coexistence and what are the driving coexistence mechanisms, assuming all interspecific interactions are equally strong (see Appendix S1 for derivation). We first examine how assembly (addition of new species) in one trophic level affects coexistence within that same level (traditional focus in Figure 1). Higher species richness within a trophic level increases fitness differences among species (Figure 2d,j), but does not affect their niche differences (Figure 2a,g). This pattern holds across all trophic levels (Appendix S2) and generalizes the earlier findings by Spaak, Carpentier, and De Laender (2021) for multitrophic communities. A heuristic explanation is that fitness differences reflect the competitive strength of a focal species relative to its competitors, and increase with the number of competitors, while niche differences compare the niche of a focal species to the average niche of its competitors and are unaffected by species richness (Spaak, Carpentier, & De Laender, 2021).

We then examine how assembly in one trophic level affects the coexistence of the adjacent trophic level (alternative focus in Figure 1). Increasing species richness in a trophic level reduces niche differences (Figure 2b,h) and fitness differences (Figure 2e,k) of the adjacent trophic level. A heuristic explanation behind this pattern is that the effective interaction between species in the focal trophic level is a combination of actual inter-trophic interactions (i.e., $A^{(11)}$ for the lower trophic), and interactions stemming from (apparent) competition (i.e., $A^{(12)}(A^{(22)})^{-1}A^{(21)}$ for the lower trophic; Equation 4). Our parametrization assumes that species in the focal trophic level have on average identical interactions with all species from the adjacent trophic level, making the (apparent) competition term for these species independent of the species pair (i.e., $A^{(12)}(A^{(22)})^{-1}A^{(21)}$ is the same for all species and the same for inter- and intra-specific interactions). Moreover, increasing species richness in the adjacent level increases the strength of (apparent) competition, making it more species-independent and decreasing niche and fitness differences. More careful mathematical analysis shows that increasing species richness has a stronger effect on niche differences than on fitness differences; specifically, the rate of change of fitness differences is $(1 - 1/n_1)$ times that of niche differences (Appendix S1), where n_1 represents the number of species at the lower trophic level. Therefore, coexistence

becomes less likely, as niche differences decrease faster than fitness differences, i.e., the distance to the coexistence boundary, $\mathcal{N}_i - \mathcal{F}_i$ decreases. This difference is most pronounced when communities have few species.

Lastly, we analyse the community-level effects of assembly on coexistence by computing niche and fitness differences for all species in a community simultaneously (community focus in Figure 1). For lower trophic species, we find that increasing species richness, either of the higher or lower trophic level, does not affect niche differences of the lower trophic species (Figure 2c,i), but increases their fitness differences (Figure 2f,l and Appendix S4). Intuitively, niche differences are a weighted average of the pairwise niche differences that a species has with the other species (Spaak, Carpentier, & De Laender, 2021), which is not affected by species richness for lower trophic species. In contrast, fitness differences are the weighted sum of the pair-wise fitness differences (Spaak, Ke, et al., 2023), which increase with higher species richness as the sum has more terms.

Then focusing on higher trophic species, we find that increasing species richness decreases both niche (Figure 2c,i) and fitness differences (Figure 2f,l) of the higher trophic level. Intuitively, increasing species richness of the higher trophic level decreases the total biomass of the lower trophic level due to increased predation, but increases the total biomass of the higher trophic level due to overyielding known from biodiversity-ecosystem functioning relationship (Bannar-Martin et al., 2018; Loreau, 2004; Loreau & Hector, 2001). Therefore, increasing species richness in the higher trophic level decreases niche differences of the higher trophic level, as more interspecific interactions are competitive (low niche difference) and fewer interactions are predation (high niche differences). Interestingly, increasing the species richness at the lower trophic level also decreases niche differences at the higher trophic level. This is because the higher species richness of the lower trophic level increases the biomass of the lower trophic level due to overyielding, it even more strongly increases the total biomass of the higher trophic level due to predation. Therefore, a random interaction with another species is more likely to be competitive than to be a predator–prey interaction. The fitness differences are driven by total biomass, which increases with both increasing species richness of the lower and of the higher trophic level. However, for the higher trophic level, this implies a decrease in species richness, as fitness differences exceed 1.

We have seen that the higher and lower trophic levels behave similarly if analysed by the traditional and alternative focus. Conversely, the community focus reveals differences between trophic levels. Specifically, community composition affects fitness differences of the lower trophic level, but does not affect their niche differences. Conversely, increasing species richness
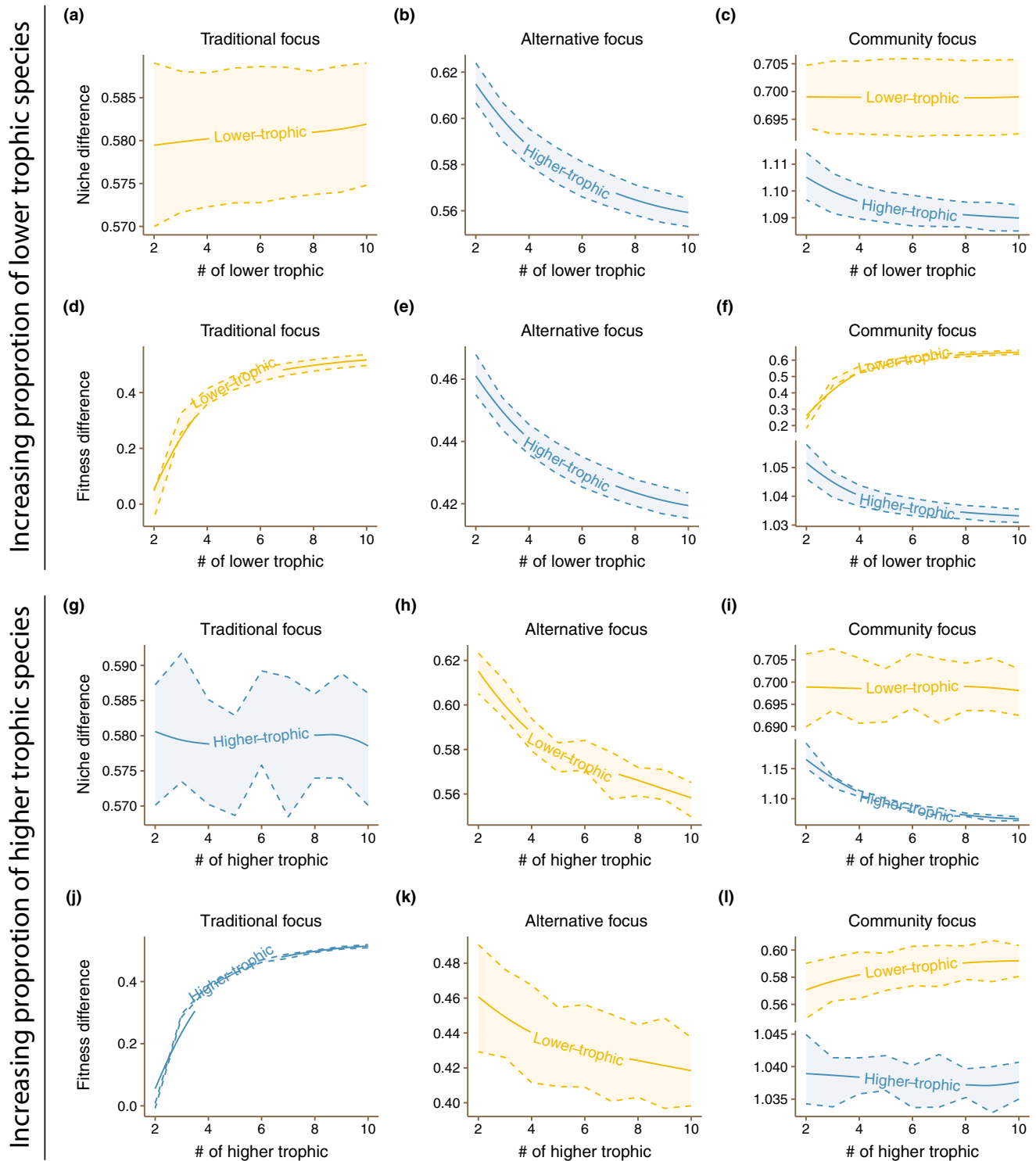
FIGURE 2 How species richness affects niche and fitness differences. The solid line represents the mean of niche and fitness differences across all species within the respective trophic level. The shaded region around the solid line denotes the 95% percentile range, indicating the variability in niche and fitness differences across species. The first two rows (a–f) show a change in lower trophic species richness, while the last two rows (g–l) show a change in higher trophic species richness. According to the traditional focus (the first column), increasing species richness does not affect niche differences (a and g), but increases fitness differences (d and j). According to the alternative focus (the second column), increasing species richness decreases both niche (b and h) and fitness differences (e and k), whereas the effect on niche differences is slightly stronger. Finally, according to the community focus (the third column), niche differences of the lower trophic species are not affected (c and i), while fitness differences of the lower trophic species increase (f and l). Both niche and fitness differences of the higher trophic species decrease with increasing species richness (c, f, i and l). Note that y-axes have drastically different ranges, indicating different magnitudes of the effects.

in the higher trophic level strongly affected niche differences of the higher trophic level (Figure 2f), while other changes in community composition had relatively small effects on niche and fitness differences of the higher trophic level (Figure 2c,i,l). These results prove that a holistic understanding of multi-trophic assembly can only be achieved via the community focus. Thus, we only focus on the community focus in the following sections.

Robustness of assembly patterns

Theory predicts that fitness differences govern coexistence in the lower trophic level, while niche differences govern coexistence in the higher trophic level. However, these results are based on some oversimplifying assumptions of the interaction strength. To substantiate the robustness of these patterns, we relaxed these assumptions with two additional approaches corresponding to higher realism. In the first approach, we assumed random species interactions corresponding to a high-dimensional niche space. In the second approach, we assumed that species interactions are governed by one underlying trait.

We quantify the ranges of niche or fitness differences among species during assembly (i.e., the range of values in the vertical axis in Figure 2). The ranges allow us to identify the key operating coexistence mechanism in multitrophic assembly. Specifically, a narrow range of niche or fitness variation in assembly indicates that it is not a limiting factor for species coexistence, and vice versa. As community focus is the most holistic view, we show the patterns for the community focus. Figure 3 (random interactions) and Figure S2 (trait-based interactions) both confirm that diversity at lower (respectively higher) trophic is primarily constrained by fitness (respectively niche) differences. Additional simulations with alternative assumptions also confirm the same result (Appendix S3). Collectively, these extensive analyses and consistent results reinforce the robustness of these coexistence patterns in multitrophic assembly.

Assembly in empirical food webs

Finally, we confront our predictions with empirically parameterized models. We compute the niche and fitness differences of each species during both the summer and winter seasons of the empirical data (Figure 4). All species of the lower trophic level have comparable niche differences, while fitness differences span a broad range. Conversely, all species of the higher trophic level have comparable fitness differences, but niche differences span a wider range. These trophic-specific patterns are observed across both seasons and align with our theoretical prediction (Figure 3): diversity at the

lower (respectively higher) trophic level is primarily constrained by fitness (respectively niche) differences.
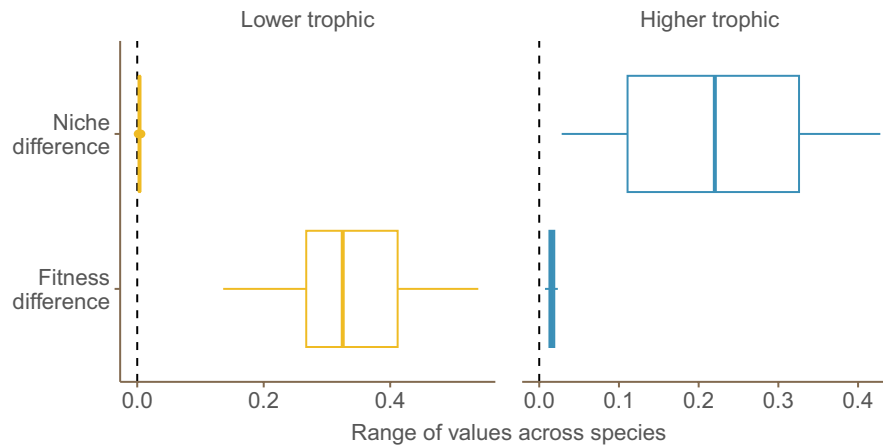
Additionally, niche differences of lower trophic species remain largely constant across seasons, while their fitness differences generally increase from summer to winter. Conversely, fitness differences of higher trophic species remain largely constant, while their niche differences generally increase from summer to winter (Appendix S5).

DISCUSSION

Our work has filled a gap in modern coexistence theory on the null expectation of multitrophic assembly. Specifically, we have studied how changes in species richness in one trophic level would affect the coexistence of other trophic levels or the community as a whole. We have established a baseline expectation of coexistence mechanisms in multitrophic assembly: diversity in lower level trophics is primarily constrained by fitness differences, while diversity in higher level trophics is primarily constrained by niche differences. This insight is based on theoretical derivations, computer simulations and empirically parameterized models.

Our findings show that increasing species richness within a trophic level makes coexistence less robust due to increased fitness differences and unaffected niche differences. Similarly, increasing species richness in an adjacent trophic level reduces coexistence because niche differences decrease more than fitness differences. This result is consistent with previous theoretical studies arguing that increasing species richness decreases coexistence (Allesina & Tang, 2015; Gardner & Ashby, 1970; May, 1972; Spaak, Carpentier, & De Laender, 2021). Notably, it differs from previous empirical findings that the inclusion of a higher trophic species only affects fitness differences of the lower trophic species, not their niche differences (Petry et al., 2018; Terry et al., 2021). This discrepancy may stem from the inclusion of more than one higher trophic species in our study, which is typical in natural communities, or the single-generation experiment did not allow any apparent competition.

Our theoretical predictions align with observed empirical patterns in predator–prey communities from a primeval forest. In both summer and winter seasons, diversity at the lower trophic level is primarily constrained by fitness differences, while diversity at the higher trophic level is primarily constrained by niche differences. In addition, the different proportions of lower trophic species have shifted niche and fitness differences in directions that match our theoretical predictions. This case study serves as a proof-of-concept, demonstrating how our theoretical results can be tested and reveal new insights from empirical data. Of course, it is unclear how

FIGURE 3 Diversity at lower (respectively higher) trophic is primarily constrained by fitness (respectively niche) differences. To validate the generality of our analytic results, we adopted a full-factorial simulation approach by relaxing various assumptions (see Methods section for details). The horizontal axis quantifies the range of values in niche or fitness differences across species throughout assembly (i.e., ranges of values in the *y*-axis in Figure 2). A smaller value indicates that species do not differ much in their niche or fitness difference. The vertical dashed line represents the baseline of no difference. The box plots show the distribution of these ranges across different simulation scenarios. Despite adopting more relaxed and realistic conditions, the observed trends closely mirror our analytical predictions. For lower trophic species (denoted in yellow), a higher proportion of lower trophic species shows an almost null impact on their niche differentiation (Upper Left) but a strong increase in fitness disparity (Lower Left). Conversely, for higher trophic species (denoted in blue), the trend is reversed, with their niche differences becoming higher and fitness differences remaining almost constant. These findings further confirm that species diversity in trophic levels is constrained by contrasting coexistence mechanisms. Simulations have considered a full factorial combination of all parameters: different species richness ($S = 5, 10, 15$), different mean interaction strength ($\mathbb{E}[A] = 0.1, 0.2, \ldots, 0.5$), different variance in interaction strength ($\text{Var}[A] = 0.01, 0.02, 0.03$), different energy efficiency ($s = 0.1, 0.5, 1$).
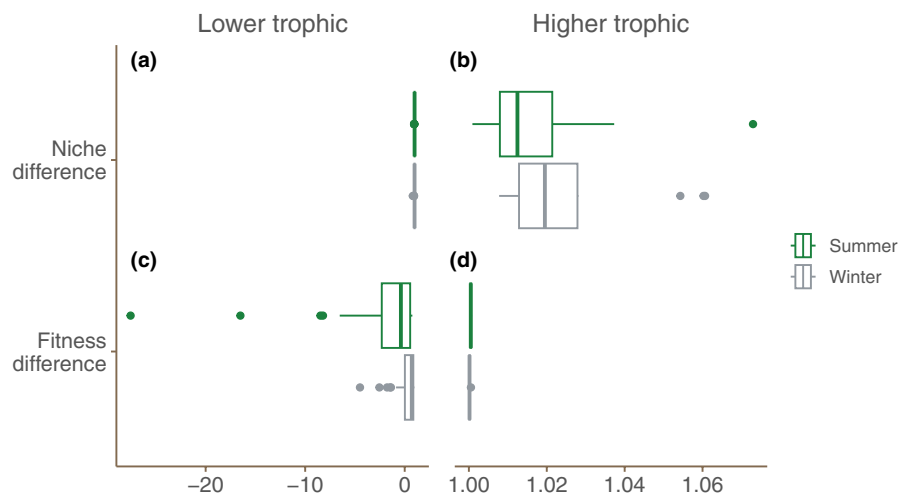
FIGURE 4 Patterns of niche and fitness differences in a seasonal food web. We analysed a thoroughly surveyed and parametrized food web from a primeval forest, calculating the niche and fitness differences for each species during both the summer (represented in green) and winter (represented in silver) seasons. For species at the lower trophic level (left column), niche differences remain relatively constant (Panel a), while fitness differences exhibit a wide range (Panel c). In contrast, for species at higher trophic levels (right column), niche differences vary widely (Panel b), while fitness differences remain relatively constant (Panel d). These patterns hold true across both seasons and align with our theoretical predictions. When comparing these patterns across seasons, we observe that the fitness differences of lower trophic species generally increase from summer to winter (Panel c), while the niche differences of higher trophic species generally increase (Panel d). This pattern also aligns with our theoretical predictions, as the food web in summer has relatively more lower trophic species compared to winter.

generalizable this case study might be. We advocate taking our results as null expectations. Any deviation from these baselines could potentially signal the presence of more complex ecological structures and mechanisms in the natural world.

While we have exclusively focused on two-trophic communities in the main text, we have expanded our analysis to include three-trophic communities (Appendix S4). Analytic derivation becomes intractable with the inclusion of an additional trophic level, hence, we opted for a numerical simulation approach. Patterns observed in three-trophic communities have remained qualitatively similar to those observed in two-trophic communities. Given the absence of quantitatively

parameterized data for three-trophic communities, we have focused on testing the prediction about the distribution of species richness across trophic levels.

Our results are not possible without recent advancements in the theoretical foundation of modern coexistence theory, which allows for analysing the coexistence of complex multitrophic communities. The traditional measure of niche and fitness differences in modern coexistence theory was constrained to two-species competitive communities (Chesson, 1990, 2013; Godoy & Levine, 2014). The incorporation of additional trophic levels has usually been accomplished through trophic separation. For instance, Chesson and Kuang (2008) studied a tri-trophic community by examining the coexistence of two competing species within the same trophic level. Unfortunately, this theoretical constraint has curtailed the capacity of modern co-existence theory to analyse empirical data (reviewed in Buche et al., 2022). To address this limitation, Spaak and De Laender (2020) generalized the classical measure of niche and fitness differences to communities with multiple species and facilitative interactions. Additionally, Spaak, Godoy, and De Laender (2021) expanded the measure to include communities with predation interactions. Nevertheless, these methodologies remained restricted to communities with a relatively low number of species. To address this limitation, Spaak and Schreiber (2023b) further advanced the approach to analyse species-rich communities. Building upon the extended theoretical foundation, Spaak, Carpentier, and De Laender (2021) have shown that fitness difference, not niche difference, limits coexistence in a single trophic level. In this line, we have generalized previous results on horizontal communities to multitrophic communities.

In addition to modern coexistence theory, there exist other theoretical frameworks capable of studying multitrophic assembly. Modern coexistence theory primarily uses invasibility to study coexistence. In contrast, other theoretical frameworks delve into various aspects of coexistence: random matrix theory focuses on perturbations of species abundances (Allesina et al., 2015), sensitivity analysis focuses on infinitesimal perturbations of model parameters (Barabás et al., 2014), and the structuralist approach focuses on large perturbations of intrinsic growth rates (Song & Saavedra, 2018a). These approaches are highly complementary to each other. Beyond these phenomenological approaches, an alternative approach is mechanistic modelling, where all coefficients are determined by biological details. For instance, McPeek (2022), while also using invasibility as a criterion for coexistence, has modelled multitrophic assembly via a fully mechanistic approach. We posit that integrating phenomenological and mechanistic approaches can offer a more holistic understanding of multitrophic assembly (Letten et al., 2017).

Overall, we argue that studying the entire multitrophic structure is essential to understanding the mechanisms that sustain biodiversity in nature. This perspective is not new and has previously been championed (Beckage et al., 2011; Godoy et al., 2018). However, it is unclear a priori whether coexistence mechanisms should differ from one trophic level to another. Here, we have found that traditional or alternative approaches—focusing only on a horizontal sub-community in a multitrophic community—would lead to incorrect identification of coexistence mechanisms. Thus, only by incorporating multitrophic structures can modern coexistence theory fulfil its promise as a truly unifying framework. We hope that our work will stimulate more empirical tests on multitrophic assembly using modern coexistence theory in the future.

Limitations and future work

The null expectations we established are predicated on simplified representations of natural communities. Here, we identify three areas in which we could further integrate ecological complexity, particularly from the field of food webs, into the null model:

First, we have adopted a simple trophic network structure. Our findings are generalizable to tri-trophic communities (Appendix S4). However, we have not considered omnivory, given that all species in our null model belong to a specific trophic level. In addition, we assume each species interacted not only with each species from the adjacent trophic levels but also with every species at the same trophic level. While such a simplified network is for the tractability of model analysis and underscores the prevailing practices of traditional and alternative focuses, empirical networks typically incorporate a significant degree of omnivory and exhibit sparsity of species interactions (Holt & Bonsall, 2017; Pimm et al., 1991). Food web theory has provided various approaches to model the structure of food webs. Just to name a few, niche-based approach (Williams & Martinez, 2000), allometric- (Otto et al., 2007) and phylogenetic-based approach (Cattin et al., 2004), and integrative approaches (Allesina et al., 2008; Lafferty et al., 2015; McCann, 2011; Rohr et al., 2010). Incorporating these realistic structures of food webs is challenging for analytic tractability, but should be achievable with simulations (Spaak, Adler, & Ellner, 2023b; Spaak & De Laender, 2021). A caveat in that case, though, is that the trophic level is not clearly defined. We hypothesize that many species with identical trophic identities (i.e., same resources and same predators) will make coexistence in the food web less likely. Similarly, we hypothesize that composition will

affect fitness differences of lower trophic species, but niche differences of higher trophic species.

Second, we have simplified the distribution of species interactions. For example, we have assumed that trophic interactions are derived from some independent and identical distribution. However, food web theory and empirical data indicate that their interaction strengths are typically characterized by many weak interactions and a few strong ones (McCann et al., 1998; Neutel et al., 2002, 2007; Wootton & Stouffer, 2016). To more accurately represent this, we may model these interactions with the constraints of food web motifs (Baiser et al., 2016; Bascompte et al., 2005; Losapio et al., 2021; Song et al., 2023). In addition to modelling trophic interactions, we also need to model within-trophic ones. However, we lack a comprehensive understanding of trophic interaction strength in empirical communities. This is mainly due to the challenges in measuring them empirically. For example, Kawatsu et al. (2021) found that roughly a fourth of all species interactions were not driven by trophic interactions. Furthermore, Spaak, Adler, and Ellner (2023b) found that predation was much more important than resource competition in simulated plankton communities, but they did not include any within-trophic interactions.

Third, our analysis is based on the Lotka-Volterra model. This model only captures linear species interactions. However, non-linear species interactions are ubiquitous in multitrophic communities (Abrams, 2022; Coblentz et al., 2023; Novak & Stouffer, 2021). To address this limitation, a promising solution is to integrate with the generalized modelling approach, which allows a holistic understanding of food webs with nonlinear interactions (Gross et al., 2009; Lade & Gross, 2012). In addition to non-linear interaction, there is also potential for higher order interactions (Gibbs et al., 2022; Kleinhesselink et al., 2022; Mickalide & Kuehn, 2019). However, it is not straightforward to extend our theory to include nonlinear functional responses or higher order interactions. With these dynamics, a community can have multiple stable equilibria with all species coexisting (AlAdwani & Saavedra, 2020; Barabás et al., 2018). This renders invasion growth rate, consequently niche and fitness differences, ill-defined. Nonetheless, recent advancements in invasion graph theory hold potential for overcoming this challenge (Hofbauer & Schreiber, 2022; Serván & Allesina, 2021; Song et al., 2021; Spaak & Schreiber, 2023b).

AUTHOR CONTRIBUTIONS
Both authors contributed equally. J.W.S. and C.S. conceived the study. J.W.S. and C.S. performed the study. J.W.S. and C.S. wrote the manuscript.

PEER REVIEW
The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14409.

DATA AVAILABILITY STATEMENT
Empirical data of seasonal networks is available from doi.org/10.1111/1365-2656.13227. The source code to produce the results is available on GitHub at https://github.com/clsong/Reproduce_Song_Spaak_2024.

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SUPPORTING INFORMATION

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