



# Climate change can disrupt ecological interactions in mysterious ways: Using ecological generalists to forecast community-wide effects

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## ABSTRACT

Ecological interactions are the backbone of biodiversity. Like individual species, interactions are threatened by drivers of biodiversity loss, among which climate change operates at a broader scale and can exacerbate the effects of land-use change, overharvesting, and invasive species. As temperature increases, we expect that some species may alter their distribution towards more amenable conditions. However, a warmer and drier climate may impose local effects on plants and animals, disrupting their interactions before noticeable changes in distribution are observed. We used a mutualistic trio from the temperate forests of South America to theoretically illustrate how climate change can disrupt ecological interactions, based on our current knowledge on this system. This study system comprises three generalist species with intersecting roles: a keystone mistletoe, a pollinator hummingbird, and a frugivorous marsupial that disperses the seeds of many species. On the one hand, drought causes water stress, increasing mortality of both mistletoe and host plants, and reducing the production of flowers and fruits. These resource shortages negatively impact animal's foraging opportunities, depleting energy reserves and compromising reproduction and survival. Finally, warmer temperatures disrupt hibernation cycles in the seed-dispersing marsupial. The combined result of these intersecting stressors depresses interaction rates and may trigger an extinction vortex if fail to adapt, with deep community-wide implications. Through negatively affecting generalist mutualists which provide resilience and stability to interaction networks, local-scale climate impacts may precipitate community-wide extinction cascades. We urge future studies to assess climate change effects on interaction networks rather than on singular species or pairwise partnerships.

## 1. Introduction

Ecological interactions are the backbone of biodiversity [1–3]. The way in which species within a community interact with each other determines species diversity, community composition, and ecosystem dynamics [4]. However, ecological interactions are also affected by the drivers of biodiversity change worldwide (i.e., land-use change, invasive species, overharvesting, and climate change [5]) that threaten populations and compromise its persistence. Climate change operates at a broader scale than other drivers and can exacerbate the effects that land-use change, invasive species, and overharvesting impose upon biodiversity [5, 6]. The temperature increase that Earth is currently facing is changing the game rules for most species, already manifesting in no-analog scenarios (i.e., combinations of novel climates and species ar-

rangements [7]) that impose strong selective forces upon biota [8–10]. Those novel climate change scenarios may favor some species and disadvantage many others, but its effects on ecological interactions are likely far more complex and intertwined [11, 12]. In many cases, species loss is a consequence of the disruption of ecological interactions [13, 14], which usually take place before we notice significant changes in the abundance and occurrence of individual species [15].

As temperature increases, we expect species to alter their geographic distribution. Under a climate change scenario, species can either move, go extinct, or adapt. Therefore, those species able to disperse beyond their original range are expected to move towards the poles or higher altitudes, where climate conditions are more amenable [16]. Rare events like waif dispersal and vagrancy are becoming disproportionately important as individuals colonize new areas beyond their known distributional ranges [17]. However, not all species are able to change their

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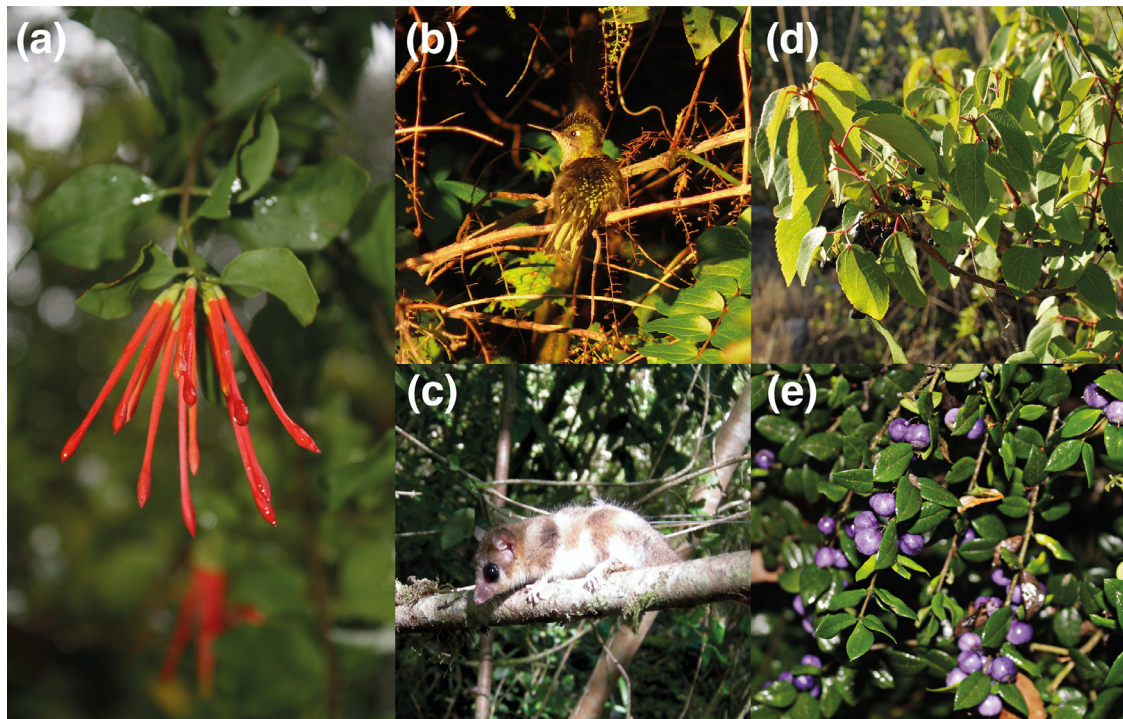
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**Fig. 1.** Common species from the temperate forest of South America: (a) the mistletoe *Tristerix corymbosus*, (b) the hummingbird *Sephanoides sephaniodes*, (c) the arboreal marsupial *Dromiciops gliroides*, and the most common mistletoe host plants (d) *Aristotelia chilensis*, and (e) *Rhaphithamnus spinosus*. Photo credits: panel (a) Johana Villagra, panels (b), and (c) Francisco E. Fontúrbel, panels (d) and (e) Sebastián Cordero.

ranges in the same way or at the same time, resulting in drastic range reductions in taxa with poor dispersal abilities (e.g., bumble bees [18]). In this sense, plants would be among the most affected species as they are sessile organisms that cannot shift their ecological niches in short time periods. Some members of co-dependent species assemblages may have different dispersal abilities (and consequently different probabilities of altering their range), leading to spatial mismatches that may disrupt assemblage-wide interactions [19]. Likewise, changes in species' phenology resulting from temperature increases can produce temporal mismatches among interacting species [20]. While these mismatches have solid theoretical foundations, they are mainly invoked to model long-term consequences of climate change and usually assume that other local conditions remain constant. Nevertheless, recent evidence suggests that short-term local changes may be taking place [e.g., 11, 12], disrupting ecological interactions before changes in distributional ranges are apparent. To illustrate this point and to understand how local effects can disrupt ecological interactions as a consequence of climate change, we used a highly-specialized mutualist system (composed of a keystone mistletoe, its generalist mutualists, and its host plants; Fig. 1) from the temperate forest of South America sensu [21] as a worked example to highlight the value of focusing on interactions as modules of climate change impacts and stimulate new research in this topic. Unlike previous work that has focused on ecological specialists, our mutualistic trio are all ecological generalists, providing a window into the direct and indirect impacts of climate perturbations and showcasing how those disrupted interactions can send ripples of change throughout ecological communities.

### 1.1. The study system—a mutualistic trio of generalists

Our study system is composed of species inhabiting the temperate forest of South America, considered a biodiversity hotspot due to its high levels of endemism, in terms of both species but also deeper and older lineages [22, 23]. These forests are characterized by an oceanic

climate with Mediterranean influence with annual precipitation ranging from 2350 to 4000 mm [24]. Within these temperate forests three interdependent species coexist: a mistletoe, a hummingbird, and an arboreal marsupial (Fig. 2). The main species is the hemiparasitic mistletoe *Tristerix corymbosus* (Loranthaceae), a widely distributed species along central and southern Chile [25]. As with other mistletoe species (more than 1300 species worldwide), *Tristerix corymbosus* depends on hosts where it establishes and on animals that pollinate its flowers and disperse its seeds to suitable hosts (appropriate host and suitable branch size [26]). Like most mistletoes, *T. corymbosus* is considered as a forest keystone species [27] because it provides food resources for animal species during periods of scarcity (i.e., austral winter [28]). This mistletoe flowers between March and September, and fruits throughout summer, from October to February. Also, it facilitates host reproduction by attracting mutualists (i.e., pollinators and frugivores), increasing recruitment up to four times compared to non-parasitized plants [29]. While *T. corymbosus* has a wide host range (~30 plant species) and could be considered a generalist parasite across its geographic range, which ranges from 30 to 42°S, comprising sclerophyllous forests and temperate rainforests [30], it displays clear host preferences at local scales. Within the temperate forest of South America, the principal host is *Aristotelia chilensis* (Eleocarpaceae) [30] representing 36% of the infected hosts.

The second species is the main pollinator. Mistletoe pollination is effected by the generalist hummingbird *Sephanoides sephaniodes* (insects are infrequent pollinators) [28, 31]. Resident *S. sephaniodes* populations heavily rely on *T. corymbosus* winter flowering to obtain nectar resources that are particularly scarce during this period [28]. Also, *S. sephaniodes* is the main vertebrate pollinator within these forests, responsible for pollinating ca. 20% of its vascular flora [32] including many dominant plant species (e.g., *Fuchsia magellanica*, *Rhaphithamnus spinosus*, and *Embothrium coccineum*). The third species is the frugivore that disperses mistletoe seeds. In the temperate forest of South America, mistletoe seed dispersal is almost exclusively performed by the nocturnal arboreal marsupial *Dromiciops gliroides* [33], and its activity period



**Fig. 2.** Distributions of *Tristerix corymbosus*, *Sephanoides sephanioides*, and *Dromiciops gliroides* in Chile. The distribution of these three species overlap in the temperate rainforest ecoregion, which is highlighted in green color.

(during the austral spring and summer) overlaps with *T. corymbosus*' fruiting period. During the cold months (April to August), *D. gliroides* is hibernating to reduce the metabolic costs [34, 35]. *Dromiciops gliroides*, the sole living member of the order Microbiotheria, is a generalist frugivore responsible for dispersing the seeds of at least 16 plant species [36]. A fruit color polymorphism is likely to be the reason of such specialized interaction (ripe fruits remain green, precluding detection by seed-consuming birds [25]). This highly asymmetric relationship between the mistletoe and its mutualists (i.e., the mistletoe depends more on the mutualist than the mutualist depends on the mistletoe) allows us to study changes in this system without the confounding effects of redundant species (i.e., other pollinators and seed dispersers) [37]. Given the tight association between the mistletoe and its seed disperser [38], it has been established that *T. corymbosus* local extinction is coupled with *D. gliroides* local extinction as a consequence of habitat loss and fragmentation [13]. Also, this mistletoe depends on some host plant species [30], which are also facing climatic and biotic constraints in a warming world.

## 2. The local effects of climate change

### 2.1. Local effects on plants

One of the most striking consequences of climate change is the increasing drought incidence. Globally, drought events are getting more frequent and more severe [39, 40]. Such unusual drought events may exceed plant's ability to tolerate water shortage, imposing severe water stress conditions [40, 41]. Water stress limits flower and fruit production on both the mistletoe and its host plants, affecting food availability to those animals that feed upon those plants, which largely influence the outcome of pollination and seed dispersal processes [11, 12]. Furthermore, water stress can increase plant mortality and reduce growth rates, ultimately impacting primary productivity [42]. Mistletoes have more negative water potentials than their hosts to ensure uninterrupted water supply from them [43–45]. Consequently, mistletoes have high transpiration rates, which result in large water demands [46, 47]. This is not a problem in normal conditions, but under severe water shortage



conditions, mistletoes dry out the host [48, 49]. If the host dies, the mistletoe will inevitably die within a short time as well which will have direct negative impacts on nectar and fruit availability.

The 2010–2018 megadrought across south-central Chile had a severe impact on precipitation regimes and vegetation [40, 50]. Precipitation declines were up to 90%, which caused dramatic reductions on soil moisture that resulted in extensive vegetation mortality [39, 51]. In our study system, this is the most severe drought in the last 50 years (12 standard deviations below the historical mean, representing a precipitation reduction of 97.5%), and caused a significant reduction in flower and fruit production of *T. corymbosus* [11]. While flower production reduced by ~50% during the drought year, *S. sephanioides* visitation rates were similar. As there were less flowers, fruit production was also reduced by ~50%, and *D. gliroides* visitation rates have reduced by ~65% during the drought year, compared to a regular year (2012 vs. 2015 in this case). Also, mistletoe mortality doubled in the same period [52], largely driven by an increase in the mortality of their host plants. For instance, laboratory experiments showed that *A. chilensis* are sensitive to severe drought conditions, in which leaf water potential significantly decreases along with the number of young leaves [53].

## 2.2. Local effects on animals

The drought-induced reduction of flower and fruit production had a direct impact on the animals that feed upon them. At the community level, water shortage reduced not only resource quantity but also resource diversity and quality [12, 54]. Therefore, relying on decimated resources negatively affect animal body condition and energy reserves, ultimately compromising their reproduction and survival [55].

This issue may be particularly critical for hibernating animals (such as *Dromiciops gliroides*), which interrupt their euthermic thermoregulation to save energy and survive when resources become scarce (e.g., winter [56]). These animals may be disproportionately affected by changes in overall annual temperature and seasonal fluctuations. Recent evidence from field studies indicates contrasting effects because climatic change may be beneficial in one season but detrimental in another because life-history strategies vary between these time periods [57] or because animals modulate torpor frequency and depth depending on food availability [58, 59].

A recent field study by Nespolo et al. [35] confirmed that this is the case with *Dromiciops gliroides*, which changes its torpor frequency during hibernation depending on both food availability and ambient temperature. Thus, local effects of climate change can impact these animals via multiple pathways. First, the reduction in fruit availability (as explained in Section 2.1) will affect energy reserves (fat) gathered during the active period (i.e., austral summer), making the hibernation period riskier. Second, the occurrence of warmer winter days (i.e., days with ambient temperature over 5 °C) force *D. gliroides* individuals to arouse earlier from hibernation (which has a very high cost in energetic terms), increasing daily energy expenditure tenfold [34]. From this evidence, we determined that *D. gliroides* needs a minimum number of cold days per year to be able to survive the winter with the energy reserves. When hibernating, a 30-g *D. gliroides* individual consumes approximately 10% of the energy needs of an active animal. Given that this marsupial arouses from torpor when temperatures surpass ~13 °C (or when fat reserves are exhausted), then increasing energy expenditure above food availability in winter, the minimum cold days per year that a *D. gliroides* need to survive is approximately 60–70 days. Another important factor is synchronization with flowering. Given that simple sugars are crucial for this species to maintain activity, during emergence from hibernation it is important that they find fruits. Otherwise, they suffer a malnutrition syndrome that kills them in a few days, even if food is available (RFN unpublished data). Therefore, the combination of depleted energy reserves and increased energy expenditure during periods of scarcity periods is likely to reduce survival. Furthermore, being an animal from a humid environment, *D. gliroides* exhibits low drought resistance [60],

thus becoming more vulnerable to warming and dehydration. This was demonstrated by Balazote-Oliver et al. [61] with a longitudinal study in Argentina, in which significantly lower *D. gliroides* abundances were reported during an unusually dry summer.

## 3. Effects on ecological interactions

The local effects of climate change on plants and animals can affect their ecological interactions in many ways (Fig. 3). Water stress can also alter floral traits that are relevant for interactions with pollinators. For example, plants experiencing water stress have smaller corollas and produce less nectar, being both less attractive and less rewarding to pollinators [54]. Likewise, water stress can compromise fruit size and quality [62]. Therefore, water shortage is likely to compromise both quantity and quality of flower and fruit resources available, particularly for those species that are not adapted to xeric conditions. Looking beyond mistletoes, host plants are also severely affected by drought events. Therefore, parasitized plants will experience more acute water stress [43], increasing its mortality probability compared to non-parasitized plants. Thus, plant-plant interactions can also be affected by the relative sensitivity to water shortage of each host plant species.

In our study system, the results reported by Fontúrbel et al. [11] imply a larger pollen transfer during drought years but also a greater nectar resource limitation. In the case of seed dispersal, the scenario is more critical as fewer fruits plus fewer visits result in a dramatic reduction of seed dispersal services. Considering that water stress not only impact mistletoes but also other fleshy-fruited plant species as well (mainly *Aristotelia chilensis*, *Rhaphithamnus spinosus*, and *Ugni molinae*, which are common sub-canopy species), overall resource availability for *D. gliroides* has dramatically reduced, impacting its energy reserves for the winter [34]. Further, the mutualists associated with *T. corymbosus* are also responsible for the pollination and seed dispersal of many native plant species at these forests [28], leading to cascading effects at the community level. The keystone mistletoe *Tristerix corymbosus* is particularly affected, which is the main food source for the hummingbird *Sephanoides sephanioides* (the main vertebrate pollinator in this system, which relies on this mistletoe for nectar provision during the winter) and for the relict arboreal marsupial *Dromiciops gliroides* (the main frugivorous vertebrate of these forests, responsible for the seed dispersal of many plant species).

This example illustrates the complexity of climate change effects on ecological interactions beyond potential long-term distributional mismatches. There is more than meets the eye: ecological interactions may be more susceptible than we initially expected. These interactions can be disrupted long before major distribution changes occur, especially if those species are unable to adapt to the novel climatic conditions. Such phenomena would be stronger in highly seasonal (e.g., temperate forests) and biologically depauperate (e.g., islands) ecosystems. While most studies stress the effects of biodiversity loss on specialist species, generalist species are usually overlooked. We contend that the network of interactions that define generalist species acts as a scaffold that ties communities together, buffering them against stochastic disturbances and, therefore maximizing lineage persistence through evolutionary time. In our study system, the three mutualistic species involved are ecological generalists, which are connected with many co-occurring plants that serve as hosts for mistletoes, provide flower resources that attract *S. sephanioides* pollinators, and provide fruits to attract *D. gliroides* dispersers (Fig. 4). In many cases, the same plant species that serve as mistletoe hosts are pollinated by *S. sephanioides* and dispersed by *D. gliroides*. These three generalist species constitute central nodes within the temperate forest network. Therefore, if those three generalist species are impacted by climate change, cascading effects would rapidly spread to other plant species reliant on them and other animal species interacting with those plants.

Beyond pollination and seed dispersal interactions, other less evident interactions can be affected, as is the case of plant-plant facilitation [29],

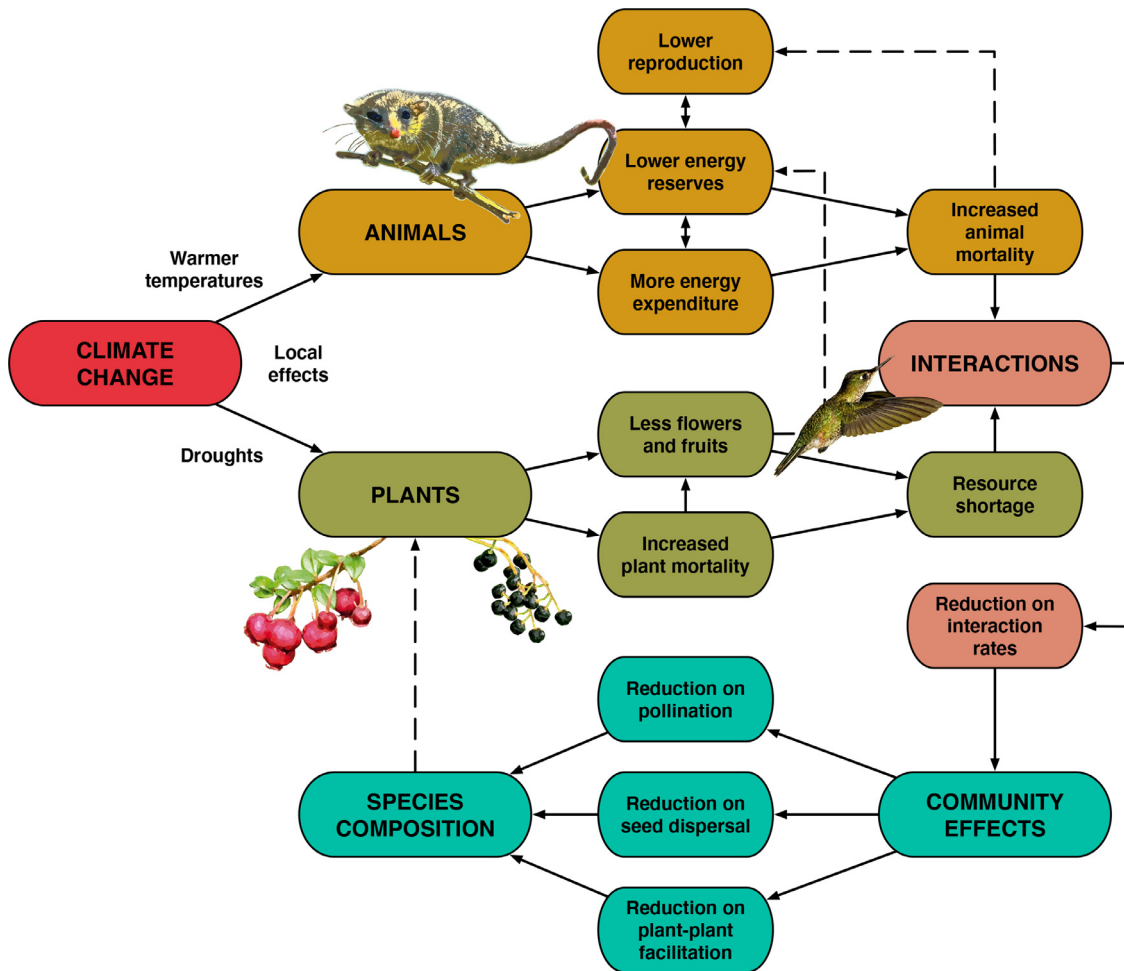


Fig. 3. Flowchart of climate change local and community-wide effects. Solid lines represent direct effects and dashed lines represent indirect effects. Arrows indicate the direction of the effect. Different colors are used to differentiate the different processes involved.

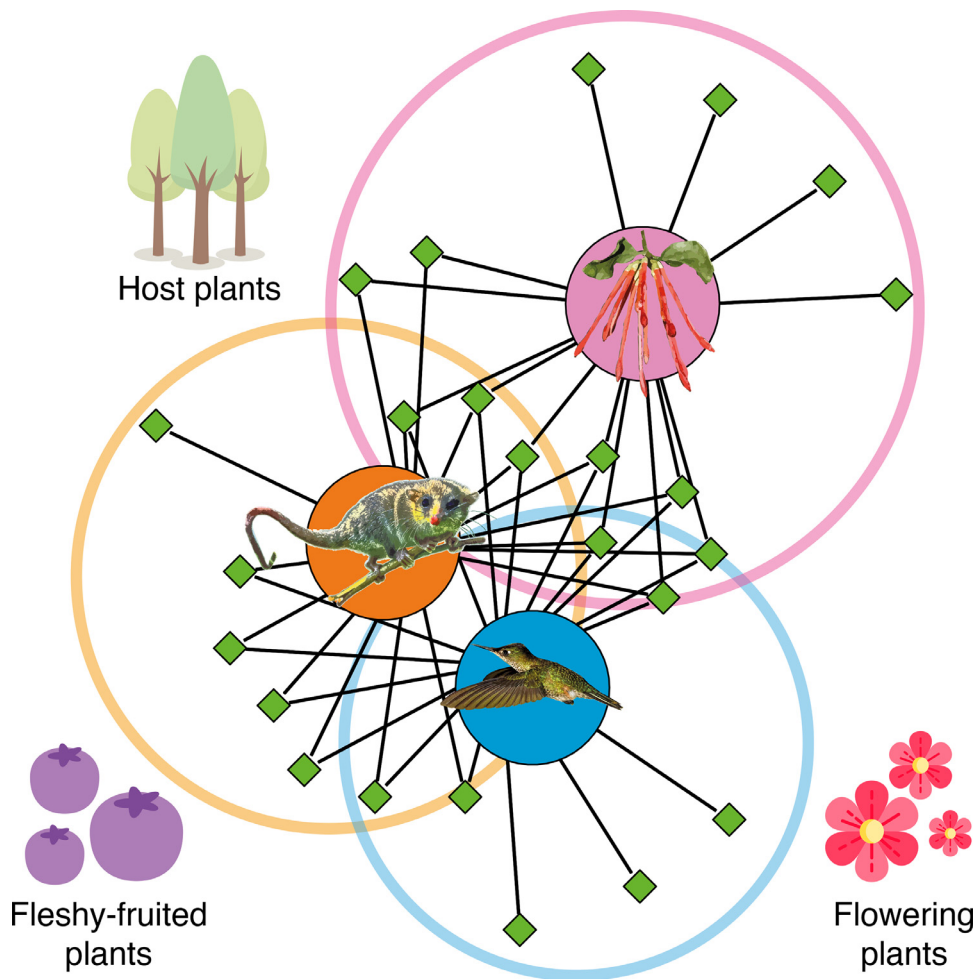
63]. Besides attracting mutualists [29], mistletoes play a remarkable facilitation role in many ecosystems. They can provide a significant nutrient input to the system via litter deposition and create microhabitat for many animal species [64, 65]. Therefore, an increase in mistletoe mortality due to drought stress [11, 52] is likely to disrupt plant-plant facilitation interactions and nutrient cycling pathways along with plant-pollinator and plant-frugivore interactions.

#### 4. Climate change as an ecological trap

The evidence compiled here could be interpreted as a particularly complex kind of ecological trap for these species. In our study system, the climatic and historical factors that promoted specialization are effectively backing them both into a corner. This ecological trap will be particularly critical for *D. gliroides*, today recognized as the last living representative of Microbiotheria, an ancient marsupial line [66, 67]. It has been postulated that mistletoes first colonized the canopy (transitioning from root to stem parasitic plants) via seed dispersal by arboreal marsupials like *D. gliroides* in the Eocene [68, 69], paving the way for subsequent diversification with the rise of fruit and nectar-feeding birds [68, 70]. Ancestors of today's *D. gliroides* (about 13 fossil Microbiotheriid species, [71]) played an important role as seed dispersers in this group of plants, and the continued presence of *T. corymbosus* within the temperate forest of South America is reliant upon *D. gliroides* [25]. This longstanding mutualistic interaction catalyzed key innovations in the evolution of mistletoes and now are in danger due to climate change.

We can expect some local extinctions of the interacting species if they are unable to move to other areas with more amenable climate conditions or to adapt to the novel climate. In this case, mistletoes would be the more sensitive component, as they are the species with the least movement capabilities. In a more critical scenario, however, warmer and dryer summers may result in population-wide starvation for *D. gliroides*. The physiological traits that made *D. gliroides* a successful species capable of persisting for over 60 million years in seasonally cold environments [34, 56], might now condemn it to extinction.

The eventual extinction of *D. gliroides* would lead to the extinction of *T. corymbosus* within the temperate forest of South America (where birds do not disperse it), which will indirectly compromise the persistence of resident *S. sephanioides* populations. Thus, this cascade of events may result in different possible scenarios, from rapid adaptation and reorganization of interactions under novel climate conditions, to triggering an extinction vortex if they fail to adapt. Either way, these changes would entrain irreversible alterations to community composition. An example of these cascade effects is the introduction of exotic herbivores into this system, which feed upon host plants, reducing mistletoe abundance and consequently reducing food resources for pollinators and frugivores [14]. Therefore, with the two main mutualistic interactions disrupted, pollination and seed dispersal patterns will be reshuffled, resulting in non-analog communities dominated by wind-pollinated and -dispersed plant species [72]. Ecological interactions are the core unit of climate change impacts. Based on Janzen's [1] original idea, what escapes the eye is a much more insidious kind of extinction: the extinction of ecolog-



**Fig. 4.** Hypothetical ecological relationships of three generalist species within the forest community (this generalization was made upon real data), arranged as an interaction network. Circles represent the generalist species: pink circle represents the mistletoe *Tristerix corymbosus*, the blue circle represents the hummingbird *Sephanoides sephanioides*, and the orange circle represents the arboreal marsupial *Dromiciops gliroides*. Green squares represent plant species that serve as mistletoe hosts, are pollinated by the hummingbird, or dispersed by the marsupial. Intersecting circles represent the ecological associations driven by the three generalist species.

ical interactions [15]. This is valid for any system, in which we may find the critical points that are likely to be more affected by climate change and have community-wide cascade effects. In this regard, network analysis may be particularly useful to identify those nodes that are likely to be more sensitive to climate change (e.g., mosses [73]) and may disrupt key ecological interactions.

## 5. Conclusion and perspectives

Climate change is likely to alter and disrupt ecological interactions before significant changes in species composition and distribution become apparent. Local effects impact plant and animal species in different ways, which have direct and indirect effects on ecological interactions. In this regard, the community-wide effects of climate change would be more severe when generalist species are compromised, as they confer resilience and stability to their interaction networks. Therefore, focusing analysis on those ecological generalists that play a central role in the ecosystem (as the triad of mistletoe-hummingbird-marsupial that we used to illustrate this point) may provide a window into the direct and indirect mechanisms underlying climate change impacts.

We urge future studies on climate change impacts to focus on ecological interactions rather than individual species. Usually, interactions are disrupted before species extinction, leading to complex cascade effects that are hard to predict on species-by-species or site-by-site assessments. While specialist species are often used to forecast the effects of climate change due to their sensitivity and ecological singularity, generalist species—particularly generalist mutualists—are the backbone of biological communities and can also be affected by climate change, compromising many other species interacting with them across the commu-

nity. Despite being largely overlooked in this kind of studies, ecological generalists can provide valuable insights on short- and long-term effects of climate change.

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