

REVIEW

Estimating co-extinction threats in terrestrial ecosystems

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Abstract

The biosphere is changing rapidly due to human endeavour. Because ecological communities underlie networks of interacting species, changes that directly affect some species can have indirect effects on others. Accurate tools to predict these direct and indirect effects are therefore required to guide conservation strategies. However, most extinction-risk studies only consider the direct effects of global change—such as predicting which species will breach their thermal limits under different warming scenarios—with predictions of trophic cascades and co-extinction risks remaining mostly speculative. To predict the potential indirect effects of primary extinctions, data describing community interactions and network modelling can estimate how extinctions cascade through communities. While theoretical studies have demonstrated the usefulness of models in predicting how communities react to threats like climate change, few have applied such methods to real-world communities. This gap partly reflects challenges in constructing trophic network models of real-world food webs, highlighting the need to develop approaches for quantifying co-extinction risk more accurately. We propose a framework for constructing ecological network models representing real-world food webs in terrestrial ecosystems and subjecting these models to co-extinction scenarios triggered by probable future environmental perturbations. Adopting our framework will improve estimates of how environmental perturbations affect whole ecological communities. Identifying species at risk of co-extinction (or those that might trigger co-extinctions) will also guide conservation interventions aiming to reduce the probability of co-extinction cascades and additional species losses.

KEYWORDS

climate change, co-extinctions, conservation, ecological network models, terrestrial ecosystems, trophic cascades

1 | INTRODUCTION

Over the last 50 years, much of the biosphere has been destroyed or degraded (Díaz et al., 2020) as a result of human endeavour. Unsustainable land use, resource-intensive agriculture, invasive

species, emerging diseases and natural resource extraction have degraded environments and exacerbated the impacts of natural disasters (e.g. droughts and fires; Heleno et al., 2020; Shukla et al., 2019). Among current pressures, climate change is one of the greatest threats to biodiversity (Newbold, 2018), with expectations

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that it will soon become the primary driver of species extinctions (Urban, 2015). According to the Intergovernmental Panel on Climate Change (Allen et al., 2019), even under the unlikely lowest rates of projected warming (SSP1-1.9: <2°C above pre-industrial temperatures by 2100; Masson-Delmotte et al., 2021), climate change is expected to disrupt ecological communities and processes beyond natural variation, degrading their structure (Holmgren et al., 2013), composition (de la Fuente et al., 2022) and function (Garcia et al., 2014; Seddon et al., 2016). Together, human modification of the biosphere will likely continue in the short term and amplify the effects of climate change in the long term.

Ecological communities—assemblages of species living together in a particular area—are simultaneously threatened by anthropogenic climate change and other perturbations (Barnosky et al., 2011; Pecl et al., 2017), with these changes having already simplified the structure and complexity of most ecological communities (Heleno et al., 2020; Ledger et al., 2013; Woodward et al., 2012), and modified species' distributions, body size, abundance, and seasonal movements (Brondizio et al., 2019; Ernakovich et al., 2014; Hatfield & Prueger, 2015; Shukla et al., 2019). Natural communities are organised into multiple **networks** (see Glossary) where species are linked to one another based on different kinds of ecological interactions, such as those between plants and pollinators, predators and prey and hosts and parasites. Both the species in a community and the interactions among them are necessary for sustaining biodiversity overall and are a fundamental component in determining how communities respond to ecological disruption (Ives & Carpenter, 2007; Suttle et al., 2007). It is because of these interactions and interdependencies, however, that threats directly affecting some species often also have secondary effects on others in the same community (Ripple et al., 2016; Strona & Bradshaw, 2018). Therefore, quantifying how species interact within their community and modelling how biodiversity loss can propagate through network links (ecological cascades) are important to predict entire community responses to future environmental conditions.

The component of climate change expressed as global warming directly affects species by challenging their thermal tolerances (Hickling et al., 2006), with predictions of how it threatens species relying primarily on estimating when temperatures will breach these tolerance limits. However, the indirect effects of these threats on communities through species interactions (Dorresteijn et al., 2015) are less clear. For example, if a species depends on the persistence of another, the extinction of the latter can cause the former to become *co-extinct*, which can in turn elicit a trophic cascade leading to more *co-extinctions* in a community (Garcia et al., 2014). These cascades are generally either *bottomup* (affecting consumers losing their food resources) or *topdown* (affecting resources losing their consumers; Feit et al., 2020; Letnic et al., 2009), potentially disrupting entire ecological communities and increasing the overall rate of extinction.

These changes to species assemblages often involve the arrival of new species (e.g. invasive or naturally range-expanding) that have never interacted with endemic species, generating new interactions (Wallingford et al., 2020). Measuring the cascading implications of

invading alien species will become increasingly important as no-analogue climate change will engender no-analogue communities (Williams et al., 2007). Most research on trophic networks (food webs) has focused on examining the effects of environmental perturbations on trophic guilds (Feit et al., 2020), with many examples documented in marine (Batten et al., 2018) and freshwater (Jones et al., 2017) environments. Yet, there has been little focus on terrestrial ecosystems, suggesting that we have underestimated extinction risks in that realm. Understanding the effects of environmental perturbations from a more complete ecological perspective will provide greater insights into how ecosystems respond to climate change and other pressures, thereby guiding more effective conservation strategies.

In this review, we delve into the complexities of characterising and measuring species interactions and community responses to environmental change, while highlighting the intricacies of defining ecological communities and the consequential implications of developing comprehensive food webs. This exploration is underpinned by a critical assessment of the limitations, issues and methods associated with quantifying and modelling biotic interactions. To enhance our understanding of biotic interactions in ecosystem-level processes and consequences, we introduce a novel framework for constructing ecological network models that can capture food webs more realistically within terrestrial ecosystems. We further discuss how this framework can allow researchers to simulate trophic cascades that are influenced by plausible future environmental perturbations, with a focus on advancing environmental policies and the management of terrestrial biodiversity (Figure 1).

2 | CHALLENGES IN MEASURING SPECIES INTERACTIONS AND COMMUNITY RESPONSES TO ENVIRONMENTAL CHANGE

Our understanding of why some species in a community interact and others do not is relatively nascent (Blanchet et al., 2020), compared to what we now understand about species distributions, despite this information being essential to predict community change (Bartomeus et al., 2016). Indeed, measuring interactions and determining how they change through time as part of complex, interconnected structures are challenging endeavours (Jordano, 2016). This is made even more difficult because most trophic interactions include >2 species (Golubski et al., 2016), and current and historical interaction data are sparse (Hortal et al., 2015). Data describing phenotypic plasticity and genetic variation that permit species some capacity for adjustment or adaptation in terms of the species with whom they interact and the strength/importance of these interactions are also rare. This rarity thereby weakens inferences on the extent to which food webs can 'rewire' (e.g. develop new interactions between previously non-interacting species or shift the strength/importance of pre-existing interactions) following the loss or gain of species in a community (Gilljam et al., 2015). Moreover, this paucity of information prevents discriminating potential and realised

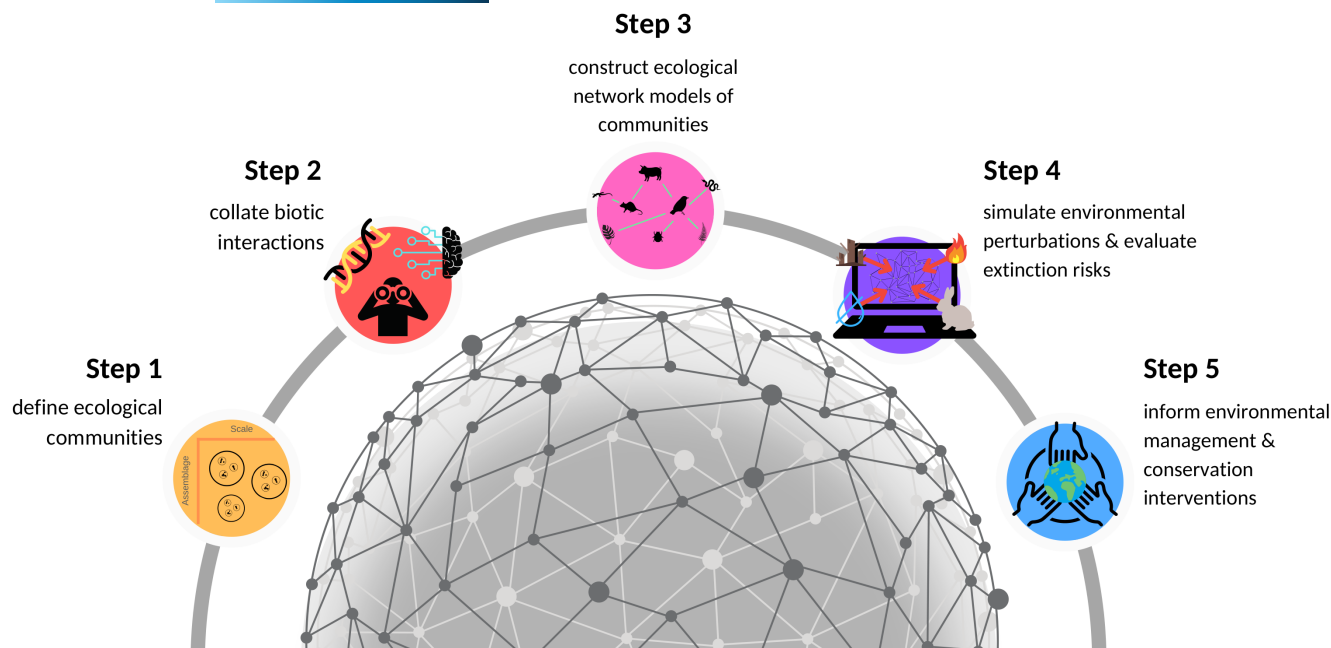


FIGURE 1 Main steps for estimating co-extinction risks in terrestrial ecosystems. The process involves five main steps: (1) define ecological communities — identify specific biotic components that make up a community of interest, for example, a list of species observed in a given space and time (see Section 3). (2) collate biotic interaction data — gather pre-existing data on biotic interactions within defined communities (Figure 2); gaps filled by (i) collecting new interaction data, for example, by making field observations or running feeding trials, and/or (ii) inferring interactions using, for example, machine-learning algorithms (see Section 4). (3) construct ecological network models of defined communities based on collated biotic interaction data; modelling communities can apply network theory to make realistic networks (see Section 5). (4) simulate environmental perturbations, for example, use models to simulate probable future environmental perturbations and apply these disturbances to the network models to investigate the trophic cascades they trigger (see Section 6). (5) inform environmental management & conservation interventions, for example, identifying conservation target such as key species that, if lost, could have significant detrimental effects on communities (see Section 7).

interactions (Strona & Veech, 2017), further masking how ecological communities might respond to environmental change.

Anthropogenic threats can affect interactions among species in terrestrial ecosystems. However, data regarding the impacts of such threats on interactions among species are rare, largely due to the difficulty of distinguishing the effects of human-driven environmental change, such as climate change, from changes attributed to natural stochasticity (McCann, 2007). For example, while we know that climate change can alter plant–herbivore interactions by directly and indirectly inducing greater food consumption by herbivores (Lemoine et al., 2013), comprehensive data documenting these impacts is scarce (Tylianakis et al., 2008). Despite these challenges, recent research has begun to examine the potential for extinction cascades in marine and freshwater ecosystems (Donohue et al., 2017). Global estimates of species extinction rates from climate change initially excluded co-extinctions (Thomas et al., 2004), but recent research has attempted to include their contribution (Hughes, 2013; Strona & Bradshaw, 2018, 2022). However, this empirical research has predominantly focused on marine and freshwater ecosystems (Anaya-Rojas et al., 2019; Donohue et al., 2017; Hayden et al., 2015; Smith et al., 2011) because aquatic communities include species with predictable, linear relationships between predator and prey body sizes (Arditi & Ginzburg, 2012), and many studies (especially in fisheries) provided detailed diet information

from gut-content and stable-isotope analyses (Davis et al., 2012). Aquatic ecosystems (e.g. lakes) also tend to function as **quasi-closed systems** with more distinct trophic levels than in terrestrial ecosystems (Estes et al., 1998), making the former easier to model. In contrast, co-extinction processes in terrestrial systems remain poorly understood and have garnered comparatively less attention (Strona & Bradshaw, 2018).

The sparser literature on terrestrial ecosystems has contrarily focused more on networks of plants and pollinators (Dallas & Cornelius, 2015), and plants and herbivores (Pearse & Altermatt, 2013); even the few studies on terrestrial predator–prey networks are concentrated mainly on specific taxonomic groups such as invertebrates, mammals, or birds (Letnic et al., 2009). Furthermore, most terrestrial networks consider only top-down effects, with few exceptions (Kagata et al., 2005; Scherber et al., 2010), likely due to the complexity and lack of data on basal resources (e.g. plants and invertebrates) needed to predict bottom-up processes. For example, the reintroduction of wolves (*Canis lupus*) in Yellowstone National Park in the United States elicited a trophic cascade, positively increasing woody browse species and bison (*Bison bison*), while simultaneously decreasing elk (*Cervus canadensis*), the wolf's main prey (Ripple & Beschta, 2012). Most other terrestrial ecological networks have been constructed to estimate the impacts of invasive species because of the availability of research funding for investigating the

economic costs of their impacts (Bradshaw et al., 2021; Crystal-Ornelas et al., 2021). For example, the invasion of the cane toad (*Rhinella marina*) across mainland Australia (Doody et al., 2015), and the yellow crazy ant (*Anoploepis gracilipes*) on oceanic archipelagos (Sugden, 2003), have caused both trophic cascades and species compositional changes in their respective communities. Despite the challenges and limitations in quantifying the effects of co-extinction cascades in terrestrial ecosystems, additional research is necessary to predict future community change and guide conservation interventions.

3 | INCOMPLETE FOOD WEBS

Model food webs are simplified representations of real food webs constructed to study the dynamics of an ecosystem or test hypotheses about how it functions (Susanne et al., 2015). However, despite their efficacy, these models have inherent limitations for capturing the complexities of real ecosystems. Such food web models, that quantify the trophic interactions among species or feeding guilds, provide an objectively useful starting point to predict community responses to environmental change (Pringle & Hutchinson, 2020) and to estimate extinction risk more generally (Llewelyn et al., 2022; Strona & Bradshaw, 2018). Yet, the intricate nature of real food webs makes the construction of realistic models for entire communities challenging. Indeed, it is not logistically practicable to record all the interactions among species in complex communities, especially due to variation in species composition and interactions through space and time. By virtue of this variation, the few detailed food webs that have been built are necessarily incomplete at one spatial and/or temporal scale or another, such as at the microhabitat or seasonal scale, making most available empirical food webs snapshots that are not necessarily loyal to ecological reality—an observation supported by the scarcity of relevant literature on terrestrial food webs (Pocock et al., 2012). Although many data on species interactions exist (e.g. open-access databases like *Global Biotic Interactions—GloBI*; Bohan et al., 2017; Carscadden et al., 2012; Poelen et al., 2014), these data often refer to a few known pairwise interactions with a focus on individual species, and cannot therefore be used to build complete food webs (Figure 2).

Despite the higher taxonomic resolution of contemporary data used in food web models (Ings et al., 2009), the prediction accuracy of these models remains hindered by persistent issues and limitations, particularly the lack of a standard method for defining a 'community' (Herrando-Pérez et al., 2012, 2014; Krebs, 1985). Ideally, one can quantify trophic interactions among species without considering how its associated community is defined, but clearly defining the community can help researchers ensure that all relevant species are considered, and standardise the terminology used to describe trophic interactions. Furthermore, a well-defined characterisation of the community structure offers insight into the intricate trophic relationships between various species in a complex food web (e.g. better characterising the relationships or interdependencies between different trophic levels).

While ecological communities can be defined simplistically as 'all organisms within a prescribed area' (Diamond, 1986), there is a more nuanced understanding that acknowledges temporal scales and the variability of species' presence and their contribution to community processes within these boundaries. For instance, some definitions describe a community as the 'group of species that occur together in space and time', indicating that temporal scale is an equally important component of the definition (Harper et al., 1990; Stroud et al., 2015). Among the various methods for defining a community, spatiotemporal movement data are required when defining boundaries (Harper et al., 1990; Stroud et al., 2015) because implicit temporal averaging means that not all species are always present in a defined area, such that membership and relative importance vary through time. In terms of categorical boundaries, a community can also be defined by a taxonomic group (e.g. mammals), or by a group of species serving a specific ecological function or role (e.g. herbivores; Begon et al., 2006). This is often defined artificially to suit a study's criteria or by outlining the boundary where separately defined communities (i.e. using the aforementioned definitions) overlap. This boundary can be defined, often in combination, by the number of species observed in a given area (Cadotte & Tucker, 2017), biotic interactions (Dodds et al., 2006), diversity indices or rank-abundance diagrams (Begon et al., 2006; Shaheen et al., 2012), pattern limits (e.g. checkerboarding; Cody et al., 1975), comparing local and regional species richness (Szava-Kovats et al., 2013), species traits (Kraft & Ackerly, 2014), and/or by functional trait diversity (Lamanna et al., 2014), or using other variables (Begon & Townsend, 2020).

Carefully considering the methods for defining a community should be an essential first step, with elements such as structure, biotic interactions, spatiotemporal scale and the specific research questions asked playing important roles in this determination. This process demands collecting as much data as possible, taking into account the spatial and temporal scale of the study. The resultant improvement in the accuracy and reliability of model outputs can ultimately reveal more practical and effective conservation strategies for at-risk communities. But, obtaining comprehensive data on trophic interactions within ecological communities can be challenging due to the lack of clear boundaries and the difficulties in collecting data describing interactions. Historically, the primary method for assigning biotic interactions was via directly observed relationships in terrestrial ecosystems (e.g. through standardised field surveys, feeding trials, and gut/faecal content analyses; Carmel et al., 2013; Figure 2). However, collecting empirical interaction data is usually costly and onerous, meaning that incomplete data are often used to construct entire networks (Lau et al., 2017). The questionable accuracy of such networks has been compounded by sampling biases (Blüthgen, 2010) and an unknown proportion of misidentified species (Egli et al., 2020), meaning that past inferences made from trophic networks need to be interpreted with caution (Bortolus, 2008).

The presence of cryptic species, which are commonly found across a variety of taxonomic groups and regions (Struck et al., 2018), can undermine the realism of resultant networks (Pringle & Hutchinson, 2020). For example, treating two morphologically identical species as a single

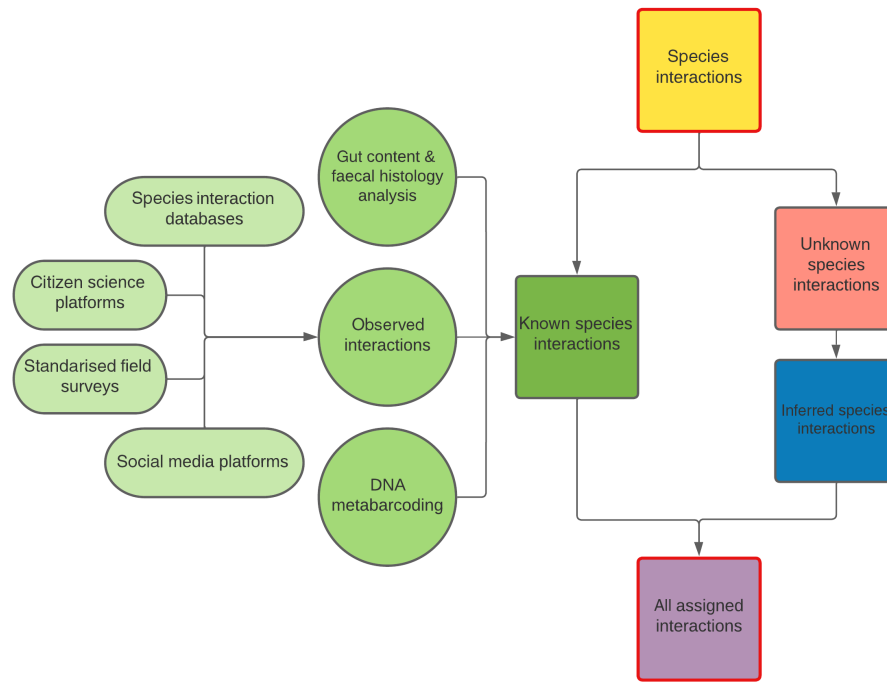


FIGURE 2 Sources, gaps, and pathways for interaction data. For species interactions (yellow: start), known interactions (green) are typically derived from one of three sources: (i) observed interactions (e.g. *GloBi*, *iNaturalist*, *Mangal*, and *Facebook*), (ii) gut contents and faecal histology (e.g. Carscallen et al., 2012), or (iii) DNA metabarcoding (e.g. Bohan et al., 2017). Several interrelating factors have made classifying the interactions for most species difficult (red). Methods to infer interactions (blue) (e.g. Desjardins-Proulx et al., 2017) have been used to address this gap, including supervised machine-learning methods. Known biotic interaction data derived from various sources, combined with methods to address unknown interactions, can provide a more comprehensive list of all assigned (or potential) interactions (purple: finish) within an ecological community.

species (i.e. by observation) (Parker, 2004) could overestimate or underestimate diet breadths (Smith et al., 2008). Cryptic interactions (those that are not easily observed) generally missed by conventional field surveys (e.g. interaction observation, scat analyses) can arise from intraspecific variation in size, behaviour, habitat, and activity (Pringle & Hutchinson, 2020). Furthermore, cryptic, non-consumptive predator-prey interactions (e.g. the mere presence of predators creating 'landscapes of fear') in ecological communities can potentially limit the distribution, habitat use and abundance of species, and therefore, the interactions in a community (Pringle et al., 2019).

Considering that most interactions among species are infrequent and fluctuate across diverse spatial and temporal scales (Parker, 2004), they are not likely detected by short-term or seasonal field surveys. Although an interaction might be rare, it can still potentially alter community processes (Arditi & Ginzburg, 1989; Leitão et al., 2016), especially if it involves top predators (Duffy, 2003). Additionally, intraspecific variation (e.g. phenotypic plasticity) can indirectly modify the true expression of an individual's diet (e.g. ontogenetic shifts, behavioural specialisation and habitat-restrictive prey availability; Pringle & Hutchinson, 2020), but it is so far unclear if such variation affects the accuracy of inferred trophic interactions, and therefore, the ecological realism of constructed networks.

Due to uneven taxonomic/disciplinary foci and research specialisations, the quantification of ecological interactions, especially in terrestrial ecosystems, often falls short, exacerbating the existing

methodological limitations and data gaps in species interactions. For example, there are geographical biases in study location and a disproportionate focus on functions indirectly related to interactions per se (e.g. invasion biology; Cameron et al., 2019). Although alternative methods to observational field surveys have been developed (e.g. faecal microhistology and dietary databasing), such methods are labour-intensive, exceed the budget and time frames of most studies and have limited resolution and accuracy (Pringle & Hutchinson, 2020). While other methods, such as DNA metabarcoding, are emerging, they can be costly (Bohan et al., 2017). Citizen science and public platforms are also a potential source of species interaction data (Maritz & Maritz, 2020), but these too have their own issues with quality control (Anhalt-Depies et al., 2019) and coverage. Together, these methodological limitations create data gaps in species interactions that have flow-on consequences for inferring high-resolution trophic networks and quantifying the relationships between biotic components in communities (mainly terrestrial). However, the increasing accessibility and development of new technologies will provide more relevant data.

4 | INFERRING BIOTIC INTERACTIONS

Awareness of the importance of biotic interactions in determining species' responses to environmental change has motivated a recent surge in modelling ecological communities and associated methods

to infer species interactions (Gravel et al., 2013). However, due to the limitations in documenting new interactions, such as those between previously non-co-occurring species, predicting potential interactions is necessary to predict and potentially manage the impacts of changing environments, and the consequences of emerging alien species.

Earlier methods to infer trophic interactions were generally derived from predator–prey body-size relationships (Gravel et al., 2013; Warren & Lawton, 1987), but these inferences are limited in ecosystems with poorly resolved diversity, or for whose interactions are not easily described by such relationships, particularly in terrestrial ecosystems. This limitation has spawned the development of alternative techniques for inferring biotic interactions. Examples include calculating the probability of interactions among species using functional traits (e.g. morphological, physiological, behavioural) or phylogeny as a proxy of these traits (Morales-Castilla et al., 2015), or abundance data to infer pairwise interactions among species. However, these methods are also limited by the data available to construct matching relationships empirically (Bartomeus et al., 2016). Co-occurrence data have been used to infer species interactions (Ibarra-Cerdena et al., 2017), but these have been criticised as poor proxies (Blanchet et al., 2020; Yackulic et al., 2018). Joint species distribution models can also be adapted to infer species interactions based on environmental conditions and presence/absence or abundance data. By combining multispecies occurrences with hypothesised environmental predictors, these models can assess the residual probability of co-occurrence after controlling for environmental conditions (Momal et al., 2020), although co-occurrence is not always evidence of direct interaction (Anhalt-Depies et al., 2019; Blanchet et al., 2020), and such models require expansive datasets (Sinclair et al., 2010). Trait-matching using generalised linear models (Desjardins-Proulx et al., 2017; Pichler et al., 2020) can also infer species interactions, although other methods often have higher predictive capacity (Caron et al., 2022).

To alleviate issues of data scarcity and inference limitations, newly emerging tools such as supervised machine-learning algorithms have become popular means for predictive interactions for different network types (Murphy, 2012). In particular, *k*-nearest neighbour and **random forest** have been applied to infer species interactions accurately by using both trait and observed trophic interaction/non-trophic interaction data (Desjardins-Proulx et al., 2017; Llewelyn et al., 2022; McConkey & Brockelman, 2011), providing a tool to predict novel species interactions under environmental change (Pomeranz et al., 2019). Despite supervised algorithms like random forest requiring extensive training data to be used effectively and having uncertainties about their ability to infer trophic interactions in highly **nested** networks, machine learning remains one of the most promising methods available for inferring biotic interactions (Desjardins-Proulx et al., 2019). While predicting individual interactions can provide insight into the dynamics of food webs, the methods used might not be sufficient for quantifying the overall food web structure of communities (Poisot, 2023). Predicting interactions alone does not necessarily reveal the real position of each

species in a food web nor the relationships between species that are not directly linked by trophic interactions. For example, methods that perform well when inferring species interactions might not do as well when inferring whole community structures (Poisot, 2023). Deciding which methods to use should depend on whether inferring more realistic trophic interactions or constructing more realistic food web structures are more important for addressing particular research aims.

Another issue beyond inferring just the potential interactions between biotic components is assessing the importance of those relationships, because quantifying the strength of interactions is necessary to attribute ecosystem dynamics and predict their responses to perturbation (Laska & Wootton, 1998). For example, the strength of a predator's interaction with a prey species depends on many components, including predator abundance (Yousef et al., 2021). However, how interaction strength is measured can complicate its quantification. For example, interaction strength can refer to different aspects of ecological relationships, from the increase in fitness (e.g. thermal tolerance) that a species experiences in a mutualistic association (Xie et al., 2013), to the influence of cross-species reproductive disturbances and competitive struggles for resources (Kishi & Nakazawa, 2013). This multiplicity of measures and the inherent variability of ecological interactions poses a challenge to their comparison of, and integration into, model food webs, with choice depending on the assumptions underpinning particular ecological theories or the method of quantification applied. Although empirical data such as field observations quantifying interaction frequency and intensity (Wootton & Emmerson, 2005) can be used to infer an interaction strength between species, alternative approaches are necessary when such data are not available (as is often the case). Various mechanistic models can account for such effects, including those that use traits to incorporate the frequency of prey items in predator diets (Pocock et al., 2021), or those based on bioenergetic-mechanistic models that link the energy flow between species and describe how they acquire and transform resources into traits (e.g. body size) that influence relationships (Passoni et al., 2022).

Although the previous examples are valid methods to quantify interaction strengths, one should carefully consider the underlying assumptions when evaluating co-extinction risks. Assuming the strength of interaction between any two species remains constant through time and regardless of changes in the ecological community in which they occur, as well as assuming that interactions between species are linear and that their strength is invariant to the densities of interacting species (Vázquez et al., 2015) need to be determined. However, methods outlined to quantify interaction strengths demonstrate situations where these assumptions are not always met, and might, therefore, not fully mimic reality. For example, ignoring the synergistic or antagonistic, non-additive effects of environmental perturbations on species interactions—that is, the effect of ≥ 2 species interacting is not equal to the sum of their individual effects—can modify estimated extinction risk (Thompson et al., 2018).

5 | MODELLING SPECIES INTERACTIONS AND COMMUNITY CHANGE

Analytical, correlative and numerical simulation models are becoming more tractable and popular for describing structure and processes within ecosystems and to predict community changes arising from environmental perturbations (Strona & Bradshaw, 2018). Network models, such as those representing relationships between individual species (Llewelyn et al., 2022), can represent trophic, mutualistic, competitive, or other interactions within a community, or be simplistic representations of pre-existing or existing ecosystems typically based on unweighted interaction links (Geary et al., 2020).

Basic predator–prey models describing the dynamic relationship between two guilds have long been used to characterise species interactions (Lotka, 1910). Such models have traditionally been based on standard predator–prey differential equations like the Lotka–Volterra to quantify the effects of biodiversity loss on the vulnerability of communities to secondary extinctions (Sanders et al., 2018), and the subsequent compensatory Rosenzweig–MacArthur (Rosenzweig & MacArthur, 1963) and ratio-dependent Arditi–Ginzburg variants (Arditi & Ginzburg, 1989), to model ecological systems (Åkesson et al., 2021; Nonaka & Kuparinen, 2021). These models highlight the importance of accounting for trophic interactions between organisms when modelling ecosystems (McCann, 2007).

Single-species population and distribution models have been used to predict the implications of anthropogenic climate change (Araújo & Luoto, 2007), yet their inherent limitations prevent a comprehensive assessment of species extinction risk. These types of models do not consider biotic interactions and physical processes (Elith & Leathwick, 2009; Figure 3), and therefore, only provide a limited assessment of species vulnerability (Carmel et al., 2013); the exception is some studies modelling multispecies dynamics (Säterberg et al., 2013). Correlative species distribution models can include interactions, but they cannot predict variation in these interactions under changing environmental conditions. As a result, such models cannot account for co-extinction processes and are likely to underestimate extinction risks under future climate change (Strona & Bradshaw, 2018).

As an alternative modelling tool, ecological network models based on network theory include interactions by using a flexible mathematical framework accounting for a specified number of biotic components and relationships within a parameterised network (i.e. species interactions can be **weighted** or **unweighted**; Delmas et al., 2019). These models can be defined as a network (G) comprised of **nodes** (N) and **edges** or links (E) (Geary et al., 2020; Landi et al., 2018), formulated generically as $G = (N, E)$, that represent one or more interactions between nodes (Lau et al., 2017). These models are typically represented as **bipartite networks** (Geary et al., 2020), although can also be used to represent trophic interactions among species in a community (Pocock et al., 2012).

Ecological network models representing biotic interactions can test hypotheses about variation in food web structure and resilience to perturbation (Säterberg et al., 2013). Because these

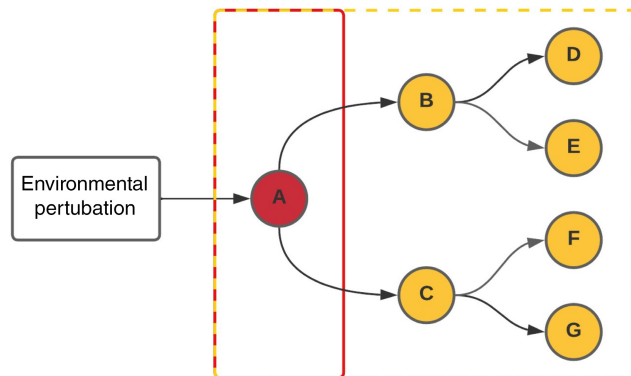


FIGURE 3 Single- versus multiple-species extinction models. Extinction estimates based on single-species models (solid red box) (e.g. species distribution models) can only predict direct effects caused by environmental perturbations (e.g. climate change; red circle 'A' representing a primary extinction). These models consider each species as a disconnected entity and do not account for the indirect effects of species co-extinctions and population changes. In contrast, multiple-species models (e.g. network-based models; dotted yellow box) consider both direct (red circles: primary extinctions) and indirect effects (yellow circles: co-extinctions and population changes). For example, a decline in the population of one species (B) can lead to the co-extinction of other species (D and E) that depend on B for food or other resources. By accounting for these indirect effects, multiple-species models provide a more accurate and comprehensive analysis of the impact of environmental perturbations on ecosystems and the risk of species extinctions.

models ideally encapsulate most nodes in a community and identify (and possibly quantify) the interactions among them, ecological network models can simulate co-extinctions more realistically than other types of models (Geary et al., 2020; Figure 3), with many examples of network models applied to reveal ecosystem-wide effects or predict the relative impacts of different management scenarios (Wallach et al., 2017). Ecological network modelling can be applied not only to evaluate multiple extinction drivers in addition to co-extinction effects (e.g. invasive species or land-use changes; Strona & Bradshaw, 2022), they also assess how these stressors might, in turn, affect different parts of the same network. Furthermore, the graphical representation of species interactions in ecological network models can be more effectively used to explore the potential for cascading effects and other nonlinear interactions arising from anthropogenic threats. This is more useful compared to other mechanistic frameworks that can represent ecological communities, such as the Madingley model (Flores et al., 2019) that is more suited to studying ecological processes and dynamics on species populations (e.g. competition) and how these affect communities. Although network models attempt to represent entire ecological communities, they too have operational limitations beyond the availability and quality of the constituent data. Model nodes representing entire populations are necessarily oversimplified, given that these might not account for all the associated qualities of a biotic component. For example,

when a node represents an individual species, all associated traits (e.g. phylogeny, morphology, physiology) are encapsulated by this single node and can never fully represent the real-world variation within the species. This limitation can generate errors in inferred network dynamics and responses (Bolnick et al., 2011). Population dynamics (e.g. age structure, density compensation) within nodes are usually ignored, either because they can make a network unwieldy, or because of data gaps for all species within the community, preventing network models from weighting nodes by variation in abundance and its influence on extinction risk (Wilmers, 2007). However, community viability models where particularly influential nodes are expanded to account for population structure and abundance could potentially increase the ecological realism of network models.

Furthermore, it is possible to attach dynamical models to important nodes in a network. For example, in predator–prey systems with large fluctuations in abundances, such as cycling predator–prey dynamics (e.g. hare *Lepus americanus*–lynx *Lynx canadensis*; Elton, 1924), dynamical models can be used to modify edge weights when those fluctuations occur. This approach would enable network models to capture more of the complexity of fluctuating interactions between species. Beyond population dynamics, accounting for spatial and temporal dynamics associated with various ecological processes is also important for modelling biotic interactions. However, dividing community spatial units according to temporal processes that vary interaction potential, such as migration patterns, seasonal changes, or disturbances, can be challenging. For instance, the migration of one species could fundamentally alter the ecological interactions within a given spatial unit (Bauer & Hoye, 2014), introducing new complexities into the community when that species is present. Likewise, natural disasters such as bushfires, floods, or other extreme events can alter food webs (e.g. by facilitating biological invasions; Spencer et al., 2020), leading to different dynamics that temporally static models are not able to capture. To account for such temporal variability in community composition, one could potentially iteratively modify a species' ability to interact as a proxy for time (e.g. through shifting migration patterns; Rickbeil et al., 2019), and by simulating the rate of movement (e.g. through elevation change; Freeman et al., 2018), by coupling network models with species distribution models. Of course, higher model complexity increases data requirements (e.g. ontogenetic variation in traits; Lau et al., 2017).

Modelling a subset of interactions within a community, although useful for quantifying binary relationships (Dallas & Cornelius, 2015), can also limit the utility of network models. For example, focusing only on trophic interactions disregards the potential offsetting effects of other interaction types, such as host–parasite (García-Callejas et al., 2018) or plant–pollinator relationships (Bartomeus et al., 2021), which could also bias estimates of extinction risk (Lafferty et al., 2008). A more realistic approach would ideally include multiple interaction types simultaneously (Hutchinson et al., 2019). Such 'multiplex' networks could theoretically encapsulate most interaction types among species in a community, account

for spatiotemporal heterogeneity, context dependency (Stella et al., 2016) and characterise the structure, function, dynamics and co-extinction risk of entire ecosystems (Pilosof et al., 2017). For example, a multiplex approach has been used to produce a framework for a multispecies food web model that allows for non-trophic interactions as functional classes (Kéfi et al., 2012). However, because most interaction types (e.g. plant–seed dispersers) are not linked explicitly to trophic interactions, they cannot be applied easily to all species in a community. Although some multiplex networks can bypass this problem by including both trophic (e.g. predator–prey relationships) and non-trophic (e.g. mutualistic partnerships) interaction networks represented as separate layers and interconnected by shared species (Pilosof et al., 2017; Figure 4), they require expansive datasets to build (Strona, 2022). For example, non-trophic interactions such as predator interference (e.g. 'landscape of fear' exclusion of potential prey; Brown et al., 1999) can modify the functional relationships between predators and prey beyond simple inference of potential trophic interaction. Accounting for such phenomena that modify the shape of the functional response (Kéfi et al., 2012) would require different network topologies to those inferred solely from trophic inference.

General consumer–resource models, which are fundamentally based on the direct relationships between consumer and resource species (MacArthur, 1970), have also been designed to integrate multiple interaction types (Lafferty et al., 2015). Furthermore, there is still no unifying theory to account for the trait space a species occupies, and therefore, no method for weighting the links between species in different networks (Figure 4). Developing methods to allow node parameters to affect different types of interactions with other parts of the network, with additional consideration to spatial and temporal influences, is a clear avenue for development.

While methods have been developed to quantify co-extinction risk across non-trophic interactions networks (Dallas & Cornelius, 2015), few studies have constructed complex networks consisting of multiple, mutualistic networks (e.g. facilitation, pollination, seed dispersal; Valiente-Banuet & Verdú, 2013) or interaction types (e.g. predation, mutualistic, parasitic interactions; Pocock et al., 2012). In contrast, most research on ecological networks has focused on comparatively simplified, empirically based parasitic (e.g. host–parasite; Dallas & Cornelius, 2015) and mutualistic (e.g., plant–pollinator) networks (Koh, Sodhi, et al., 2004), with no current framework developed for quantifying the co-extinction risk for many other non-trophic interaction networks.

6 | SIMULATING TROPHIC CASCADES IN ECOLOGICAL NETWORKS

Simulation models are a common tool applied to predict relative extinction risk, encompassing diverse methodologies and approaches. These approaches range from simple statistical models to estimate secondary extinctions as an effect of primary extinctions, to modelling co-extinctions and trophic cascades accounting for the rewiring

Multiplex network

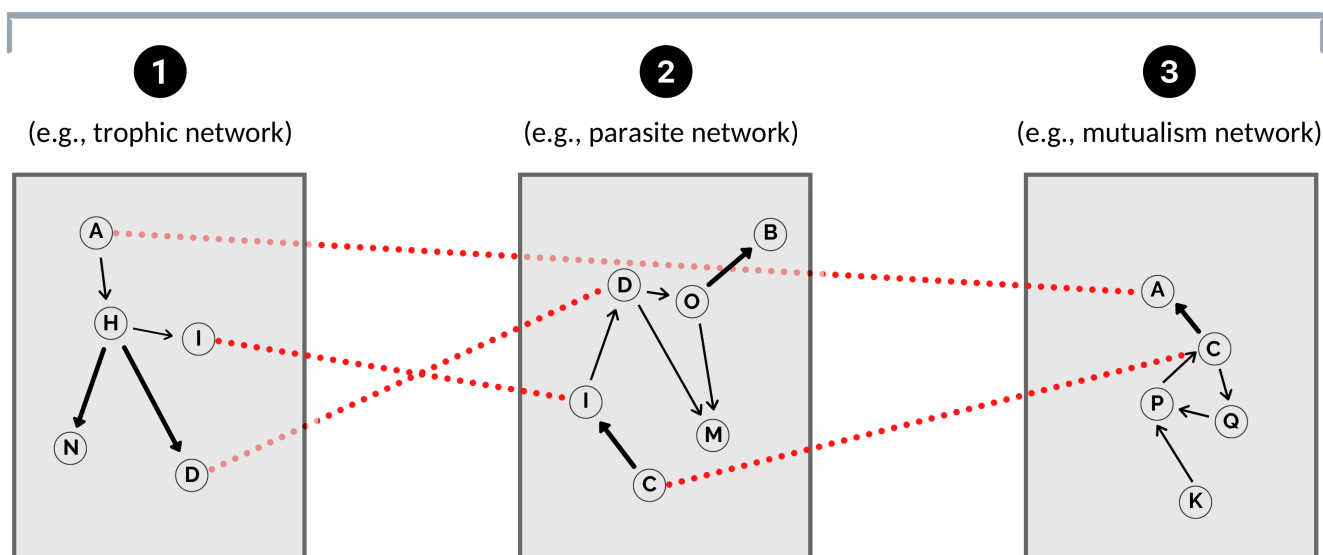


FIGURE 4 A theoretical multiplex network. A multiplex network can include two or more network layers (e.g. layers 1, 2 and 3). Using a model based on network theory, nodes (represented as letters) can be used to characterise biotic components such as species or functional groups, while edges or links represent their interactions within each interaction network. For example, nodes 'D' and 'I' could represent shared prey or host species from predation and parasitic networks, respectively. These nodes could be connected by 'C' as a shared host in both the parasite and mutualism networks, connecting all biotic components trophically, either directly or indirectly. The thickness of the black arrows representing these interactions can be weighted according to ecological effect. However, full-community multiplex networks are difficult to construct because they require extensive datasets that are unavailable for most systems. Interactions between networks can be linked by shared species, but no current theory exists for weighting links between trophic and non-trophic networks (indicated by red dotted lines).

of interaction matrices (Colwell et al., 2012). Various hypothetical and empirically based co-extinction simulation models have been constructed across different biome and interaction network types (Strona & Bradshaw, 2018), with a particular focus on simulating primary and secondary extinctions in **unipartite** and bipartite networks (Dallas & Cornelius, 2015; Koh, Dunn, et al., 2004; Strona & Bradshaw, 2018; Valiente-Banuet & Verdú, 2013).

While showing that the primary extinction of a species can precipitate the secondary extinction of others, the process of predicting relative extinction risk is a more complex task. Computer simulations and network theory are modern tools that can evaluate extinction risk (Traveset et al., 2017), facilitated by simulations in large-scale studies (Baumgartner et al., 2020) and by supervised inferences of the relationships between biotic components (Poisot et al., 2016). Simulations are generally constructed under a set of user-defined assumptions, with extinction risk for a given species estimated from different exposures to a theoretical list of different conditions (Baumgartner et al., 2020). However, the main challenges limiting the realism of such simulations are devising realistic assumptions to trigger secondary extinctions for species in a network, and the difficulty of accounting for the effects of complex trophic and non-trophic interactions.

Co-extinction simulations, conventionally derived from probability-based co-extinction models (Koh, Dunn, et al., 2004; Memmott et al., 2004), provide estimations of potential species

extinctions linked to the loss of associated species. Such simulations rely on the premise that affiliated extinctions occur in a random sequence, typically within bipartite networks, and have since developed into an array of more advanced methods. These include topological models that simulate co-extinction when a non-basal species loses all or most other species in the food chain on which it relies (Dunne et al., 2002), stochastic models that also account for variation in demographic dependencies among species (Vieira & Almeida-Neto, 2015), and hybrid co-extinction models that combine topological and simulation models for different species types (Traveset et al., 2017) to estimate complex extinction probabilities based on the removal and persistence of nodes. Other approaches include the dependent random-search co-extinction model (Baumgartner et al., 2020) that improves the realism of extinction estimates by accounting for how extinction processes affect not only node removal, but also how their interactions change or are rewired following node extinctions where novel interactions are designated randomly 'depending' on similarities among nodes.

Although many existing simulation models can account for processes of co-extinction and trophic cascades, several complications and limitations need to be addressed. Techniques to simulate co-extinctions are usually designed for specific studies or network types (Dunn et al., 2009; Koh, Dunn, et al., 2004). For example, simulations designed for bipartite networks with two trophic guilds cannot normally accommodate the multiple trophic levels

making up entire food webs. Much of the research in community ecology has also attempted to estimate the resilience of ecological networks under various perturbations (Dallas & Cornelius, 2015; Wilmers, 2007), as opposed to quantifying the co-extinction risk of specific nodes within networks. Moreover, simulation methods that can be applied to networks with multiple trophic guilds are primarily restricted to simulating hypothetical scenarios that are focused on either top-down or bottom-up trophic cascades, but not both (Llewelyn et al., 2022; Strona & Bradshaw, 2018).

While many existing simulation models consider processes of co-extinction and trophic cascades, the functional importance of different species within a community can potentially alter how inferred linkages emerge (Brodie et al., 2014). Functional importance can be quantified by relative position within a trait hypervolume—that is, all traits (e.g. morphology, behaviour, life history; Kissling et al., 2018) represented by all species within a given space and time. These traits together represent the functional diversity or richness of a particular hypervolume (Lundgren et al., 2020; Pimienta et al., 2020) describing the community's total trait variation (Roscher et al., 2012). The more trait redundancy in the hypervolume, the greater a community's resilience to perturbation, and therefore, its potential to resist extinction cascades (Lundgren et al., 2021). Species-level trait databases (Pimienta et al., 2020) analysed using Gower similarity or dissimilarity matrices (Gower, 1971) can be used to construct such trait hypervolumes (Lundgren et al., 2020; McLean et al., 2019) that contextualise community composition and interaction potential based on their functional compatibility. The position of species within a network can also be used as a measure of functional importance (Bello et al., 2023), although different measures (e.g. degree, which surmises the total number of edges connected to a node) reflect different aspects of 'importance' (Cirtwill et al., 2018).

By ascertaining the functional importance of species within a community, we are equipped to determine the functional compatibility and potential interactions between species. This process can reveal which traits play pivotal roles in facilitating interactions with other species (Lavorel & Garnier, 2002). Furthermore, estimating the functional importance of a species within a community can reveal emergent properties of the relative functional roles of specific taxonomic groups (Dehling & Stouffer, 2018). Species that are functionally unique or that contribute disproportionately more to the functional diversity of a community are more likely to form foundational linkages within that community (Estes et al., 2016). The loss of such species might, therefore, have a higher relative probability of eliciting cascades.

7 | IMPLICATIONS FOR MANAGEMENT AND CONSERVATION

Not considering most biotic interactions in an ecosystem likely underestimates future extinction risk (Strona & Bradshaw, 2018); therefore, network-based analyses provide a relevant framework to clarify ecosystem-level processes and consequences (Harvey

et al., 2017). Quantifying, inferring and simulating biotic interactions give deeper insights into how anthropogenic threats will erode entire ecosystems via co-extinctions (Desjardins-Proulx et al., 2017; Pomeranz et al., 2019; Tylianakis et al., 2008). As climate disruption compounds other extinction drivers like habitat loss (Benton et al., 2021) and invasive species (Essl et al., 2020), network models offer a useful way to explore the potential ecosystem-wide effects of future biodiversity loss and change, by simulating emerging interactions and the loss of existing interactions that can rearrange species assemblages in otherwise unpredictable ways. Measuring how the topology of interactions within a community degrades in response to perturbations can also identify the extent to which resilience to future environmental change declines concomitantly (Strona & Bradshaw, 2022).

Single-species management frameworks have historically dominated environmental decision-making (Lindenmayer et al., 2007), but sensible environmental policy relies on identifying and avoiding environmental tipping points (Hillebrand et al., 2020) (i.e. events that depend on species' interactions and multiple scales of complexity; Landi et al., 2018; Wolanski & McLusky, 2011). Comprehensive ecological network models can represent these interactions over different scales of complexity and so improve the accuracy of predictions, enabling policies that will have a higher probability of avoiding negative tipping points (Dunne & Pascual, 2006). Ecological network modelling might better inform environmental management by simulating possible outcomes under a broad set of assumptions; for example, network models can be applied to predict and mitigate the effects of biological invasions on native communities, or even possibly to evaluate different intervention strategies and avoid ineffective species translocations (Morris et al., 2021). Extended outcomes of this type of research could also assist with recognising co-extinction risk in threatened-species assessments and policies (Moir & Brennan, 2020). As such, ecological network modelling is poised to add considerable power to the management of biodiversity (Schuwirth et al., 2019), although in practical applications, there are many issues relating to model feasibility, data availability and communication transparency that could limit the utility of these methods (Schuwirth et al., 2019).

8 | CONCLUSIONS

The trophic complexity of some terrestrial ecosystems and the spatial and temporal uncertainties of community boundaries have made resolving trophic networks difficult. Combined with the dearth of empirical data on species interactions (Momal et al., 2020) and the difficulty and costs associated with collecting such data (Pringle & Hutchinson, 2020), quantifying how species interact within a community remains a challenge. Comprehensive research for constructing trophic networks that realistically model ecological interdependencies, coupled with robust methods for quantifying extinction risk, are still needed to predict and manage the indirect effects of climate change and other anthropogenic threats. More research to

test assumed processes and inference accuracy will make these approaches more realistic, guiding current and future decisions in the management of terrestrial ecosystems (see Section 9).

9 | OUTSTANDING QUESTIONS

- How do anthropogenic threats like climate change affect the extinction risk of vertebrate species through the processes of co-extinction and trophic cascades at fine spatiotemporal scales? Previous research has tended to focus on either marine or freshwater ecosystems, with comparatively little research on terrestrial ecosystems. Understanding how anthropogenic threats affect these communities, specifically between multi-trophic and non-trophic networks at fine spatiotemporal scales, will be necessary for effective multispecies conservation.
- Can machine-learning algorithms be used to infer all predator-prey interactions for vertebrates in terrestrial communities? Although many trophic networks have been constructed, few studies have attempted to model all the interactions in entire (and diverse) terrestrial systems, with many difficulties surrounding the quantification of trophic relationships between species.
- How might a change in a community's detail (e.g. intraspecific variation) and composition affect how trophic cascades and co-extinctions occur in co-extinction models? Identifying all potential trophic interactions among species in an ecosystem is a complex element that is typically neglected in many co-extinction models that instead progressively remove species and ignore how species might rewire their interactions when other species are lost or join the community. Furthermore, basal resources (e.g. invertebrates and plants) in terrestrial network models are typically ignored or clumped due to a dearth of data, developing a gap in our understanding of the dynamics of food webs.

GLOSSARY

Bipartite network	An interacting relationship between two groups of species, such as that between plants and pollinators within a biological community.
Co-extinction	The cascading process in which the primary extinction of a species results in the secondary extinction of another, dependent species.
Edge	In an ecological network model, edges represent the relationship (e.g. biomass flow, trophic interaction) between nodes.
Nestedness	The pattern in which species interactions within a network are organised such that

less-connected species tend to interact with only a subset of the species that are more connected. This results in a nested structure, where the interactions of the less-connected species are a subset of those of the more connected species.

Networks

A complex system of interactions between different biotic components, where the interactions can be direct or indirect and can involve a variety of mechanisms and functions. These components can include individual organisms, populations, communities or ecosystems, and they can be connected through different types of relationships, such as mutualism, predation, parasitism, competition or facilitation.

Node

In an ecological network model, nodes can represent a biotic component (e.g. species, functional groups) connected by edges.

Random forest

A supervised machine-learning algorithm based on ensemble learning that uses input data to construct and merge decision trees to predict an outcome.

Single-species management frameworks

A management strategy that specifically focuses on conserving individual species, excluding other associated or dependent species from direct intervention.

Top-down and bottom-up trophic cascades

The process by which species going extinct at one trophic level (consumers) causes species occupying lower trophic levels (resources) also to go extinct (top-down) or vice versa (bottom-up).

Unweighted and weighted relationships

A weighted interaction link is a relationship between two species in which a numerical value represents the strength of the interaction; an unweighted link does not account for interaction strength.

Unipartite network

An interacting relationship such as predation in which only one group of species interacts with all other species within a biological community.

Quasi-closed ecosystem

An ecosystem that functions as if it is closed to external influences, with little exchange of matter or energy with its surroundings

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CONFLICT OF INTEREST STATEMENT

All authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

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