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# Eco-evolutionary dynamics in different environments : implication for the maintenance and structure of ecological communities

Avril Weinbach

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# Sorbonne Université

École doctorale 227

*Sciences de la Nature et de l'Homme : écologie et évolution*

Thèse de doctorat d'Écologie

## **Eco-evolutionary dynamics in different environments: implication for the maintenance and structure of ecological communities**

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## Introduction

A cold running water stream and its nearby warmer and calmer pond will share some common species and trophic groups, like benthic algae, phyto- and zooplanktons, amphibians, herbivorous, omnivorous and carnivorous fishes and even insects or mammals like birds feeding at the surface. However, upon a closer look, you will find differences in the structure and abundances within these two communities. In the pond, you might find newts and their larvae only if no carnivorous fish is present. Only some type of strongly fixed benthic algae will survive in the stream current, providing food and shelter for animals. You will seldom find duckweed in the stream, while it might be quite abundant in the nearby pond. The interactions and the temporal dynamics of these two communities might also differ, as does the environment they live in. But what makes them unique? And what is the part played by their environment in their uniqueness?

## 1 Ecological communities in different environments

### 1.1 What is a community

In this thesis, we consider communities as a group of co-occurring species in interaction. While the word community is often used only to designate a group of co-occurring species from the same phylogenetic clade (order, genera, family...) (e.g. in empirical (CaraDonna et al., 2014) or theoretical studies (Chapman and Purse, 2011)) or from the same functional group (e.g. primary producers), we explicitly chose to focus on them via the interactions they are bound by. Their interaction strength could vary according to the species abundances and traits and their abiotic environment. We voluntarily avoid the term network, which implies numerous interacting species. In the following, the studied communities will range from very simple modules of two interacting species to full complex networks of dozens of species. All of these community studies are however intended to be answering the same research

questions, and this general term allows us to encompass all of them. Communities, therefore, vary in their number of species, relative abundance and type of interactions that connect the different populations they are composed of.

## 1.2 From species traits to an interacting community

Communities composition, structure and dynamics are of course influence by the co-occurrence of species in a specific locality (e.g. see Cazelles et al., 2016), but they show that co-occurrence data alone are not enough for a realistic communities assembly), and the relative abundance (e.g. Stang et al., 2006a) of each species. Studies like that of Proulx et al., (2005) point out the fact that ecological communities' assembly, structure and dynamics differ strongly from random networks. However, species traits are also controlling strongly the interaction between species and the response of the community to different environments. Below are some examples of different traits controlling species interaction type, strength and specificity. Later I develop the impact of the abiotic environment on the communities mediated by the species traits. Hereafter we define traits as the species characteristics evolution acts on, like morphological, functional, or life-history traits.

### 1.2.1 Trait type and interaction type

Eklöf et al., (2013) did a thorough study on the number of traits needed to explain interactions among species in communities (i.e. community structure). This question arose from niche theory, and the real dimensionality of the niche that needs to be considered in order to explain the structure and dynamics of a given community. They explore different types of interactions networks (food webs, antagonistic and mutualistic ones), and showed that only a very small number of critical traits was useful to explain a given ecological structure. The nature of the traits that seem to constrain the most the interactions within the communities differ depending on the interaction type.

Body-size ratio is of good use to predict interactions between predator and their preys. Aside from parasitic systems, predators are often larger and rarer than their prey (Brose et al., 2006; Naisbit et al., 2011). This trait as been shown by Eklöf et al., (2013) to be consistently essential in predicting the observed community structure. Being so informative, abundance and size distribution of each species can be sometimes alone used to predict a food web structure, as developed later in this introduction. Other consumer-resources interactions are best explained by the mouth part dimension of the forager and its mobility, as in many of the plant-pollinator systems (e.g. Alexandersson and Johnson, 2002), as well as constraining their metabolic requirement.

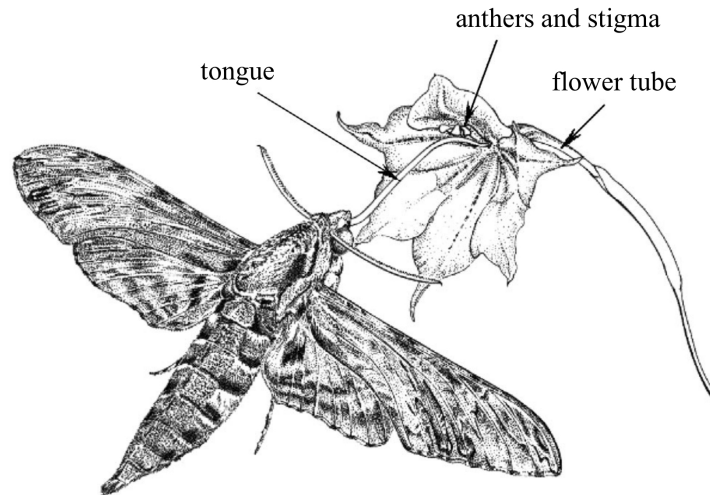
Mutualistic interaction have been shown to be mostly govern by traits like the species phenologies, as it is the case for flowering plants and foraging pollinators (Peralta et al., 2020; Sonne et al., 2020). Attractiveness traits of one species for the others are also good predictors of mutualistic interaction (some of them are consumer resources as they are based at least partly on a resource trade, e.g. as in plant-pollinator interaction). This is for example the case of flower height and floral reflectance, both influencing their visibility to potential pollinator (Junker et al., 2013).

### 1.2.2 Trait matching and interaction strength

The strength or intensity of an interaction is partly driven by the species co-occurrence, the species abundance but also the trait match (or trait difference depending on the interaction type, e.g for competition or for some types of predation (Yoder and Nuismer, 2010)) between two species.

A strong match between morphological traits can for example increase the efficiency of pollen transfer for pollination networks. Klumpers et al., (2019) recently focused on size matching between nectar tube and proboscis (the mouthpart insect pollinators use for sucking and feeding) in relation to foraging efficiency. They found that a proboscis shorter than the

nectar tube increases handling time and therefore decreases foraging efficiency. A proboscis longer than the nectar tube decreases nectar reward. This altogether led to close size matching (Klumpers et al., 2019). A similar trait match has been followed by Alexandersson and Johnson, (2002) on the hawkmoth *Agrius convolvuli*, with tongue length of 85-135 mm, and the hawkmoth-pollinated South African iris, *Gladiolus longicollis*, with nectar tube ranging from 56 to 129 mm (see figure 1 for a graphical representation of an interaction). They show that flowers with nectar tube below the hawkmoth tongue length were much less pollinated, potentially influencing the plant fitness and ultimately leading to the selection of a close match between the flower nectar tube size and the moth tongue size. Such traits could therefore be used to predict community structure in a given area (Crea et al., 2016). This trait-matching between the interactors can strongly impact the interaction strength and can override the effect of abundance by creating “forbidden links”, pairs of species that will never interact whatever their co-occurrence and abundance patterns (Vizentin-Bugoni et al., 2014).



*Figure 1: Classical example of a trait matching between a South African Iris and its hawkmoth pollinator, here represented with the moth feeding on the plant nectar at the bottom of the flower tube. Alexandersson and Johnson showed that when the hawkmoth tongue is longer than the flower tube, pollen from the anthers is not properly deposited on the moth and stigma do not receive exogenous pollen, strongly reducing the pollination rate of the plant. From Alexandersson and Johnson, (2002).*

Trait-matching can also take the form of a given ratio in between the trait values of two interactors. It is the case for the body mass-ratio between a predator and its prey. Empirical evidences are numerous to show the relationship between body size value and trophic position in food webs, especially in aquatic systems (Brose et al., 2006; Cohen et al., 1993, 2003; Emmrich et al., 2014; Jonsson et al., 2005). The food web observed in 1984 at Tuesday lake and schematized by Cohen et al., (2003), shows nicely the distribution of body size and biomass along the trophic levels, lower level preys having way smaller body masses than top predators (figure 2). On the contrary, species at the bottom of the food web are much more abundant than top predators. But how to explain these observed patterns? The size of the prey a predator feeds on depends on its searching and handling abilities, but its size also controls its metabolic requirements, ingestion rate, growth rate, abundance and other allometric scalings (Peters, 1983). This link between species body mass and metabolic rates and

requirements has been expressed formally by Brown et al., (2004), and named by them the metabolic theory of Ecology or MTE. This scaling relationship differs depending on the species but allows to include body mass in various traits and behaviours related to predation. This ratio is of very good use to predict a network structure, as shown in Cohen et al., (1993) and Gravel et al., (2013). They used a simple model with predator-prey body size relationships provided by statistical analysis, and observed great matching of their obtained community structures with empirical food webs dataset provided by Brose et al., (2006) meta-analysis . This body-size ratio between consumer and resource has already been used to successfully predict the structure of numerous food webs, and is employed in a growing body of theoretical models producing results that often match with experiments and observations (as early as this model by Yodzis and Innes, 1992, see also e.g. Allhoff et al., 2015; Loeuille and Loreau, 2005).

However there is no universal ratio value between predator and prey body mass, and the interaction strength also depends for example on the habitat and predator types (Brose et al., 2006). In another more recent study, they associate a certain body mass ratio with specific species traits, and explore especially the traits characteristic of predator groups with high body-size ratio with their prey (e.g. small vertebrates and large swimming and flying predators (Brose et al., 2019)).

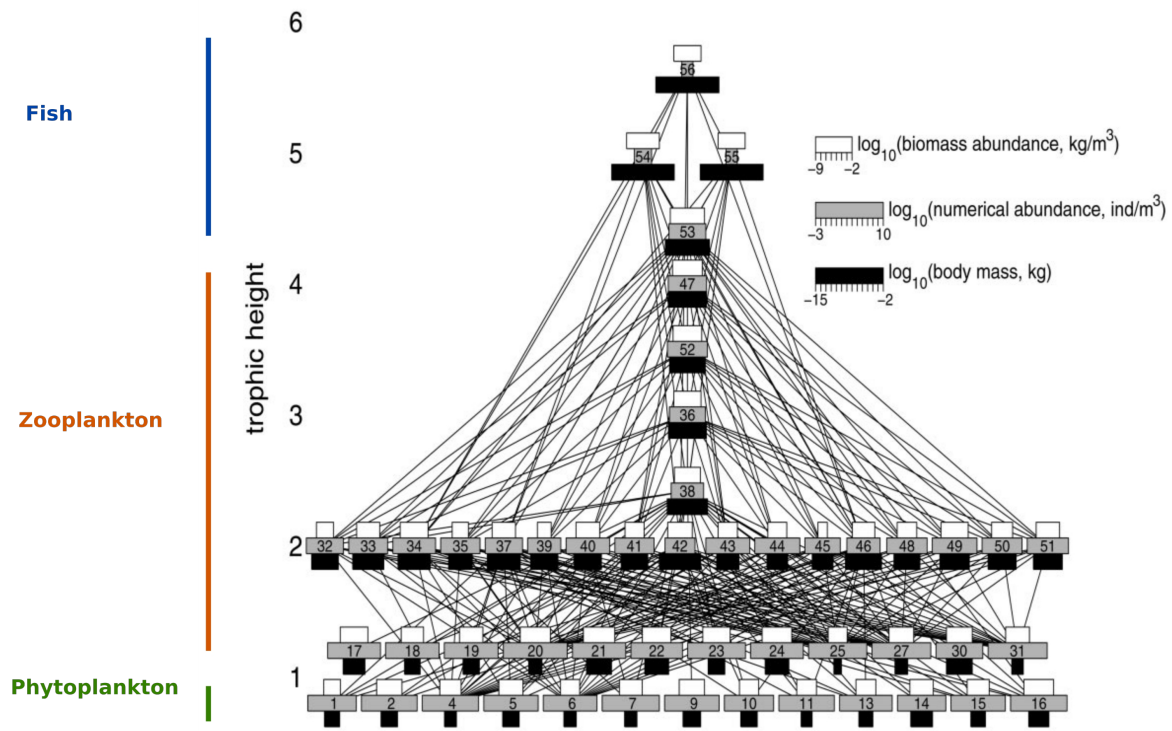


Figure 2: Schematic representation of a pelagic food web observed at Tuesday lake in 1984. The numbers represent the different species observed, correspondence to species names can be found in (Jonsson et al., 2005). The width of the black, grey and with bars. correspond to the log of the body mass, numerical and biomass abundances respectively. Adapted from Cohen et al., (2003).

Adding to abundance, spatial co-occurrence and morphological trait matching, another condition that controls the interaction between species and the resulting community in a certain locality is the temporal co-occurrence of potential interactors, also called phenological synchrony or match. Several articles point out the importance of this phenological match, especially in mutualistic plant-pollinator networks. This phenological overlap can drive the community assembly and the observed interaction patterns (Encinas-Viso et al., 2012). Using field data from a 2 years study in the arctic, Olesen et al., (2008) observed that the species turnover in the network was explained by the phenophase (the length of the phenological event) of plant flowering and pollinator activity. Recent studies even go further with very detailed empirical data. Using a 6-year data sets with specific information about species morphological trait, phenology abundance, specialisation, and pollination efficiency in a plant-pollinator community. Peralta et al., (2020), showed that the main drivers of temporal



stability and pollination efficiency was a strong morphological trait-matching and temporal overlap of the interacting species, above the potential importance of plant and pollinator abundance. Sonne et al., (2020) found similar results with 24 plant-hummingbirds interactions datasets. They also observed that morphological trait-matching and phenological overlap outperform abundance in explaining interaction frequency.

Species phenology can directly drive their position in a biological network. Taking into account this phenological trait also uncovers network properties that will otherwise be hidden. Morente-López et al., (2018) for example showed that phenological synchrony is a strong determinant of pollination networks modularity, which itself is a characteristic that influences the network stability. Mutualistic systems with numerous species are often composed of different modules of strongly interacting species, themselves loosely connected to one another. Hub species, at the centre of these modules, are key species whose loss often creates extinction cascades in the community (Olesen et al., 2007).

However, while most of these studies point out the necessity of a strong trait-matching to increase interaction intensity, numerous interaction mismatches have been reported in literature (Bolmgren and Eriksson, 2015; Kharouba et al., 2018; Miller-Rushing et al., 2010; Thackeray et al., 2010; Visser and Gienapp, 2019). Are these trait-mismatches detrimental to species interactions? While interactions that rely strongly on trait matching might suffer from a decrease in trait-match, some interaction types will on the contrary increase with it. In that case, one preferably uses the term trait difference. This is true for all interactions when one of the interactors is more efficient when outcompeting its partner species, as in competition, or for predation that requires a larger trait value from the predator than its prey (e.g. larger body size, faster running abilities). This armed race is, for example, visible in several populations competing for the same niche (Calsbeek, 2009), or, for predator-prey interactions, driving the coevolution of toxicity and tolerance, as with the garter snakes and their toxic newt preys

(Brodie et al., 2002). These interactions will on the contrary to the previous ones that are stabilised by stabilising selection, promote species diversification (Yoder and Nuismer, 2010).

### 1.2.3 Trait value and interaction specificity

While the trait type might determine the type of interaction species will contract and the intensity of the trait match or trait difference the frequency and/or intensity of their interaction, its value can also rule the degree of specificity (or oppositely its degree of generalism).

Morphological traits can predict the functional role of species and their degree of specialisation. A study on the link between morphological traits and functional roles in a frugivorous community showed that morphologically different birds foraged in different sets of plant species and had specialised functional roles in the community (Dehling et al., 2016). They used relevant traits like beak length and beak width or body mass for birds and fruit size and diameter, crop mass and plant height for fruiting plants.

For predator-preys interaction, especially those that are constrained by body-size ratio, the feeding behaviour of the predator can limit its predation ability and the variety of accessible preys that will make him a specialist or generalist in a given environment. Snakes are for example predators that cannot reduce their prey size via mastication, and are therefore very limited in the maximal prey size and shape they can feed on (Willson and Hopkins, 2011).

As for mutualistic interactions, plant-pollinators traits are often used to measure their degree of specialisation. In Peralta et al., (2020), in addition to showing a higher interaction frequency of species with well-matched traits and high phenological overlap, they point out that an increased specialisation between partners is also promoting pollination network stability. Sonne et al., (2020) also note a specialisation pattern in their plant-hummingbirds study, with increased resource specialisation at lower latitude. In their system, they explain this pattern with the specific morphological constraints imposed on tropical species. Olesen et

al., (2008) looking at some of their network properties, saw that linkage-level, i.e. the number of links per species, was positively correlated to the length of the species phenophase, and for plants to their abundance. Linkage level affects a community connectance (number of observed links between species divided by the number of potential ones) and nestedness (describing the degree in which specialist species links are a subset of generalist species ones). Those two parameters (and many others) are often used to describe a community structure, and their values give insights into the community's potential stability (Lau et al., 2017).

Specialised interactions seem therefore to be at the core of many networks, especially mutualistic ones as mentioned above (Fortuna et al., 2020). This strength of the specialised interaction is one of the key elements of networks' ecological stability in time (Olesen et al., 2008; Peralta et al., 2020). However, because of their high specificity, resulting from a long co-evolutionary process or via ecological fitting, the extinction of one of the partner species can be fatal to its interactor, and ultimately destabilise the entire community. Are these specialised species more fragile than generalist ones to changes in their environment?

### 1.3 Environmental gradients or environmental changes?

Environments are not fixed in time but vary, whether because of human activities or not. Some studies measured temporal changes in the environment and their impacts on the communities but long-term data that allow having ecological and evolutionary responses are rare (more on that in part 3 of this introduction). Instead, many studies focus on environmental gradients (Emmrich et al., 2014; Sentis et al., 2017; Tylianakis and Morris, 2017). In the following, to explore the impact of the environment on the communities we will use both examples from environmental changes and environmental gradient studies. However note that using environmental gradient requires making space for time substitution when comparing the impact of a given environmental change across studies (Blois et al., 2013). We

consider here both environmental gradients and changes caused by natural phenomena or by human activities indifferently, as they have the same impact on species, albeit sometimes with different intensities (same approach as in Tylianakis and Morris, 2017). See box 1 for more information about temporal environmental changes with human origin, i.e. Global Change, and its potential impacts on communities.

*Box 1: A rapid review of some human-induced environmental changes*

Environmental changes can be side products of human activities, and if they are at a large spatial scale and have a directional effect in time, they are referred to as global change. Some of these environmental changes can have strong impacts on communities, by changing environmental parameters they are sensitive to.

A combination of various human activities is now producing what is known as climate warming. By changing the spatial distribution of thermal niches, this global warming creates species ranges shifts (Kelly and Goulden, 2008; Parmesan and Yohe, 2003), potentially disrupting their interactions with other species. It increases the aridity period and region (Kertész and Mika, 1999), and produces catastrophic heat waves sometimes leading to the extinction of species (McKechnie and Wolf, 2010). It is also creating phenological changes, among whom the often reviewed shift toward earlier phenologies (Cleland et al., 2007). This again can potentially disrupt interactions and lead some populations to local extinction (Petanidou et al., 2014; Singer and Parmesan, 2010). Climate warming also impacts species' body-mass and the associated metabolic activities, perturbing energetic flows into trophic networks (Daufresne et al., 2009; Sheridan and Bickford, 2011).

Land-use changes have also strong impacts on natural communities. It breaks-up suitable habitats, creating mosaics of refuges in an inhospitable matrix. Land-use changes create

gradients of land-use intensification. The intensively managed areas often suffer from biotic homogenisation and simplification (Gámez-Virués et al., 2015).

These land-use changes, as well as other human-induced changes, also bring new invasive species and increase some managed species to the disadvantage of other native ones (Grass et al., 2013). These species are known as massively introduced managed species, or MIMS, and comprise the conspicuous massively flowering crops (MCF) (Geslin et al., 2017). Their interference with native biota is currently under study, and they could also be a source of strong selective pressure (Geslin et al., 2017; Holzschuh et al., 2016).

Human pollutions have various impacts on wild biota, decreasing some species abundance, disturbing their natural sensors, or perturbing resource or partner detection (McFrederick et al., 2008). Reviews on wild pollinators show a global worldwide decline (Biesmeijer et al., 2006; Potts et al., 2010) caused by a combination of pesticides and pollutant (van der Sluijs et al., 2013), parasites and diseases, invasive predators and competition with domesticated bees (Ropars et al., 2019).

Overexploitation and selective harvesting of some natural environments also strongly impact local communities. A classic phenomenon resulting from massive selective harvesting is known as “fishing down the food web”. Most marine catches focus on top predators, long-living fishes. This repeated selective harvesting has induced a decline of mean trophic position in the food web, first observed between 1950 and 1994 (Pauly et al., 1998). In response, humans have started to fish down the marine food webs, first increasing their catches. They are now decreasing, showing that current practices are unsustainable (Pauly et al., 1998) but see (Caddy et al., 1998). This disappearance of top predators has completely disrupted marine food webs, potentially leading to cascading effects on marine communities (Pauly et al., 2000).

A few human habitats and activities are however also favouring some wild communities. Urban areas are for example seen as potential refuges for pollinators (increased flowering period because of heat island effect, managed nectar sources, or reduced pesticides) (Hall et al., 2017a; Hicks et al., 2016). Offshore wind farms are another classical example of artificial constructs that are today a hotspot of biodiversity (Langhamer, 2012), the pillars of the wind turbines acting, like other hard substrates in the marine environment, as an artificial reef quickly colonised by epibenthic species (Kerckhof et al., 2010), thus leading to the settlement of complex coral communities. However, their global impact on the environment is still controversial, and biodiversity offset often forgotten in the evaluation processes (Vaissière et al., 2014).

#### 1.4 How environmental parameters affect species traits

Why do communities differ in different environments? If we compare similar community types in different environments, or follow the temporal pattern of a community in a changing environment, we can notice changes in the species abundance and diversity, the strength of the interaction and their distribution within the community. Environmental constraints can be said to act as an “environmental filter”, only authorizing the co-existence and interaction of species based on their specific traits.

##### 1.4.1 Environment as a filter of species traits

Environment filter is often defined as the local abiotic factors that constrain the establishment and persistence of species in a community via their trait states (Kraft et al., 2015; Venn et al., 2011). Therefore it is expected to also constrain the interactions within the community. Among the potential filters, the timing of snowmelt is for example crucial for the alpine communities. Focusing on plant traits like leaf area, plant height and seed mass, Venn et al., (2011) showed that earlier snowmelt favours tall and leafy plants. Light intensity is also a

very common abiotic factor tested as a filter for plant species traits. As expected, limited light affects especially slow-growing and late flowering plants in a fen community (Kotowski and Diggelen, 2004). Among many others, some studies also focus on the filtering effects of urban areas (e.g. Croci et al., 2008 for passerine birds), or the impact of landscape heterogeneity on carabid beetles traits (Dufлот et al., 2014). However, because most of these studied communities correspond to a homogeneous functional or phylogenetic group (see part 1.1 to see how this definition of a community differs from ours and why), they tend to completely put aside the potential effect of species interactions as a “biotic filter” for communities composition. If some interactions are rarely if ever present in communities thus defined (e.g. trophic interactions), others, like mutualistic and antagonistic interactions, can still impact the community assembly and persistence. A classical example of biotic filter is the strong grazing pressure imposed by an abundant herbivore in a given community. Begley-Miller et al., (2014) e.g. observed that the white-tailed deer reduced by 12 % the diversity, by 17% the richness and by 63% the phylogenetic diversity of plant species when comparing enclosure with nearby grassland. This obviously favoured a small number of browse tolerant grass species.

This is why the concept of a “filter” in itself is today challenged (e.g. Cadotte and Tucker, 2017; Kraft et al., 2015), as it is hard to properly measure in the wild, but more importantly, can be mingled and often override by biotic constraints (the majority of studies focusing on environmental filtering aren’t controlling for the impact of the present/absence of key interactors of the focal species). These filters being strong ecological pressure on the species, environmental differences can affect many of the community’s ecological parameters (abundance, behaviour, persistence).

#### 1.4.2 Changes in abundance related to species traits

We do not consider here abundance as a species trait, but trait values can affect a species abundance, which will, in turn, have consequences on the ecological dynamics of the population and communities. The relationship between body size and species abundance has been studied many times (e.g. Greenwood et al., 1996). A review by White et al., (2007) identifies four different, but interrelated, mechanisms that link a species body size to its global or local abundance. These different relationships depend on the considered scales and, while commonly observed in many empirical systems, are still uneasy to be explained via ecological processes (global energy availability, local resource partitioning among services, distribution of individual size and resource limitation at the community level). The general and intuitive pattern, also explained by metabolic scaling, is always that the greater the body size, the lower the species abundance (Peters and Wassenberg, 1983). Phenological traits are often measured alongside local abundance, but a clear link between the two is uneasy to make. However, because there is often an optimal timing for each phenological event according to the environmental condition, variation in a phenological trait can lead to diverse local abundance. The phenologies fitting most optimally to the temporal environmental conditions leads to the highest local abundance (e.g. as with the first flowering day of these grassland species, whose environmental condition favours the earliest phenological values (Craine et al., 2012)). Finally, local abundance is one of the many traits that can be considered when measuring the attractiveness of a species for a partner, and a high local abundance can increase the interaction strength and probability (Cagnolo et al., 2011; Vázquez et al., 2009). High abundance can also preserve highly connected species when environmental changes provoke the disassembly of a network, like in this plant-pollinator one (Winfrey et al., 2014).



### 1.4.3 The species versatility and interaction rewiring

Changes in the environment might affect not only the intensity of the existing interactions but also the behavioural traits of species, and especially with whom they interact. The fact that species can switch partner throughout time, i.e. interaction rewiring, is a mechanism that stabilise communities facing environmental changes. Some studies already showed that climate can change the behaviour of species in a food web, influencing the dominant energy pathways of top predators. Guzzo et al., (2017) for example studied the changes in the foraging behaviour of a lake trout in response to temperature variation. In more stressful years with shorter springs and longer summers, lake trout had reduced access to littoral habitats (with bigger preys) and assimilated less energy (small preys from deep offshore regions), therefore growing less one those years. They especially show that annual variations in preys distribution changes the trout foraging tactics (number and duration of forages) (Guzzo et al., 2017). But rewiring can sometimes change entirely the structure of a given community in cascading effects. This is frequently caused by the introduction of new species after environmental changes. With warming, large body-sized fish are moving from southern to northern latitudes. Those fish are often generalists and change the structure of the extant community (Blanchard, 2015). Arctic marine food webs are known to be species and link poor with high modularity. All these characteristics are expected to favour the community robustness to changes. With the arrival of these new top predators, the community rewiring leads to richer and more connected systems with lower modularity. Whether or not this will temporally stabilise the community on a long time scale is however uneasy to predict. Models confirm this stabilising effect of interaction rewiring. Kaiser Bunbury et al., (2010) simulated random and non-random (of either the stronger and weaker interactor) extinctions within a quantitative empirical pollination network, and observed that allowing for rewiring temporally stabilised networks compared to static ones.

Of course, that ability of a species to rewire will depend on its versatility, e.g its degree of generalism for consumer-resource interaction. A generalist species with a wider niche and more potential interactors to choose from will have a greater probability of being maintained even if its interactors change in temporal and spatial abundance (Bartley et al., 2019). Being less able to undergo rewiring, specialist species could be more fragile to environmental changes than generalist ones...

#### 1.4.4 The species persistence within the community and species turnover

Biodiversity can help maintaining species and links throughout time despite environmental changes. Many studies showed that the more diverse a community is, the more stable and robust to change it becomes (Loreau and Mazancourt, 2013; Loreau et al., 2002; Tilman and Downing, 1994). It has for example been shown to help plant-pollinator keep synchrony despite climate change (Bartomeus et al., 2013), or to increase the resistance of ecosystem productivity against climate extremes (Isbell et al., 2015).

Aside from interaction rewiring, links within a community can vary according to species turnover. This turnover results from species introduction, abundance variation and species extinction. Species introduction into a given community can result from environmental changes that render the local environment more favourable to that species. Ranges shifts due to climate changes have been numerous observed, e.g. as with this migration of Swedish tree and shrub species toward northern latitude with warming (Kullman, 2002). Species introduction can also be actively controlled by humans via agricultural and breeding practices. These land-use and management changes often result in the concentration of few species at a high abundance in a locality, i.e. massively introduced managed species like rapeseed or honeybees, interfering with local species and their interactions (Geslin et al., 2017). Alien bees are e.g. known to reduce abundance and interactions of native ones (Madjidian et al.,

2008; Ropars et al., 2019), while crops can temporarily dilute pollination efficiency and reduce wild pollinator population (Holzschuh et al., 2016).

Species extinction can be due to various environmental changes, among what the increasing temperature and phenological shifts previously mentioned. Temperature has various disturbing effects on natural communities. Experiments showed that warming alters the size spectrum and shifts the distribution of biomass on freshwater ecosystems (Yvon-Durocher et al., 2011). A meta-analyse of warming effects on food webs showed that warming first stabilises the systems until a threshold where predators die of starvation (Fussmann et al., 2014). Models (e.g. Binzer et al., 2012) and experiments (e.g. Sentis et al., 2015) also explore the effect of a temperature gradient combined with nutrient enrichments. Binzer et al., (2012) for example found that at low temperature, warming counteracts the paradox of enrichments by bottom-up and top-down effect, and that warming increases the risk of starvation of large species in low-fertility systems (Binzer et al., 2012), potentially leading to top predators extinction (Sentis et al., 2017). Changes in resources phenology can impact consumer-resource communities. Its impact on the consumer ecological dynamics differs if the resource emerges before or after the consumer. If the resource emerges before the consumer, co-existence is often maintained up to a certain consumer abundance level where the consumer goes extinct. When the resource emerges after, the consumer survival is reduced progressively with its abundance increase (model by Bewick et al., 2016). Phenological shifts, e.g. due to the increase in atmospheric CO<sub>2</sub>, can also lead to interaction disappearance, even without species extinction. Memmott et al., (2007) simulated such changes on a highly resolve empirical pollination network. They observe a decrease of 17% to 50% of plant resource availability for pollinators. This reduced species overlap also decreases the pollinators diet breadth, and all these changes could lead to interactions and species disappearance. In general, if changes are too strong or too fast, the population sometimes does not have time to

evolve and goes extinct, potentially destabilising the entire community. Many studies have shown that the loss of key species that are linked to many others can lead to catastrophic disassembly, unless the community rewires into new interactions (Thierry et al., 2011).

An illustration from CaraDonna et al., (2017) presented in figure 3, wraps up nicely these two potential outcomes, also showing that they could work in concert in reshaping a plant-pollinator community (or whatever community in question).



Figure 3: Illustration of interaction rewiring and species turnover after a change in the community's environment. Rewiring can be caused by changes in abundance and interaction intensity e.g. via species behavioural trait. Turnovers occur after extinction and invasion of species. Adapted from CaraDonna et al., (2017).

## 2 Evolution of communities in different environments

The traits previously shown as shaping the communities in different environments also influence the relative fitness value of the individuals carrying them. Individuals with traits adapted to the environment will be selected, and their increase in frequency can reshape the ecological community. Part of the trait changes are of course due to plasticity, but studies also record long-term changes owed to natural selection. Plasticity itself can result from evolutionary processes, and the variability it offers in response to changes can be of special importance in rescuing populations in very fluctuating environments (de Jong, 1995).

Species specific interactions can shape their evolutionary responses. A review by Elzinga et (2007) showed the importance of interaction in constraining the evolution of species traits. Plant flowering phenology is partly driven by its interacting pollinators (often foraging mostly

early or on the flowering peak), seed disperser preferring on the contrary off-peak and late phenologies. This affects individuals fitness and constrains the evolution of their phenology. The direction of the evolutionary pressures then depends on the interaction types (Elzinga et al., 2007). Other reviewing works found similar results. Pollinator feeding type can for example influence the efficiency of the pollination process (nectar-feeding pollinators groom less and transfer pollen more efficiently), adaptive foraging pollinators also change of resource plants more often, transferring more efficiently pollen out of a flower, decreasing geitonogamous fertilization (i.e. self-pollination by pollens of a different flower from the same plant) (Devaux et al., 2014). These can impact the efficiency of plant reproduction and the strength of the interaction with different pollinator types. The previously presented behavioural changes in different environments are also premises of potential adaptive responses.

## 2.1 Trait evolution in different environments

Environmental changes or differences in the environment can be strong selective pressures on species traits, but it can also be a diversification driver. Some rapid and strong environmental changes have already been associated with general evolutionary responses. Temperature rise is frequently associated with phenological shift (Cleland et al., 2007), species distribution changes (Kullman, 2002), and variation in body size (Gardner et al., 2011). Temperature is a strong diversification force as it increases population sizes and mutation rates (e.g. Zhang et al., 2018). A general tendency is the evolution toward earlier phenologies, shift toward northerner ranges and decreased body size with warming, but these patterns are not universals (e.g. see Gardner et al., 2011). Intensive human harvesting also selects for smaller individuals, with earlier reproduction and life cycles. Increased nitrogen enrichment with human activities is also responsible for mutualism switch to antagonism and mutualism abandonment in plant-mycorrhizae communities (Egerton-Warburton et al., 2007; Johnson et al., 2003).

All in all, the fate of an evolving community could be very diverse, especially because different types of communities are sensitive to different types of environmental changes and drivers, and will therefore respond differently to these selective pressures. Toby Kiers et al., (2010) encapsulated several environmental drivers and the potential ecological and evolutionary outcomes on different mutualistic systems. You can find a reproduction of this summarizing table in figure 4, showing for example that plant-pollinator are especially sensitive to climate change and fragmentation which affect for example the phenological synchrony and species gene flow. Plant-mycorrhizae are more sensitive to nutrient enrichment which could result in a switch to antagonism (but see Frederickson, 2017). They categorised the potential outcomes into co-extinction, switch from mutualism to antagonism, switch to novel partner and mutualism abandonment. While this table emphasises the fact that different mutualistic interaction types are sensitive to different pressures, we could extend that observation and wonder if different interaction types (e.g. antagonistic and mutualistic) results in different sensitivities to environmental changes.

Driver	Mutualism type	Ecological and evolutionary responses	Critical conservation questions
Climate change	Coral–zooxanthellae mutualisms	Expulsion and/or switching of mutualist partners <sup>1-3</sup>	Does switching facilitate invasion by antagonistic partners or increase host resilience?
	Plant–pollinator mutualisms	Changes in phenologies decouple plant and pollinator partners <sup>4-7</sup>	How resilient are hosts to changes in partner densities?
Nutrient enrichment	Plant–rhizosphere mutualisms	Spread of less effective but highly competitive mutualist partners <sup>8-10</sup>	Can evolutionary shifts towards antagonism be reversed?
Habitat fragmentation	Plant–pollinator mutualisms	Reductions in pollinator abundance and richness <sup>11,12</sup> ; changes in recruitment, gene flow and selection regimes for mutualistic partners <sup>13-14</sup>	Will 'rescue' partner species effectively replace native partners?
Overhunting	Plant–disperser mutualisms	Changes in tree recruitment patterns leading to shifts in forest composition <sup>15</sup> ; reduction of long-distance dispersal events crucial for maintaining genetic structure of tree populations <sup>16</sup>	Can landscape-level effects be predicted?
Exotic species introductions	Plant–rhizosphere mutualisms	Contrasting effects: degradation of native rhizosphere communities <sup>17</sup> vs. enhancement of exotics by native mutualists <sup>18,19</sup>	Can evolutionary shifts towards antagonism be reversed?
	Ant–plant mutualisms	Changes in seed dispersal and pollination patterns upon exotic ant invasion <sup>20,21</sup>	How rapidly can hosts respond to changes in partner species?
	Coral–zooxanthellae mutualisms	Naturalization of exotic symbiont into coral ecosystem with unknown evolutionary consequences <sup>22</sup>	Do exotic mutualistic partners displace natives? How will displacement affect hosts?
Loss of third species	Ant–plant mutualisms	Shifts in cost:benefit ratios of a mutualism via loss of an external species (e.g., herbivores) <sup>23</sup>	What is the role of external species in directing mutualistic outcomes between two partners?

Figure 4: Example of anthropogenic perturbations on different mutualistic systems, and the potential ecological and evolutionary challenges they create. From Toby Kiers et al., (2010).

## 2.2 The fate of an evolving community?

### 2.2.1 Adaptation and evolutionary rescue

In response to a non-optimal environment, new traits are potentially selected and the species may adapt and maintain their populations in the new environment. This evolution can be

rapid, especially if the population has a high abundance, high mutation rate or high reproduction rate (providing more variants and adaptation potential), and/ or a short life cycle (Gandon and Michalakis, 2002). Rapid evolution has already been observed, especially in experimental evolution studies. Rapid evolution caused by pollinator loss in *Mimulus guttatus* has been observed in an experiment comparing the flowering traits and fecundation rate when exposed to high bumblebee abundance or no pollinator (Bodbyl Roels and Kelly, 2011). The plant population with no pollinator exposure first decreases, then rebound to a viable abundance. Parallel to this rebound plant traits associated with selfing increase in this population (e.g. pollen viability or anther and stigma separation) as well as reproduction via plant selfing (Bodbyl Roels and Kelly, 2011). This rapid evolution has also been shown to slows extinction in food webs (Zee et al., 2017).

This experiment and others (e.g. Gervasi and Schiestl, 2017) are good illustrations of evolutionary rescue. In that case, natural selection prevents species extinction. Gomulkiewicz and Holt, (1995) present the two potential outcomes of a maladapted population, represented here in figure 5. With evolution, a declining population can sometimes rebound, if it contains a phenotype with higher fitness in the new environment (see figure 6A). However, as illustrated in figure 5, even with an evolutionary potential, if the rescue process is too slow, a small population can be too vulnerable and still go extinct because of stochastic demography, Allee effect, inbreeding depression or genetic drift. Empirical and experimental examples of this evolutionary mechanism are often detected by an increase in frequency of a genotype (and associated phenotype) responsible for a fitness increase in the new environment. A review by Carlson et al., (2014) presents some of these examples, among what the one illustrated in figure 6B. These outcomes are often observed when there is a strong selective pressure arising in the environment, for example the massive introduction of chemicals



leading to rapid insecticide (e.g. Mallet, 1989) and antibiotic resistance (e.g. Hermsen et al., 2012).

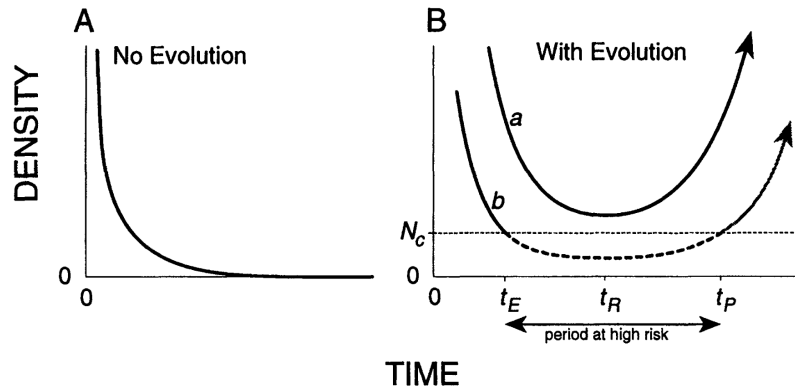


Figure 5: A) Without evolution, the maladapted population goes extinct. B) With evolution, the maladapted population can, after a first decline, rebound to a viable population. (a) If this phenomenon happens fast enough, the population never crosses the threshold of critical viability. (b) If the rebound goes slower there is a risk period below the threshold of critical viability, and stochastic demographic variation can lead to population extinction. From Gomulkiewicz and Holt, (1995).

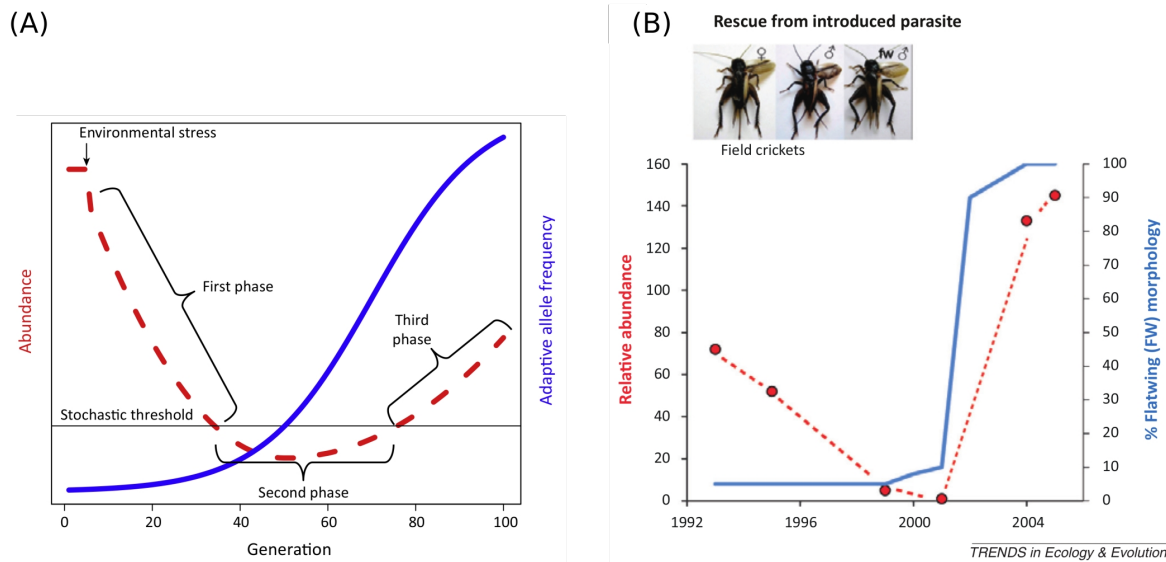


Figure 6: A) Schematic representation of the abundance and adaptive allele frequency variations during an evolutionary rescue process. In the first phase the population declines, in the second phase it is below the stochastic threshold and endangered of extinction, in the third phase it regrows, parallelly to the increase of frequency of the adaptive allele. B) A real case of evolutionary rescue. A field cricket population affected by a parasite on males declined. The parasite was attracted by males sexual wing sound. Scientist rapidly observed the increase of frequency of silent male (flatwing morphology or fw), and a rebound of the population abundance. From Carlson et al., (2014).

### 2.2.2 Extinctions and evolutionary murder

If a population is depressed, selection will have a lower impact on its response to environmental changes, and other mechanisms like Allee effect, genetic drifts or inbreeding depression could lead the population to extinction (Ellstrand and Elam, 1993).

However, sometimes selection itself produces responses that lead to the extinction, or event co-extinction of species and their interactors, as reviewed by Diamond and Martin, (2020). This phenomenon is known as “evolutionary suicide” (Parvinen, 2005), but is also mentioned by Webb, (2003) as Darwinian extinction, or simply evolution to extinction (Dieckmann et al., 1995). While theoretically, it is easy to exhibit such a behaviour in mathematical models, it is not so easily observed in Nature. Experimentally, it is rare to lead one’s own experimental population to extinction purposely. However, because evolution acts at the individual level, the ones’ favoured, that produce more offspring, change their environment, which can thereafter be detrimental to the entire population. This is for example the case of overharvested cod populations (Olsen et al., 2004). This strong selection pressure favours smaller and quicker maturing cods. While their relative fitness outperforms that of larger cods, they still produce fewer offspring in the longer term, ultimately dangerously decreasing the fish population.

A last possibility is that the evolution of a species leads another to extinction, especially close interactors. This outcome depends on how essential to the species the interaction is, the type of interaction considered, and the evolutionary potential of both partners. A figure from Loeuille, (2019) represents different case scenarios where all these parameters vary but the interaction dependence, that is considered essential in all cases (figure 7). When one species evolves faster than its interactor, it reduces the synchrony between the two species (see section 1.2.3 on phenological synchrony). In the example, the shift is toward earlier phenology. If the mutualistic interactor or the herbivore that shift the earlier is too much in

advance, its earliest individuals will not be able to feed on the plant resource, in panel A or B, or for the plant in panel D, its earliest flowering plants will not be pollinated. The rest of the herbivore, pollinator or plant population is still able to interact with the slower responding plant or pollinator and will maintain a population with a similar phenological shift. In all these cases evolution is slowed down because these too early individuals will not reproduce and their too early phenotype will be lost. However, in the case of an antagonistic consumer-resource interaction (panel C), if the plant shift toward earlier phenology than its specialist consumer, the consumer will miss the plant phenological peak and will not be able to maintain its population. In that last case, the strong evolutionary response of one species (here the plant) kills its interactor (the herbivore) that cannot track the change. This phenomenon of one species evolution causing the extinction of its interactor is known as an evolutionary murder (Parvinen, 2005). It shows that the obtained evolutionary outcome both depends on the evolutionary potential of the considered species, but also on the type of interaction it is engaged in. We deeper explore the effect of different interaction types on species eco-evolutionary responses to environmental changes later in this thesis.

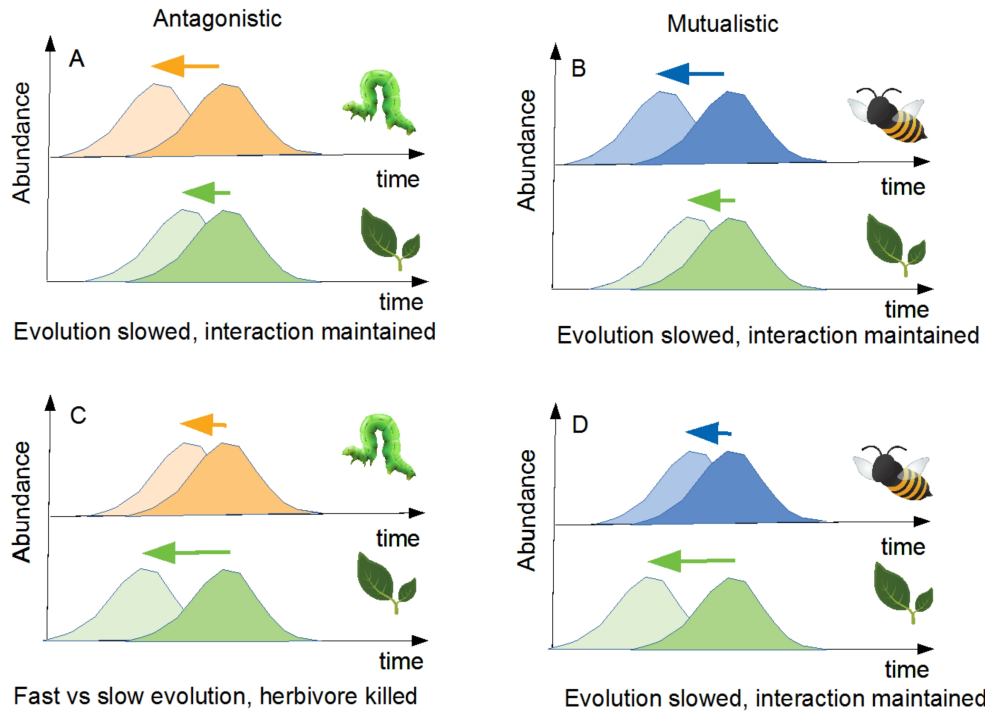


Figure 7: Different phenological shifts of two interactors with environmental change. On the left (panels A and C) are represented antagonistic interactors, like a plant and an herbivore. On the right (panels B and D) one finds mutualistic interactors, e.g. a plant and a pollinator. The interactions are supposed to be essential to both partners. The intensity of the interaction therefore directly drives the resulting abundance of each species. The arrows represent the species evolutionary potential following the perturbation. On panel A and B, the plant phenology shifts less than its interactor, whereas its phenology responds more than that of its interactor on panel C and D. The evolutionary outcome is stated below each graph. From Loeuille, (2019).

Species trait type and value are influencing both the ecological and evolutionary response of species facing environmental changes. Could we link the study of these two dynamics to explore their combined effect on populations and interactions responses to environmental changes?

### 3 Linking ecological and evolutionary dynamics

#### 3.1 What does eco-evolutionary dynamics mean?

Eco-evolutionary dynamics is a term of growing use in the past decades. This term states that there is a link between the modelled, observed and/or measured ecological and evolutionary

dynamics. More explicitly, it implies that the ecological dynamics can impact the observed evolutionary pattern, which can, in turn, affect the ecological ones. How does this feedback loop between ecological and evolutionary dynamics explain the fate of a community in a specific environment? While the effects of ecological dynamics and especially demographical effect on the evolution of a trait is very well known (e.g. thorough review of this mechanism in plant demography and evolution in Solbrig, (1980), are their clear evidence for feedback of evolutionary trajectories on ecological dynamics?

Evolutionary rescue is one example of a link between ecological and evolutionary processes because the increase in frequency of the adaptive allele is correlated to the rebound of the population (Carlson et al., 2014). However, while it shows the evolutionary impact on the ecological persistence, what is missing is the impact of ecology on the evolution of a population.

Another straightforward argument is that, after part 1 and 2, one sees that traits controlling the interaction between species are both influencing the ecological and the evolutionary dynamics of the species. Moreover, by linking the species to a common fate, evolution affecting the interaction trait can have repercussions on the demography of the interactor, as seen in the “evolutionary murder” example (Loeuille, 2019). There is indeed a feedback loop between those two processes, demography influencing the way a trait is selected within a population, and this trait evolution having demographic consequences on the focal species and its interactors. Eco-evolutionary dynamics, or the fact of considering both ecology and evolution as acting together to create species fate, is particularly important when considering interacting populations in a community.

A last argument to consider both ecological and evolutionary forces in the same system, is that they are often acting on the same time scale. For long, evolution was considered to act on a very long time scale, imperceptible to humans, therefore not acting on the scale of a human

lifetime. However, a progressive shift in the community of research in the evolution research field (Reznick et al., 2019), has led to the idea that, depending on the species characteristics, rapid evolution could be contemporary to ecological timescale (Hairston et al., 2005). This idea opened the research field of experimental evolution. Evolution has been experimentally shown to be very rapid (e.g. significant morphological and reproductive changes were observed in 5 generations in Bodbyl Roels and Kelly, 2011, and in 11 in Gervasi and Schiestl, 2017), and can therefore act in feedback with demographic dynamics. More and more field studies report observations of very rapid evolution following an environmental change. Franks et al., (2007) observed a flowering phenological shift of 1.9 to 8.6 days after summer drought in only a few generations of a herbaceous plant, while Cheptou et al., (2008) observe a strong decrease in dispersal investment of a weed when switching from a rural to an urban environment in only 5 to 12 generations. This idea of rapid evolution was already theorised in the early 60's by Pimentel, (1961). It paved the work for the study of species co-evolution; progressively making more complex the ecological conditions (Dieckmann and Law, 1996; Geritz et al., 1998), and then to later include the feedbacks between ecological and evolutionary dynamics, even leading to *concepts* like “community genetics” (Agrawal, 2003; Neuhauser et al., 2003).

## 3.2 Measuring and modelling eco-evolutionary feedbacks

### 3.2.1 Experimental and empirical eco-evolutionary dynamics

While all the previous arguments are in favour of considering both the ecological and evolutionary dynamics in feedback within a community, is this degree of complexity always necessary to analyse the observed pattern? Are their empirical and experimental proofs that eco-evolutionary dynamics explains more than just ecology or evolution alone?

Now that the concept of eco-evolutionary dynamics has fully arisen, there are regular experimental studies on the eco-evolutionary feedback loops of a single species, often using experimental evolution (e.g. Turcotte et al., 2013, on peach aphids). De Meester et al., (2019) point out the importance of considering the eco-evolutionary dynamics of more than one focal species because it can be involved in co-evolutionary dynamics. To fully understand its dynamics, one might not neglect the species interacting community (see earlier work of the same team with predators and competitors (Turcotte et al., 2011)). There are very few experiments and empirical studies that consider both ecological dynamics (often following the demography of the species) and evolution of focal traits within a community. Some rare are reviewed in Fussmann et al., (2007) and Schoener, (2011). In their review, Fussmann et al., (2007) clearly note that in the few empirical studies that follow both ecological and evolutionary dynamics, they are acting on the same timescale and are both essential to explain the observed fate of the community. De Meester et al., (2019) even advocate for studies of eco-evolutionary feedback on multispecies communities and point out that so far (in 2019) only a few microbial community experiments have looked at this, and in very artificial constructs. This, however, requires a new definition for eco-evolutionary feedbacks, because they are often used in a single species context.

Nowadays, there are several growing sources of observation and data. They are provided by experimental evolution, the growing literature body assessing strong global changes impact on species rapid evolution, e.g. urbanisation, selective harvesting or the assessment of invasive species' impact on indigenous communities. Turcotte et al., (2011) for example studied aphids exposed or not to predators and competitors while grazing on their host plants. They insist on doing field experiments to have a more realistic set up, and to follow aside clonal non evolving controls. Indeed, according to Schoener (2011), good experimental studies on eco-evolutionary feedbacks must track demography and genetic frequencies over

many generations, have a plausible mechanistic explanation for the eco-evolutionary feedback loop observed and include a non-evolving clonal control. He is also advocating for long term field experiments to better study this feedback loop, although this would be time and resource consuming. Other studies tried to distinguish the effect of the evolution of only one interacting species, compared to the co-evolution of both partners. Cairns et al., (2020) studied the experimental evolution and coevolution of a predator-prey system, using different preys (bacteria) on the same ciliate predator to compare evolving histories. Evolution of the predator traits (morphological and behavioural) increases its search efficiency, but does not clearly increase the growth efficiency by feeding on the ancestral prey (Cairns et al., 2020). Indeed, experimental evolution, while not being very convincing because it may not mimic natural pressure and the complexity of real system, is very useful to identify mechanism that could be at stake in explaining the current observed dynamics. This is nicely shown by Yoshida et al., (2003) experiments. They compare predator-prey (rotifer-algal) cycles with and without allowing the prey to evolve, and observe the well known out of phase and stabilising predator-prey demographical oscillation only when the prey is able to evolve. On the opposite, as expected, evolution of the prey decreases the population densities and growth rate of the predator, the effect varying depending on the prey type. One of the most studied cases of empirical eco-evolutionary feedbacks with invasive species is the system between rabbits and the myxoma virus causing the myxomatosis disease in Australia (see box 2 for a more detailed review of this). Other biological invasions are often controlled with biological agents, especially in Australia that was colonized very recently by European species (e.g. see table 1 in Fenner, 1983). Because the demography of these species is closely monitored, as well as their evolutionary responses to control attempts, it makes them good candidates for field eco-evolutionary dynamics studies (Huey et al., 2005). More and more example of rapid evolution following a strong environmental pressure are observed, from the impact of



urbanisation on the allocation to dispersal mechanisms of a weed (Cheptou et al., 2008), the long-term shift in phenology following short but intense summer drought on an annual plant species (Franks et al., 2007), or the impact of overharvesting in marine communities (Olsen et al., 2004).

*Box 2: Eco-evolutionary dynamics of the invasive European wild rabbits in Australia and control attempts*

One of the better-known cases of invasion is that of the wild rabbits in Australia. White and Newton-Cross, (2000) gave a good summary of the invasion history. Wild rabbits (*Oryctolagus cuniculus*) are native to the Iberian peninsula, and were first introduced in quite reasonable quantities in Victoria, Australia, for shooting game purpose in 1859. By 1880, after spreading by 20 to 100km each year due to their very high reproduction and dispersal rates, they had reached pest status (Ratcliffe, 1959). They created ecological damages both by an overgrazing pressure on the sheep pastures (sheep close cropping are ideal for rabbits), and by acting as a reservoir of diseases, decreasing primary productivity and threatening native endangered species persistence. They especially reduced the food supply for stock and endemic grazing marsupials, destroyed shelters and prevented grass regeneration (White and Newton-Cross, 2000). While one would expect an evolution of grasses to be more grazing tolerant or resistant, some studies showed that, because of indirect interactions at the community level, it is not always the case. Some experiments e.g. showed that decreasing rabbit grazing on *Rumex acetosa* was not always leading to reduced defences production, resistance or tolerance to herbivory as expected, but instead caused an evolutionary decrease in plant growth rate (Turley et al., 2013).

A first major controlling attempt was made releasing the Myxomatosis virus after specificity checks in quarantine in the 1930s, and then again after World War II (Fenner, 1983). It first

worked until coevolution between the rabbit and the virus arise, with an equilibrium reached where 30-50% of the rabbits survive (Thompson and King, 1994). As the co-evolution process was in fields, following the populations infection was not easy. First attempts were made in 1951-1952 with serological and in-lab examinations, observing in real time the appearance of new strains and a reduction in the virus virulence (Fenner, 1983). This mixture of intermediate virulent strains and their maintenance over generations can be explained by a theoretical model, as a trade-off between virulence and transmissibility (May et al., 1983, figure 8). They showed that intermediate virulence optimizes the rabbit survival for virus transmission. Rabbit mortality drop from 90% to 30% in only 8 years, probably due to mortality induced selection, but non-genetic factors may have also played a role (Dwyer et al., 1990). In-depth following of the rabbit genetic background would have added information, but it is clear that this is a good example of co-evolution of a host-parasite system, with clear impacts on the host demography, as detailed in (Pimentel, 1961).

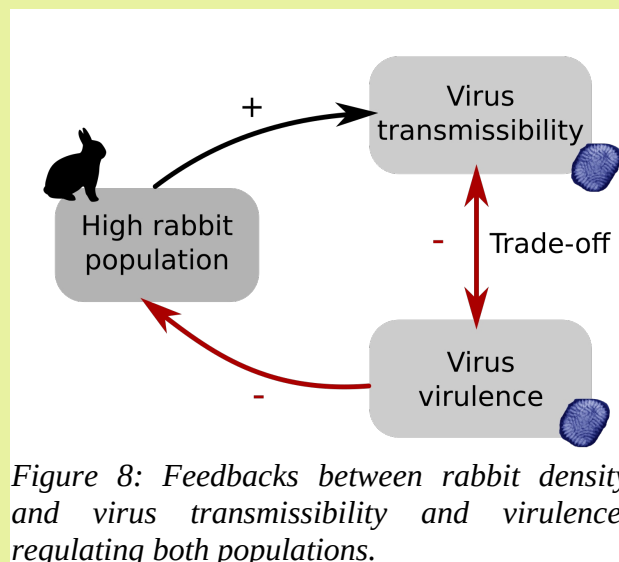


Figure 8: Feedbacks between rabbit density and virus transmissibility and virulence, regulating both populations.

After the discovery of another disease specific to European rabbits, the RHDV (or RDC), i.e. the rabbit hemorrhagic disease virus, it was tested on Australian fauna and the invasive rabbit. Proven very specific to the European wild rabbit it was released in quarantine, and thereafter on the full continent (Cooke and Fenner, 2002) spreading mainly through biting insects. It

was not equally efficient in all regions, probably due to climate differences (Saunders et al., 1999). New strains are nowadays emerging again, as with the myxoma virus (Mahar et al., 2018), and its evolution and the demographic consequences are still under study today. It is also of good use to follow long term evolution, as both the virus and rabbits have short reproduction cycles (Hall et al., 2017b).

### 3.2.2 Models using eco-evolutionary feedbacks

As explained before, theoretical models were the firsts to incorporate feedbacks between ecological and evolutionary dynamics, and helped to formulate hypotheses on the impact of such a reciprocity.

One of the first models with the reciprocal loop of evolution on ecology was made by Pimentel in 1961. It was based on the link formulated earlier by Haldane, (1956) coupling density of a population and natural selection. Pimentel, (1961) used the rabbit myxomatosis system (see box 2) and then a plant-herbivore system to illustrate an allele frequency model at a single locus. In this model the expression of the animal density at the beginning depends on the plant genotypes it feeds on and the selective pressure exerted on the plant by the animal. From this he derived the proportion of surviving plants and proportion of different plant genotypes after herbivore consumption. By random mating, he obtained the plant allele distribution at the next generation. In his model demography is therefore clearly linked to density of both the focal species and its interactor. He then detailed the model even further, adding explicit genetic description on the animal side. He afterward obtained the very famous resource-consumer cycles, often observed in these types of eco-evolutionary systems. He acknowledged that in natural systems, traits expression and feedbacks will be multifactorial, more flexible but also more complex. However this simple model integrates traits within the biological rate, thus allowing the environment and other species to impact the focal species

demography and evolution. It also links present and future density via the selective process, clearly putting into action this eco-evolutionary feedback loop.

As expressed in more recent reviews (e.g. Fussmann et al., 2007; Govaert et al., 2019), many of today's theoretical models are incorporating this feedback loop. However they are often separated between quantitative genetics models (e.g. Zee et al., 2017), following the ecology and the evolution of a focal species, and game theory models (e.g. Brown and Vincent, 1992), adaptive dynamics (e.g. Loeuille, 2010) and inclusive fitness theory (e.g. Van Cleve, 2015) that can be used in a multi-species system but with separate time scales between ecology and evolution. Lion, (2018) recently published a review trying to reunify these theoretical models, by showing that they all rest on the same principle. It is the species sensitivity to changes in the environment (often via its specific traits) that mediates the eco-evolutionary feedback loop considered. Earlier synthesis by Abrams, (2001) emphasises the proportional link these methods procure between trait(s) variations and the individual fitness gradient. Among those different models, we chose to use the adaptive dynamics tools. It enables to follow the evolution of a focal trait (or several), and how it feedbacks with the ecological dynamics of a multi-species system. The specificities of this method allows to account for frequency dependence via an explicit demographical dynamics that also provides the basis to define the appropriate fitness function related to the evolving trait.

### 3.2.3 Modelling eco-evolutionary feedbacks with Adaptive Dynamics

Adaptive dynamics is a modelling technique that is used to take into account the feedbacks between ecological and evolutionary dynamics. As explained before it extends principles from Game theory to study continuous traits evolution.

Contrary to frameworks like population and quantitative genetics that focus on the trait frequency in infinite populations, adaptive dynamics accounts for ecology explicitly via the demographic dynamics of each species in the system. It considers the evolution of one or

more trait(s), that is affecting the focal population demography and potentially that of its interactors. Because the method rests on a tight link between population dynamics and trait evolution, a system starting with a homogeneous trait can either maintain its trait in time (evolutionary endpoint) or diversify in several subpopulations (trait branching). Parallel to that these evolutionary trajectories can increase or decrease the population size, even leading them to extreme situations like maximum environmental capacity or extinction.

Adaptive dynamics has been theorised in the nineties (Dieckmann and Law, 1996; Geritz et al., 1998; Metz et al., 1992, 1996), but also vulgarised in more recent papers (Brännström et al., 2013; Dieckmann, 2004). It has specific prerequisites: populations are asexual, the considered trait is linked to a precise genotype affecting the individuals' fitness, mutations are small and happen when the population is at ecological equilibrium. However, relaxation of these classical assumptions, and especially the asexual reproduction (Geritz and Kisdi, 2000) and the separate timescales of ecological and evolutionary processes often lead to similar results. Explicit sexual models could, however, give better insight into the dynamics of polymorphic populations (Geritz and Kisdi, 2000), which we will not consider here. Contemporaneous ecological and evolutionary process are indeed more realistic and could reinforce the eco-evolutionary feedbacks that we previously discussed in this introduction. Note that adaptive dynamics always requires that the evolving trait(s) varies quantitatively and at the individual level. A method assessing for quantitative trait variations is useful to follow continuous morphological traits like body size, or complex and diffuse ones like the investment in an interaction (e.g. via nectar or organic compound production).

Once define a demographic model (e.g. modelling the population size variation, expressed in abundance or biomass) adaptive dynamics rests on two major principles. The resident population of the evolving species is at ecological equilibrium when a new and rare mutant appears in the population. The fate of this mutant population can be drawn from the initial

growth rate or invasion fitness. A positive invasion fitness will lead in most cases to the complete invasion of the resident population by the new mutant with trait variant, while a negative one to the extinction of this new mutant subpopulation.

The link between the variation of the trait value and the invasion fitness is given by the canonical equation of adaptive dynamics. This is a deterministic approximation of the stochastic process resulting in the trait evolution. In a monomorphic population, it is expressed as follow, with  $x$  the trait value of the resident individuals, and  $x_m$  of the mutant ones (Dieckmann and Law, 1996):

$$\frac{dx}{dt} = \frac{1}{2} \mu \sigma^2 P^*(x) \left. \frac{\partial \omega(x_m, x)}{\partial x_m} \right|_{x_m \rightarrow x} \quad (1)$$

The term  $\frac{1}{2} \mu \sigma^2 P^*(x)$  encapsulates the phenotypic variability brought by the mutation process on which selection can act.  $P^*$  is the population size at equilibrium,  $\mu$  the per individual mutation rate and  $\sigma^2$  the variance of the phenotypic effect of the mutation. The last term, called the selective gradient, is based on the variations of the relative fitness of mutants  $x_m$  given a resident  $x$ , i.e. the derivation of the invasion fitness. It signs gives the direction of evolution; a positive gradient selects larger trait values, while a negative gradient selects smaller ones.

In a monomorphic population, the invasion fitness is expressed as the *per capita* growth rate of the rare mutant population in the resident population at ecological equilibrium, with  $P_m$  the population size of the mutant:

$$\omega(x_m, x) = \left. \frac{1}{P_m} \frac{dP_m}{dt} \right|_{P_m \rightarrow 0} \quad (2)$$

Its explicit expression depends on the chosen demographic model. Contrary to other methods, the strong point of adaptive dynamics is to define the fitness function from the ecological equation of the population. This link between ecological and evolutionary dynamics is absent in methods using ad hoc functions.

Of particular interest are points when the phenotypic trait value stops varying, i.e. when equation 1 goes to 0. This means that the first derivation of the fitness function 2 goes to zero. This specific point value is called a singular strategy. It can afterward be characterised by its convergence (are mutant trait values close to the eco-evolutionary equilibrium converging toward it or not?), and invasibility (once reached, is that trait value maintained in time or can new mutants with different trait invade the system?). These two characteristics can be drawn in the monomorphic case from the second and cross derivation of this fitness function (for more detailed explanations, see for example the step by step summary by Brännström et al., (2013).

Pairwise invasibility plots or PIPs are useful graphical tools to visualise these singular strategies and their convergence and invasibility potential. They represent the invasion fitness sign for combinations of resident and mutant trait values, areas of positive fitness corresponding to pairs of traits values for which the mutant successfully invade the resident population. Figure 9 represents PIPs with the four possible singular strategy types. The specific names corresponding to the different singular strategies types are listed under each PIPS.

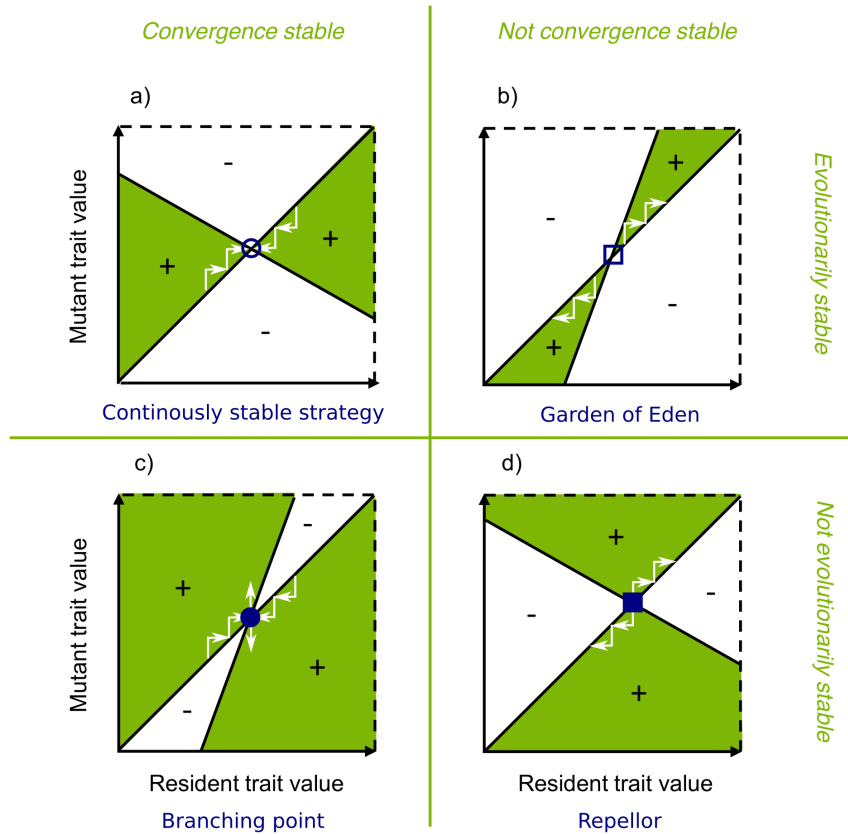


Figure 9: Pairwise invasibility plots (PIPs) representing the invasibility potential of a rare mutant within a resident population at ecological equilibrium. Green areas represent combinations of parameters for which the invasion fitness is positive and the mutant invade the resident population. White arrows correspond to evolutionary trajectories. Blue symbols correspond to the singular strategies type, with circle corresponding to convergent strategies and square to divergent ones, filled symbols representing invulnerable strategies even with small mutation steps. Unfilled symbols are non-invasible strategies with small mutation steps, but could sometimes be with larger ones, and are considered evolutionarily stable. Adapted from (Brännström et al., 2013).

It arises that, while some strategies like the continuously stable strategy will lead to an evolutionary endpoint, the system stabilizing for a specific trait value and demography, others like branching point can lead to the system diversification. PIPs can also be used to obtain the region of coexistence of protected dimorphism, e.g. once the diversification arises (see example in Brännström et al., (2013). Under such conditions we could observe polymorphism in the population, maintained via disruptive selection, and, on an even longer period, to speciation events.



While mathematically more complex and less easy to read into biological phenomena, methods have been developed to follow the evolution of multiples traits. These multiple traits can coexist after the branching event or the system can be already considered to start its eco-evolutionary process with different evolving traits in the same or multiple populations ((Kisdi, 2006) for an example of two co-evolving traits), or even after successive radiation events (Ito and Dieckmann, 2007). This method has also been generalised to the analysis of function-valued traits, i.e. the fact that individual characteristics have no fixed values but are continuous traits, and are especially useful to physically structured populations (e.g. by age), adding integrals to the expression of the fitness functions (Dieckmann et al., 2006; Parvinen et al., 2013).

In the following, we will use this method to only analyse evolution in monomorphic populations, as we wish to interpret the obtained analytical results in the light of biological mechanisms.

## 4 The impact of eco-evolutionary dynamics on communities responses to different environments

### 4.1 The chosen conditions explored in this thesis

As thoroughly presented before, communities are both characterised by their ecological and evolutionary dynamics, both sensitive to the traits of the species they are composed of. Therefore in the following, we choose to focus on different species traits evolution, and their impact on the eco-evolutionary feedbacks within the community. The different traits we explore have been previously presented. We focus on three traits, species body mass, that controls both the species internal rate and its interaction with other, the level of attractiveness of a species to an interactor (e.g. size of a floral display or quantity of nectar for a plant species), and the temporal availability for interactions of each species within a year, characterised by the duration and mean availability for interactions in time, e.g. their

phenology. Like the body mass, both last traits also control the potentiality and intensity of interaction with other species from the community e.g. see part 1.2.3 of this introduction.

There is a great diversity of communities on earth. Here we chose to focus only on resource-consumer interactions. While this interaction type is, of course, the basis of food web communities, we also explore its role in mutualistic communities where the energetic exchange is often, at least on one side, of food origin (e.g. plants providing food for pollinators or seed dispersers, plant-fungi nutrient exchanges). As seen earlier in this introduction, e.g. in part 2.2.2, these different interaction types could condition different ecological and evolutionary responses of species facing environmental changes.

As for the environmental impact, the previous parts showed that both abiotic and biotic environmental impacts can affect the species and their trait. We investigate further the impact of an abiotic change in the environment that can both influence species traits and their interactions, namely the temperature. We also explore biotic environmental changes, that can result from abiotic one. Those changes are also impacting the intensity of the interactions as they affect the availability of the partner species. We study the impact of a strong decline in a consumer population, and differences in the temporal availability of alternative resources for a consumer species.

## 4.2 The different studied models and environmental effects

Trying to explore these different aspects in the following parts we distinguish three different ecological systems, with different environmental impacts and traits evolution.

- In a first part, we explore the effect of temperature difference in the building-up and maintenance of a complex food web, whose interactions are directed by the species body size, itself influenced by temperature. In this part, we study the system at two levels. A simple predator-prey module is explored with analytical calculations to study thoroughly the mechanisms leading the eco-evolutionary feedbacks and the emergence

and starting conditions for diversification toward a complex food web. We also analyse via numerical simulations the building up and maintenance of a whole food web, and the body size distribution and system stability throughout time at different temperatures. Moreover, because the precise impact of temperature on a consumer's attack rate is not yet well known, we investigate this temperature effect in different case scenarios, where a consumer's attack rate is unaffected, increases or exhibits an optimum when temperature increase.

- In a second part we follow the evolution of a species attractiveness when its interactor species decline. We start again with a simple two-species model, this time considering that the consumer-resource interaction is, in fact, a mutualistic one, and the interaction with the resource increases its growth rate, e.g. via pollination or the exudate of nutrient by the partner species. This allows us to explicitly compare the system equilibria with different densities of interactors, and even increasing or declining ones, with or without evolution.
- In a third part we explore the evolution of a consumer's foraging phenology with different temporal distributions of two alternative resources, and the potential cases when it leads to the system diversification or extinction. These differences in the resources' distribution can be also of environmental origins, as presented in parts 1 and 2. Indeed these phenological shifts in the resources' distribution can be caused by climate change, land-use change and/or other human impacts. We especially explore the impact of an increasing gap of resource in the middle of the season, and the effect of asymmetric durations of resource availability for the consumer (i.e. one resource that is available in limited quantity on a long time period, and the other available in great quantity over a very short time period).

Here is a summary of the different models characteristics

Chapter	Community type	Type of consumer-resource interaction	Evolving parameter	Environmental constrain	Methods
1	Two species (one consumer and one resource) and a full multi-trophic network	Antagonistic, predator-prey type	Consumer body size, and preferred feeding range in the multi-trophic model	Different temperatures. Test 3 scenario for the impact of temperature on attack rate (no effect, increasing attack rate with temperature, hump-shaped variation with temperature increase)	Analytical tools, Pairwise invasibility plots (PIPs) and simulations
2	Two species	Mutualistic, the consumer also increases the resource demography via the interaction (e.g. plant-pollinator interaction)	Investment in the mutualism (e.g. attractiveness via nectar or flower production for a pollinated plant)	Decrease in the intrinsic growth rate of the partner species	Analytical tools and graphs
3	One consumer and two resources	No feedback yet, can be either an antagonistic or mutualistic one in future analyses	Foraging phenology of the consumer ( duration and mean date)	Changes in resources phenology, either an increased gap between the resources peaks or an asymmetry in their distribution trough time via various phenology duration	Analytical tools, PIPs and simulations

### 4.3 PhD general questions

All the systems that are simple enough to be analytically analysed are explored using the adaptive dynamics techniques presented above. The variety of environmental impacts and observed traits allow us to answer general questions regarding the eco-evolutionary dynamics within a community. In each chapter we investigate how a particular change linked with environmental human impacts affect the eco-evolutionary dynamics of a community and the resulting community structure. By contrasting our different results, we have also the possibility of comparing the responses of different interaction types, their strengths and the effects at the partner and community levels. This Ph.D. thus allow us to discuss the following questions:

- Are mutualistic interactions more sensitive to different environments than antagonistic ones?
- Does the eco-evolutionary response of a species depend on its degree of generalism?
- Do we find the most generally observed empirical evolutionary patterns associated with environmental differences we studied?

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## Chapter 1: Selective effects of temperature on body mass depend on trophic interactions and network position

The present chapter has been submitted for revision to the *American Naturalist*. The present version is available in bioRxiv 233742; doi: <https://doi.org/10.1101/233742>. A new version of this manuscript will soon be resubmitted, with modifications in the model structure: energy input is now via an inorganic chemostat independent of temperature and the feeding preference of a predator is a fixed size ratio with its prey. With this new model we explore more specifically the impact of the degree of generalism on the eco-evolutionary response to different temperature.

# Selective effects of temperature on body mass depend on trophic interactions and network position

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Online appendices (including table A1, table B1 and fig. C1.)

*Keywords:* Global warming, body mass evolution, adaptive dynamics, predator-prey interactions, attack rate

## Abstract

Body mass is a key trait constraining interspecific interactions in food webs through changes  
3 in metabolic requirements. Because climate warming affects metabolic rates, it creates direct  
selective effects on body mass. Many empirical studies suggest that body mass decreases un-  
der warming, although important exceptions have been noted. We first analyze the evolution of  
6 body mass in a simple consumer-resource model to provide conditions under which a body mass  
increase or decrease may be expected. We then extend our model to a multi-trophic food web  
context that allows for the coevolution of body mass and of feeding preferences. We focus here on  
9 how the trophic position of a consumer influences its evolutionary response to warming under  
different scenarios for the temperature dependence of attack rates. We observe that body masses  
can remain constant or increase with temperature when attack rates are constant or increasing  
12 with temperature, while body mass reductions in response to warming are only expected when  
attack rates have a thermal optimum and populations are initially locally adapted. We also found  
that body masses at lower trophic levels vary less under warming than body masses at higher  
15 trophic levels, which may be explained by decreasing levels of stabilizing selection along food  
chains.



## 18 Introduction

Accumulating evidence suggests that current global change, and in particular climate warming, affects the evolution of body masses. Many researchers regard decreases in body mass as one  
21 of the “universal responses” to warming, next to range shifts and changes in life-history traits (Brose et al., 2012; Daufresne et al., 2009; Emmrich et al., 2014; Sheridan and Bickford, 2011). Such downsizing is more pronounced for aquatic compared to terrestrial species (Forster et al.,  
24 2012), but it has been found for systems as diverse as phytoplankton (Yvon-Durocher et al., 2011), carnivorous mammals (Yom-Tov et al., 2010), fishes (Edeline et al., 2013), amphibians (Reading, 2007) or birds (Yom-Tov et al., 2006).

27 Body mass is considered to be a key ecological trait largely defining ecological rates and life history traits (Peters, 1986; Woodward et al., 2005). It constrains average home range size (Lindstedt et al., 1986), life spans and metabolic requirements (Brown et al., 2004) and also affects species  
30 interactions, e.g. when predators favor species in a given mass window (Brose et al., 2006a). Such allometric relationships have been extensively studied during the past decades and are known to enhance stability in complex food webs (Brose et al., 2006b). Body mass evolution can therefore  
33 affect individual metabolism and demography, as well as multi-species interactions, with important consequences for the structure and functioning of ecosystems (Loeuille and Loreau, 2006) and their ability to provide essential services (Ohlberger, 2013; Woodward et al., 2005). It is thus  
36 an urgent challenge to understand how increasing temperatures affect body mass evolution and the responses of complex ecosystems incurred by such eco-evolutionary feedbacks.

Warming-induced responses of average body mass of homeotherms are often explained in  
39 terms of physiological or metabolic constraints (Brown et al., 2004; Gillooly et al., 2001). Consider the classic Bergmann’s rule, which describes a geographical pattern where species of smaller body mass are typically found in warmer environments. Bergmann explained the observed pat-  
42 tern with a higher surface-to-volume ratio that allows for increased heat radiation per unit body mass (Bergmann, 1848). However, not all of the empirical studies agree with such variations (e.g. in insects, Shelomi 2012). A number of cases in which body mass shows instead a variable  
45 response, or even an increase, are summarized in the review by Gardner et al. (2011). Such deviations can neither be explained by Bergmann’s surface-to-volume argument, nor by metabolic constraints.

48 While not denying that variations in body mass are partly driven by individual scale con-  
straints (metabolic or physiological), such variations also largely alter the ecological context for  
the considered population. It may lead to mass-dependent feedbacks at the population level, as  
51 well as changes in competitive and predatory interactions in the community (Ohlberger, 2013).  
Body mass is therefore likely selected not only by direct metabolic or energetic requirements, but  
also by changes in the network context. For example, Yom-Tov and Yom-Tov (2005) show that  
54 the body mass of Palearctic shrews in Alaska increased during the second half of the twentieth  
century in response to warming, contradicting the prediction of Bergmann's rule. They proposed  
that such increases may be explained by a higher food supply, resulting from improved weather  
57 conditions for the shrew's prey in milder winters. This study highlights that the evolutionary  
response of a target species to warming can depend on its trophic interactions with other species.

It is important to address such a dynamic community context, since empirical evidence sug-  
60 gests that global environmental changes exert pervasive impacts on both antagonistic and mu-  
tualistic species interactions, leading to major changes in network composition and ecosystem  
processes (Tylianakis et al., 2008). Biotic interactions and feedback processes can lead to highly  
63 complex, nonlinear and sometimes abrupt responses to climate change (Walther, 2010). A syn-  
thesis of species ecology, species evolution and biotic interactions is thus needed to generate  
reliable predictions of species responses to changing environments, but these fields have so far  
66 mostly been studied separately (Lavergne et al., 2010). In this context, it is not yet clear in which  
cases the network context will accelerate, hamper or even counteract selection for smaller body  
mass due to metabolic or energetic constraints.

69 Trophic interactions between species shape selective pressures on body mass among species  
and trophic levels because predator/prey body mass ratios are constrained by the physical abil-  
ity of predators to ingest prey of a certain mass. Moreover, these interactions are at the same  
72 time temperature-dependent (Englund et al., 2011; Rall et al., 2012). The most common ways of  
dealing with temperature-dependent (trophic) interaction rates is to either assume temperature  
dependency is weak enough to be ignored completely, or that trophic interactions increase fol-  
75 lowing the Arrhenius equation (as for example done in Binzer et al. 2016; Fussmann et al. 2007;  
Vasseur and McCann 2005). The latter can be a good approximation within a certain thermal  
window, but it neglects additional processes occurring at higher or lower temperature regimes

78 (see for example Peck 2016; Pörtner and Knust 2007; Tansey and Brock 1972; West and Post 2016).  
For instance, Sinervo et al. (2010) found that a whole group of lizard species can be so physi-  
ologically stressed by warming that they may not maintain any efficient activity, contradicting  
81 the prediction of monotonically increasing attack rates with temperature. A hump-shaped re-  
lationship between temperature and attack rates is thus more realistic when considering wide  
temperature ranges and has indeed been found in a large meta-analysis by Englund et al. (2011).

84 Several theoretical studies based on allometric relationships have already investigated the  
impact of warming on interaction networks. For example, it has been shown that warming  
stabilizes predator–prey dynamics at the risk of predator extinction (Fussmann et al., 2014), and  
87 strongly decreases the diversity of mass-structured predator–prey networks (Binzer et al., 2016).  
These studies only use the Arrhenius approach for attack rates and do not consider evolutionary  
dynamics. There is thus a lack of studies exploring how the relationship between temperature  
90 and attack rates affect food web evolution on broad thermal scales.

The first goal of our study is to understand how predator-prey interactions may interfere  
with metabolic and energetic constraints in shaping the evolutionary response of body mass to  
93 warming climate. More precisely, we ask how the temperature dependence of the attack rates can  
lead to increasing or decreasing body masses with temperature. We tackle this first question by  
focusing on a simple consumer-resource model that accounts for the evolution of the consumer  
96 body mass in addition to ecological dynamics. The temperature dependency of the attack rate  
is included via three different scenarios, namely a null hypothesis of temperature-independent  
attack rates, the Arrhenius approach and a hump-shaped relation with temperature, reflecting  
99 the underlying complexity of the foraging and ingestion processes. We use the adaptive dynam-  
ics framework (Dieckmann and Law, 1996; Geritz et al., 1998; Metz et al., 1992) to investigate  
consumer body mass evolution. The simplicity of the model allows us to obtain exact analytical  
102 solutions for variations in the selected body mass and conditions of consumer-resource coexis-  
tence in this eco-evolutionary context.

The second goal of the study is to understand how selection on body mass changes depend-  
105 ing on the position of the evolving species in the food web. We therefore study variations in  
body mass at different trophic levels using a large community evolution model (for a review on  
such models see Brännström et al. 2012; Drossel and McKane 2005; Fussmann et al. 2007). The

108 model produces, via numerical simulations, multi-trophic networks that emerge and evolve in a  
self-organized, temperature-dependent manner. This temperature dependence is implemented in  
exactly the same way as in the simplified consumer-resource model, allowing us to assess which  
111 patterns observed in the simple model hold across trophic levels in complex, multi-species com-  
munities.

## Models and Methods

114 We use a two-step approach to study the impact of warming on body mass evolution. A simple  
 consumer-resource model is used to study the impact of temperature on consumer body mass  
 evolution. This two-species model is a simplification of a more complex, multi-trophic com-  
 117 munity evolution model, which is used to study how body mass response depends on trophic  
 position in complex networks. Our two models are based on the same ecological assumptions,  
 but differ in their treatment of evolutionary dynamics, as explained in the following. In the fol-  
 120 lowing parts, asterisks (\*) indicate the ecological equilibrium, and tilde ( $\tilde{\cdot}$ ) the evolutionary one.  
 Whenever mentioned, log corresponds to the decimal logarithm.

### Ecological Processes

In both models, a consumer morph  $i$  is characterized by its average adult body mass  $x_i$  (measured  
 in kg) and its preferred prey body mass  $f_i$ . These traits determine the feeding interactions, as  
 illustrated in fig. 1. The rate of change of a consumer biomass density  $B_i$  (measured in kg per  
 $\text{m}^2$ ) is given by:

$$\frac{dB_i}{dt} = \sum_{j=\text{resource/prey}} e a_{ij} B_i B_j - \sum_{j=\text{consumers}} a_{ji} B_j B_i - \sum_{j=\text{competitors}} c_{ij} B_i B_j - d_i B_i, \quad (1)$$

123 where  $e$  is the conversion efficiency,  $a_{ij}$  is the mass-specific consumption rate at which morph  $i$   
 consumes morph  $j$ ,  $c_{ij}$  describes interference competition among consumers  $i$  and  $j$ , and  $d_i$  is the  
 respiration and mortality loss rate of consumer  $i$ . All ecological parameters are summarized in  
 126 Table 1.

Body mass and temperature dependence can affect the consumer loss rate,  $d_i = d_i(x_i, T)$ , and  
 the consumption rates,  $a_{ij} = a_{ij}(x_i, x_j, f_i, T)$ . The different scenarios of temperature dependence  
 are explained below. For a given temperature  $T$ , we assume that the consumer loss rate is  
 constrained by body mass (Brown et al., 2004),  $d_i \propto x_i^{-0.25}$ , and that the consumption rate is a  
 product of a metabolic scaling factor and a Gaussian feeding kernel,  $a_{ij} \propto x_i^{-0.25} \cdot N_{ij}$ . The feeding  
 kernel (also illustrated in fig. 1) is defined as:

$$N_{ij} = \frac{1}{s\sqrt{2\pi}} \cdot \exp \left[ -\frac{(\log f_i - \log x_j)^2}{2s^2} \right], \quad (2)$$

where the standard deviation  $s$  describes the degree of generalism of the consumer.

Following limiting similarity theory (MacArthur and Levins, 1967), we propose that competition increases when morphs have similar feeding niches. Their similarity is measured via the overlap of feeding kernels,  $I_{il} = \int [N_{ij} \cdot N_{lj}] dw_j$ , with  $w_j = \log x_j$ . We therefore write competition interaction as:

$$c_{ij} = c \cdot \frac{I_{ij}}{I_{ii}} \quad \text{for } i \neq j. \quad (3)$$

The model parameter  $c$  sets the overall competition strength in the system.

Energy input into the system is provided by an external resource with body mass  $x_0 = 1$ . The rate of change of its biomass density  $B_0$  is given by

$$\frac{dB_0}{dt} = r \left(1 - \frac{B_0}{K}\right) B_0 - \sum_{j=\text{consumers}} a_{j0} B_j B_0, \quad (4)$$

129 where  $r = r(T)$  and  $K = K(T)$  represent the temperature-dependent resource growth rate and carrying capacity, respectively.

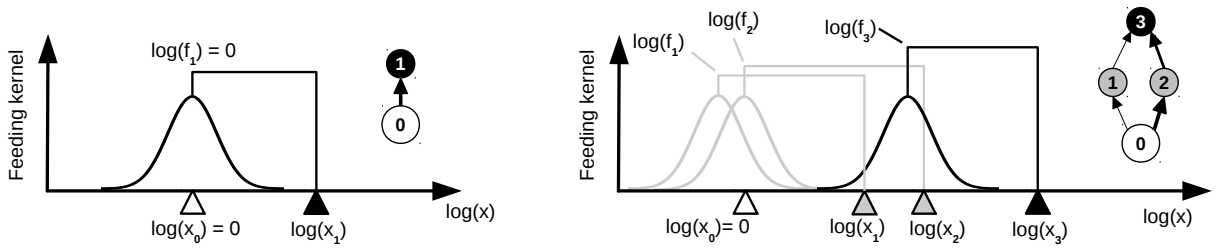


Figure 1: Illustration of the ecological rules in the two versions of the model. Left: A simple consumer-resource model. The consumer (black triangle) is characterized by its body mass  $x_1$  and the center of its feeding range  $f_1$ . The Gaussian function (black curve) describes its attack rate kernel on potential prey, as explained in equation (2). The consumer thus feeds on the external resource (white triangle) with its maximum attack rate. Only the body mass  $x_1$  can evolve. Right: A more complex, multi-trophic model. Shown is a snapshot with three consumer morphs. Morph 3 (black triangle) feeds on morph 2 and 1 (gray triangles) with a high, resp. low, attack rate. Morph 1 and 2 are consumers of the external resource (white triangle). Note that both the body masses and the feeding centers can evolve, meaning that the network structures generated by this model are dynamic and typically more complex than this snapshot.

Definition	Value(s) <sup>a</sup>	Unity
$e$ : Consumption efficiency, see (1) and (5)	0.85 <sup>b</sup>	[1]
$s$ : Standard deviation of the feeding niche, see (2)	0.25	[log(kg)]
$c$ : Scaling factor for interference competition, see (3)	0.15	$\left[\frac{\text{m}^2}{\text{s}\cdot\text{kg}}\right]$
$r$ : Resource growth rate, see (7)	1	$\left[\frac{1}{\text{s}}\right]$
$K$ : Resource carrying capacity, see (8)	10	$\left[\frac{\text{kg}}{\text{m}^2}\right]$
$d$ : Scaling factor for consumer loss rate, see (9)	0.3 <sup>b</sup>	$\left[\frac{1}{\text{s}}\right]$
$E_a$ : Activation energy used in (7), (8) and (9)	0.65 <sup>c</sup>	eV
$E'_a$ : Activation energy used for $a_{ij}$ in (11)	0.35 <sup>d</sup>	eV
$T_{ref}$ : Reference temperature used in (7) - (9), (11) and (12)	293	K
$T$ : Local temperature used in (7) - (9), (11) and (12)	273-313	K
$k$ : Boltzmann constant used in (7) - (9), (11) and (12)	$8.617 \cdot 10^{-5}$	$\frac{\text{eV}}{\text{K}}$
$b$ : coefficient of the hump-shaped temperature dependency used in (12)	$b^e = -0.256$	[1]
$q$ : coefficient of the hump-shaped temperature dependency used in (12)	$q^e = -0.691$	[1]

Table 1: A summary of all ecological model parameters both for the simplified consumer-resource model and for the more complex multi-trophic community evolution model. The models differ in the evolutionary rules, as explained in the methods section. <sup>a</sup> Values most commonly used in the analyses, and referred to as the typical values. <sup>b</sup> Values based on the work by Yodzis and Innes (1992). <sup>c</sup> Following the results of Gillooly et al. (2001) and Brown et al. (2004). <sup>d</sup> Values based on work from Binzer et al. (2016); Fussmann et al. (2014); Rall et al. (2012). <sup>e</sup> These parameters are chosen in a way that the attack rate is close to zero in case of  $T = 273\text{K}$  or  $T = 313\text{K}$  and maximal for  $T_{opt} = 291, 64\text{K}$ .

## Evolutionary processes

In our first model, we consider a simple two-species system consisting only of the external resource and a single consumer population. Only the consumer body mass  $x_1$  is evolving, whereas its feeding center is fixed and matches the resource body mass,  $f_1 = x_0 = 1$ . In this simplified case, the population dynamics become:

$$\begin{aligned}\frac{dB_1}{dt} &= ea_{10}B_1B_0 - [a_{11}(1 - e) + c]B_1^2 - d_1B_1 \\ \frac{dB_0}{dt} &= r \left(1 - \frac{B_0}{K}\right) B_0 - a_{10}B_1B_0\end{aligned}\quad (5)$$

132 We follow the evolution of the consumer body mass  $x_1$  using the adaptive dynamics frame-  
work (Dieckmann and Law, 1996; Geritz et al., 1998; Metz et al., 1992). It assumes that evolution  
occurs via small mutation steps and that the system reaches the ecological equilibrium in be-  
135 tween two mutations. Within this framework, the evolutionary dynamics of  $x_1$  is described by  
the canonical equation of adaptive dynamics (Dieckmann and Law, 1996):

$$\frac{dx_1}{dt} = \frac{1}{2}\mu\sigma^2 \frac{B_1^*(x_1)}{x_1} \left. \frac{\partial\omega(x_m, x_1)}{\partial x_m} \right|_{x_m \rightarrow x_1}, \quad (6)$$

where  $\mu\sigma^2 \frac{B_1^*(x_1)}{x_1}$  embodies the phenotypic variability on which selection can act, with  $\mu$  the per  
138 individual rate of mutation,  $\sigma^2$  the variance of the phenotypic effect of the mutation and  $\frac{B_1^*(x_1)}{x_1}$  the  
density of the resident consumer population at equilibrium. The last term embodies variations  
in the fitness landscape around the resident value, thereby the effects of natural selection. The  
141 mutant is assumed to have a slightly different body mass value ( $x_m$ ) compared to a resident  
population fixing the ecological community (Metz et al., 1992). Because the part of the equation  
embodying the phenotypic variability is always positive, only the sign of the fitness gradient  
144 constrains the direction of trait variation. If the gradient is positive (resp. negative) then a  
higher (resp. lower) value of body mass is selected. In the results section, we use equation (6) to  
determine the position of evolutionary singularities and associated evolutionary dynamics.

147 In our second model, we consider not only the evolution of body masses, but also of feeding  
preferences, and we relax the strict assumptions of small mutation steps and separate ecological  
and evolutionary time scales. Such modifications facilitate the emergence of higher trophic levels  
and complex food webs. Each numerical simulation starts with a single consumer morph with  
150 body mass  $x_1 = 100$  and feeding center  $f_1 = 1$ , which is thus feeding on the external resource



with its maximum attack rate. The initial biomass densities are  $B_0 = K = 10$  for the resource and  
153  $B_1 = \epsilon$  for the ancestor morph, where  $\epsilon$  is the consumer extinction threshold. Every 100 model  
time steps, we introduce a new morph into our network, which makes a total number of  $5 \cdot 10^6$   
morph additions during a simulation runtime of  $5 \cdot 10^8$  time units. One of the extant morphs  
156 (but not the external resource) is chosen randomly as "parent" morph  $i$  for a "mutant" morph  
 $j$ . The mutation probability for a given morph is proportional to its individual density, meaning  
that morphs with small body masses on low trophic levels, which have the highest individual  
159 densities, have the potential to evolve fastest. The initial biomass density of mutants is taken  
from the parent morph and set to  $B_j = \epsilon$ . The logarithm of the mutant's body mass  $\log(x_j)$  is  
randomly chosen from a normal distribution around the logarithm of the parent's body mass  
162  $\log(x_i)$ , with a standard deviation of 0.25. The same rule applies also for the logarithm of the  
mutant's feeding center  $\log(f_j)$ . Parent and mutant morphs have thus typically similar traits, but  
bigger mutation steps can occasionally occur.

165 Whether or not a new mutant population is viable in a given environment created by the other  
morphs is determined by the population dynamics in equations (1-4). The resulting food web  
structures are not static, but emerge and evolve in a self-organized manner. Related community  
168 evolution models have been shown to produce complex networks with properties very similar  
to available empirical food web data (Allhoff and Drossel, 2013; Allhoff et al., 2015; Loeuille and  
Loreau, 2005). More details on the model that we use here, including exemplary simulation runs,  
171 can be found in the online appendix C.

## Temperature dependence

For both models, we include temperature dependence into the resource growth rate and carrying  
capacity, as well as into the consumer respiration and mortality loss rates:

$$r(T) = r \cdot \exp \left[ \frac{E_a \cdot (T - T_{ref})}{kTT_{ref}} \right], \quad (7)$$

$$K(T) = K \cdot \exp \left[ -\frac{E_a \cdot (T - T_{ref})}{kTT_{ref}} \right], \quad (8)$$

$$d_i(x_i, T) = d \cdot x_i^{-1/4} \cdot \exp \left[ \frac{E_a \cdot (T - T_{ref})}{kTT_{ref}} \right]. \quad (9)$$

Here,  $E_a$  is the activation energy,  $T$  is the local temperature,  $T_{ref}$  is the reference temperature and  
174  $k$  is the Boltzmann constant.  $r$ ,  $K$  and  $d$  are scaling factors (see Table 1). Using this Arrhenius  
approach in order to include the temperature dependency into the resource growth rate  $r$  and  
into the respiration and mortality loss rate  $d_i$  is consistent with previous studies by Gilbert et al.  
177 (2014) and Vasseur and McCann (2005). Our approach for the temperature dependency of the  
carrying capacity  $K$  is motivated by previous work from Binzer et al. (2012) and Meehan (2006),  
and consistent with the empirical observations reported in the analysis by Fussmann et al. (2014).  
180 For simplicity, we chose identical activation energies in all three cases.

We compare three different scenarios linking temperature with feeding interactions. Empirical data on attack rates reveal that the relationship with temperature is weak compared to the influence of temperature on parameters reported above (Fussmann et al., 2014; Rall et al., 2012, 2010). Thus, as a first approximation, we consider attack rates to be independent from temperature (scenario (a)), which serves as a null model:

$$a_{ij}^{(a)} = x_i^{-0.25} \cdot \frac{1}{s\sqrt{2\pi}} \cdot \exp \left[ -\frac{(\log f_i - \log x_j)^2}{2s^2} \right]. \quad (10)$$

Scenario (b) assumes that temperature dependence of attack rates follow the Arrhenius equation (Binzer et al., 2016; Fussmann et al., 2007; Vasseur and McCann, 2005):

$$a_{ij}^{(b)} = a_{ij}^{(a)} \cdot \exp \left( \frac{E'_a \cdot (T - T_{ref})}{kTT_{ref}} \right). \quad (11)$$

Following Rall et al. (2010), Rall et al. (2012) and Fussmann et al. (2014), we use a relatively low value for the activation energy  $E'_a$  compared to the activation energy for the resource parameters  
183 and consumer loss rates,  $E_a$ .

As explained in the introduction, continuous increases in attack rates under warming (as in scenario (b)) is only valid within a certain temperature range and is not suitable to describe temperature dependencies above the thermal optimum. In scenario (c), we therefore follow the results from Englund et al. (2011), and assume a modal relationship with a peak of attack rates at an optimal temperature ( $T_{opt} = 291,64$  K):

$$a_{ij}^{(c)} = a_{ij}^{(a)} \cdot \exp \left( \frac{b \cdot (T - T_{ref})}{kTT_{ref}} + \frac{q \cdot (T - T_{ref})^2}{k^2 T^2 T_{ref}^2} \right), \quad (12)$$

## Data collection

For both models and all three scenarios of temperature-dependent attack rates, we investigate how the consumer body mass(es), as well as the distribution of biomasses respond to warming. The simplified consumer-resource model can partly be treated analytically. We first study the ecological dynamics of the system, investigating the conditions for consumer-resource coexistence at a given temperature and for a given consumer body mass  $x_1$ . We then study the evolution of consumer body mass using adaptive dynamics (Dieckmann and Law, 1996; Geritz et al., 1998; Metz et al., 1992). All analytical results from the consumer-resource model are corroborated by numerical simulations. Whenever adaptive dynamics equations are analytically intractable, graphical exploration of the possible evolutionary outcomes are made using pairwise invasibility plots (PIPs) (Geritz et al., 1998). Such PIPs visualize the invasion success of potential mutant populations given resident populations via the sign of their relative fitness. They allow us to investigate whether evolutionary singularities occur and whether they are convergent and invulnerable.

The multi-trophic community evolution model is analyzed via numerical simulations only. Each simulation allows the emergence of a network. After an initial period of diversification, the network size and structure stays approximately constant and fluctuates around a temperature-dependent average. We are particularly interested in the fluctuations in network structure and biomass flow after this initial build-up, and therefore deliberately exclude the first  $5 \cdot 10^7$  time units from the analysis. Throughout the simulations, we calculate the trophic positions of all morphs via the average, flow-based trophic position of their prey plus one. We round these trophic positions to integer values in order to group the morphs into distinct trophic levels. We then determine the average body mass and the total biomass of all morphs found at each trophic level and finally calculate the time average of these measures. More detailed information on this procedure, including exemplary simulation runs, can be found in the online appendix C.

## Results

### 210 Ecological equilibria

We start with the analytical investigation of the simplified consumer-resource model. System (5) leads to three possible ecological equilibria. Two of those are trivial, because either the consumer ( $B_0^* = K$  and  $B_1^* = 0$ ) or both species ( $B_0^* = B_1^* = 0$ ) go extinct. A third equilibrium allows for the coexistence of both species and is therefore of particular interest. The equilibrium biomass of resource and consumer are given by:

$$\begin{cases} B_0^* = \frac{K ([a_{11} (1 - e) + c] r + a_{10} d_1)}{a_{10}^2 e K + [a_{11} (1 - e) + c] r} \\ B_1^* = \frac{r [a_{10} e K - d_1]}{a_{10}^2 e K + [a_{11} (1 - e) + c] r} \end{cases} \quad (13)$$

Note that this equilibrium depends on all parameters and in particular on the consumer body mass  $x_1$  that affects the metabolic scaling of loss ( $d_1$ ) and attack rates ( $a_{10}$  and  $a_{11}$ ). Feasibility and stability conditions required to maintain the coexistence are detailed in the online appendix A.

### 216 Impact of temperature-dependent attack rates on body mass evolution and biomass densities

In this part, the parameters depending on body mass are rewritten as functions of this trait (e.g.  $a_{10}$  becomes  $a(x_1, x_0)$ ). As explained in the methods section, evolution of the consumer body mass is determined by the fitness gradient (see equation(6)). The relative fitness  $\omega(x_m, x_1)$  of mutant consumer  $m$  (with biomass density  $B_m$  and body mass  $x_m$ ) given the resident consumer 1 (with biomass density  $B_1^*$  and body mass  $x_1$ ) is determined by the mutant population growth rate when rare and the resident being at ecological equilibrium:

$$\begin{aligned} \omega(x_m, x_1) &= \frac{1}{B_m} \frac{dB_m}{dt} \Big|_{\substack{B_0, B_1 \rightarrow B_0^*, B_1^* \\ B_m \rightarrow 0}} \\ &= e \cdot a(x_m, x_0) B_0^* - [a(x_1, x_m) + c - e \cdot a(x_m, x_1)] B_1^* - d(x_m), \end{aligned} \quad (14)$$

where  $a(x_1, x_m)$  describes the predation rate of the mutant by the resident,  $a(x_m, x_1)$  is the predation rate of mutants on residents, and  $d(x_m)$  is the mutant death rate.

The fitness function can be used to determine evolutionary singular strategies, which occur when trait variations are null. This correspond to the roots of equation (6). Because other parts of the equation (6) are strictly positive, evolutionary singularities correspond to the roots of the fitness gradient  $\frac{\partial \omega(x_m, x_1)}{\partial x_m} |_{x_m \rightarrow x_1}$ . Computing this fitness gradient yields the following evolutionary singularities:

$$c - a(\tilde{x}_1, \tilde{x}_1) \left[ \frac{4(\log \tilde{x}_1 - \log f_1)}{s^2 \ln(10)} - 1 \right] = 0 \quad (15)$$

219 where the tilde indicates singular strategies. The complete proof of this result, as well as numerical conditions for non-invasibility (i.e., conditions under which such strategies cannot be invaded by any nearby mutant) differentiated from this equation, can be found in the online  
222 appendix B.

While equation does not allow an explicit expression for selected consumer body mass  $\tilde{x}_1$  (15), it reveals which parameters affect its evolution under warming. More precisely,  $\tilde{x}_1$  clearly  
225 depends on competition and predation rates, but not on resource parameters or consumer loss rates. Effects of temperature changes can then be directly analyzed. Taking the derivative of (15) with respect to T shows that variations the singular strategy  $\tilde{x}_1$  are positively related to variations  
228 of the consumer attack rate with temperature (none in scenario (a), Arrhenius-shaped in scenario (b) and hump-shaped in scenario (c)), for the vast majority of parameter sets. The direction of body mass evolution in response to warming is thus entirely determined by the direction of the  
231 effect of temperature on consumer attack rate. A complete analysis can be found in the online appendix B.

Pairwise invasibility plots (PIP) (Geritz et al., 1998) corroborate these findings (fig. 2). For all  
234 three scenarios and for the whole temperature range considered in our study, we always find two singular strategies: a repellor and a continuously stable strategy (CSS). Consumers with a body mass close to the repellor will evolve away from it (as shown on panel C), whereas a population  
237 near a CSS will evolve towards the singular strategy and settle there (as shown in panels B and C). Consistent with our analysis of equation (15), the position of the CSS is temperature independent in scenario a). Panels D, E and F confirm that increasing temperature leads to  
240 continuously increasing consumer body mass under scenario (b). Scenario (c) first leads to an increase (panel G and H) then to a decrease (panel I) of consumer body mass.

Fig. 3 further illustrates the variations in body mass due to temperature, as well as their

243 implication for distribution of biomasses. Panels A, C and E show the variations in the selected  
(CSS) body mass for a wide range of temperature and for each of the three scenarios tested.  
Increasing attack rates (as in scenario (b) or scenario (c) when below the thermal optimum) lead  
246 to increasing body masses under warming. Decreasing attack rates (as for high temperature in  
scenario (c)), in turn result in decreasing body masses under warming.

The final distribution of biomasses at the end of the eco-evolutionary process also depends  
249 on the considered scenario for the consumer attack rate (fig. 3B, D, and F). In scenario (a), both  
 $B_0^*(\tilde{x}_1)$  and  $B_1^*(\tilde{x}_1)$  increase with temperature (panel B), as a direct consequence of increasing  
resource growth rates (equation (7)). The decline in carrying capacity under warming (equation  
252 (8)) gets more important at even higher temperatures, and eventually leads to consumer extinc-  
tion, but plays only a minor role in the temperature window considered here. Such a pattern  
is also consistent with relaxed top-down controls (Oksanen et al., 1981), as the consumer suffers  
255 increasing loss rates (equation (9)). Warming eventually leads to a decreasing consumer-resource  
biomass ratio.

A similar pattern of increasing biomass densities, but with an increasing consumer-resource  
258 biomass ratio, emerges from scenario (b), because increasing attack rates (equation (11)) partly  
compensate increased loss rates (panel D). In contrast, the pattern emerging from scenario (c) is  
more complex (panel F). Coexistence of resource and consumer is only possible within a certain  
261 temperature window. At high temperature, the reduced attack rate does not allow the mainte-  
nance of the consumer (equation (12)). Maximum attack rates at intermediate temperatures lead  
to resource depletion, explaining the U-shape of the resource biomass density with temperature.

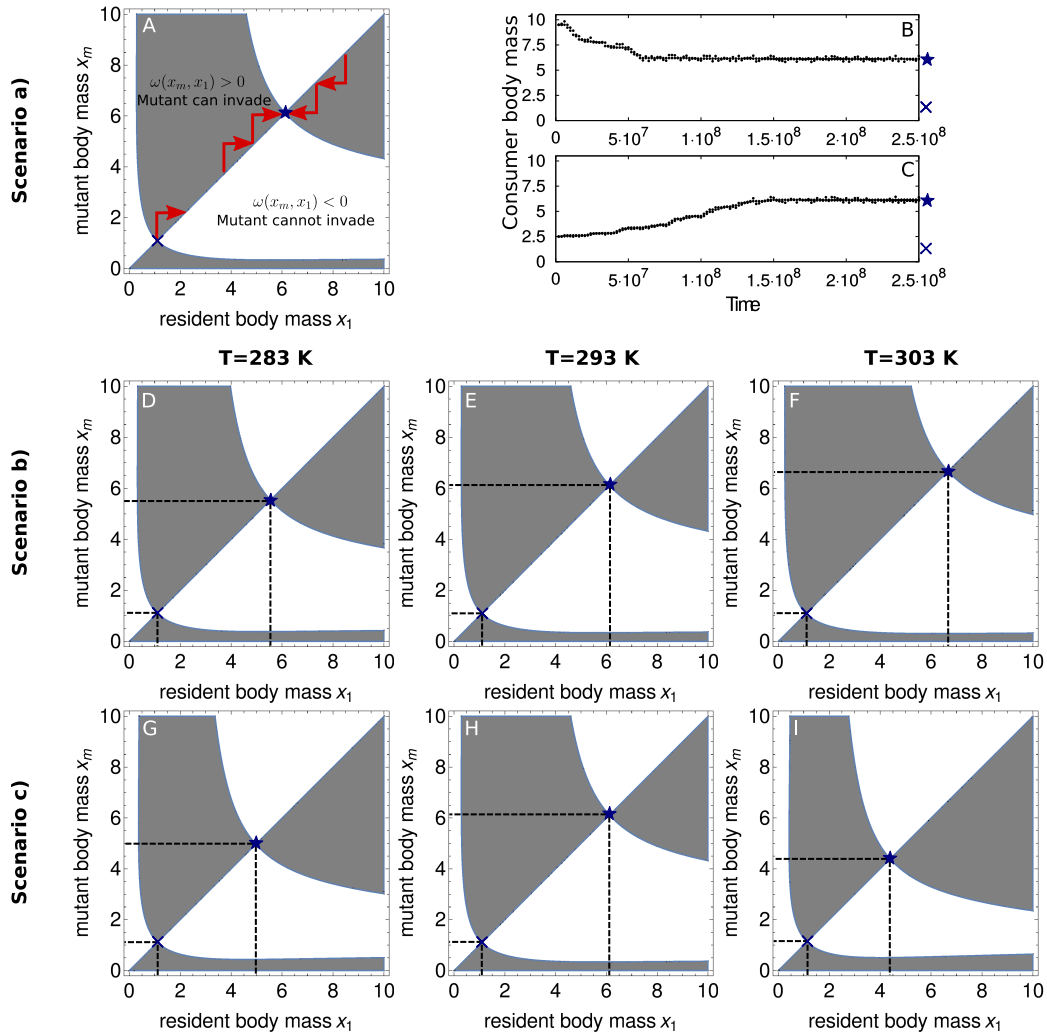


Figure 2: A, D to I: Pairwise invasibility plots (PIP) representing the potential invasibility of a rare mutant with body mass  $x_m$  within a population of resident consumers at the ecological equilibrium with body mass  $x_1$ . In A,  $\omega(x_m, x_1)$  is the relative fitness of a mutant with trait value  $x_m$  compared to a resident with trait value  $x_1$ . Evolutionary trajectories are represented by red arrows. The system has two evolutionary singular strategies, one non-convergent and invulnerable (the blue cross, called a repeller) and one convergent and non-invasible (the blue star, called a continuously stable strategy or CSS). B and C: Simulations of consumer body mass evolution under scenario (a) starting at  $x_1 = 10$  (B) and  $x_1 = 2.5$  (C).

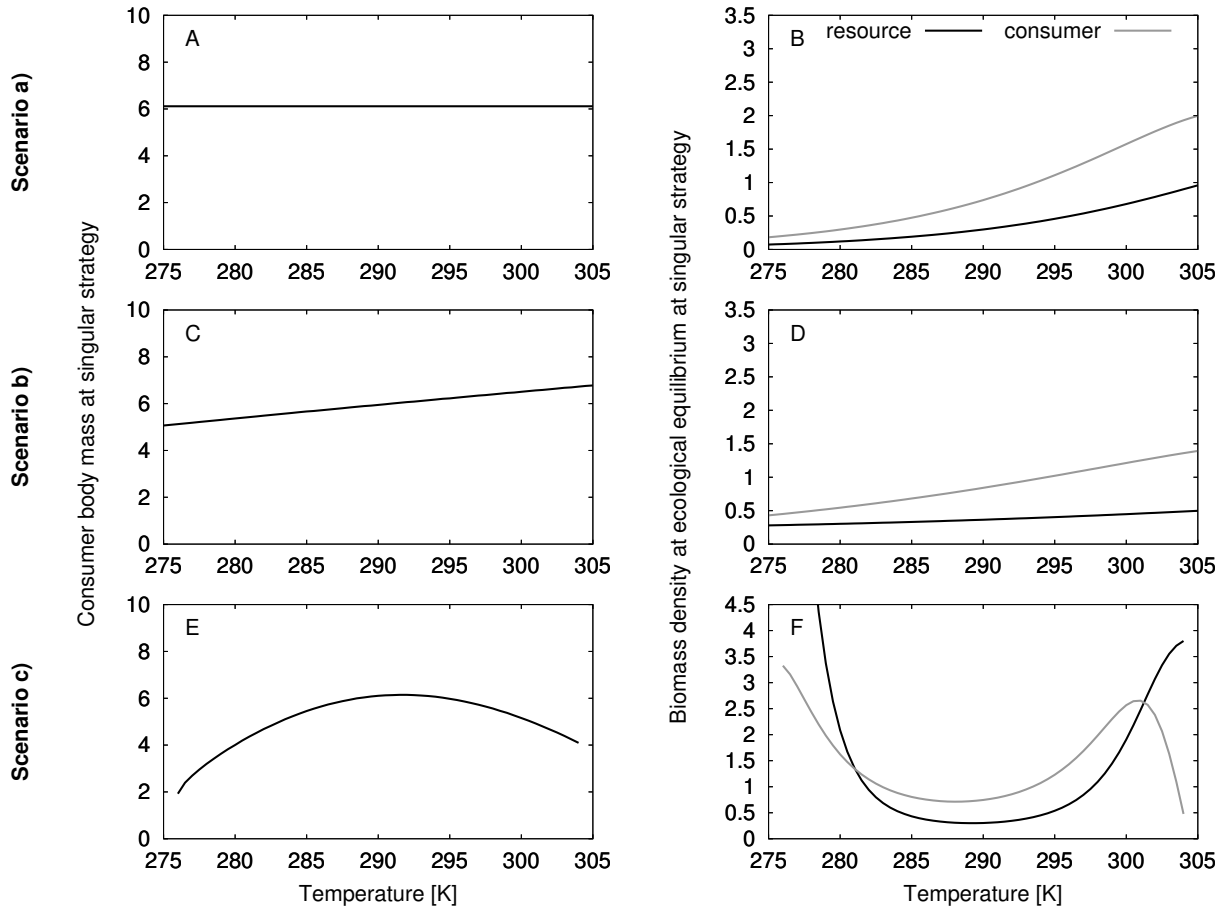


Figure 3: Analysis of the consumer-resource model with three scenarios of temperature-dependent interaction rates. A, C, E: Impact of temperature on final consumer body mass  $\tilde{x}_1$ . B, D, F: Impact of temperature on biomass densities  $B_0^*$  and  $B_1^*$ . Parameters values are the typical one specified in Tab.1.



## 264 **Impact of trophic positions on body mass evolution and biomass densities**

The multi-trophic community evolution model allows us to check whether the results that we obtain from the simplified consumer-resource model, hold across trophic levels in a more complex network context. We therefore explore whether and how the trophic position of a consumer affects its evolutionary response to warming. In general, we obtain results that are very similar to the results from the simplified consumer-resource model, as shown in panels A, C and E of fig. 4: Consumer body masses do not change in response to warming under scenario (a), increase under scenario (b) and show a hump-shaped response under scenario (c). However, we observe that the variation in body mass observed in scenario (b) and (c) is systematically larger at higher compared to lower trophic levels. Changing temperatures trigger evolutionary responses on all trophic levels, meaning that consumers not only react directly to changing temperatures, as in the simplified model version, but also to changing prey and/or predator body masses. Evolutionary changes in body masses thus cascade through the whole food web and trigger eco-evolutionary feedbacks. While lower levels are heavily constrained (selected body mass being a compromise of many effects, including body mass of both predators and prey), top levels evolve more freely (as their body mass is not constrained by any predator above). This results in decreased levels of stabilizing selection at higher trophic positions.

The response of biomass densities to warming is a straightforward generalization of the consumer-resource model, as shown in panel B, D and F of fig. 4. Warming in scenario (a) leads to an increase in resource biomass density, but decreasing consumer efficiency hampers the biomass flow from lower to higher trophic levels and therefore leads to starvation of top predators in hot temperature regimes. Scenario (b) leads again to a similar, but less pronounced pattern, reflecting the fact that increasing attack rates compensate for increasing consumer loss rates. Scenario (c) leads to resource depletion at intermediate temperatures, where attack rates are maximal. Increasing (or decreasing) temperature first leads to starvation of top predators, which temporally releases the next lower trophic level from predation pressure, and then these new top predators also go extinct, and so on, until consumer survival is impossible.

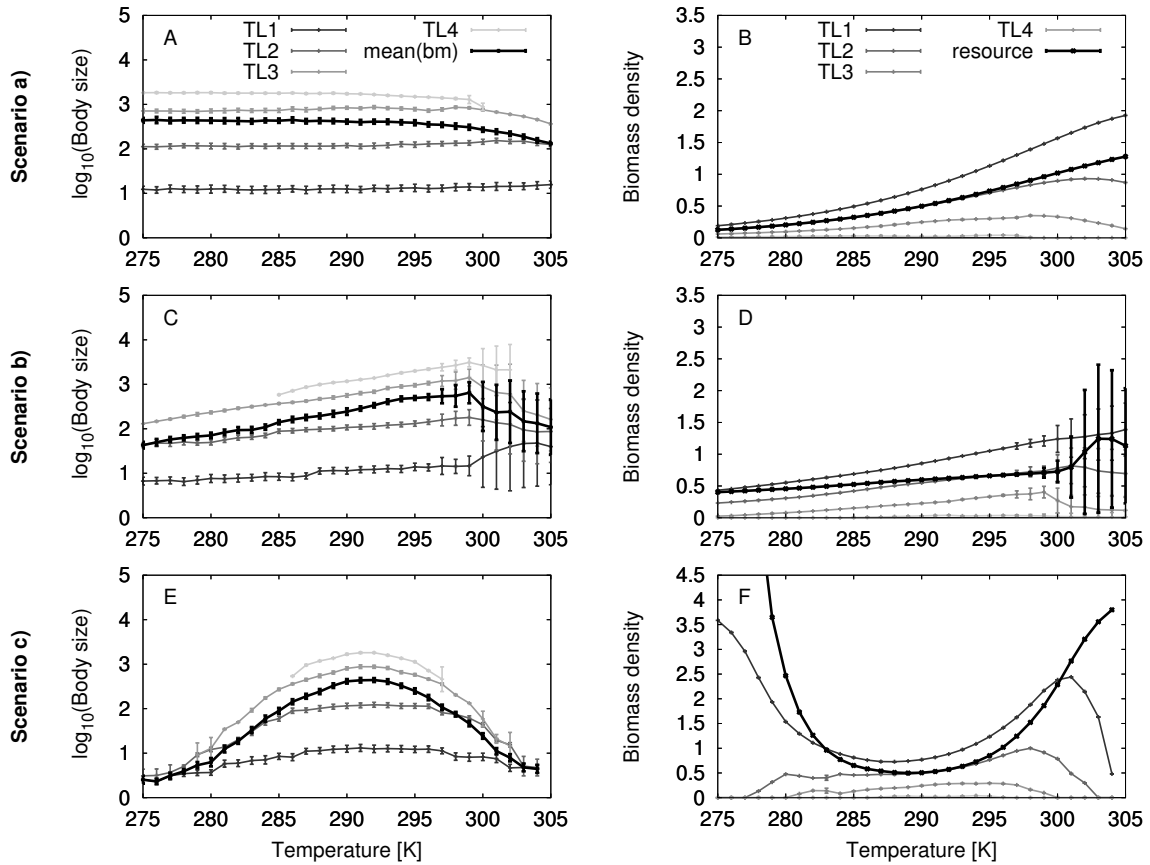


Figure 4: Same analysis as in fig. 3, but with the multi-trophic community evolution model. A, C, E: Body mass response to warming. Shown is the mean body mass of all consumer morphs in the network and of all consumers morphs within a given trophic level. Each data point represents an average over time and over 10 simulations runs. Error bars represent standard deviations describing the variation among simulations. The initial network build-up is not taken into account. B, D, F: Response of the biomass distribution across trophic levels to warming. Shown is the biomass density of the resource and the total biomass density of all consumer morphs within a given trophic level. Each data point represents again an average over time and over 10 simulations runs.

## 291 Discussion

Our results reveal that evolution of body mass in response to warming can greatly depend on the temperature dependence of consumer attack rates and that such body mass changes cascade through the whole food web. We investigated three different scenarios: (a) Temperature-independent attack rates, (b) attack rates increasing with temperature, following the Arrhenius approach, and (c) a hump-shaped relation between temperature and attack rates. By comparing results obtained under these three different scenarios, we uncovered that body mass increase or decrease follow the variations of attack rates, throughout the network. Our approach considers both organism-level metabolic and ecological constraints linking temperature and body mass (i.e. temperature-dependent resource growth, respiration and attack rates, and temperature-dependent resource capacity), but does not account for developmental or cell-level metabolic rationales (such as those invoked by Arendt, 2007; Kozłowski et al., 2004; Perrin, 1995; van der Have and de Jong, 1996). Our approach thus assigns body mass variations to the result of ecological selective pressures acting directly at the organism mass level (Atkinson and Sibly, 1997; Daufresne et al., 2009; Hessen et al., 2013).

The simplified model suggests that temperature effects on body mass greatly depend on how temperature constrains attack rates. We find that scenario (a) and (b) lead respectively to no change and to an increase in consumer body mass under warming, whereas scenario (c) results in a hump-shaped relation of body masses with temperature. The decline in consumer body mass, as observed in numerous empirical studies (Brose et al., 2012; Daufresne et al., 2009; Emmrich et al., 2014; Sheridan and Bickford, 2011), thus only occurs under scenario (c), under the assumption that the consumer was initially adapted to thermal constraints and now displays decreasing attack rates with warming. The assumption of an increase in attack rates as a first response to warming (such as in scenario b) may be justified as consumers first need increased energy levels to face new metabolic requirements. During this first response we therefore expect, according to our results, an increase in selected body mass. However, empirical evidence shows that many species may already be limited in their daily activities, including foraging, as they have to spend time in refugia to prevent overheating (Sinervo et al., 2010). Such observations suggest that such species have passed their thermal optimum, so that attack rates decline, as in scenario c. We then expect, consistent with most reported empirical results, that declines in

321 selected body mass should be expected for such species. In a world that has already warmed significantly, scenarios (a) or (b) might be limited in scope, so that no variation or increases in body mass may seldom be observed.

324 By allowing different outcomes in terms of body mass variation, our model helps to account for the important exceptions to the supposed universal rule of declining body masses with climate warming (Gardner et al., 2011). Empirical examples related to scenario (a), which show no  
327 body mass response to warming, are likely to be under-reported in the empirical literature, as negative results are more prone to self-censorship, and/or harder to publish. However, according to our model, we still expect frequent evolution to smaller body masses. Indeed, the assumption  
330 leading to such an outcome (locally adapted consumers, which suffer from decreased consumption efficiency when being forced to leave their thermal optimum under global warming), seems to be reasonable in many cases. This assumption of local adaptation even forms the cornerstone  
333 of so-called climate envelope models that take current species distributions as reflections of their niches to predict future species distributions under changing environmental conditions (Thomas et al., 2004). It is likely fulfilled for species with large populations and large spatial ranges, as  
336 selective pressures then have ample opportunities to act and allow local adaptation.

The mechanistic explanation for this direct link between attack rate and body mass variation is as follows: in the simplified consumer-resource model, the selected consumer body mass is  
339 constrained by two conflicting pressures. The first pressure is energetic and corresponds to the balance between feeding input and biomass loss terms. It favors rather small body masses. All of these terms indeed scale with body mass, except for competition, so that a smaller morph overall  
342 experiences less competition pressure. By contrast, the second pressure is due to cannibalism and favors big body masses that suffer less such additional mortality. Scenario (b) reinforces the strength of the second component (by increasing attack rates under warming) relative to the  
345 first force, so that the body mass increases with warming. The same argumentation also holds for scenario (c) when temperature is below the optimum. Above the optimum, the trends get reversed and lead to decreasing body masses.

348 The direct link between evolved body mass and the temperature-dependence of consumer attack rate is confirmed by our mathematical analysis of the simple model. Note however that it relies on the assumption that resource parameters and consumer loss rates have identical acti-

351 vation energies. Temperature dependencies may however largely vary among parameters, as for  
example suggested for the resource carrying capacity by Uszko et al. (2017) and O’Gorman et al.  
(2017). In this light, a complete understanding of the temperature dependencies remains an im-  
354 portant question, that goes beyond the scope of this article. We can nevertheless assume that our  
first key result, which states that substantial decreases in body masses are only observed under  
scenario (c) as a consequence of decreased attack rates, is at least robust against choosing slightly  
357 different activation energies in (7), (8) and (9), because their impact would be overcompensated  
by the impact of considering or neglecting temperature-dependent attack rates. This interpreta-  
tion is perfectly in line with the study by Edeline et al. (2013), who predict that warming-induced  
360 body downsizing emerges through both ‘direct’ (ecology-independent, e.g. thermal constraints  
on physiology) and ‘indirect’ (ecology-mediated, e.g. shifts in selection induced by species in-  
teractions) effects of temperature, but that ecology provides the overwhelming forces driving  
363 thermal clines in fish body mass.

Direct links between attack rate and selected body mass variations may be empirically tested  
in different ways. A first test could focus on selected examples of body mass responses con-  
366 firming or contradicting the universal rule of declining body masses with temperature (Atkinson  
and Sibly, 1997). Targeted experiments on variation in performance and attack rates in response  
to temperature would allow to determine whether the considered species or populations are  
369 at a particular position of their thermal niches (see e.g. Dreisig, 1981; Englund et al., 2011; Fe-  
dorenko, 1975; Gresens et al., 1982; Mohaghegh et al., 2001; Thompson, 1978, for classic studies  
and a meta-analyses investigating interaction rates at various temperatures). We predict that an  
372 increase (resp. decrease) in body mass is related to consumers that were initially adapted to  
temperatures warmer (resp. colder) than their environment and therefore benefit (resp. suffer)  
from warming. We further predict that those cases where no body mass response is observed  
375 reflect virtually temperature-independent attack rates (as might be the case for small tempera-  
ture changes around the consumer thermal optimum) or situations where the species had no  
evolutionary potential to follow the temperature change (e.g. because it is very rare, has a low  
378 genetic variability or long generation times compared to the pace of climate warming).

A second test could be based on experiments using organisms with a short generation time  
such as phytoplankton and zooplankton species, which have often been successfully used to

381 investigate eco-evolutionary processes (e.g. Yoshida et al. 2003, Pantel et al. 2015). Growing  
several populations at different temperatures and confronting these pre-selected populations  
with different temperature regimes would allow a manipulation of the species position relative  
384 to its thermal optimum. Based on our scenario (c), we predict that the body masses of organisms  
selected at temperatures below (resp. above) the species' thermal optimum will increase (resp.  
decrease) with warming.

387 Interestingly, the qualitative variations of body masses observed in the simplified consumer-  
resource model hold in more complex, multi-trophic communities. We find, however, that the  
observed relative changes in body mass are larger at higher trophic levels compared to lower  
390 trophic levels. Although all consumers are directly affected by changes in temperature through  
their attack and death rates, as in the simplified model, most consumers also have to adapt to  
changes in prey and/or predator body mass. As a consequence, we observe that body mass  
393 changes cascade through the whole food web. Higher trophic level species undergo less stabiliz-  
ing selection than those at lower trophic levels, because low trophic levels are constrained by the  
body masses of both resource and predator species, whereas top predators are not constrained  
396 by any predator and thus evolve more freely.

That temperature changes interact with trophic interactions to select body mass variations  
is in line with empirical observations. Gibert and DeLong (2014), who analyzed a large marine  
399 data set uncovered that prey mass selection depends on predator body mass, temperature and the  
interaction between the two. Our finding that sensitivity to warming increases with increasing  
trophic position is also in line with data from multi-trophic grassland communities (Voigt et al.,  
402 2003). While top predators show larger evolutionary responses of body masses in our model,  
they also are the first to go extinct under warming. This finding is again in line with several  
empirical observations (Beisner et al., 1997; Gibert and DeLong, 2014; Petchey et al., 1999) and  
405 can be explained by the low abundance at the top trophic levels. Increased respiration/death  
rates due to warming then lower the population growth rates of morphs that are already rare.  
Such extinctions are therefore coherent with classic works on top down controls (Oksanen et al.,  
408 1981) or with other works that link trophic length and energy availability (Pimm, 1982; Post,  
2002).

While the flattening of trophic networks under warming agrees with previous results (Arim

411 et al., 2007; Fussmann et al., 2014), most previous works rely on ecological processes only, ignor-  
ing the role of (eco-)evolutionary dynamics. One might for example imagine that those trophic  
levels that disappear in response to warming can re-emerge, meaning that evolution eventually  
414 "repairs" the damage that took place (Kokko et al., 2017), or that body mass evolution helps to  
maintain constant consumer-resource biomass ratios and buffer the community from extinctions  
in the first place (Osmond et al., 2017). Our model, relying on eco-evolutionary dynamics, can  
417 thus help clarifying this question. Evolution is clearly not sufficient to completely restore (or  
maintain) the network structure after (during) warming. Instead, we predict that warming will  
significantly change the food web structure not only through variations in population density due  
420 to changes in ecological dynamics, but also due to changes in selected body mass. A related  
study by Stegen et al. (2011) predicts diversity to increase with temperature if resource supply  
is temperature-dependent, whereas temperature-dependent consumer vital rates cause diversity  
423 to decrease with increasing temperature. Combining both thermal dependencies (similar to our  
scenario b) results in a unimodal temperature–diversity pattern. A more detailed analysis of how  
temperature shapes evolving food web structures is, at least to our knowledge, still lacking.

426 Our observation that consumer body mass evolution is more sensitive to warming at higher  
trophic levels, could be tested with empirical data, since body mass distributions are now widely  
measured in food webs (Brose et al., 2006a; Cohen et al., 2003; Petchey et al., 2008; Riede et al.,  
429 2010; Woodward et al., 2005). However, we are confronted with two major difficulties when using  
such data sets. First, we would need to have these distributions on many generations, which is  
challenging, especially since high trophic levels are typically occupied by long generation species.  
432 This first obstacle can be overcome by using palaeontological data (Willis and MacDonald, 2011)  
or indirect evidence, e.g. from a space-for-time substitution, with the usual caveat that latitu-  
dinal gradients correlate not only with temperature changes, but also with other environmental  
435 variables (eg, growth season duration) (Hessen et al., 2013).

Second, current systems are not only stressed by warming, but also by other changes, such  
as nutrient availability or habitat fragmentation, which are already known to affect food web  
438 complexity (Calcagno et al., 2011; Pillai et al., 2011; Post, 2002). These simultaneous changes can  
affect body mass evolution and food web dynamics in ways that are antagonistic or synergistic  
to warming effects. This second obstacle can only be addressed with controlled experiments, for

441 example using mesocosm experiments. While such mesocosm experiments may have some limits  
in terms of representing natural network complexity (eg, aquatic mesocosm most often rely on  
phytoplankton-zooplankton, but may oversimplify diversity at upper trophic levels), they have  
444 provided important tests for ecological theories (see for example (Hulot et al., 2000) or (Downing  
and Leibold, 2002)) and are currently developed to understand the effects of global changes on  
complex system assemblages (Yvon-Durocher et al., 2011).

447 Based on our investigation, we see two important challenges for future research. The first  
challenge focuses on food web structure and stability, as already indicated above. A recent  
modeling approach by Binzer et al. (2016) led to the conclusion that the persistence and the  
450 connectance of complex, mass-structured predator-prey networks decrease with warming. It is,  
however, unclear whether these predictions hold when evolutionary dynamics, and in particu-  
lar body mass evolution, is taken into account. We know that eco-evolutionary feedbacks can  
453 provoke surprises concerning species coexistence, through evolutionary rescue effects (Bell and  
Gonzalez, 2009; Ferriere and Legendre, 2013; Gonzalez et al., 2013) or evolutionary extinction  
debts (Norberg et al., 2012). In some cases, body mass evolution might help to maintain biodi-  
456 versity by modifying consumer-resource mass ratios and thereby altering interaction strengths  
and energetic efficiencies (Osmond et al., 2017; Sentis et al., 2017), but the differential sensitivity  
of trophic levels to warming might also lead to community destabilization (Voigt et al., 2003).  
459 A change in network structure in response to warming also influences the functioning of the  
network and hence its ability to provide essential ecosystem services (Allhoff and Drossel, 2016).  
We therefore strongly suggest further research on the question how food web structures change  
462 in responses to warming, how evolution shapes these responses, and consequently what changes  
in the stability and functioning can be expected.

The second challenge addresses spatial aspects of food web eco-evolutionary dynamics. In  
465 our study, we assumed well-mixed populations in a homogeneous landscape and neglected any  
kind of spatial dynamics. It has, however, been predicted that gene flow and invasions have the  
potential to affect local adaptation and vice versa, depending on the relative timescale of spatial  
468 and evolutionary dynamics (Calcagno et al., 2017; Kirkpatrick and Barton, 1997; Norberg et al.,  
2012; Urban et al., 2012). It has also been predicted that spatial dynamics occurring between  
coupled habitats have the potential to change selection pressures in local food webs (Bolchoun



471 et al., 2017). Evolutionary metacommunities, which integrate large community evolution models  
(Brännström et al., 2012) with the concept of metacommunities (Leibold et al., 2004; Pillai et al.,  
2011), might thus be key to generate a thorough understanding of evolutionary responses to  
474 global warming.

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## **Author contribution statement**

483 AW and KTA share the first authorship for this article. All authors participated in designing the  
models. AW performed the analytic calculations of the consumer-resource model, while KTA  
performed all numeric simulations of both models. All authors discussed the results. AW and  
486 KTA wrote the first draft of the manuscript. All authors then participated in the manuscript  
writing.

## Online Appendices

### 489 **A: Ecological analysis of the consumer-resource model**

#### **Method**

Variations of the consumer and resource biomass densities with time (ecological dynamics) are  
492 described by equation (5) in the main article. Of special interest are conditions that determine the  
equilibrium of consumer and resource biomass densities, meaning the solutions of equation (5)  
equal to (0,0). The evolutionary analysis we undertake requires that the equilibrium is feasible  
495 and stable, so that we need to determine the parameters ranges for equilibrium feasibility and  
stability.

Feasibility simply means that biomasses are non negative. Studies usually consider positive or  
498 null biomasses, but because we focus here on species interactions, we consider strict positive  
biomasses for both species:  $B_0^* > 0$  and  $B_1^* > 0$ .

Local stability is investigated by analyzing the associated Jacobian matrix ( $J$ ). Stability requires:  
501  $\det(J) < 0$  and  $Tr(J) > 0$ .

## Results

Feasibility and stability conditions for the three scenarios are presented in table A1 below. We  
 504 can show that in our case, if feasible, the equilibrium is always locally stable.

Table A1: Feasibility and stability conditions

	Feasibility <sup>a</sup> conditions at low K	Feasibility conditions at high K
Scenario (a)	$0 < T < T_{lim} = \frac{T_{ref}E_a}{E_a - T_{ref}k \ln\left(\sqrt{\frac{a_{10}eK}{d}}\right)}$ and $0 < K < \frac{d \exp\left(\frac{2E_a}{T_{ref}k}\right)}{a_{10}e}$	$0 < T \text{ and } K \geq \frac{d \exp\left(\frac{2E_a}{T_{ref}k}\right)}{a_{10}e}$
Scenario (b)	$0 < T < T_{lim} = \frac{T_{ref}(2E_a - E'_a)}{2E_a - E'_a + T_{ref}k \ln\left(\frac{a_{10}eK}{d}\right)}$ and $0 < K < \frac{d}{a_{10}e}$	$0 < T \text{ and } K \geq \frac{d}{a_{10}e}$
Scenario (c) <sup>b</sup>	There is a lower and upper $T_{lim}$	

<sup>a</sup>: The stability conditions are always the same or less restrictive than the feasibility conditions.

Thus, when a system is feasible, it is always stable. <sup>b</sup>: Conditions for stability and feasibility are

507 given by the interval between the roots ( $T_{lim1}$  and  $T_{lim2}$ ) of the following inequality:

$$\frac{\alpha}{T^2} + \frac{\beta}{T} + \gamma > 0 \text{ with } \alpha = \frac{q}{k^2}, \beta = \frac{2E_a - b}{k} - \frac{2q}{k^2 T_{ref}} \text{ and } \gamma = \frac{1}{T_{ref}} \left( \frac{b - 2E_a}{k} + \frac{q}{k^2 T_{ref}} - \ln\left(\frac{d}{K e a_{10}}\right) \right)$$

## B: Evolutionary analysis of the consumer-resource model

### 510 Proof of the singular strategy formula

Adaptive dynamics are formalized by the canonical equation (Dieckmann and Law, 1996):

$$\frac{dx_1}{dt} = \frac{1}{2} \mu \sigma^2 \frac{B_1^*(x_1)}{x_1} \left. \frac{\partial \omega(x_m, x_1)}{\partial x_m} \right|_{x_m \rightarrow x_1} \quad (\text{B1})$$

with all terms explained in the methods section of the main article. In this equation, the last  
 513 term corresponds to the selection gradient, whose sign controls the evolutionary outcome (all  
 the other terms are always positive and are therefore not influencing the direction of evolution  
 of our focal trait  $x_1$ ). If the gradient is positive (resp. negative) then a bigger (resp. smaller)  
 516 body mass is selected. Here the selection gradient is the derivative of the relative fitness of a  
 rare mutant within a resident population. The selected trait is the body mass, with mutant body  
 mass  $x_m$  slightly different from that of the resident  $x_1$ .

Calculation of the selection gradient requires the expression of the relative fitness function. In  
 simple deterministic continuous-time models such as ours, relative fitness  $\omega(x_m, x_1)$  of a mutant  
 strategy  $x_m$  is measured as the growth rate of a rare mutant population, given that the resident  
 population is at its ecological equilibrium. It corresponds to equation (B2):

$$\omega(x_m, x_1) = \frac{1}{B_m} \left. \frac{dB_m}{dt} \right|_{\substack{B_0, B_1 \rightarrow B_0^*, B_1^* \\ B_m \rightarrow 0}} \quad (\text{B2})$$

519 Let us consider interactions between the mutant and the resident in our present model, with  
 the resource and resident consumer biomasses at ecological equilibrium and a rare mutant con-  
 sumer. The growth rate is given by:

$$\omega(x_m, x_1) = e \cdot a(x_m, x_0) B_0^* - (a(x_1, x_m) + c - e \cdot a(x_m, x_1)) B_1^* - d(x_m) \quad (\text{B3})$$

The first derivative of this fitness function gives the following selection gradient:

$$\begin{aligned} \frac{\partial \omega(x_m, x_1)}{\partial x_m} &= B_0^* e \cdot \frac{\partial a(x_m, x_0)}{\partial x_m} - \left( \frac{\partial a(x_1, x_m)}{\partial x_m} - e \frac{\partial a(x_m, x_1)}{\partial x_m} \right) B_1^* - d'(x_m) \\ &= B_0^* e \cdot \frac{-1}{4x_m} a(x_m, x_0) - \left( \frac{(\log f_1 - \log x_m)}{x_m s^2 \ln(10)} a(x_1, x_m) - e \frac{-1}{4x_m} a(x_m, x_1) \right) B_1^* - \frac{-1}{4x_m} \cdot d(x_m) \\ &= -\frac{1}{4x_m} \left[ \omega(x_m, x_1) + B_1^* \left( c - a(x_1, x_m) \left[ \frac{4(\log x_m - \log f_1)}{s^2 \ln(10)} - 1 \right] \right) \right]. \end{aligned} \quad (\text{B4})$$

Evolutionary singularities occur at trait values which make the canonical equation (B1) equal to zero. Because other parts of equation (B1) are strictly positive, evolutionary singularities correspond to the roots of the selection gradient. Here the singular strategies  $\tilde{x}_1$  therefore correspond to the roots of equation  $\frac{\partial \omega(x_m, x_1)}{\partial x_m} \Big|_{x_m \rightarrow x_1} = 0$ . As mutations are small ( $x_m$  goes to  $x_1$ ), and remembering that  $\omega(x_1, x_1) = 0$ , equation B4 simplifies to:

$$\frac{\partial \omega[x_m, x_1]}{\partial x_m} \Big|_{x_m \rightarrow x_1} = -\frac{1}{4x_1} B_1^* \left( c - a(x_1, x_1) \left[ \frac{4(\log x_1 - \log f_1)}{s^2 \ln(10)} - 1 \right] \right) \quad (\text{B5})$$

522 Remembering that  $B_1^* > 0$ , such singular strategies follow the equation:

$$c - a(\tilde{x}_1, \tilde{x}_1) \left[ \frac{4(\log \tilde{x}_1 - \log f_1)}{s^2 \ln(10)} - 1 \right] = 0 \quad (\text{B6})$$

where the tilde indicates body mass values at the singular strategy.

### Temperature dependence of the singular strategy

525 In order to study the variation of  $\tilde{x}_1$  with the temperature  $T$ , we can differentiate (B6). Consider now  $a(\tilde{x}_1, \tilde{x}_1) = a(\tilde{x}_1[T])g(T)$ , with  $g(T)$  the impact of temperature on the attack rate.  $g(T) = 1$  in scenario (a),  $g(T) = \exp\left(\frac{E_a \cdot (T - T_{ref})}{kT T_{ref}}\right)$  in scenario (b) and  $g(T) = \exp\left(\frac{b \cdot (T - T_{ref})}{kT T_{ref}} + \frac{q \cdot (T - T_{ref})^2}{k^2 T^2 T_{ref}^2}\right)$  in scenario (c), with all the terms defined in table 1. Finally let us set  $h(\tilde{x}_1[T]) = \frac{4(\log \tilde{x}_1 - \log f_1)}{s^2 \ln(10)} - 1$ .

With these new notations, (B6) becomes:

$$c - a(\tilde{x}_1[T])g(T)h(\tilde{x}_1[T]) = 0. \quad (\text{B7})$$

To understand the impact of temperature on the consumer body mass at the singular strategy 531  $\tilde{x}_1[T]$ , we differentiate (B7) with respect to temperature  $T$ :

$$-g(T) \frac{\partial \tilde{x}_1[T]}{\partial T} \frac{\partial a(\tilde{x}_1[T])h(\tilde{x}_1[T])}{\partial \tilde{x}_1} - a(\tilde{x}_1[T])h(\tilde{x}_1[T]) \frac{\partial g(T)}{\partial T} = 0. \quad (\text{B8})$$

Then the sensitivity of  $\tilde{x}_1[T]$  to changes in T is equal to:

$$\frac{\partial \tilde{x}_1[T]}{\partial T} = a(\tilde{x}_1[T])h(\tilde{x}_1[T]) \frac{1}{g(T)} \frac{\partial g(T)}{\partial T} \frac{-1}{\frac{\partial a(\tilde{x}_1[T])h(\tilde{x}_1[T])}{\partial \tilde{x}_1}}. \quad (\text{B9})$$

Because  $a(\tilde{x}_1[T])h(\tilde{x}_1[T])$  is always positive, then if  $\frac{\partial a(\tilde{x}_1[T])h(\tilde{x}_1[T])}{\partial \tilde{x}_1}$  is negative (resp. positive) the sensitivity of  $\tilde{x}_1[T]$  to changes in T is similar (resp. opposite) to that of  $g(T)$  to changes in T (i.e.  $\frac{1}{g(T)} \frac{\partial g(T)}{\partial T}$ ).

The sensitivity of  $\tilde{x}_1[T]$  to changes in T depends on the sign of  $\frac{\partial a(\tilde{x}_1[T])h(\tilde{x}_1[T])}{\partial \tilde{x}_1}$ .

$$\begin{aligned} \frac{\partial a(\tilde{x}_1[T])h(\tilde{x}_1[T])}{\partial \tilde{x}_1} &= \frac{\partial \left( \tilde{x}_1[T]^{-0.25} \cdot \frac{1}{s\sqrt{2\pi}} \cdot \exp \left[ -\frac{(\log f_1 - \log \tilde{x}_1[T])^2}{2s^2} \right] \right)}{\partial \tilde{x}_1} \left( \frac{4(\log \tilde{x}_1 - \log f_1)}{s^2 \ln(10)} - 1 \right) \\ &= \frac{a(\tilde{x}_1[T])}{4s^4(\ln(10))^2} (16(\log \tilde{x}_1 - \log f_1)^2 + s^2(16 + s^2)). \end{aligned} \quad (\text{B10})$$

Because  $\frac{a(\tilde{x}_1[T])}{4s^4(\ln(10))^2}$  is always positive, we focus on finding the roots of  $16(Y - \log f_1)^2 + s^2(16 + s^2)$ , with  $Y = \log \tilde{x}_1$ . This polynomial of degree 2 is negative (meaning similar impact of temperature on attack rate and consumer body mass) if and only if:

$$Y < \frac{-\sqrt{s^2(16 + s^2)}}{4} + \log f_1 \text{ or } Y > \frac{\sqrt{s^2(16 + s^2)}}{4} + \log f_1 \quad (\text{B11})$$

Whether temperature affects consumer body mass similarly to how it affects consumer attack rate thus depends on the relative values of consumer body mass at the singular strategy, degree of generalism  $s$  and feeding center  $f_1$ . For the typical values used in this analysis, the consumer body mass values at the singular strategy are always above the larger root  $\frac{\sqrt{s^2(16+s^2)}}{4} + \log f_1 \approx 0.25$ . This is coherent with our results on fig. 3A, C and D where the relation between body mass and temperature follows the same direction than the relation between attack rate and temperature. More generally, we expect consumer body masses to be often above the bigger root. Indeed, all consumers in our model have by definition a larger body mass than the external resource, meaning that at evolutionary equilibrium  $\tilde{x}_1 > x_0 = 1$ , and therefore,  $Y > 0$ . Values below the larger root would require a high degree of generalism  $s$  and a consumer with above-optimum feeding center ( $f_1 > x_0 = 1$ ), such values are thus unlikely.

### Evolutionary stability analysis - Invasibility

Study of the singular strategy invasibility (i.e. evolutionary stability) requires the second derivative of the fitness with respect to  $x_m$  (Marrow et al., 1996). The singular strategy is evolutionarily stable if  $\frac{\partial^2 \omega[x_m, x_1]}{\partial x_m^2} < 0$ . We find that

$$\begin{aligned}
\frac{\partial^2 \omega[x_m, x_1]}{\partial x_m^2} &= B_0^* e \cdot \frac{\partial^2 a[x_m, x_0]}{\partial x_m^2} - \left( \frac{\partial^2 a[x_1, x_m]}{\partial x_m^2} - e \frac{\partial^2 a[x_m, x_1]}{\partial x_m^2} \right) B_1^* - d''[x_m] \\
&= \frac{5}{16x_m^2} [B_0^* e \cdot a(x_m, x_0) + e \cdot a(x_m, x_1)] B_1^* - d(x_m) \\
&\quad + B_1^* a(x_1, x_m) \left( \frac{s^2 \ln(10) X_m + X_m^2 - s^2 \ln 10}{s^4 \ln(10)^2} \right),
\end{aligned} \tag{B12}$$

with  $X_m = \log x_m - \log f_1$ , which simplifies into:

$$\begin{aligned}
\frac{\partial^2 \omega[x_m, x_1]}{\partial x_m^2} &= \frac{5}{16x_m^2} \omega(x_m, x_1) \\
&+ \frac{5}{16x_m^2} * B_1^* \left( c - a(x_1, x_m) \left[ \frac{16X_m^2 + 16s^2 \ln(10) X_m - 16s^2 \ln(10) - 5s^4 \ln(10)^2}{5s^4 \ln(10)^2} \right] \right).
\end{aligned} \tag{B13}$$

We know that  $\omega[x_m, x_1] \rightarrow 0$  in case  $x_m \rightarrow x_1$ . In consequence, we have:

$$\frac{\partial^2 \omega[x_m, x_1]}{\partial x_m^2} \Big|_{x_m \rightarrow x_1} = \frac{5}{16x_1^2} B_1^* \left( c - a(x_1, x_1) \left[ \frac{16X_1^2 + 16s^2 \ln(10) X_1 - 16s^2 \ln(10) - 5s^4 \ln(10)^2}{5s^4 \ln(10)^2} \right] \right), \tag{B14}$$

with  $X_1 = \log x_1 - \log f_1$ .

Note that  $\frac{16X_1^2 + 16s^2 \ln(10) X_1 - 16s^2 \ln(10) - 5s^4 \ln(10)^2}{5s^4 \ln(10)^2} = \frac{4(4X_1^2 - X_1 s^2 \ln(10) - 4s^2 \ln(10))}{5s^4 \ln(10)^2} + \frac{4X_1}{s^2 \ln(10)} - 1$ .

Therefore, using equation (B5), we can write:

$$\begin{aligned}
\frac{\partial^2 \omega[x_m, x_1]}{\partial x_m^2} \Big|_{x_m \rightarrow x_1} &= \frac{-5}{4x_1} \left( \frac{-1}{4x_1} B_1^* \left[ c - a[x_1, x_1] \left( \frac{4(4X_1^2 - s^2 \ln(10) X_1 - 4s^2 \ln(10))}{5s^4 (\ln(10))^2} + \frac{4X_1}{s^2 \ln(10)} - 1 \right) \right] \right) \\
&= \frac{-5}{4x_1} \left( \frac{\partial \omega[x_m, x_1]}{\partial x_m} \Big|_{x_m \rightarrow x_1} + \frac{1}{x_1} B_1^* a[x_1, x_1] \frac{(4X_1^2 - s^2 \ln(10) X_1 - 4s^2 \ln(10))}{5s^4 (\ln(10))^2} \right)
\end{aligned} \tag{B15}$$

555 When  $x_1 \rightarrow \tilde{x}_1$  (the predator body mass reaches the singular strategy), then  $\frac{\partial \omega[x_m, x_1]}{\partial x_m} \Big|_{x_m \rightarrow x_1} = 0$

by definition. In summary, we find:

$$\frac{\partial^2 \omega[x_m, x_1]}{\partial x_m^2} \Big|_{x_m \rightarrow \tilde{x}_1} = \frac{-B_1^* a[\tilde{x}_1, \tilde{x}_1]}{4(\tilde{x}_1)^2 s^4 (\ln(10))^2} (4\tilde{X}_1^2 - s^2 \ln(10) \tilde{X}_1 - 4s^2 \ln(10)), \tag{B16}$$

with  $\tilde{X}_1 = \log \tilde{x}_1 - \log f_1$ .

558 Since  $\frac{-B_1^* a[\tilde{x}_1, \tilde{x}_1]}{4(\tilde{x}_1)^2 s^4 (\ln(10))^2} < 0$ , the singular strategy is evolutionarily stable if and only if we have  $4\tilde{X}_1^2 - s^2 \ln(10) \tilde{X}_1 - 4s^2 \ln(10) > 0$ . Because the value of  $\tilde{x}_1$  is fixed by equation (15), the sign of equation (B16) will depend on the values of  $f_1$  and  $s$  that describe the predator feeding niche.

561 Results of such parameter variation are mentioned in the next part on convergence stability.

With the typical parameters used in the main article ( $f_1 = 1$  and  $s = 0.25$ ), the bigger singular



strategies  $\tilde{x}_1$  is approximately equal to 6.115 for the standard temperature  $T_{ref} = 293K$  and  
564  $4\tilde{X}_1^2 - s^2 \ln(10)\tilde{X}_1 - 4s^2 \ln(10) \approx 2.111$ . It ensures non-invasibility of this strategy, in consistency  
with our simulation results.

### Evolutionary stability analysis - Convergence

567 Convergence stability conditions are normally computed via either the sum of two second partial  
derivatives or the derivative of the selection gradient. The singular strategy is convergent stable  
if:

$$\frac{\partial^2 \omega[x_m, x_1]}{\partial x_m^2} + \frac{\partial^2 \omega[x_m, x_1]}{\partial x_1 \partial x_m} < 0 \quad (\text{B17})$$

570 Formula of the first term of this equation is given by equation (B12). The calculation of the  
cross-derivative is, however, more complex. It corresponds to:

$$\frac{\partial^2 \omega[x_m, x_1]}{\partial x_1 \partial x_m} = \frac{\partial}{\partial x_1} \left[ \frac{\partial \omega[x_m, x_1]}{\partial x_m} \right]. \quad (\text{B18})$$

Using the expression of the first derivative  $\frac{\partial \omega[x_m, x_1]}{\partial x_m}$  from equation (B4) gives:

$$\frac{\partial^2 \omega[x_m, x_1]}{\partial x_1 \partial x_m} = -\frac{1}{4x_m} \left[ \frac{\partial \omega(x_m, x_1)}{\partial x_1} + \frac{\partial B_1^*}{\partial x_1} (c - a(x_1, x_m)h(x_m)) + B_1^* \left( c - \frac{\partial a(x_1, x_m)}{\partial x_1} h(x_m) \right) \right] \quad (\text{B19})$$

573 with  $h(x_m) = \frac{4(\log x_m - \log f_1)}{s^2} - 1$  as in equation (B7), and  $\frac{\partial a(x_1, x_m)}{\partial x_1} = \frac{-1}{x_1} a(x_1, x_m)$ .

Derivative of the fitness function with respect to  $x_1$  gives:

$$\begin{aligned} \frac{\partial \omega(x_m, x_1)}{\partial x_1} &= ea(x_m, x_0) \frac{\partial B_0^*}{\partial x_1} - \left( \frac{\partial a(x_1, x_m)}{\partial x_1} - e \frac{\partial a(x_m, x_1)}{\partial x_1} \right) B_1^* - \frac{\partial B_1^*}{\partial x_1} (a(x_1, x_m) - ea(x_m, x_1) + c) \\ &= ea(x_m, x_0) \frac{\partial B_0^*}{\partial x_1} + \frac{1}{x_1} \left( a(x_1, x_m) - \frac{eh(x_1)}{4} a(x_m, x_1) \right) B_1^* - \frac{\partial B_1^*}{\partial x_1} (a(x_1, x_m) - ea(x_m, x_1) + c) \end{aligned} \quad (\text{B20})$$

Derivative of  $B_0^*$  with respect to  $x_1$  gives:

$$\frac{\partial B_0^*}{\partial x_1} = \frac{1}{4x_1} \left( B_0^*(1 - K) + \frac{\gamma(K - 1) + Ka(x_1, x_0) [d(x_1) - ea(x_1, x_0)]}{v} \right) \quad (\text{B21})$$

Derivative of  $B_1^*$  with respect to  $x_1$  gives:

$$\frac{\partial B_1^*}{\partial x_1} = \frac{B_1^*}{4x_1} \frac{a(x_1, x_0)^2 eK - Ra(x_1, x_1)(1 - e)(h(x_1) + 1)}{v} \quad (\text{B22})$$

with  $\gamma = -R[c - a(x_1, x_1)(1 - e)h(x_1)]$  and  $v = a(x_1, x_0)^2 eK + R[a(x_1, x_1)(1 - e) + c]$ . The full cross derivative has then a complex expression. Added to the second derivative, conditions for non-invasibility using equation (B17) are non tractable. Convergence stability of the singular strategy is therefore checked by varying one parameter at a time within the feasibility range. Convergence stability (and evolutionary stability) can then be visually checked by PIPs, and by the calculation of the fitness at  $(\tilde{x}_1 - \delta, \tilde{x}_1)$ ,  $(\tilde{x}_1 + \delta, \tilde{x}_1)$ ,  $(\tilde{x}_1, \tilde{x}_1 - \delta)$  and  $(\tilde{x}_1, \tilde{x}_1 + \delta)$ , with  $\delta = 0.001$  kg, around the singular strategy. Convergence stability (resp. evolutionary repelling quality) requires the fitness of  $(x_m = \tilde{x}_1, x_1 = \tilde{x}_1 \pm \delta)$  to be positive (resp. negative), because a resident close to the singular strategy can be replaced by a mutant. In this case the mutant reaches the singular strategy, no further mutation is possible. Evolutionary stability requires the fitness of  $(x_m = \tilde{x}_1 \pm \delta, x_1 = \tilde{x}_1)$  to be negative because a mutant with a slightly bigger or lower body mass than the resident at equilibrium then cannot invade the system.

Parameter variations are given in table B1. For all the parameter values tested in the ranges indicated in table B1, the smallest singular strategy is always a repellor (not convergent stable, not evolutionarily stable), and the biggest always convergent and evolutionarily stable (i.e. a CSS).

Table B1: Robustness check for all the model parameters.

Parameter <sup>1</sup>	Variation range <sup>2</sup>
$R$	[0.5, 10] with a 0.5 step
$K$	[5, 1000] with a 5 step
$x_0$	[0.5, 2.5] <sup>3</sup> with a 0.05 step
$f_1$	[0.5, 2.5] <sup>3</sup> with a 0.05 step
$s$	[0.05, 1] with a 0.05 step
$d$	[0.05, 1] with a 0.05 step
$e$	[0.3, 1] <sup>3</sup> with a 0.05 step
$c$	[0.05, 1] with a 0.05 step

<sup>1</sup> When varying one parameter, all the other are fixed at the typical values specified in table 1.

<sup>2</sup>For all parameter values, we tested all T values in the range [273K,  $\min(T_{lim}, 313K)$ ], with  $T_{lim}$  the limit temperature for coexistence, calculated via the formula specified in table A1.

<sup>3</sup> The upper (lower) range value is taken just below (above) the limit value of the parameter for coexistence, with  $T = T_{ref}$ .

## 591 **C: More information on the multi-trophic model**

In this appendix, we present three simulations of the multi-trophic community evolution model in detail, in order to clarify how we collected the data shown in fig. 4 of our main article. The time series of these three simulation runs are shown in fig. C1. They differ only in the temperature (280, 290 or 300 K) and in the set of the random numbers. Temperature dependence is included following scenario (a).

597 The topmost two panels show the evolution of body masses and feeding centers over time. Each line represents the life span of a morph. Please note that lines might overlap, indicating that several morphs share practically the same trait. Dots represents morphs that emerged, but were not able to establish themselves in the current network. Our mutation rule favors populations with big individual densities, which explains why we generally observe more mutations of morphs with smaller body masses, which typically have the biggest populations.

603 In the middle panel, we use exactly the same presentation to show the trophic positions of all morphs that are present at a given time. The trophic position of a consumer is calculated as the average, flow-based trophic position of its prey plus one. The trophic position of the external resource is considered to be zero. We round these trophic positions to the next integer value in order to assert all morphs into distinct trophic levels. At a given time, we can now determine how many morphs exist within a given trophic level, as shown in the forth panel, and how much biomass these morphs accumulate, as shown in the fifth panel.

The food webs emerge in a self-organized manner starting with only one single ancestor consumer, which feeds on the external resource. The beginning of the simulations is typically characterized by a period of strong diversification, where higher trophic levels emerge one after the other and where the network structure gets more and more complex. After this initial build-up, we observe that the network size and structure stays approximately the same and only fluctuates around a temperature-dependent average. We are particularly interested in this long-term behavior and therefore deliberately exclude the data from the first  $5 \cdot 10^7$  time units from our analysis. Instead, we take only data between  $t = 5 \cdot 10^7$  and the end of the simulation into account. Note that for better clarity fig. C1 shows only the first  $10^8$  time steps, although the simulations analyzed for fig. 4 in the main article actually had a much longer runtime of  $5 \cdot 10^8$  time units.

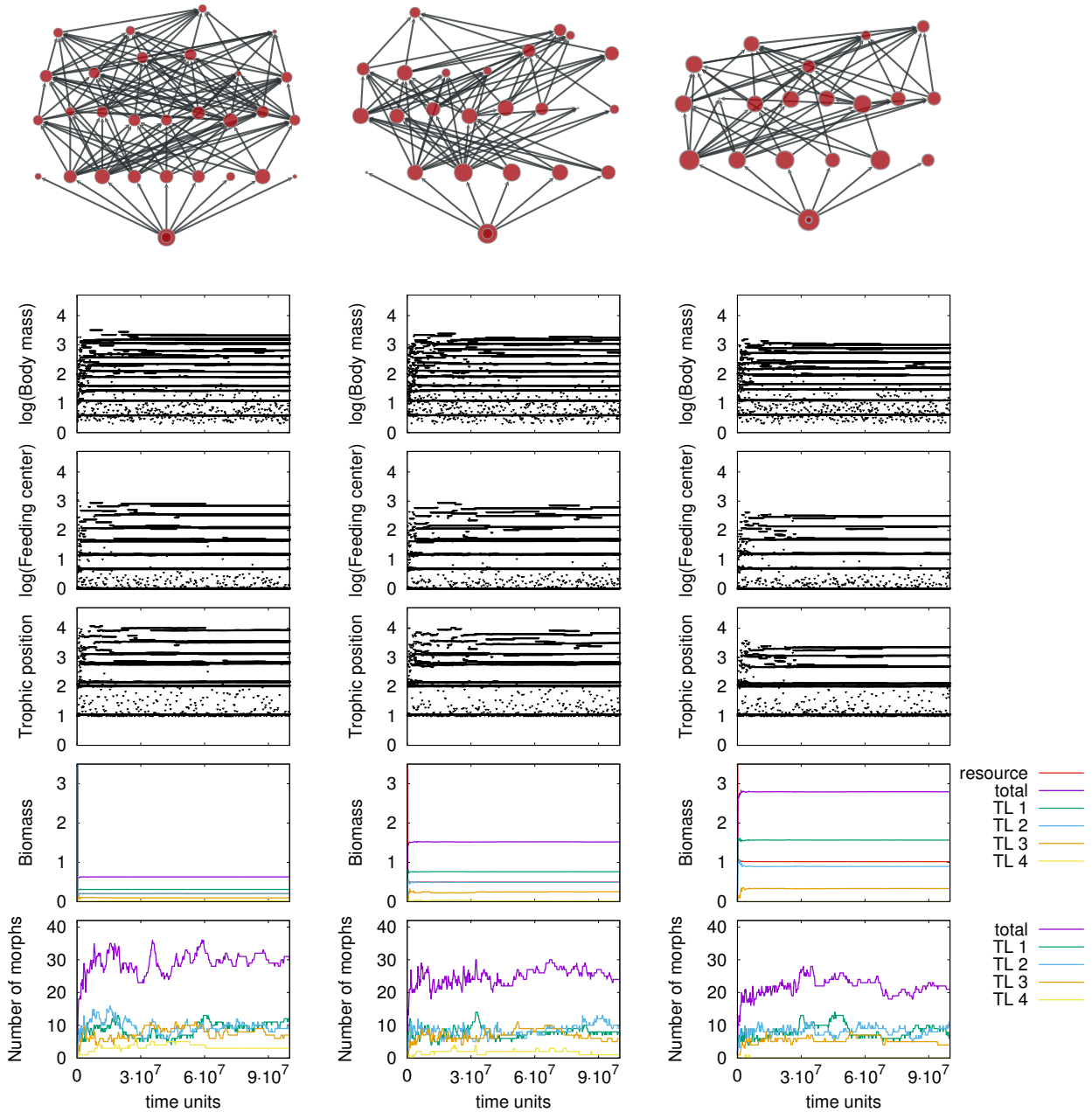


Figure C1: Three exemplary simulation runs of the multi-trophic community evolution model with low (left,  $T = 280\text{K}$ ), intermediate (middle,  $T = 290\text{K}$ ) and high (right,  $T = 300\text{K}$ ) temperature. Temperature dependence is included following scenario (a). The network visualizations at the top of the figure represent the food webs after  $t = 10^8$  time units.

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## Chapter 2: Eco-evolutionary dynamics further weaken mutualistic interaction and coexistence under partner decline.

The present chapter is currently under revision via the PCI Ecology process.

# **Eco-evolutionary dynamics further weakens mutualistic interaction and coexistence under population decline**

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## **Abstract**

With current environmental changes, evolution can rescue declining populations, but what happens to their interacting species? Mutualistic interactions can help species sustain each other when their environment worsens. However, mutualism is often costly to maintain, and evolution might counter-select it when not profitable enough. We investigate how evolution of mutualism affects the coexistence of two mutualistic species, e.g. a plant-pollinator or plant-fungi system. Specifically, using eco-evolutionary dynamics, we study the evolution of the focal species investment in the mutualistic interaction of a focal species (e.g. plant attractiveness via flower or nectar production for pollinators or carbon exudate for mycorrhizal fungi), and how it is affected by the decline of the partner population with which it is interacting. We assume an allocation trade-off so that investment in the mutualistic interaction reduces the species intrinsic growth rate. First, we investigate how evolution changes species persistence, biomass production, and the intensity of the mutualistic interaction. We show that concave trade-offs allow evolutionary convergence to stable coexistence. We next assume an external disturbance that decreases the partner population by lowering its intrinsic growth rate. Such declines result in the evolution of lower investment of the focal species in the mutualistic interaction, which eventually leads to the extinction of the partner species. With



asymmetric mutualism favouring the partner, the evolutionary disappearance of the mutualistic interaction is delayed. Our results suggest that evolution may account for the current collapse of some mutualistic system like plant-pollinator ones, and that restoration attempts should be enforced early enough to prevent potential negative effects driven by evolution.

*Keywords:* adaptive dynamics, plant attractiveness, pollinators decline, evolutionary murder, asymmetrical interactions, alternative stable states

## Introduction

Facing current global change, evolutionary mechanisms can help maintain biodiversity. Evolutionary rescue [1,2] corresponds to the selection of new traits in population collapsing with environmental changes, that allow for a demographic bounce. The signature for evolutionary rescue is the increase in frequency of the allele and corresponding phenotype robust to the new environment, correlatively to the population bounce. While this can be easily highlighted in lab experiments, it has so far been seldom observed in nature. In their review Carlson and collaborators [2] cite, for example, a previous study showing the adaptation of some *Chlorella* species, but not all, after strong acidification of many Canadian lakes with industrial pollution.

However, species are not isolated from one another and interaction might interfere with this evolutionary process. Mutualism is an interaction that has already been intensively studied, and proven to be fragile to Global Changes [3]. Echoing to that loss of interactions is that of biodiversity and system services such as pollination [4] and seed dispersal [3] and effective carbon and nutrient cycles [6]. While several reviews like that of Potts and collaborators [7] point out the critical ecological crises we are undergoing, Toby Kiers and collaborators [3] add that mutualism, by binding species to a common fate, could create an evolutionary breakdown. With environmental changes, mutualism can become costly to maintain. Aside from co-extinction of the two interacting

species, evolution can lead to mutualism loss, partner switch, or even a shift to antagonism. They thoroughly present how the different types of mutualisms are specifically sensitive or resistant to breakdown depending on the global change drivers. For example, plant-pollinator mutualism could be strongly affected by climate change and habitat fragmentation, while plant-rhizosphere mutualisms will be more affected by nutrient enrichment and the introduction of exotic species.

Mutualist systems, like all other systems of interacting species, will respond differently to global change [8]. One species can strongly decrease its density, following for example an environmental worsening, while the other might adapt faster to the new environment. This inertia decreases the interaction strength. We then observe a perverse positive feedback loop, where the decrease of one species is worsened by the evolution of the other, as illustrated in [9]. For mutualism, and especially obligatory ones, this might lead to species extinction, driven by the evolutionary disinvestment of its interactor. This effect is called an evolutionary murder (name suggested by [10]).

For instance, plants have been shown to evolve rapidly to changing pollinator populations [11–13]. A recent study from Gervasi and Schiestl [14] experimentally showed that changes in pollinator communities affect plant trait evolution after only eleven generations. Exposed to bumblebees, which are very efficient pollinators of *Brassica rapa*, the plants evolved toward more attractive traits to those pollinators (e.g. traits attracting pollinators such as volatile organic compounds, flower size, or plant height). Moreover, hoverflies, which are less efficient pollinators of *B. rapa*, caused a 15-fold increase in self-reproduction and a reduction in plant attractiveness. Given these experimental results, the current change and reshaping of pollinator communities may affect the evolution of plant species, which in turn could influence coexistence with their interacting pollinators, i.e., an eco-evolutionary feedback loop.

Plant-mycorrhizal fungi interaction is another type of mutualism affected by global changes. The mycorrhizal fungi can for example fix inorganic nitrogen and provides this essential nutrient to the plant, who, in exchange, transfers via its roots carbon products to the fungi. Several experiments

already showed that enriching the soil in nitrogen (often from anthropogenic sources in natural environments) disturbs this mutualistic exchange, by inducing a shift in the allocation to the mycorrhizal structures [15] and the composition of the mycorrhizal community [16]. This can in turn affect the plant community, and can even facilitate the invasion of alien plant species [17].

Theoretical studies have investigated the ecological [18–21] and evolutionary dynamics [3,22–25] of mutualistic communities such as plant-pollinators or plant-fungi. In particular, the evolution of plant selfing with changing pollinator communities has been studied in several papers [26–28].

Thomann and collaborators [29] even suggested that the decrease in pollinator richness and density could intensify pollen limitation. They propose that plants could in turn adapt either by increasing autonomous selfing or reinforcing the interaction with pollinators. Here we study the consequences of a declining population (e.g. pollinator collapse) on the eco-evolutionary dynamics of a two-species mutualistic system (e.g. plant-pollinator or plant-fungi). Specifically, we study the eco-evolution of the investment in mutualism of a focal species. To do so, we use the adaptive dynamics framework. This framework explicitly accounts for the eco-evolutionary feedback loop between the two species. We clarify when evolution leads to high or low investment in mutualism and determine the conditions under which evolution leads to the coexistence of the whole system. We then show that a declining partner population often results in a counter-selection of the investment in mutualism of the focal species, which eventually enhances the population declines. For simplicity, in the following, we will use the example of a plant-pollinator system. The adaptive trait is the plant investment, and the declining population is the pollinator. However, our approach remains general and can be applied to other mutualistic systems.

## Plant-pollinator model and ecological dynamics

We consider a simple system with two interacting species; a plant with biomass density  $P$ , and a pollinator with biomass density  $A$ . Note that this model is formulated as a general model of

mutualism rather than very specifically tied to plant-pollinator interactions so that results may also concern other mutualistic systems. The community dynamics are given by a Lotka-Volterra type model:

$$\begin{cases} \frac{dA}{dt} = A(r_A - c_A A + \alpha \gamma_P P) \\ \frac{dP}{dt} = P(r_P - c_P P + \alpha \gamma_A A) \end{cases} \quad (3)$$

A schematic view of the system is given in figure 10. The parameters  $r_A$  and  $r_P$  correspond to the intrinsic growth rate of the pollinator and plant populations, respectively. We assume  $r_P$  to be strictly positive because of other reproduction means, e.g. vegetative reproduction or autogamy. The intrinsic growth rate of the pollinator ( $r_A$ ) can be positive (e.g., interaction with other plants) or negative. Parameters  $c_A$  and  $c_P$  modulates intraspecific competition for the two species. Mutualistic interactions are given by  $\alpha \gamma_A$  and  $\alpha \gamma_P$ , with  $\gamma_P$  the energetic gain provided by the plant (via nectar, pollen and/or other plant exudates) to the pollinator, and  $\gamma_A$  the fertilisation provided by the pollinator to the plant. Because we consider mutualism as the net benefice obtained by both species, both  $\gamma$  parameter values are assumed positive in our model. We modulate the intensity of the interaction between the two species with the parameter  $\alpha$ . While the interaction depends on biological traits from both interactors (e.g. pollinator morphology or flight capacities, plant attractiveness), we have chosen to model it as a plant dependant trait and have therefore linked it to other plant traits via a trade-off function, Fig 11. We interpret it here as the attractiveness of the plant for the pollinator, and it corresponds to the trait that is under selection in the rest of the study. This plant attractiveness includes investment in various characters such as the number of flowers, their shape, their colour, volatile organic compound (VOCs) that attract insects with their odour, plant height, flowering duration or nectar quantity and quality (see part II in Willmer (2011) [28]).

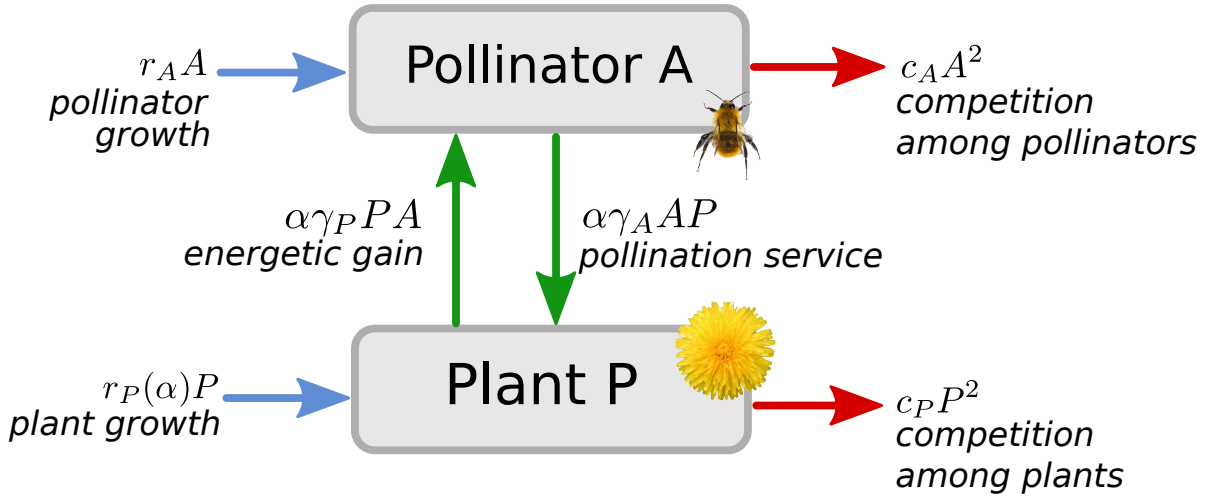


Figure 10: **Population variation rates of plant  $P$  and pollinator  $A$** . Blue arrows indicate the density variations independent of the mutualistic interaction, green arrows the effects of the mutualistic interaction, and red arrows the effects of intraspecific competition. The parameters are described in the main text. B)

Extrapolating from previous results [21], coexistence is stable provided:

$$\left\{ \begin{array}{l} \frac{\alpha \gamma_P r_P + c_P r_A}{c_A c_P - \alpha^2 \gamma_A \gamma_P} > 0 \\ \frac{\alpha \gamma_A r_A + c_A r_P}{c_A c_P - \alpha^2 \gamma_A \gamma_P} > 0 \\ \alpha^2 \gamma_A \gamma_P < c_A c_P \end{array} \right. \quad (4)$$

The first two inequalities give the condition for the existence of an equilibrium point allowing positive densities (i.e. feasibility conditions). The last inequality ensures the dynamical stability of the equilibrium. In the case of two interacting species, this local stability condition implies the global stability of the feasible equilibrium. The globally stable equilibrium is then:

$$\left\{ \begin{array}{l} A^* = \frac{\alpha \gamma_P r_P + c_P r_A}{c_A c_P - \alpha^2 \gamma_A \gamma_P} \\ P^* = \frac{\alpha \gamma_A r_A + c_A r_P}{c_A c_P - \alpha^2 \gamma_A \gamma_P} \end{array} \right. \quad (5)$$

If the stability condition is not fulfilled, i.e., interspecific mutualism is stronger than intraspecific competition, the positive feedback loop resulting from interspecific mutualism may drive the system towards infinite growth. In such cases, other limiting factors (e.g. pathogen, predators, or

new competitors) eventually regulate the populations. Since these factors are not taken into account in our model assumptions, we define a maximum plant attractiveness  $\alpha_{cl}$  below which stability is warranted:

$$\alpha_{cl} = \sqrt{\frac{C_A C_P}{Y_A Y_P}}. \quad (6)$$

We allow the evolution of  $\alpha$  between zero (no investment in attractiveness) and this maximal level  $\alpha_{max} < \alpha_{cl}$ . We could also have controlled the infinite growth of our system by choosing a saturating function for the mutualistic interaction (Holling type II or other, e.g. [30]). Our choice of a linear functional response, however, allows explicit analytical computations and has the advantage to keep the model general and applicable to mutualistic interactions other than pollination.

## Evolution of plant attractiveness

We study the evolution of plant attractiveness ( $\alpha$ ), assuming an allocation trade-off affecting the plant intrinsic growth rate  $r_P$  [31]. Its biomass can grow either via a reproduction process dependent on the interaction with its mutualist (e.g. pollination) whose intensity is controlled by its attractiveness  $\alpha$ , or via intrinsic growth (e.g. vegetative growth) and self-reproduction. The plant has a given quantity of energy that is divided between these two growth modes. [31,32], so that we assume  $r_P$  to be a decreasing function of the attractiveness  $\alpha$ :

$$\left(\frac{r_P}{r_{Pmax}}\right)^s + \left(\frac{\alpha}{\alpha_{max}}\right)^s = 1. \quad (7)$$

The plant maximal intrinsic growth rate  $r_{Pmax}$  can be fixed to one without loss of generality, by rescaling time unit:

$$r_P = \left(1 - \left(\frac{\alpha}{\alpha_{max}}\right)^s\right)^{1/s}. \quad (8)$$

The  $s$  exponent controls the trade-off shape. When  $s=1$  there is a linear relationship between  $r_P$  and  $\alpha$ . When  $0 < s < 1$  the trade-off is convex. On the opposite,  $s > 1$  produces a concave trade-off (as shown in figure 11).

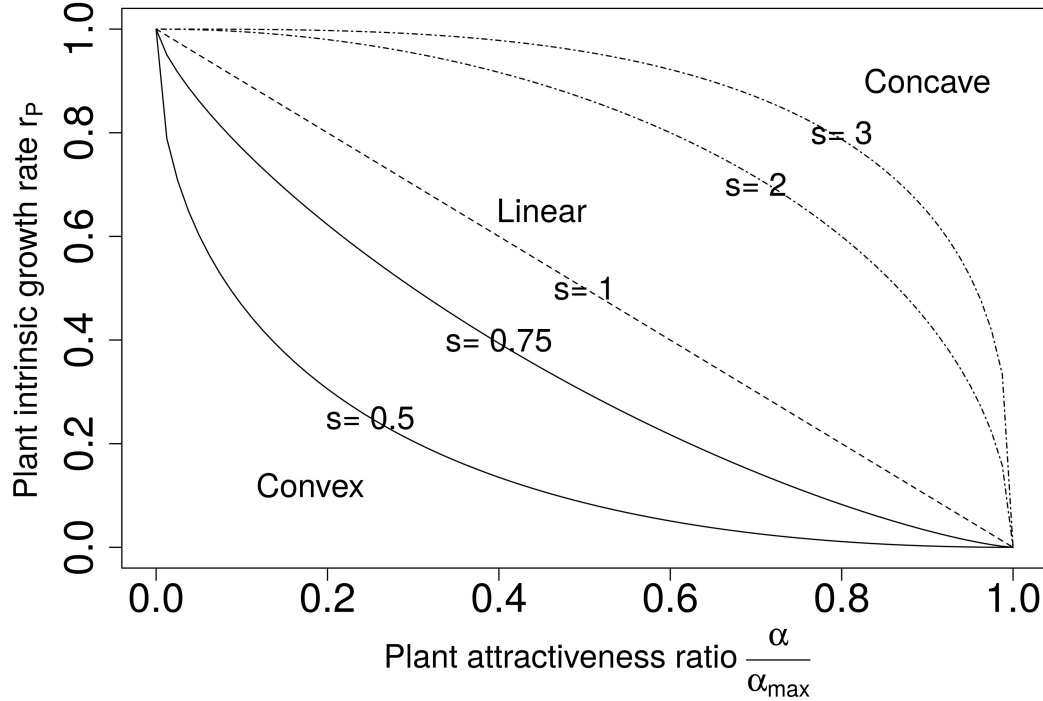


Figure 11: **Variation of the attractiveness ratio  $\frac{\alpha}{\alpha_{max}}$  with the plant intrinsic growth rate  $r_P$  depending on the trade-off strength.** Continuous lines show convex trade-offs, the dashed line a linear trade-off, and dashed-dotted lines concave trade-offs.

We follow the evolution of plant attractiveness using adaptive dynamics techniques [32,33]. Under adaptive dynamics hypotheses (see supplementary material for a full description of the method and hypotheses) we can model the evolution of plant attractiveness and its consequences on species density dynamics, and the feedback of species density on the evolutionary process [33]. Evolution then proceeds by the successive invasions and replacements of resident by mutant populations. Such dynamics are approximated, given rare and small mutations, by the canonical equation [33]:

$$\frac{d\alpha}{dt} = \frac{1}{2} \mu \sigma^2 P^*(\alpha) \left. \frac{\partial \omega(\alpha_m, \alpha)}{\partial \alpha_m} \right|_{\alpha_m \rightarrow \alpha} \quad (9)$$

The term  $\frac{1}{2} \mu \sigma^2 P^*(\alpha)$  encapsulates the phenotypic variability brought by the mutation process on which selection can act. The last term, called the selective gradient, is based on the variations of the

relative fitness of mutants  $\alpha_m$  given a resident  $\alpha$ . It gives the direction of evolution; a positive gradient selects larger attractiveness, while a negative gradient selects smaller trait values. The relative fitness of the mutant is computed as the *per capita* growth rate of a rare mutant population in a resident population at ecological equilibrium (5):

$$\omega(\alpha_m, \alpha) = \frac{1}{P_m} \frac{dP_m}{dt} \Big|_{P_m \rightarrow 0} = r_P(\alpha_m) - c_P P^*(\alpha) + \alpha_m \gamma_A A^*(\alpha), \quad (10)$$

Eco-evolutionary equilibrium (called a singular strategy) occurs when the phenotypic trait stops varying, i.e. equation 9 equals 0. Since its first part is always positive, it corresponds to  $\hat{\alpha}$  values for which the selective gradient is null:

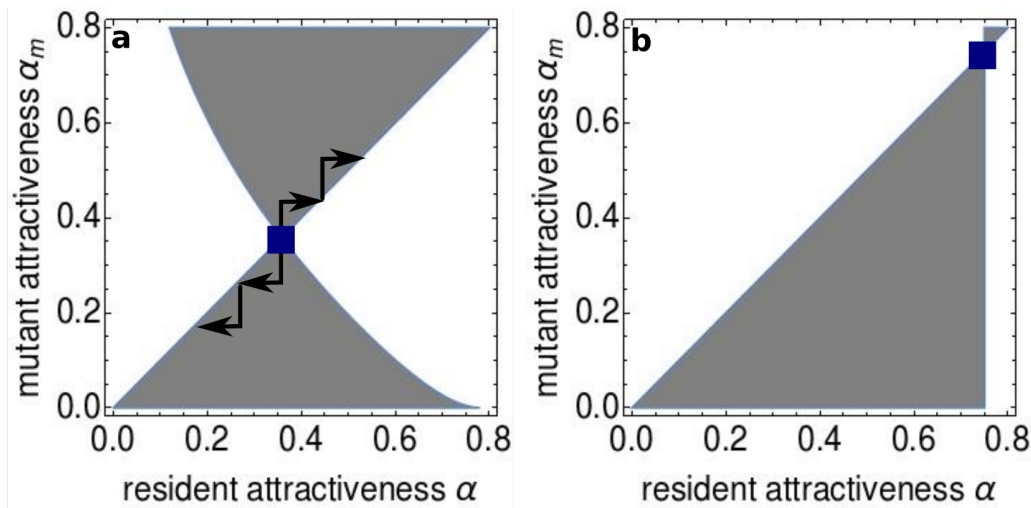
$$\frac{\partial \omega(\alpha_m, \alpha)}{\partial \alpha_m} \Big|_{\alpha_m, \alpha \rightarrow \hat{\alpha}} = \frac{dr_P(\hat{\alpha})}{d\hat{\alpha}} + \gamma_A A^*(\hat{\alpha}) = 0. \quad (11)$$

At singularities, costs in terms of energy dedicated to alternative means of reproduction ( $dr_P(\hat{\alpha})/d\hat{\alpha}$ ) therefore match pollination benefits ( $\gamma_A A^*(\hat{\alpha})$ ). The existence of a singular strategy is not enough to guarantee that evolutionary dynamics locally lead to it (convergence condition) or that it persists (non-invasibility condition, i.e. resistance to invasion by nearby mutants). A singular strategy that is both convergent and non-invasible is called a continuously stable strategy (CSS) [35]. Evolution toward a CSS guarantees the coexistence of the two species. This and other singularity types are presented in figure 12. Calculation of the second and cross-derivative of the fitness function determines criteria for convergence and invasibility [36]. The mathematical computation for the existence of singular strategies and their convergence and invasibility properties are detailed in the supplementary material.

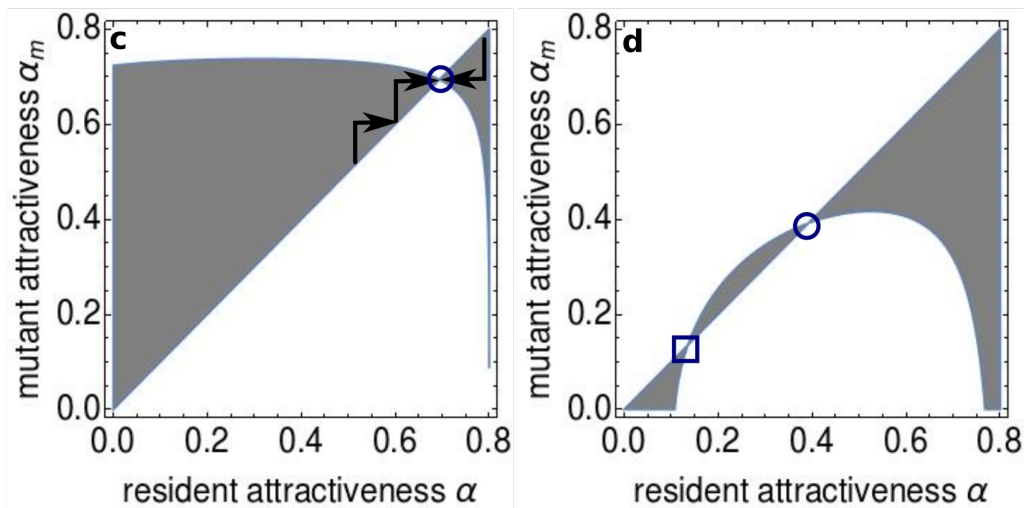
Equation (11) can be solved analytically for particular sets of parameters (see supplementary material). For other cases, we graphically determine convergence and invasibility using pairwise invasibility plots (figure 12). It is possible to show (supplementary material), as illustrated in figure 4, that among the particular trade-offs that we study (eq. 8), only concave allocation trade-offs lead to non-invasible strategies. Therefore, CSSs are only obtained with a concave trade-off function.



Convergence depends on the pollinator's intrinsic growth rate (figure 12c and 12d). Mathematical analyses show that linear trade-offs lead to singular strategies that are not convergent. For non-linear trade-offs, convergence criteria cannot be solved and we rely on numerical investigations and PIPs. For positive pollinator intrinsic growth rate, given concave trade-offs, we obtain only one convergent stable singular strategies (CSS) at which ecological coexistence is granted. For negative pollinator intrinsic growth rate, the system exhibits a second singular strategy that is a Garden of Eden (non-convergent and non-invasible), i.e. a stable strategy that can never be reached by nearby mutants. For convex trade-offs (figure 12a and 12b), we always observe repellers (non-convergent and invasible). Starting above the repellor, attractiveness increases to reach the maximum value (  $\alpha = \alpha_{max}$  ) and the plant growth relies only on the mutualistic interaction. Starting below the repellor, attractiveness evolves to zero, so that the two species no longer interact at the end of the evolutionary dynamics (e.g. complete selfing or clonal reproduction). In the following, we only study concave trade-off functions (i.e.  $s > 1$  ).



convex trade-off ( $s = 0.5$ ) linear trade-off ( $s = 1$ )  
 $r_A = 0.5$   $r_A = 0.5$



concave trade-off ( $s = 3$ ) concave trade-off ( $s = 3$ )  
 $r_A = 0.5$   $r_A = -0.1$

Figure 12: **Pairwise invasibility plots (PIPs) representing the invasibility potential of a rare mutant  $\alpha_m$  within a resident plant population  $\alpha$  at ecological equilibrium.** Grey areas indicate that the mutant relative fitness  $\omega(\alpha_m, \alpha)$  is positive, so that it invades and replaces the resident population. In panels a and c, arrows show the direction of evolutionary trajectories. The system exhibits several singular strategies depending on the parameter values. Circles represent convergent strategies, whereas squares are non-convergent. Filled symbols represent invulnerable strategy, while not filled symbols are non-invulnerable. In panels a and b, the singular strategy is non-convergent and invulnerable (repellor). In panel c, the singular strategy is convergent and non-invulnerable (CSS). Panel d displays two strategies, one CSS and one which is non-convergent and non-invulnerable (Garden of Eden). Parameter values are:  $c_A = c_P = \gamma_A = \gamma_P = 1$ , and  $\alpha_{max} = 0.8 * \alpha_{cl}$ .

## Consequences of pollinator population decline

Now that we have characterised the eco-evolutionary dynamics of the plant-pollinator system, we study how pollinator decline may affect its outcome. We simulate less favourable environmental conditions for pollinators (e.g. habitat fragmentation, pesticides, diseases) by decreasing their intrinsic growth rate ( $r_A$ ). We illustrate the effects of this disturbance through Ecology-Evolution-Environment ( $E^3$ ) diagrams [1,37]. These diagrams, presented in figures 13 and 14, show the outcome of eco-evolutionary dynamics as a function of the environmental parameter, here the pollinator intrinsic growth rate  $r_A$ . Figure 13 exhibits two types of singular strategies: a convergent and stable singular strategy (CSS, continuous line), and Garden of Eden (GOE, dashed line). The Garden of Eden singular strategy is present only for negative pollinator intrinsic growth rates, i.e. in bad environments for the pollinator. In this case, the system exhibits evolutionary alternative stable states. When plant attractiveness is above the Garden of Eden value, the evolution converges toward the CSS, while when below the GOE value, selection leads to ever-decreasing attractiveness, weakening the mutualistic interaction and eventually leading to the extinction of the pollinator (arrow (7) in figure 5a).

For positive pollinator intrinsic growth rates ( $r_A > 0$ ), i.e. in “good pollinator environments”, the system converges toward intermediate attractiveness  $\alpha$  (arrows (1) and (2) in figure 13a). Now consider an environmental degradation (red arrow (3) in figure 13a). In the absence of evolution, both plant and pollinator populations have positive biomass densities. However, considering evolution, plant attractiveness is counter selected as pollinators are too rare to compensate for the intrinsic costs of attractiveness. Eventually, evolution drives pollinator populations to extinction; an evolutionary murder depicted by arrow (4) in figure 13a. Faced with the crash of pollinator populations, restoration attempts may be undertaken (i.e. an increase in  $r_A$  value, e.g. by suppressing pesticides or adding other plant resources for pollinators). Early intervention, depicted by arrow (5), can restore a stable mutualistic interaction. Delayed restoration attempts (white arrow

(6)), do not allow such a rescue, as evolutionary trajectories will counteract their effects and lead to the extinction of the pollinator (arrow (7)). Note that here we separate timescales for simplicity, and consider that deterioration and restoration are fast compared to the evolutionary dynamics, hence horizontal arrows for these environmental changes.

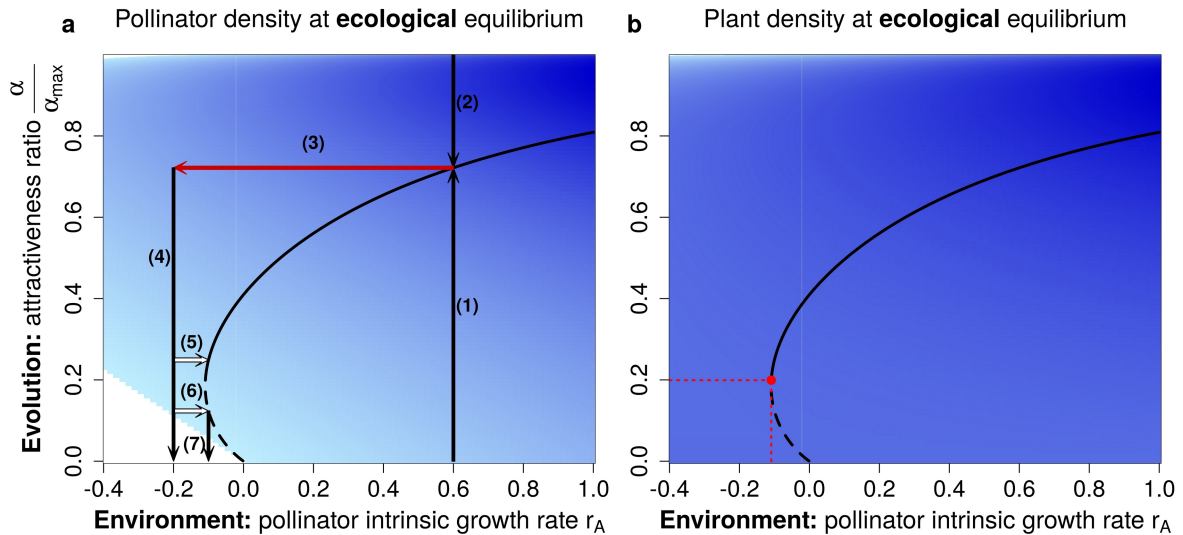


Figure 13: **Ecology-evolution-environment (  $E^3$  ) diagram representing the impact of pollinator environmental deterioration on the evolution of plant attractiveness and on pollinator (panel a) and plant (panel b) equilibrium biomass densities .** White areas show parameters for which extinction occurs for either plants or pollinators. The blue intensity correlates with population densities of pollinators (panel a) or plants (panel b). Black lines show the position of singular strategies; continuous lines show convergent and non-invasible singular strategies (CSS), and dashed lines show Garden of Edens (non-invasible, divergent). Vertical black arrows (1, 2, 4, 7) display the direction of evolution. Environmental disturbance is represented by a red arrow (3). White arrows (5, 6) represent restoration attempts at different times along the evolutionary trajectory. On panel b) the red point and dotted lines represent the lowest  $r_A$  and  $\frac{\alpha}{\alpha_{max}}$  values for allowing a CSS, therefore the maintenance of the mutualistic interaction. This point is what we call an eco-evolutionary tipping point. Parameters values are  $s=2.5$  ,  $c_A=c_P=\gamma_P=1$  ,  $\gamma_A=0.2$  , and  $\alpha_{max}=0.8*\alpha_{cl}$  . Similar  $E^3$  diagrams can be found in [1,37]

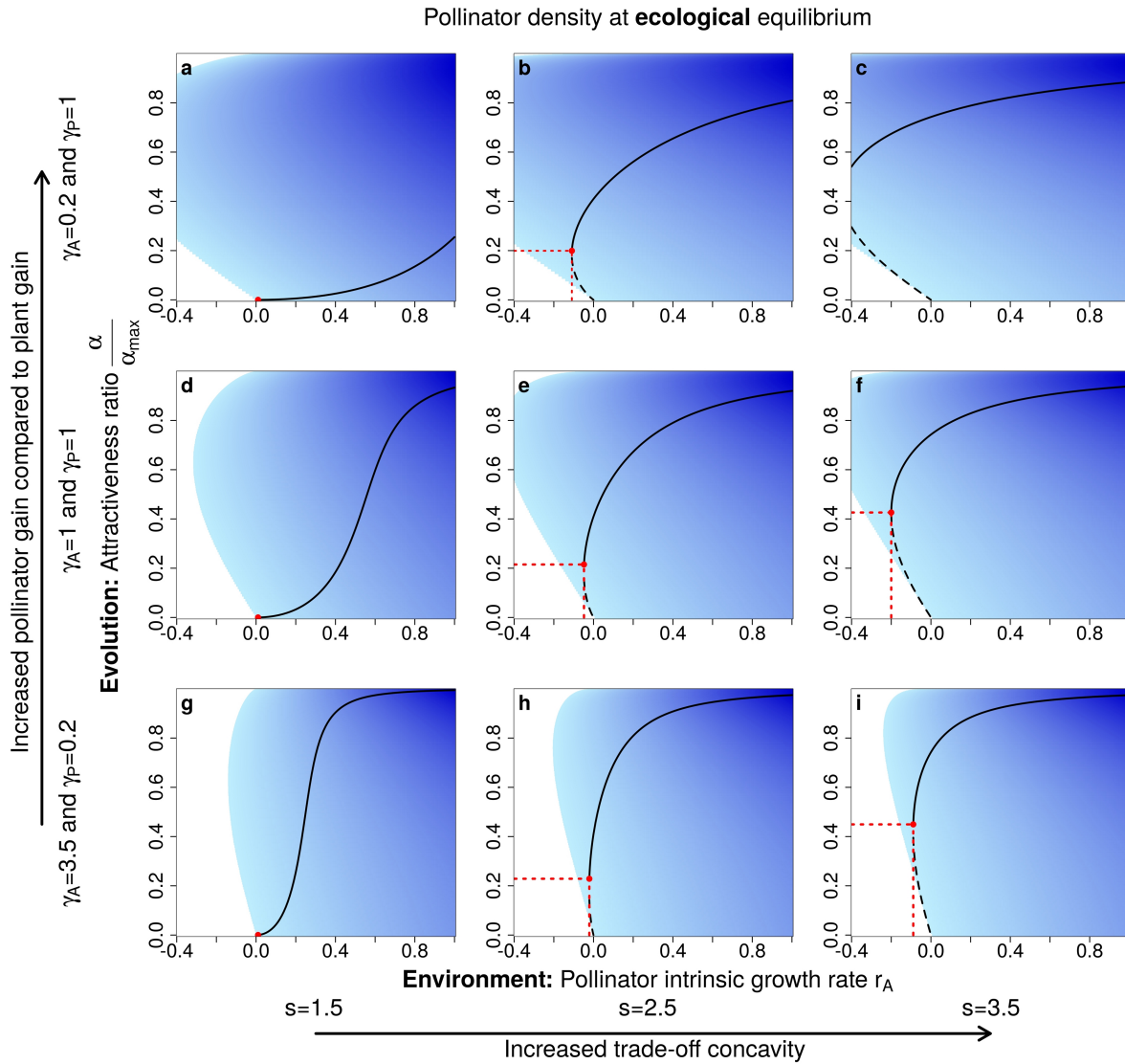


Figure 14: **Influence of trade-off shape and mutualistic gains on  $E^3$  diagrams.** Columns differ in trade-off concavity. Lines differ in the asymmetry of mutualistic gains: in the top line (panels a,b, and c) pollinators benefit more than plants; the middle line (panels d,e, and f) shows equal gains while in the bottom line plant gains are larger. Red points and dotted lines represent the lowest  $r_A$  and  $\frac{\alpha}{\alpha_{max}}$  values for maintaining a CSS, allowing the maintenance of the mutualistic interaction. Colours and lines are the same as in figure 13. The parameter values are  $c_A=c_P=1$  and  $\alpha_{max}=0.8*\alpha_{cl}$ .

Finally, we study how trade-off shapes and asymmetry of mutualistic gains affect the eco-evolutionary outcome (figure 14). More concave trade-offs allow a larger coexistence domain. For less concave trade-offs,  $s < 2$ , only a positive pollinator intrinsic growth rate  $r_A$  allows coexistence (figure 14a, d, g). Negative pollinator intrinsic growth rates lead to small benefits for the plant, so

that attractiveness is counter selected, eventually leading to the pollinator extinction . For stronger concave trade-offs,  $s > 2$ , (figure 14b, c, e, f, h, i) we observe qualitatively the same dynamics as in figure 13. For those trade-offs, asymmetric mutualistic gains favouring pollinators allow a larger range of disturbance, including negative intrinsic growth rates  $r_A$ , before attractiveness is counterselected and extinction occurs. Therefore, an increased mutualistic gain of the pollinator relative to that of the plant facilitates the long-term coexistence of the plant-pollinator system. This produces a more robust system that eases a potential restoration process. Note, however, that favouring pollinators gain over plants leads to lower selected levels of attractiveness.(compare figure 14 a, b, c vs g, h, i).

## Discussion

While from a one species perspective, evolution can help to avoid extinction by fostering adaptation and restoring positive growth rates (evolutionary rescue), we here show an example in which accounting for mutualistic interactions largely modifies this optimistic view. Here, the evolution of one species in response to disturbances acting on its mutualistic interactor selects further decreases in the interactor population, eventually leading to the demise of the mutualistic interaction. This shows that evolution within mutualistic systems can actually be detrimental to the system's persistence and could undermine restoration attempts. Because we have used a general model of mutualism, this mechanism may concern various systems. This clearly suggests that when investigating the impact of global changes, we need to account for eco-evolutionary dynamics of the species and their interactors.

The model we use is voluntarily simple to allow a more complete mathematical study of eco-evolutionary dynamics and to highlight the role of key parameters (e.g. trade-off shapes or mutualistic gains). However, it may be linked to other models that study various types of mutualism. For instance considering pollination systems and plant reproduction, in line with the

presentation of the results, our model recalls previous theoretical works on plant evolution, that detail furthers the reproductive implications (e.g. [26–28]). For instance, Lepers *et al.* [27] explicitly modelled the evolution of a plant reproduction system by taking prior selfing and inbreeding depression into account. In particular, they showed that evolution toward high prior selfing (for us of lesser attractiveness) leads first to pollinator extinction (our evolutionary murder). Because they also model the cost resulting from the inbreeding depression, they show that this evolutionary murder may further lead to the extinction of the plant population. However, the model we propose may also be adapted to consider other mutualistic systems. For instance, in plant-mycorrhizae interactions, a resource exchange takes place, where plants provide carbon-based resources (e.g., sugars) to mycorrhizae while they get nutrients from the interaction. Such a situation does fit our hypotheses. The trait  $\alpha$  would then be the quantity of resource provided by the plant (ie, its investment in the mutualistic interaction), and this production diverts resources from growth and reproduction, therefore fitting our trade-off hypotheses. As such, our model recalls the results of a study by de Mazancourt & Schwartz [23]. They show that mutualism can arise and be evolutionarily selected from a two-species competing model by including trading. Each species can trade the resource it extracts in excess with the other. In our system, this trading would correspond to the benefit  $\alpha \gamma$  provided by the mutualistic interaction. Depending on the resource availability (the intrinsic growths in our model) the plant can either perform better on its own (possibly at the detriment of the fungi, as in our model) or can benefit from the mutualistic association with a mycorrhizal fungus. The mutualistic trading interaction can extend the coexistence boundaries, i.e. the resource space the two species can live in.

Our results also highlight that mutualistic interactions could be more or less vulnerable to environmental changes and population declines. For instance, here, only concave allocation trade-offs between plant intrinsic growth rate and investment in mutualism lead to the maintenance of the mutualistic interaction. These trade-offs favour intermediate investments in the mutualistic

interaction, while in the case of convex trade-offs, either complete investment or no investment is eventually selected, depending on initial conditions. We kept our study general because trade-off shapes are extremely difficult to measure *in vivo*, and can vary deeply depending on the environment or the species types [39].

Bistability and critical transitions have been highlighted in a variety of ecological situations (e.g. [40,41] in mutualistic system), and result from a strong positive feedback loop. Here we have a similar phenomenon but on an eco-evolutionary scale. If the evolved investment in mutualism before environment deterioration is above a certain threshold, evolution reinforces the interaction, by increasing the attractiveness values, eventually leading to a stable, coexisting system. On an ecological scale, this interaction reinforcement increases the abundance of both species, which in turn favours the evolution of the focal species investment toward higher value. Below a critical level of evolved investment, the population of the mutualistic partner species is low. Evolution then further decreases investment in mutualism, eventually leading to complete disinvestment in the mutualistic interaction. This runaway selection for decreased investment leads in our case to the evolutionary murder of the partner population by the evolving species [42]. Note that the trade-off shape modulates the strength of the positive feedback loop. More concave trade-offs decrease the threshold value above which interaction is maintained, thereby facilitating the persistence of the system. Such dynamics have important implications. For instance, consider pollination as the mutualistic interaction. Current data suggest large decreases in pollinator abundances [43]. Such pollinator declines are often considered to be directly linked to environmental changes (eg, habitat change, pesticides [7]). However, our results suggest that evolutionary components may also be present. If these declines favour plant strategies that offer less resource, plant evolution may enhance the observed declines. In line with these predictions, empirical observations suggest a decline of flower resources parallel to the pollinator decline [43].



On a management side, alternative stable states and critical transitions have large implications, as systems may then shift abruptly, and large restorations are needed to recover previous states [41]. The eco-evolutionary alternative stable states we describe here have similar implications. Restoration can either be a reduction of the mortality causes of the declining species (banning pesticide, ploughing controlling pests and predators) or the increase in their alternative resource source (plant sowing or nutrient addition). Here we consider that restorations are faster than evolutionary timescales. Evolution can however act fast [14], while restoration timescales largely vary from a few months (e.g., sowing high reward plants) to much longer timescales. Changes in pesticide regulations and applying these regulations may require national or international consensus. Similarly, while a change in the agricultural mode does occur (eg, from intensive to agroecology), its dynamics happen over decades, while the evolution of plant reward may happen in just a few generations [14]. Note that, were we to consider longer restoration attempts we would still observe eco-evolutionary tipping points in our system. Such tipping points also make restoration attempts more difficult from two different points of view. First, the timing of the attempt becomes important. Restoration is only successful when achieved before the threshold attractiveness is evolved. Second, if the system becomes degraded, a small restoration attempt may not be sufficient to recover large populations, but large efforts will have to be undertaken.

While in the face of current changes in the environment, evolution can play a key role in restoring populations and maintaining diversity, our results suggest that in the case of mutualistic interactions, evolution may also favour strategies that eventually further threatens species coexistence. As such, our model echoes recent analyses that highlight the evolutionary fragility of mutualisms, given current changes [3,9]. Because our model is voluntarily simple, restricted in its number of interaction types and species, we expect evolutionary effects in complex ecological networks to be more complex and context-dependent. However, we expect that accounting for these

covariations of evolutionary dynamics and changes in ecological interactions will be important, and that the effects of evolution will then not systematically be positive.

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## Chapter 3: Effects of resource distribution on the evolution of species phenology

After some more modifications, the present chapter will be submitted to a general ecological review.

# Effects of resource distribution on the evolution of species phenology

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## Abstract

Phenology partly controls the strength of species interactions, and is constrained by intrinsic, abiotic and biotic factors. Recent changes in some of these constraints (e.g. global warming, land-use change, species invasion) affect species phenologies, potentially disrupting interactions. As a result, some consumer species might not be able to exploit their food resource any more, eventually leading to species extinction. It is difficult to predict how consumer phenology will change as a result of shifts in the phenology of its resources, especially if we consider several alternative food resources with different phenologies. To understand the ecological and evolutionary consequences of resource phenological changes on consumers, we followed, via a model, the evolution of the foraging phenology of a consumer in response to different temporal distributions of two alternative resources. We studied the evolution of either the foraging mean day of consumer phenology or the foraging duration, as well as the evolution of both phenological traits jointly. We found that diversification and the coexistence of foragers with different phenologies required an intermediate level of overlap between resource phenologies. Specialist foragers were only observed in case of a low overlap between resource phenologies, especially after a diversification event. Generalists were observed in case of higher overlap, or when only the duration of the foraging phenology evolved. However, the diversification and specialisation patterns that we observed depended largely on the evolving trait considered, or if the traits co-evolved or not. Our results thus highlight the importance of considering the length of phenological events together with mean phenology dates for understanding the demographical and evolutionary consequences of changes in species phenologies. Our results could help discussing the current implications of

species phenological mismatches, such as the one observed in plant-pollinator systems, due to current climate and land-use changes, and explore the conditions that maintain species diversity.

## Introduction

The timing of biological events within years, or phenology, is a fundamental part of species temporal dynamics. Phenology is frequently described with its onset and duration times or phenophase (e.g.[1, 2]). Indeed, when studied at the individual level, phenology describes an activity level, or a life cycle-event, over a certain period of time. It can be as sudden as a bird flying the nest for the first time, a butterfly hatching from its cocoon, the day a bear goes into hibernation, or the break of a seed from dormancy. It also corresponds to longer-lasting biological processes like the length of a tree growing season, or long mating times of some amphibian or bird species. Phenology describes a single event, but at the scale of a population it will have a long-lasting demographical effect, reflected for example by the flowering period [3] or seed fall [4] of a plant population in a certain locality.

There is extensive evidence that human activities modify species phenology. For instance many climate-dependent phenologies are advancing to earlier dates, as shown by Parmesan and Yohe [5] in a meta analysis across 279 species. This is however not a universal pattern, e.g. as noted by Dunnell and Travers [6] with historical records of prairial plants flowering phenologies. They observed a shift of 5% to 17% of the observed species, either toward an earlier or a later flowering phenology. Current climate warming and CO<sub>2</sub> increases have also extended the vegetation period of numerous plants [7]. Biological invaders can also affect native species phenologies. Invasive crayfish have e.g. shortened the availability time of leaf litter by direct consumption that accelerates its decomposition, while this resource is crucial for many freshwater consumers [8].

Such changes in species phenology can therefore strongly alter ecological interactions because interspecific interactions depend directly on the temporal synchrony between interacting partners. Evolution will select for increased synchrony or asynchrony between the interactors, depending on the interaction type [9]. Interactions beneficial to both partner like mutualism is expected to select for matching (i.e. synchronised) phenologies. The synchrony among species phenologies is known to be an important determinant of interactions between plants and pollinators. Olesen et al. [2] extensively studied an arctic plant-pollinator network during two consecutive vegetative seasons. They showed that while abundance partly explained the observed interaction pattern (12%), phenophase length explained a greater part of the observed number of links per species (51–69%). Among antagonistic interactions, competition is detrimental to both partner, and is expected to select for mismatching phenologies. Hatching asynchrony has for example been observed in numerous studies e.g. in [10]). This asynchrony reduces competition between juveniles for food resource and the brood visibility to predators. However direct proofs of competition resulting in asynchrony are rare, and often asynchrony is explained by other constraints (e.g. [11, 10]). Predation is another antagonistic interaction which is positive for the predator or consumer and negative for its prey or resource. We would expect the maintenance of a constant time-lag between the two interactors (red queen's dynamics), selection increasing synchrony for the consumer with its resource, and increasing asynchrony for the resource with its consumer (e.g. asynchronous phenology resulting from prey escape in [12]). Indeed, phenological asynchrony is not always non-adaptive, and can result from numerous combined ecological mechanism and evolutionary pressures, as thoroughly studied by Johansson et al. [13].

The evolution of a consumer foraging phenology will not only depend on the match-mismatch with a given resource, but also on the general phenological distribution of all its potential resources, which can all respond differently to climate change. Global change can decrease the length of total phenological availability of resources for consumers, by increasing



synchrony between them. For instance, in a part of Alaska, scientists observed a recent change of elderberries phenology toward earlier fruiting [14], increasing the overlap between this fruiting phenology and that of spawning salmon from a nearby river. Before that phenology shift, Kodiak brown bears population was feeding on salmons early in the summer, and then switched to consuming elderberries in late summer, feeding on a long time period on two complementary resources. With these phenological changes, scientists have observed a switch in the food diet of the bear, who start consuming berries earlier, neglecting the salmon population. The evolutionary outcome of this diet switch on the bear demography and phenology evolution is yet to be tested. This example highlights the impact of changing resource phenologies on their consumer degree of generalism.

Other global changes such as land-use also manipulate the availability of different resources for consumers, and especially the availability of plant resources. Wild resource species are strongly affected by human-induced changes [5], but this is also true for human-managed resources like cultivated or ornamental plants. Crops and urban flora can provide alternative food resources to pollinators and pests normally feeding on wild plants, cities sometimes even becoming a refuge for these species [15]. Human land use modifies the availability of floral resources not only by affecting the amount and diversity of plant resources, but also by changing the timing and duration of resource availability for consumers such as pollinators [16, 17]. Large crop patch with synchronized sowing could also create a burst of flowers (i.e. massively flowering crops or MFCs [18]) concentrating the resource availability on a short time period. On the contrary, a very diverse agricultural landscape, by providing a variety of alternative food sources, could elongate the availability of the flowering resource. The extension of urban areas at the expense of agricultural land is not always detrimental to consumer foraging on plant resources. Apart from the protective reduction or ban of pesticides by some city councils in the management of urban parks, heat island effect, exotic flower, and

the maintenance of flowerbeds along the year could extend the flowering period, hence their availability for consumers [19].

The evolutionary response of a given consumer phenology will therefore partly rest on its (potential) degree of generalism, and considering all the alternative food sources and their phenological changes is crucial in studying the evolution of a consumer's phenology. Current environmental changes, by potentially shifting differently the phenologies associated to a consumer different food resources, disturb the evolutionary synchronised or asynchronised equilibrium above discussed. Considering the relative speed of changes of the environment compared to the evolutionary potential of a species, what phenological changes in a consumer would we observe when its resources phenology changes?

Empirical studies following phenological evolution after one or several resource shift(s) are rare (e.g. see [20]), but some theoretical works give insight into the potential outcomes. While evolution of species phenology phenologies in response to the temperate changes in resource distribution has seldom been treated, it is essentially an issue of evolution of specialisation on several resources, heterogeneously distributed. As such, it can be linked to previous evolutionary works of resource specialisation or adaptation in a heterogeneous landscape. Following [21], and previous models (e.g. [22]), that all considered two alternative food resources, we expect diversification events when the two resources are intermediary separated. Pontarp et al. [23] also note that higher competition can first lead to an intermediate situation with one generalist consumer, then diversifying towards the resource peaks. With an increasing distance between the two resources peaks, they observe a shift from one generalist foraging on two resources to a specialist on the resource with the highest local abundance (e.g. a resource with short phenological length or spatial distribution, hence a high resource peak) [21, 23].

As mentioned above, human impacts can differently affect resource phenologies. Therefore we will look at the effects of different resource distributions on the evolution of a consumer phenology, focusing on the impact of:

1) an increasing gap in the middle of the season, with little to no resources for the consumer.

2) asymmetry in the resource distribution (on with of sharp peak of resource vs one producing the same total amount of resources as the other but over a longer time period). We would thereafter refer to the temporal duration of resource availability as the resource phenological length. Moreover, the relative abundances of a resource group can vary with the environmental changes. However, it produces easy to make predictions: increasing the availability of one resource will attract more the forager, and its phenology will often match that of the most available resource. Testing both questions 1) and 2) with different distributions of the resource phenologies, we focus on the conditions under which we observe:

1) diversification events and the coexistence of foragers with different foraging phenologies.

2) narrow or broad foragers phenologies, and if the mean foraging day matches with a resource peak. 3) generalists or specialists consumers. The degree of generalism results from this potential diversification and the final temporal distribution of the forager phenology(ies) relative to the resources distributions. We could observe specialists foraging mainly on one resource peak or more generalists foragers whose phenology overlap with both resource phenologies.

As in [22, 21, 23], we predict that increasing the resource gap will drive the consumer's phenology from generalist to specialist and diversification for intermediate resource overlap. According to [23] we also expect to find more generalists when the resource length is higher.

We observe similar diversification and generalisation pattern as those obtained by previous theoretical studies. The peaky resource often acts as an attractor one which at least one of the pollinator populations specialises, sometimes neglecting the other resource. However, the overlap thresholds for the diversification and specialisation patterns that we observe depend

largely on the evolving parameter considered, and differ when the two foraging phenology parameters co-evolve.

## The consumer-resources model

For simplicity, in the following, we use the example of a plant-pollinator system, with a pollinator foraging on two alternative pools of plant resources with different flowering phenologies. The different resource landscapes that we explore correspond to different flowering phenologies. However, our approach remains general and can be applied to other consumer-resources systems, e.g. of an herbivore feeding on two pool of plant resources. The model is comprised of two alternative food resources, e.g. a pool of wild plant species with population  $P_W$  and a pool of managed ones with population  $P_M$ , and a consumer, e.g. a foraging pollinator with population  $A$ .

Focusing our study on the consumer demography and evolution, we describe its biomass variations via the following equation:

$$\frac{dA}{dt} = r(\mu_A, \sigma_A)A - c(\mu_A, \sigma_A)A^2 \quad (1)$$

with  $\mu_A$  the mean foraging day of the consumer and  $\sigma_A$  the variance of its foraging period hereafter called the foraging length.

The first term of eq. (1) corresponds to the growth rate of the consumer provided by the consumption of the two resources. It is a generalisation the classical Lotka-Volterra consumption term. We express it as the integral of the product of the consumer phenology  $f_A$  and each of the resource phenologies  $f_M$  and  $f_W$ . It is an approximation of the phenological overlap between the consumer and resource phenologies.

$$r(\mu_A, \sigma_A) = \int_{-\infty}^{+\infty} f_A(\tau, \mu_A, \sigma_A) \cdot f_{P_M}(\tau) d\tau + \int_{-\infty}^{+\infty} f_A(\tau, \mu_A, \sigma_A) \cdot f_{P_W}(\tau) d\tau, \quad (2)$$

with  $\tau$  the day of the year,  $\mu_A$  and  $\sigma_A$  as previously defined.

The second term of eq. (1) corresponds to the competition rate within the consumer community. It is calculated as the overlap between the phenology of the consumer and its competitor, here himself.

$$c(\mu_A, \sigma_A) = c_{base} \int_{-\infty}^{+\infty} (f_A(\tau, \mu_A, \sigma_A))^2 d\tau, \quad (3)$$

with  $c_{base}$  the basal competition rate.

The phenologie of the resources are described by the abundance of each species throughout the year. The following function describes the temporal distribution of all the flowers from the pool of plants  $i$ :

$$f_{P_i}(\tau) = \frac{P_i}{\sigma_{P_i} \sqrt{2\pi}} * \exp\left(\frac{-(\tau - \mu_{P_i})^2}{2\sigma_{P_i}^2}\right), \quad (4)$$

with  $\tau$  the day of the year,  $\mu_{P_i}$  the mean day of resource availability, corresponding also to the day of maximal resource availability (e.g. flowering peak) and  $\sigma_{P_i}$  the flowering period variance or flowering length. In the following we will assume that the the phenology of the wild resource pool  $f_{P_W}$  is fixed, and we study different scenario for the phenology of the managed resource pool  $f_{P_M}$ , by varying  $\mu_{P_M}$  and  $\sigma_{P_M}$  values.

The forager intake phenology is similar to that of the resources. The following function describes the foraging activity of one consumer along the year:

$$f_A(\tau, \mu_A, \sigma_A) = \frac{1}{\sigma_A \sqrt{2\pi}} * \exp\left(\frac{-(\tau - \mu_A)^2}{2\sigma_A^2}\right) \quad (5)$$

with  $\tau$ ,  $\mu_A$  and  $\sigma_A$  as previously defined.

Defining the phenologies by gaussian function allows to simplify the above mentioned eqs.

(2) and (3) of the consumer growth and intraspecific competition respectively. They now become:

$$r(\mu_A, \sigma_A) = \frac{1}{\sqrt{2\pi}} \left( \frac{e\left(\frac{-(\mu_A - \mu_{P_W})^2}{2(\sigma_A^2 + \sigma_{P_W}^2)}\right) P_W}{\sqrt{\sigma_A^2 + \sigma_{P_W}^2}} + \frac{e\left(\frac{-(\mu_A - \mu_{P_M})^2}{2(\sigma_A^2 + \sigma_{P_M}^2)}\right) P_M}{\sqrt{\sigma_A^2 + \sigma_{P_M}^2}} \right) \quad (6)$$

$$c(\mu_A, \sigma_A) = \frac{c_{base}}{2\sqrt{\pi\sigma_A^2}}$$

All functions and parameters meanings are summarised in table 1 (supplementary materials). AS described in equation (2), the first term of  $r(\mu_A, \sigma_A)$  corresponds to the total energy acquired by the consumer A while foraging on the resource  $P_W$  and the second term its growth resulting from foraging on the resource  $P_M$ .

## Ecological dynamics

Ecological equilibrium is reached when the pollinator demography stops varying, i.e. when equation (1) goes to zero. Of the two possible equilibrium, the formula of the non-zero equilibrium is:

$$A^* = \frac{r(\mu_A, \sigma_A)}{c(\mu_A, \sigma_A)} \quad (7)$$

This equilibrium, which is the classical definition of the carrying capacity, is biologically relevant in our upcoming analysis only if it is feasible and stable in time.

Feasibility conditions require  $A^* > 0$  which is always true with all parameters values positive.

Stability condition is also always true with positive parameters values. Whenever the ecological equilibrium is reached, it is always feasible and locally stable. These are classical results arising from a classical logistic model. Detailed calculations of these conditions can be found in the supplementary materials.

The abundance of the consumer at ecological equilibrium will increase when the resource growth rate increases. This could be caused for example by  $\mu_A$  getting closer to one of the flowering peaks. (see expression of r and c in (6)). Influence of  $\sigma_A$  on the ecological equilibrium is less clear, because it appears in various parts of both the numerator and denominator terms of the equilibrium, and cannot be factorised.

# Evolution of the forager phenology

## 1 Method: the adaptive dynamics

Our goal is to follow the evolution of the pollinator phenology in various floral phenological landscapes. To this end we follow the evolution of either the pollinator mean foraging day  $\mu_A$ , its foraging length  $\sigma_A$ , or both combined. We use tools from adaptive dynamics [24, 25], with what we can not only follow the the evolution of the pollinator trait but also its demographic consequences and how they feedback into the evolutionary dynamics.

Evolution is followed via the invasion of a mutant population with a trait  $\mu_{Am}$  or  $\sigma_{Am}$  slightly different from  $\mu_{Ar}$  or  $\sigma_{Ar}$ , the trait of the resident population. Assuming separate ecological and evolutionary time scale evolution of the trait is given by the canonical equation of adaptive dynamics[24]:

$$\frac{dx_r}{dt} = \frac{1}{2}\mu\sigma^2 A^*(x_r) \left. \frac{\partial\omega(x_m, x_r)}{\partial x_m} \right|_{x_m \rightarrow x_r}, \quad (8)$$

with  $x_r$  the trait under selection and  $x_m$  that same trait in a mutant population.  $A^*$  is the population of the resident pollinator at ecological equilibrium (expressed in eq. (7)). The first part  $\mu\sigma^2 A^*(x_r)$  embodies the phenotypic variability on which selection can act. The last term embodies variations in the fitness landscape around the resident value  $x_r$ , thereby the effects of natural selection. Because the first part of this equation is always positive, only the sign of the fitness gradient constrains the direction of trait variation. If the gradient is positive (resp. negative) then a higher (resp. lower) value of the trait  $x_r$  is selected. We use equation (8) to determine the position of evolutionary singularities, called singular strategies, and associated evolutionary dynamics. These Eco-evolutionary equilibria or singular strategies occur when the phenotypic trait stop varying, i.e. eq. (8) equals to 0. Since its first part is always positive, it corresponds to values for which the selective gradient is null.

To study the gradient sign we need to express the relative fitness function of the mutant compared to the resident. It corresponds to the intrinsic growth rate of the mutant, the resident population being at ecological equilibrium  $A^*$  :

$$\omega(\mu_{A_m}, \mu_{A_r}) \Big|_{\substack{A_m \rightarrow 0^+ \\ A_r \rightarrow A^*}} = \frac{1}{A_m} \frac{dA_m}{dt} = r(\mu_{A_m}, \sigma_{A_m}) - c(\mu_{A_m}, \mu_{A_r}, \sigma_{A_m}, \sigma_{A_r})A^*, \quad (9)$$

The competition was previously defined within a population. Now we consider competition between the resident and the mutant consumer populations  $c(\mu_{A_m}, \mu_{A_r}, \sigma_{A_m}, \sigma_{A_r})$ . The mutant population being very small, we neglect the competition within the mutant population.  $r(\mu_{A_m}, \sigma_{A_m})$  and  $c(\mu_{A_m}, \mu_{A_r}, \sigma_{A_m}, \sigma_{A_r})$  are defined as follow:

$$r(\mu_{A_m}, \sigma_{A_m}) = \frac{1}{\sqrt{2\pi}} \left( \frac{e^{\left(\frac{-(\mu_{A_m} - \mu_{P_W})^2}{2(\sigma_{A_m}^2 + \sigma_{P_W}^2)}\right)}}{\sqrt{\sigma_{A_m}^2 + \sigma_{P_W}^2}} P_W + \frac{e^{\left(\frac{-(\mu_{A_m} - \mu_{P_M})^2}{2(\sigma_{A_m}^2 + \sigma_{P_M}^2)}\right)}}{\sqrt{\sigma_{A_m}^2 + \sigma_{P_M}^2}} P_M \right)$$

$$c(\mu_{A_m}, \mu_{A_r}, \sigma_{A_m}, \sigma_{A_r}) = \frac{c_{base} e^{\left(\frac{-(\mu_{A_m} - \mu_{A_r})^2}{2(\sigma_{A_m}^2 + \sigma_{A_r}^2)}\right)}}{2\sqrt{\pi}(\sigma_{A_m}^2 + \sigma_{A_r}^2)} \quad (10)$$

The singular strategies corresponding to a null selection gradient can be classified in different types regarding their convergence and stability (here defined as invasibility) by mutant with nearby trait values (see , and the associated texts for illustration). A convergent strategy means that individuals with a trait values nearby the strategy will evolve toward it, invasibility means that once the singular strategy trait value is reached, nearby mutants with either a bigger or lower trait value can invade the system.

In the following parts we present the evolution of the mean foraging day  $\mu_A$  and foraging length  $\sigma_A$  of the pollinator alone, then in coevolution.

## 2 Evolution of the pollinator mean foraging day

As expressed above, the dynamics of the trait under selection requires the study of the fitness gradient. After expressing the fitness function with only the evolution of the mean foraging day  $\mu_A$  (see supplementary materials) we can calculate the fitness gradient (supplementary materials for detailed calculations):

$$\frac{\partial \omega(\mu_{A_m}, \mu_{A_r})}{\partial \mu_{A_m}} \Big|_{\mu_{A_m} \rightarrow \mu_{A_r}} = \frac{1}{\sqrt{2\pi}} \left( \frac{e^{\frac{-(\mu_{A_r} - \mu_{P_W})^2}{2s_W}} (-\mu_{A_r} + \mu_{P_W}) P_W}{s_W^{3/2}} + \frac{e^{\frac{-(\mu_{A_r} - \mu_{P_M})^2}{2s_M}} (-\mu_{A_r} + \mu_{P_M}) P_M}{s_M^{3/2}} \right) \quad (11)$$



with  $s_W = \sigma_A^2 + \sigma_{P_W}^2$  and  $s_M = \sigma_{A_2} + \sigma_{P_{2M}}$ .

Note that by replacing  $A^*$  by its explicit formula, the basal competition term  $c_{base}$  does not appear in the fitness gradient anymore. While it will play a part in the ecological equilibrium values, it does not influence the variation of the fitness gradient and then the existence and characteristics of singular strategies. The value of the mean foraging day of the consumer at equilibrium only depends on the two resource phenologies (mean and length), their abundance, and the consumer foraging length values.

Adaptive dynamics hypothesises that at eco-evolutionary equilibrium, the mutant trait  $\mu_{Am}$  tends, via very small mutation steps, toward that of the resident  $\mu_{Ar}$ , who himself is at equilibrium  $\mu_A^*$ . There the fitness and the fitness gradient are null. At the eco-evolutionary equilibrium, the gradient then become:

$$\left. \frac{\partial \omega(\mu_{Am}, \mu_{Ar})}{\partial \mu_{Am}} \right|_{\substack{\mu_{Am} \rightarrow \mu_{Ar} \\ \mu_{Ar} \rightarrow \mu_A^*}} = \frac{1}{\sqrt{2\pi}} \left( \frac{e^{-\frac{(\mu_A^* - \mu_{P_W})^2}{2s_W}} (-\mu_A^* + \mu_{P_W}) P_W}{s_W^{3/2}} + \frac{e^{-\frac{(\mu_A^* - \mu_{P_M})^2}{2s_M}} (-\mu_A^* + \mu_{P_M}) P_M}{s_M^{3/2}} \right) = 0 \quad (12)$$

Solving (12), gives the analytical expression of the singular strategies  $\mu_A^*$ . We can first demonstrate that all the potential singular strategies lay in between the two flowering peaks ( $\mu_A^* \in [\mu_{P_W}; \mu_{P_M}]$ , see supplementary materials). We can further show that, when the two resources only differ by their mean flowering phenology (i.e.  $s_W = s_M$  and  $P_M = P_W$ ),  $\mu_A^* = \frac{\mu_{P_M} - \mu_{P_W}}{2}$  is the expression of one of the singular strategies (see supplementary materials). Impacts of the foraging and flowering lengths on the fitness gradients are less easy to interpret, as these parameters are in both the numerators and denominators of the fitness gradient. However, in case of a very generalist pollinator (e.g. if  $\sigma_A$  is very big) both term inside the parentheses will be very low and will not vary much with the evolution of  $\mu_A$  value. If there is a strong asymmetry between the two floral peaks, e.g. if  $\sigma_M \gg \sigma_W$  meaning a peaky flowering phenology for the wild species and a more spread out flowering peak of the managed one, the part of the fitness gradient corresponding to the spread-out flowering distribution will be very small compared to that of the other plant. Therefore, the main term driving the evolution of  $\mu_A$  toward a null selective gradient will be the difference  $\mu_A - \sigma_W$ .  $\mu_A$  will therefore evolve to a close value of that of the less spread-out flowering peak,  $\mu_W$  in this example.

However, equation (12) is not analytically tractable for the general case, we then cannot obtain an explicit formula for the position of the singular strategies. Full characterisation of

the singular strategies convergence and invasibility are unfortunately intractable, but we can explore the impact of the parameter values with adaptive dynamics plotting tools (fig. 1 (a), (d), (g) and E3 diagram) or by numerical simulations (fig. 1 (b), (e), (h)).

We can represent the sign of the relative fitness of the mutant compared to that of the resident for a set of parameters with a pairwise invasibility plot, or PIP (e.g. Metz et al 1992), as shown on figure 1 (a), (d), and (g). PIPs allow to explore the position of the singularities, and their convergence and invasibility properties depending on the set of parameters chosen.

Those particular PIPs illustrate a case where, apart from their flowering peaks, both plant pools have identical abundance and flowering length. First, note that in all PIPs we observe a singular strategy in the middle of the two flowering peaks, as predicted by the analytical calculations.

For figure 1 and the next ones, whenever possible, we have shown the evolution of or their co-evolution within the same flowering landscape. If not, it is either because the results are qualitatively similar to another one plotted on the above mentioned figures (and therefore still discuss in the results section), or one of the simulation had not reach evolutionary equilibrium yet. All of the studied floral landscapes are still represented in supplementary materials, figures 7, 8 and 9.

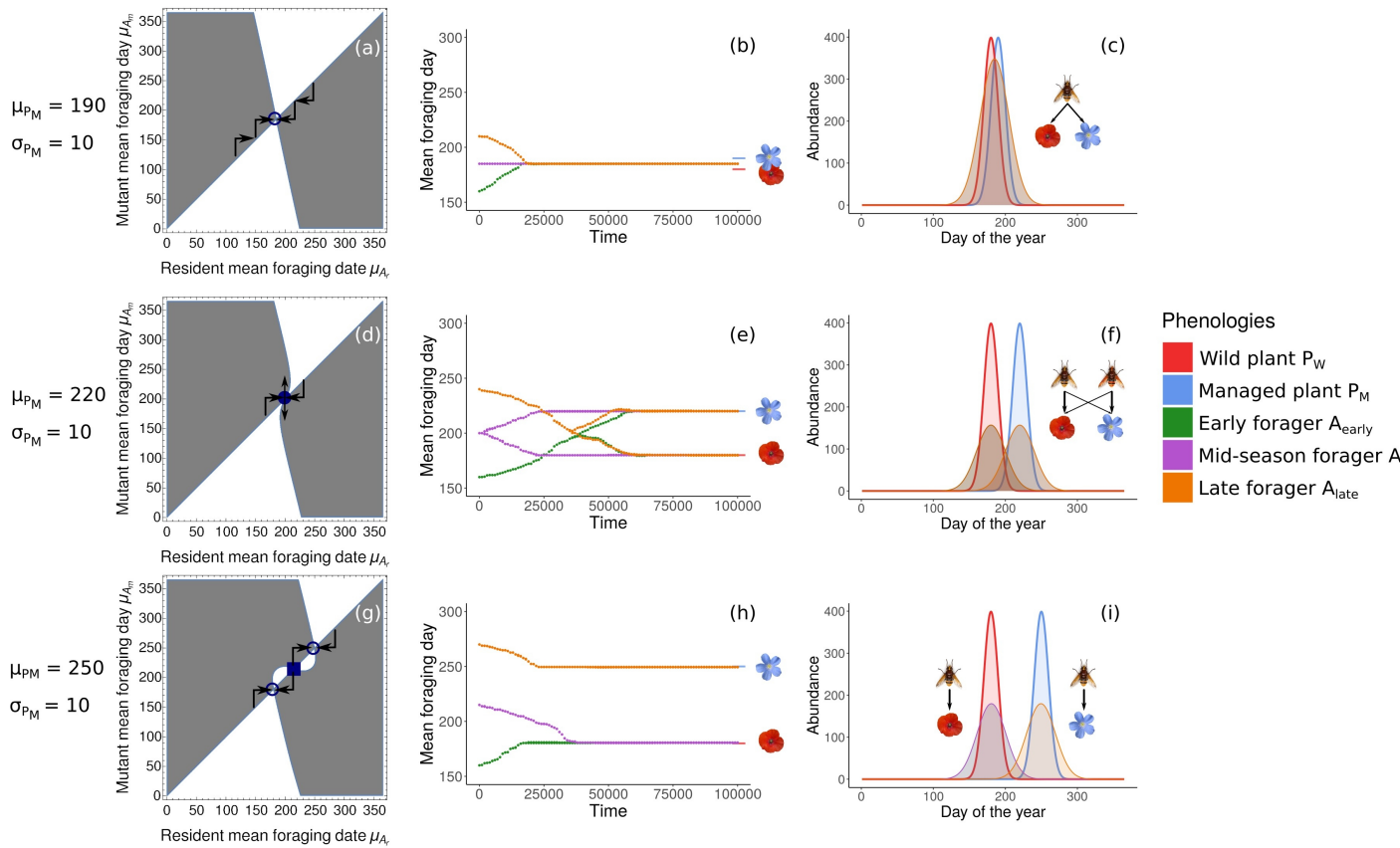


Figure 1: Evolution of the pollinator mean foraging day with an increased gap in the flowering season. Panel (a), (d) and (g) present pairwise invasibility plots. Grey areas indicate that the mutant relative fitness is positive, so that it invades and replaces the resident population. Arrows show the direction of evolutionary trajectories. The blue symbols correspond to the singular strategies and their characteristics. Circles represent convergent strategies, whereas squares are non-convergent. Filled symbols represent invasible strategy, while not filled symbols are non-invasible. Panel (b), (e) and (h) present simulations of the temporal variation of the evolving parameter, the blue and red ticks at the end corresponding to the mean flowering days of each plant group. Panel (c), (f) and (i) present the mean foraging phenologies observed at the end of the simulation. We divided the total pollinator abundance by 10 to ease visualising the phenologies. We have added schematic view of the different networks obtained. The flax and poppy flowers represent the flowering phenologies of the managed and wild groups of species, respectively. Note that while we plot three simulation situations on each graph, they are always launched separately, with only one foraging

pollinator at the beginning. Apart from that specified on the graph, parameters values are  $\sigma_{P_W}$   
 $= \sigma_{P_M} = 10$ ,  $\sigma_A = 20$ ,  $P_W = P_M = 10000$  and  $c_{base} = 0.1$ .  $\mu_A = 160$  if green, 185 if purple, and  
210 if orange. See supplementary materials for values of  $\mu_A$  at the beginning of the simulation  
and explanations.

Not that in the following part we refer with the term mid-season forager to pollinator whose  
mean foraging day is centred in between the two flowering peaks.

With a small gap between the two flowering peaks, fig. 1 panel (a), we observe a convergent  
and non-invasible strategy, called a continuously stable strategy or CSS. The simulations on  
panel (b) confirm the convergence and non-invasibility, and the resulting foraging phenology  
is shown on panel (c). This represents a stabilising selection. As represented on the interaction  
scheme, we always observe a generalist pollinator (50% of its final abundance is provided by  
the consumption of the plant flowers  $P_M$ ). When the gap increases between the two flowering  
peaks, panel (d), evolution still converges toward a singular strategy in between the two  
peaks, but this strategy is invasible. Once the singular strategy is reached, mutants with a higher  
or lower trait will be selected, leading to a dimorphic population. In this case we therefore  
observe a disruptive selection at the singular strategy. The singular strategy is called a  
branching point. Simulation in panel (e) shows that this dimorphism is maintained in time. At  
the end, on panel (f), we observe two populations, each with mean foraging day synchronised  
with a flowering peak. As shown on the interaction scheme, each pollinator population is now  
more specialised on one of the peaks ( $P_M$  is responsible for 83% of the abundance of one  
pollinator population, and 16% of the other, for all simulations). When the gap between the  
two flowering peaks increases even more, panel (g), the central singular strategy becomes a  
repellor, i.e. a non-convergent and invasible strategy. Avoiding this value, evolution  
converges towards the nearest flowering peaks. Each flowering peak is now a CSS and once  
attain the mean foraging day of the pollinator does not vary any more, as confirmed by  
simulation on panel (h). Note that for the simulation "Amiddle" (in purple) starting exactly at  
the central value, there is a fifty-fifty chance that evolution will lead to the wild or managed  
flowering peak. Panel (i) shows that at the end, one of the two flowering resources is  
completely neglected by the pollinator (for the "Aearly" simulation in green,  $P_M$  is responsible  
for only 0.7% of the pollinator abundance).

In summary, when only the mean foraging day can evolve, and the two resources are  
distributed over a short time period ( $\sigma_{P_W} = \sigma_{P_M} = 10$ ), diversification appears only for an

intermediate overlap between the two flowering peaks. Only when the two flowering peaks are very close do we observe potential generalism, when they separate we ultimately observe a specialisation on the nearest or both peaks if diversification.

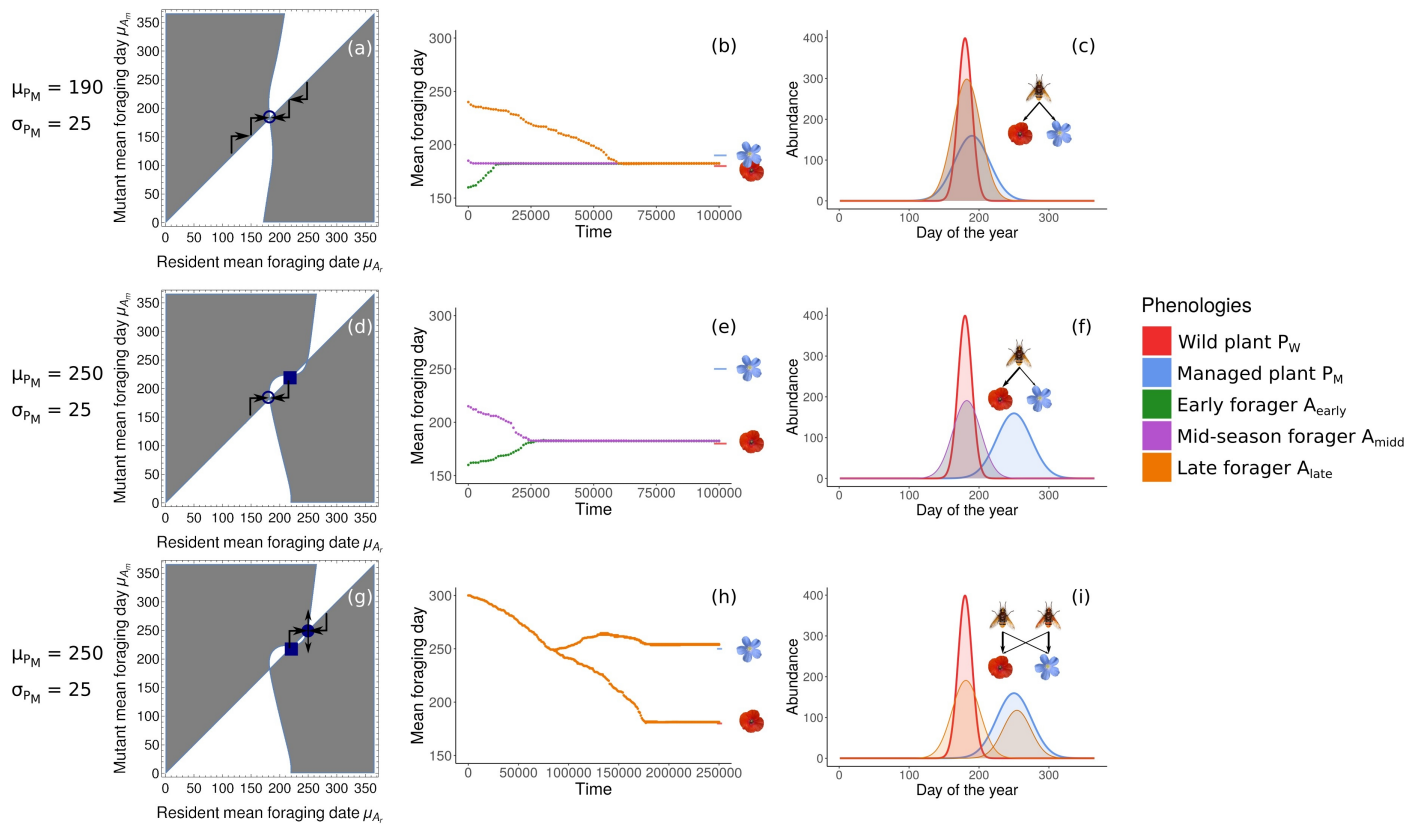


Figure 2: Evolution of the pollinator mean foraging day with an increased flowering length of the Managed species pool. Panel (a), (d) and (g) present pairwise invasibility plots. Colour codes, schemes and symbols are similar to fig. 1. Panel (b), (e) and (h) present simulations of the temporal variation of the evolving parameter, the blue and red ticks at the end corresponding to the mean flowering days of each plant group. Panel (c), (f) and (i) present the mean foraging phenologies observed at the end of the simulation. We divided the total pollinator abundance by 10 to ease visualising the phenologies. Apart from that specified on the graph, parameters values are  $\sigma_{P_W} = 10$ ,  $\sigma_A = 20$ ,  $P_W = P_M = 10000$  and  $c_{base} = 0.1$ .  $\mu_A = 160$  if green, 185 if purple on panel (b) and 215 on panel (e), and 210 if orange on panel (b) and 300 on panel (h). See supplementary materials for explanation on the chosen values of  $\mu_A$ .

Figure 2 presents the impact of increasing the flowering length of the managed pool of species. Comparing the results with that of figure 1, this lengthening causes a decrease in the attractivity of the managed species flowering peak, and the mean foraging day will almost always evolve toward the wild pool of species flowering peak, and will match its mean flowering phenology (panels (b), (c), (e), (f)). This evolutionary strategy is a CSS, stable in time. We however observe branching and dimorphic populations when starting with foraging phenology very late in the flowering season and when there is a fairly big gap between the flowering peaks but still a little overlap in the resource phenologies (panels (h) and (i), see supplementary materials figure 7 for more flowering landscapes). If we increase even more the flowering length of the managed pool of species, the diversification observed for an intermediate distance between the flowering peaks disappears, and simulations that reach equilibrium are more specialised on the highest peak of plants  $P_w$  (responsible for 75% of the pollinator abundance, panel (h) of supplementary figure 7)

As before, only with a big overlap between the two flowering peaks (10 days of differences between the peaks, and a flowering length of the managed species of maximum 25 days) do we observe a generalist foraging pattern. When the flowering length of one species increase and/or the peaks are more distant, the pollinator population tend to specialise on the nearest or most abundant peak.

In general we observe diversification patterns when the overlap between the flowering resources is neither too big (which would create a very high competition between the two population), nor too low (which will create a temporal gap of resource and render one of the two flowering peaks unreachable from the other). We observe further diversification, either when starting early or late in the season, when the managed resource is widely temporally distributed compared to the wild one, and the closest to the pollinator starting phenology.

### 3 Evolution of the pollinator foraging length

Now we follow the evolution of the pollinator foraging length  $\sigma_A$  in similar resource landscapes as in the previous section.

Expression of the relative fitness function of a mutant and a resident with different foraging lengths  $\sigma_{A_m}$  and  $\sigma_{A_r}$  is already quite complex:

$$\omega(\sigma_{A_m}, \sigma_{A_r}) = -\frac{\sigma_{A_r} \left( \frac{e^{-\frac{(\mu_A - \mu_{P_W})^2}{2(\sigma_{A_r}^2 + \sigma_{P_W}^2)}} P_W}{\sqrt{\sigma_{A_r}^2 + \sigma_{P_W}^2}} + \frac{e^{-\frac{(\mu_A - \mu_{P_M})^2}{2(\sigma_{A_r}^2 + \sigma_{P_M}^2)}} P_M}{\sqrt{\sigma_{A_r}^2 + \sigma_{P_M}^2}} \right)}{\sqrt{\pi} \sqrt{\sigma_{A_m}^2 + \sigma_{A_r}^2}} + \frac{e^{-\frac{(\mu_A - \mu_{P_W})^2}{2(\sigma_{A_m}^2 + \sigma_{P_W}^2)}} P_W}{\sqrt{2\pi} \sqrt{\sigma_{A_m}^2 + \sigma_{P_W}^2}} + \frac{e^{-\frac{(\mu_A - \mu_{P_M})^2}{2(\sigma_{A_m}^2 + \sigma_{P_M}^2)}} P_M}{\sqrt{2\pi} \sqrt{\sigma_{A_m}^2 + \sigma_{P_M}^2}} \quad (13)$$

The fitness gradient is more complex, and we cannot easily predict the impact of the values of the mean flowering days and flowering length on the evolution of the foraging length  $\sigma_A$  directly from looking at equation (13). Study of the fitness gradient sign and characteristics of potential singular strategy are unfortunately intractable (see supplementary materials). Once again, if one flowering peak is very long (e.g. if the spread-out flowering phenology is that of  $P_M$  then  $\sigma_{P_M} \gg \sigma_{P_W}$ ), the associated terms within the fitness and fitness gradient will be negligible compared to that associated to the short flowering peak. Therefore as with the evolution of  $\mu_A$ , the evolution of  $\sigma_A$  will be driven by the value corresponding to the short flowering peak ( $P_W$  in our example), and  $\sigma_A$  will evolve to capture that peak, whatever the starting mean foraging day  $\mu_A$  value. We can still further explore the effect of increased flowering gap or an asymmetrical distribution of the two flowering lengths ( $\sigma_{P_W} \neq \sigma_{P_M}$ ), with various mean foraging days, on the evolution of the consumer foraging length via numerical simulation and PIPs (figures 3 and 4).

For the simulations, as in the previous part we always start with the same foraging length  $\sigma_A = 20$  and with three possible mean foraging day (see supplementary for information on the simulation starts choice and the different flowering landscapes). This parameter cannot evolve

in this second part, but the observed results can depend on its value compared to that of the flowering resources, especially when the resources are asymmetrically distributed (figure 4). First, we examine the impact of an increased flowering gap. Figure 3 presents the evolutionary output with a low or high gap. The output is qualitatively similar to that of a high gap for a medium gap (supplementary materials figure 8 panel (b), see also figure 8 for more flowering landscapes).

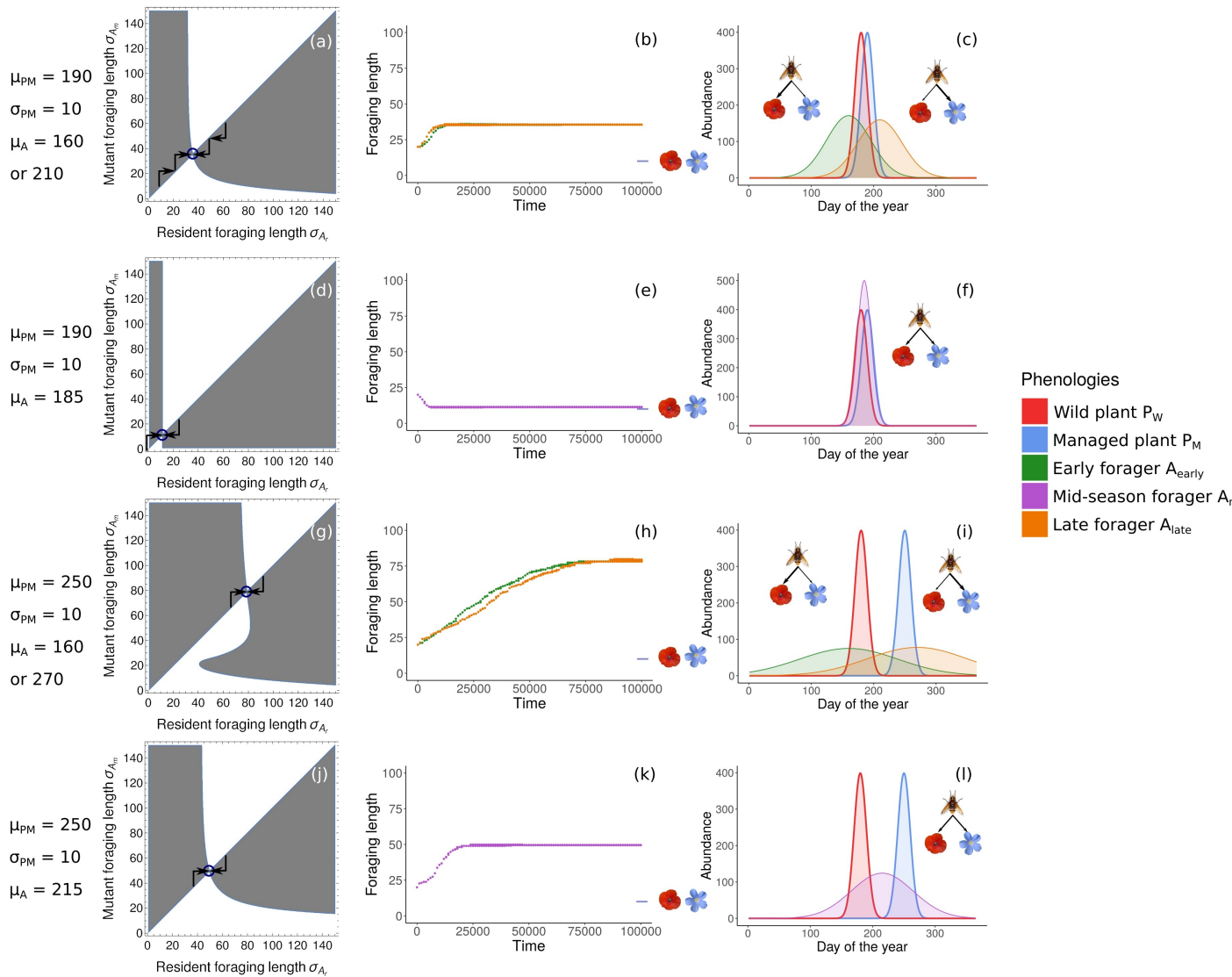


Figure 3: Evolution of the pollinator foraging length for different mean flowering day with an increasing gap between the flowering peaks. Panel (a), (d) and (g) present pairwise invasibility plots. Colour codes, schemes and symbols are similar to that of figure 1. Panel (b), (e) and (h) present simulations of the temporal variation of the evolving parameter, the blue and red ticks at the end corresponding to the mean flowering days of each plant group. Panel



(c), (f) and (i) present the mean foraging phenologies observed at the end of the simulation. We divided the total pollinator abundance by 10 to ease visualising the phenologies. Apart from that specified on the graph, parameters values are  $\sigma_{PW} = 10$ ,  $\sigma_{PM} = 25$ ,  $\sigma_A = 20$ ,  $P_W = P_M = 10000$  and  $c_{base} = 0.1$ . See supplementary materials for explanation on the chosen values of  $\mu_A$ .

Increasing the flowering gap in the middle of the flowering season leads to qualitatively similar patterns that when the gap between the flowering peaks is low. Evolution always leads to a continuously stable strategy or CSS (figure 3 (a), (d), (g) and (j)). With plants with a short flowering length we never observe branching and diversification, even for an intermediate overlap of the flowering phenologies (see supplementary figure 8 (b)), as opposed to what we observed for the evolution of  $\mu_A$  in the same flowering landscape.

The generalist or specialist pattern depends on the spread between the two flowering peaks and the value of the non-evolving mean-foraging day  $\mu_A$ . Whatever the gap values, when starting in the middle of the flowering season, the foraging length at the end of the evolutionary process always capture both peaks equally, the pollinator is generalist (panels (f) and (i)). When starting before the first flowering peaks or after the last one, the foraging length extend to capture both peaks. When the two peaks are fairly separated, the pollinator is a little more specialised on the nearest peak (e.g. on panel (h) and (i), PW provides 65% of the pollinator abundance on the "Aearly" simulation).

We then study the impact of a lengthening flowering season of the managed species pool, plotted on figure 4

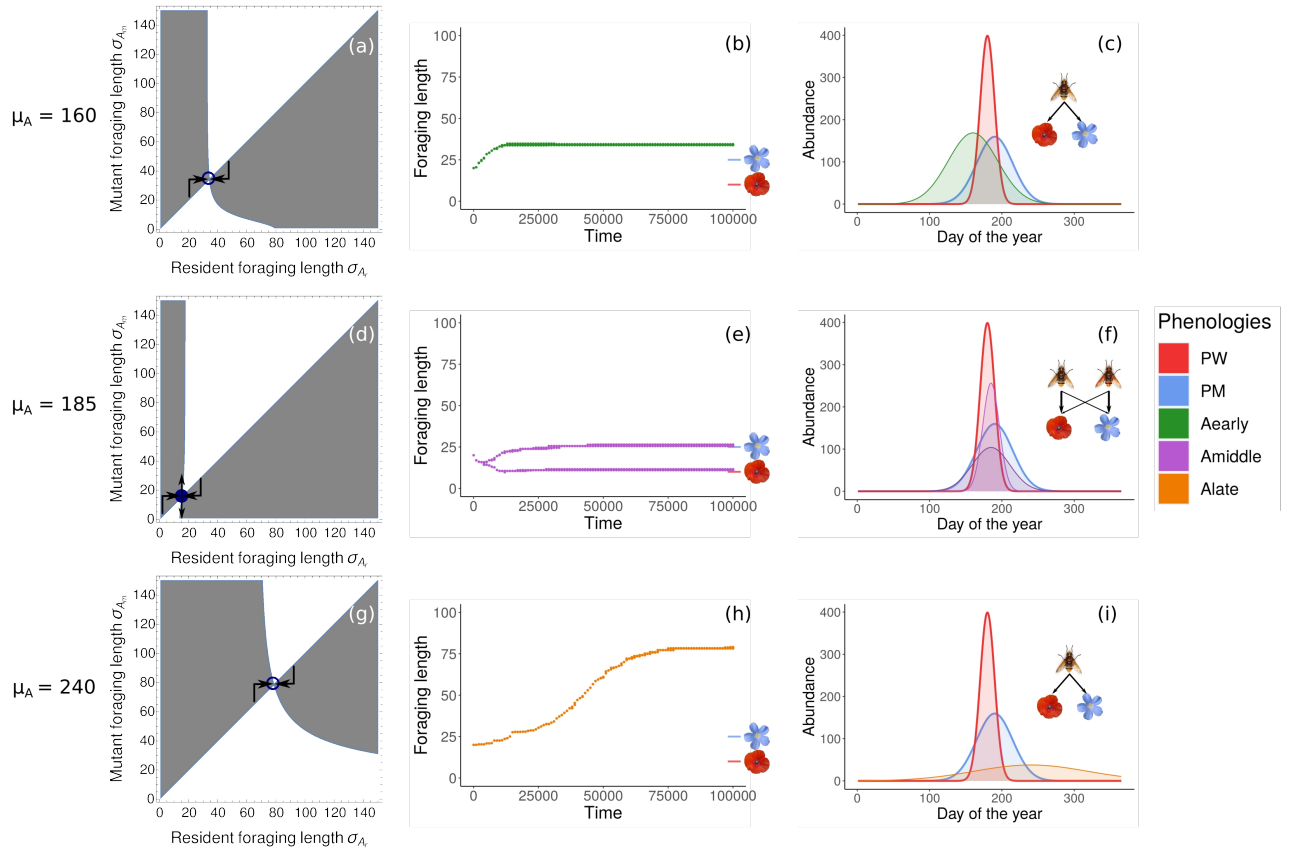


Figure 4: Evolution of the pollinator foraging length for different mean foraging day with an asymmetry in the flowering length of the two plant groups. Panel (a), (d) and (g) present pairwise invasibility plots. Colour codes, schemes and symbols are similar to that of figure 1. Panel (b), (e) and (h) present simulations of the temporal variation of the evolving parameter, the blue and red ticks at the end corresponding to the mean flowering days of each plant group. Panel (c), (f) and (i) present the mean foraging phenologies observed at the end of the simulation. We divided the total pollinator abundance by 10 to ease visualising the phenologies. Apart from that specified on the graph, parameters values are  $\mu_{PM} = 190$ ,  $\sigma_{PW} = 10$ ,  $\sigma_{PM} = 25$ ,  $\sigma_A = 20$ ,  $P_W = P_M = 10000$  and  $c_{base} = 0.1$ . See supplementary materials for explanation on the chosen values of  $\mu_A$ .

When both resources peaks are close-by and asymmetrically distributed, results depend on the starting mean foraging phenology. When starting before the first flowering peak (figure 4 (a-c)) evolution of the foraging length increases until the foraging phenology captures both flowering peaks. We observe the same pattern when starting after the last flowering peak

(figure 4 (g-i)). The further the mean foraging day at the beginning of the simulation is from the peaks, the bigger is foraging length becomes, capturing always both flowering peaks. However it is more specialised on the nearest peaks. When starting the simulation with a mean foraging day in between the two flowering peaks, we observe, after a branching phenomenon, the appearance and persistence of two pollinator morphs, each one closely matching the flowering length of each plant groups. When the managed plant group flowering length increases even more, we observe qualitatively the same pattern but for the early mean foraging day who also branches into two populations with different phenologies, each capturing mostly one of the flowering peaks (see supplementary figure8 panel (g)). However, the diversification pattern observed when starting in the middle of flowering season disappear when the distance between the two peaks increases, and diversification only happen when the managed plant flowering length is high and the simulation starts with a mean foraging day early in the season (supplementary figure figure 8 panels (h) and (i)). All this shows the importance of taking both the mean foraging day and the foraging length into account when studying the pollination (or other foraging activities) pattern. Indeed, here we have very different outcomes on the evolution of the foraging length when the mean foraging day is strongly restricted (which can be the case if it constrained by other abiotic or biotic factors). Diversification pattern when  $\sigma_A$  evolves are different from the evolution of  $\mu_A$ . They appear either when starting with an early mean foraging day in flowering landscape with managed plants with a very high flowering length, or when starting in the middle of the flowering season when the two peaks are asymmetrically distributed and close-by (10 days between the flowering peaks).

The endpoint of evolution is mainly driven by the position of the nearest flowering peak, the pollinator foraging length evolving until catching this flowering peaks. Whatever the starting point, the lengthening of the foraging length always leads to generalist pollinator, except when we observe diversification. Then, if the peaks are fairly separated and asymmetrically distributed, the pollinator whose foraging length matches the flowering length of the plant

with the highest peak ( $P_w$  in our system) is more specialised on that one, the one matching the flowering length of the more distributed species forages on both flowering peaks as his foraging length is wider to maximise intake on that flatten peak, and is de facto more generalist.

#### 4 Coevolution of the two phenological parameters

Adaptive dynamics can model the coevolution of traits [24], but the analytical outputs in our case would be intractable. We chose here to follow the coevolution of the two foraging traits via numerical simulation, using the software R version 3.4.4 (2018-03-15). At each time step we first calculate the population sizes of all present foragers. For that we integrate over one time step the corresponding demographic variation function (as expressed in (1) but generalised for multiple competing pollinator populations) with the ode function from the deSolve package [26]. Once all population variations have been taken into account we remove all the populations and associated foraging traits that are below the minimum population threshold (here equal to  $10^{-10}$ ). We now draw the new mutant populations and their associated mutant traits. First we determine which populations are going to produce new mutants on trait  $\mu_A$  and then we do the same process on trait  $\sigma_A$ . Some population can cumulate both mutation as the pool of population use for the mutation of  $\sigma_A$  is the one that includes the previously drawn  $\mu_A$  mutants. Mutant population and mutant trait values are chosen according to the population size, the mutation probability (fixed at  $10^{-7}$  on our coevolution simulations) and the mutation amplitude (0.5 for each trait). The new mutant populations that arise have a size equal to the minimum population ( $10^{-10}$ ), the mutant trait is drawn on a normal distribution centred on the parent trait and with amplitude 0.5 day, and the non-mutant trait is inherited from the parent population. The parent and mutant populations are now considered as the new population pool for a new simulation run at year+1. We run our simulations for a minimum of

$10^5$  time steps, then continue up to  $2.5 \times 10^5$  time steps if the populations size and trait values kept varying (checked via graphical plots of the temporal variations, e.g. as in 7).

We performed simulations in the same flowering landscape as studied in the previous sections, varying both the gap between the two flowering peaks and the length of the phenology of the managed plant group. For simulations in more various landscapes, see the Figure 5, supplementary materials figure 9).

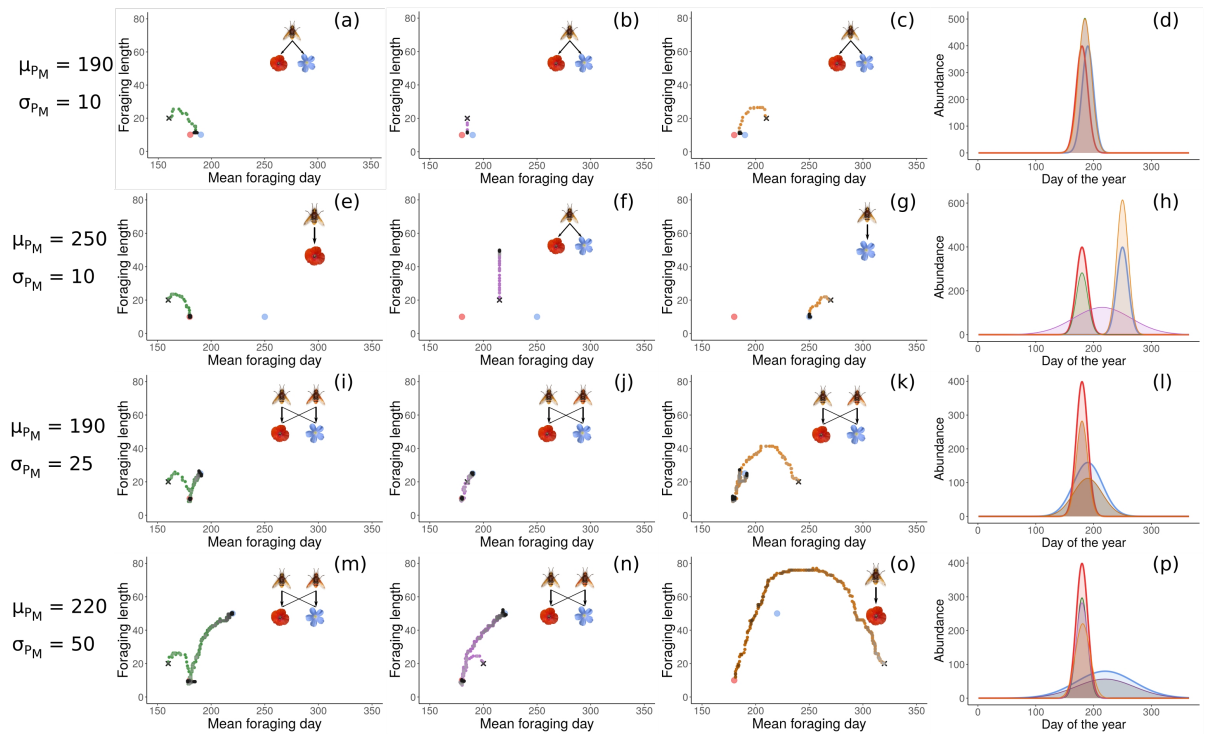


Figure 5: Coevolution of the pollinator mean foraging day and foraging length in different flowering landscapes. The first column present simulation starting before the first flowering peak, the second column in between the two peaks and the third one after the two peaks. The darker the color of the simulation point, the closer to the end of the simulation process. Simulations (a, b, c, e, f, g, i, j) were run for 100000 time steps, the others for 200000 time steps. Column four present the phenologies of the different populations at the end of the simulations. Again we divided the pollinator populations by ten to ease the phenologies visualisation. Color code is the same as in figure 1. For explanations on the starting  $\mu_A$  values, see supplementary materials.

The results obtained with the coevolution of the mean foraging date or the foraging length differ from those found when either the mean foraging date or the foraging length evolved alone, the match at the end of the eco-evolutionary process between the pollinator phenology and one (or two if there is a diversification event) of the resources distribution being larger in the former case.

First, when both plant pools have identical abundance and flowering length (fig. 5 (a-h)), we do not observe any diversification event as was found in some cases when only the mean foraging day could evolve. When the gap between the two flowering phenologies is small (fig. 5 (a-d)), the pollinator foraging phenology at the end of the evolutionary process includes both flowering peaks, the pollinator feeding equally on both resources as qualitatively found previously. However, when the flowering gap is larger (fig. 5 (e-g)), the foraging phenology evolves toward a longer phenology including both peaks when the pollinator starts in between the two peaks (fig. 5f), whereas the end phenology of the pollinator matches that of the nearest flowering peak when starting outside the period between the two flowering peaks (fig. 5e,g). In the same flowering landscape, when only the mean foraging day could evolve, we did not observe this generalist strategy with starting mean foraging day in between the two flowering peak figure 1). Instead the evolution of  $\mu_a$  only lead either to the match of the foraging phenology with alternatively one of the two flowering peaks or to a dimorphic population, each morph being characterised by a mean foraging day synchronised with a flowering peak. This generalist strategy is in fact observed in that same case when only the foraging length evolves (fig. 3).

Second, when resource distribution is asymmetric with increased flowering length of the managed pool of species (5 (i-o)), we observe a diversification event in most cases contrary to what was found in previous sections when only one of the phenology parameters of the forager evolved. In these cases, the coevolution of the mean foraging date and the foraging length leads to the coexistence of two morphs with different foraging phenologies, each one matching the flowering distribution phenology of one of the two resources. While the

evolution of the foraging length  $\sigma_A$  only could lead to a diversification pattern when the resource distribution was asymmetric this was less frequent than in the case of coevolution (fig. 2). Indeed diversification and maintenance of two foragers with different phenologies were then observed in two cases, with intermediate flowering overlap (figure 4 panel (e) and (f), or, when the flowering phenologies were very asymmetrical, for a pollinator with early starting mean foraging day, figure 8 panels (h)-(i)). It should also be noted that the evolution of  $\sigma_A$  only tends to favour larger foraging length than when  $\sigma_A$  coevolve with  $\mu_A$ . Indeed when the mean foraging day is constrained far from the main flowering peak, this leads to the evolution of even greater phenological length than when the parameters can coevolve to capture this resource peak.

Overall, we observe generalist pollinators either when the two peaks greatly overlap, or when they do not overlap but the evolution of pollinator mean foraging day starts in between the two flowering peaks. Both diversification and specialisation patterns seem to depend on the overlap between the two phenologies and whether they are asymmetrically distributed, and for specialisation, on the starting mean foraging day value. These preliminary results should be tested with systematic parameter checking to explore in particular the threshold conditions for diversification. We observe diversification when the two flowering phenologies partly overlap, are asymmetrically distributed.

## Discussion

By following the evolution of different traits describing the foraging phenology of a consumer, we observe different diversification and specialisation patterns. Our results emphasize the impact of temporal distribution of two alternative resources on the evolution of a consumer phenology, but the initial mean foraging day of the consumer is also very important in the obtained outcome. We also observe some differences in the evolutionary

outcomes if one of the two foraging parameters (mean foraging day or foraging length) is unable to evolve.

## 1 Consumer diversification patterns in different phenological landscapes of resources

The presence of gaps in floral resources over the season and of mass-flowering events are both suggested to affect the abundance and diversity of pollinators [16], potentially leading to pollinator extinctions [27, 28]. In our study, as the graphical representations of the temporal distribution of our consumer's abundance at the end of the evolutionary process show, even when only one parameter of the consumer's phenology can evolve, it always maintains a relatively high population, and is able to survive and sometimes even thrive even when starting with a phenology very different from that of its resources. While such high abundances are likely related to the parameter choices in the simulations, in our model, the consumer has always the ability to evolve to an eco-evolutionary stable strategy and never goes extinct, whatever the landscape configuration and its synchrony with it at the beginning.

Our results highlight that the resource phenological landscapes promoting consumer diversification are those that present two alternative food resources that are not totally temporally overlapping but are still not too distant from the starting forager's phenology. While diversification always leads to the exploitation of both resource peaks, a high resource gap prevents diversification by causing the temporal isolation of one of the resources. In empirical studies, a reduced resource availability during part of the foraging season is often associated to reduced pollinator abundance and diversity (e.g. [27] [28]). Long term coexistence of two sub-populations also requires a not too big phenological overlap of the resources, which reduces competition between the two consumers population and promotes coexistence [29]. The diversification that we observe for intermediate resource overlap could be an effect of niche complementarity [30]. This rather spread out distribution of resources



allows several different strategies to coexist without a too high competition rate [31]. On the contrary, when the two resources have a very high overlap or almost none, this produces very temporally narrow resource niches, with no temporally proximate alternative [32]. Strongly overlapping resources can only feed one consumer type, as two would over-compete for this narrow resource availability.

The diversification window that we observe for a certain level of resource overlap is a classical result of models representing consumer(s) foraging on two alternative resources (e.g [23] previously found in [21] or [22]). Empirical studies e.g. also observe a great diversity of pollinator species when the resource landscape provide several flowering peaks distributed all along spring and summer [28].

## 2 Specialisation patterns in different phenological landscapes of resources

Because the degree of generalism is directly linked in our model to the overlap between the two resources, we observe the greatest degree of generalism, either when all the resources are concentrated over a short season, or when one of the two resources was distributed more evenly over a long season, its presence therefore strongly overlapping that of the other resource with shorter availability. Other studies also link the degree of generalism with the temporal spread of resources. Using an arctic day-to-day pollination dataset, gathered over two years, Olesen et al. [2] showed that even more than abundance, phenophase controlled the number of links per species. In this mutualistic network, the longer the species phenophase, the more generalist the species was. This fits well with our results, and the observation that when one of the resources had a very long phenophase, it usually allowed to maintain two consumers, and consumers with a long foraging length were generalists, the timing of their phenology within the season allowing them to feed on both resources.

The most generalist consumers occur in our model when the resource phenological landscape corresponds to two strongly overlapping resources in time. Dominance of one generalist over specialists when one resource is very abundant has been potentially observed in empirical studies testing the effect of mass flowering crops (MFCs) on pollinators phenology [33]. They observe that all groups of bees are negatively impacted by MFC, and that their densities also decline in the surrounding semi-natural remnant but for the very generalist honeybee populations. While this effect of MFC was observed on other studies, it seems to disappear on the long term for non-bombus wild and managed generalist bees [34]. The degree of generalism considered here depends on two factors, the synchrony between the consumer and one resource, and the overlap between the two resources. Indeed, because we did not include any trait-matching or behavioural preference parameter, when both resources are available, the consumer forages equally on them. Therefore, in our system, synchrony is not equivalent to a high degree of specialism, and we observe a majority of generalist consumers at the end of the evolution process.

### 3 Asynchrony between consumer and resource phenologies and (co-)evolution of phenological traits

In our eco-evolutionary outcomes, we sometimes observe asynchrony between the consumer final foraging phenology and at least one of the resource. The best fit between consumer and resource phenologies are observed when the two phenological parameters of the consumer co-evolve. However, in that case, we can still observe some sort of asynchrony. In general, as previously mentioned, the peaky resource drives the evolution of the consumer's phenology. The consumer's phenology is therefore in asynchrony with the neglected food resource, and considering only pairs of interacting species when studying phenology can hide asynchrony or synchrony with other interacting partners. Many empirical studies observe asynchrony or mismatch between interacting species (e.g . [35, 36]). While current asynchrony can of course

harm species and can result from a lack of evolutionary potential and quick adaptive responses to track current change [1], it can still originate from an evolutionary process. In their review, Visser and Gienapp [20] suggest that because total fitness has multiple components, fitness optimum can correspond to a phenological mismatch with the main interactor, meaning that species asynchrony is not always counter selected [37]. Remember also that a shift in phenology does not always create a mismatch between two interactors, and that observed mismatches are not always maladaptive [38, 37]. If we draw a parallel between our models and current land-use changes, a very abundant and concentrated resource like mass flowering crops could indeed attract most of the pollinators, especially the most generalist and strongest competitors of them like honeybees. This phenological attractiveness could potentially temporally deprive the surrounding wild plant from pollination [18], especially if mass flowering crop ultimately lead to the evolution of pollinators with shortened phenologies matching that of the crop flowering peak. However note that some long term studies have noted a benefit of mass flowering crops like oilseed on pollinators biodiversity and abundance [39] [40] [34]. Those pollinators might maintain a long foraging season (either because it is constrained as in our first evolutionary part, or because it is maintained by selective pressure) that allow them to both feed on the flowering peak when present, and on other wild plants during the rest of the season.

Asynchrony increases when we consider the evolution of one parameter alone, as the constrained consumer phenological term prevents a perfect match with the resource phenologies. It is indeed possible that constraints prevent the evolution of the other phenological trait with resource changes, which make also relevant the exploration of single trait evolution. The length of a species phenology can sometimes strongly depends on intrinsic (e.g. metabolic) constraints. Short-living species, or with one short-living stage (e.g. the brief adult life of gall insects) will undergo their full life cycle in a limited amount of time, for each adult-stage, phenological variation of the phenophase length is therefore limited, especially if they need to synchronise with their food resource [41]. On the contrary, some species might

be strongly constrained in the value of their onset or mean phenology, especially if it is correlated with the maximal abundance of the interactor, and the interaction depends on this abundance level (e.g. birds nesting and egg-laying time and date of peak resource abundance [42]).

#### 4 Limits and perspectives

Our observations have several limitations: we do not consider feedbacks between the consumer and its resource, resource phenology is the only component of the consumer's fitness, and we do not consider differences in preferences (exploitation abilities) between the two resources for each consumer.

Not considering feedbacks on the resource ecological or evolutionary dynamics means that a reduced synchrony between the consumer and the resource has no impact on resource abundance and phenology. We therefore limit the effect of direct and indirect competition that could be greater in natural systems. Too much synchrony could also lead to the overexploitation of the resource by the consumer, selecting then for not too synchronized phenologies [43]. If the interaction is mutualistic (e.g. plants-pollinators or plant-mycorrhizae interactions) we could observe an even stronger match between the consumer (e.g; the pollinator or the fungi) and its (plant) resource. If it is a "true" consumer-resource interaction with a negative impact of consumption on the resource demography, on the resource side it could select for an increased asynchrony with its consumer, and increased synchrony on the consumer side, creating a red-queen dynamics that will stabilise the long term evolutionary pattern.

In our model, we consider that temporal coexistence is a necessary and sufficient condition for the interaction, which is not always the case [44]. This would correspond to the coarse grain hypothesis of Mac Arthur and Levin [45], in which individuals cannot discriminate between the different resources. But temporal synchrony, interaction can depend on spatial location

and/or morphologically or physiologically compatibility between the two interactors (fine grain hypothesis, with a species able to discriminate and select its food [45]). These added conditions could explain some discrepancies between our results and observed patterns. For example, the Kodiak brown bear presented in the introduction are feeding in an environment where both of their possible resources overlap strongly on a short time period [14, 46]. While our model predicts evolution in such a resource landscape toward a generalist consumer foraging equally on both resources, researchers have observed a selection toward the resource that reduces intraspecific competition, especially for the female bears with cubs. This selective foraging pattern, in opposition to the generalist one that we observe, is probably not adaptive in the long term, as the preferred resource, the berries, are less energy-rich and lack essential nutrients provided by the alternative food source, spawning salmons [47].

If we would have considered consumer's preferences, and the evolution of that preference trait, this would have probably lead to the diversification and coexistence of several consumers with different degrees of generalism in more divers case of resource landscapes, notably when there is a strong overlap between resources phenologies. But the coexistence of specialists, or specialists and generalists, on strongly overlapping resources is still a common pattern in the wild (e.g; [48, 29]). Morris et al. [48] explain this pattern with data on generalist and specialist rodents via a niche partitioning effect, generalist rodents coexisting with very efficient specialist ones by exploiting the habitat niches they left unused. Other models add these selective foraging traits to their consumer-resource systems, to explore conditions for coexistence. Rueffler et al. [49] for example included the evolution of behavioural flexibility in diet choices and morphological traits involved in the foraging efficiency. They observe that opportunist consumers never diversify and will stay generalist on the different food resources, while when diet choice is implemented and the ancestral population forages selectively, they observe diversification and the coexistence of several specialist consumers. Adding this diet choice parameter in our model would reduce the number of cases where we observe generalist individuals, in accordance with wild observations.

## 5 Conclusion

Our models follow the evolution of two fundamental phenological traits that are the mean foraging date and foraging length. The results we observe are different depending on the evolving parameters, showing the importance of taking both traits into account. This is also emphasized by [50], where they analyse phenological data on pairs of amphibian competitors. They often observe non-homogeneous shifts in species phenologies (e.g. a complete change in the temporal shape of the species distribution), that, instead of increasing the asynchrony between species, can increase their coexistence time, which is particularly critical for these amphibians, as they compete for sound space during reproduction. These shifts cannot be captured by typical phenological metrics used in field and empirical studies (e.g. onset and mean phenological day [5], and call for more descriptors of species phenologies. Phenology length is understudied compared to changes in the onset or mean phenology day. Most of the research questions that focus on the synchrony/asynchrony or match/mismatch question with the observed current global changes only focus on phenology with similar duration at a different time, therefore characterised easily by the onset or mid phenology parameter (e.g. studies reviewed by [20]), but very rarely by changes in the length of the phenological process at stake (but see [2]). However, our study shows that the evolution of mean phenological day and phenological length lead to very different foraging patterns, evolution of foraging length alone leading generally to less diversification and more generalist consumers. All in all, our study highlights the importance of considering the length of phenological events, in addition to phenological onset or mean dates, for understanding the demographical and evolutionary consequences of changes in seasonal dynamics of species.

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# Supplementary materials

## 1 Parameters and function table

Parameter	Description
$r$	growth rate of the consumer
$c$	competition rate within the consumer community
$\mu_{A(m,r)}^{(*)}$	mean foraging day of the ( $m,r$ : mutant or resident) consumer (*: at eco-evolutionary equilibrium)
$\sigma_{A(m,r)}^{(*)}$	foraging length of the ( $m,r$ : mutant or resident) consumer (*: at eco-evolutionary equilibrium)
$\mu_{P_i}$	mean day if resource availability, or mean flowering day of resource i
$\sigma_{P_i}$	flowering length of resource i
$f_A$	foraging activity of the consumer along the year
$f_{P_i}$	temporal distribution of the flowers of resource i
$c_{base}$	basal competition rate
$A^{(*)}$	consumer population (*: at ecological equilibrium)
$P_i$	resource i population
$\mu\sigma^2$	mean value and variance of the mutation in the canonical equation (8) of adaptive dynamics

## 2 Feasibility and stability conditions of the ecological equilibrium

Feasibility of the ecological system requires that  $A^* > 0$  which is true if and only if  $r(\mu_A, \sigma_A) > 0$  and  $c(\mu_A, \sigma_A) > 0$ . Owing to our definition of these two functions this is always true, the ecological equilibrium is always feasible.

Stability of an ecological equilibrium requires that the real part of eigenvalues of the matrix corresponding to the ecological system is negative [51]. In our case this correspond to the derivation of eq. (1) with respect to  $A$  at the ecological equilibrium  $A^*$ :

$$\left. \frac{\partial^2 A}{\partial t \partial A} \right|_{A \rightarrow A^*} = r(\mu_A, \sigma_A) - 2A^* c(\mu_A, \sigma_A) \quad (14)$$

Because  $A^* = \frac{r(\mu_A, \sigma_A)}{c(\mu_A, \sigma_A)}$  this equation becomes:

$$\left. \frac{\partial^2 A}{\partial t \partial A} \right|_{A \rightarrow A^*} = -r(\mu_A, \sigma_A) \quad (15)$$

$r(\mu_A, \sigma_A)$  is positive by definition, therefore the above equation is always negative. When feasible, the equilibrium is always stable.

### 3 Analyses of the singular strategies when the mean foraging day evolves

After equation (9), the explicit formula of the fitness function following the evolution of the pollinator mean foraging time is:

$$\omega(\mu_{A_m}, \mu_{A_r}) = \frac{1}{\sqrt{2\pi}} \left( \frac{e^{-\frac{(\mu_{A_m} - \mu_{P_W})^2}{2s_W}} P_W}{\sqrt{s_W}} + \frac{e^{-\frac{(\mu_{A_m} - \mu_{P_M})^2}{2s_M}} P_M}{\sqrt{s_M}} - e^{-\frac{(\mu_{A_m} - \mu_{A_r})^2}{4\sigma_A^2}} \left( \frac{e^{-\frac{(\mu_{A_r} - \mu_{P_W})^2}{2s_W}} P_W}{\sqrt{s_W}} + \frac{e^{-\frac{(\mu_{A_r} - \mu_{P_M})^2}{2s_M}} P_M}{\sqrt{s_M}} \right) \right) \quad (16)$$

With  $s_W = \sigma_A^2 + \sigma_{P_W}^2$  and  $s_M = \sigma_A^2 + \sigma_{P_M}^2$ .

Note that by replacing the value of the ecological equilibria  $A^*$  by its expression depending on growth and competition rates, the basal competition parameter does not appear in the fitness function any more. When derivating this fitness function with respect to the mutant mean foraging day we obtain:

$$\left. \frac{\partial \omega(\mu_{A_m}, \mu_{A_r})}{\partial \mu_{A_m}} \right|_{\mu_{A_m} \rightarrow \mu_{A_r}} = \frac{1}{\sqrt{2\pi}} \left( \frac{e^{-\frac{(\mu_{A_m} - \mu_{P_W})^2}{2s_W}} (-\mu_{A_m} + \mu_{P_W}) P_W}{S_W^{3/2}} + \frac{e^{-\frac{(\mu_{A_m} - \mu_{P_M})^2}{2s_M}} (-\mu_{A_m} + \mu_{P_M}) P_M}{S_M^{3/2}} \right. \\ \left. + \frac{e^{-\frac{(\mu_{A_m} - \mu_{A_r})^2}{4\sigma_A^2}} (\mu_{A_m} - \mu_{A_r}) \left( \frac{e^{-\frac{(\mu_{A_r} - \mu_{P_W})^2}{2s_W}} P_W}{\sqrt{s_W}} + \frac{e^{-\frac{(\mu_{A_r} - \mu_{P_M})^2}{2s_M}} P_M}{\sqrt{s_M}} \right)}{2\sigma_A^2} \right) \quad (17)$$

Adaptive dynamics hypotheses that at eco-evolutionary equilibrium, the mutant trait  $\mu_{A_m}$  tends toward that of the resident  $\mu_{A_r}$ , who himself is at equilibrium  $\mu_A^*$ . At the eco-evolutionary equilibrium, the gradient then become:

$$\left. \frac{\partial \omega(\mu_{A_m}, \mu_{A_r})}{\partial \mu_{A_m}} \right|_{\substack{\mu_{A_m} \rightarrow \mu_{A_r} \\ \mu_{A_r} \rightarrow \mu_A^*}} = \frac{1}{\sqrt{2\pi}} \left( \frac{e^{-\frac{(\mu_A^* - \mu_{P_W})^2}{2s_W}} (-\mu_A^* + \mu_{P_W}) P_W}{S_W^{3/2}} + \frac{e^{-\frac{(\mu_A^* - \mu_{P_M})^2}{2s_M}} (-\mu_A^* + \mu_{P_M}) P_M}{S_M^{3/2}} \right) \quad (18)$$

The model is symmetrical but here we randomly fixed  $\mu_{P_W} < \mu_{P_M}$ . The above formula goes to zero if and only if one of the two terms inside the parentheses are equal to zero, or if one is negative and the other positive.

All terms are positives but  $(-\mu_A^* + \mu_{P_W})$  and  $(-\mu_A^* + \mu_{P_M})$ . The two terms are null if and only if  $\mu_{P_W} = \mu_{P_M} = \mu_A^*$ . Because  $\mu_{P_W} < \mu_{P_M}$ , it means that the negative term must be  $(-\mu_A^* + \mu_{P_W})$  and the positive one  $(-\mu_A^* + \mu_{P_M})$ . Therefore  $\mu_A^* \in [\mu_{P_W}; \mu_{P_M}]$ .

Note that when  $\mu_A^* = \frac{\mu_{P_M} - \mu_{P_W}}{2}$ , i.e. the pollinator mean foraging day is equidistant of the two flowering peaks, 18 becomes:

$$\left. \frac{\partial \omega(\mu_{A_m}, \mu_{A_r})}{\partial \mu_{A_m}} \right|_{\substack{\mu_{A_m} \rightarrow \mu_{A_r} \\ \mu_{A_r} \rightarrow \mu_A^*}} = \frac{1}{\sqrt{2\pi}} \left( \frac{e^{-\frac{(\frac{\mu_{P_W} - \mu_{P_M}}{2})^2}{2s_W}} \left(\frac{\mu_{P_W} - \mu_{P_M}}{2}\right) P_W}{S_W^{3/2}} + \frac{e^{-\frac{(\frac{\mu_{P_M} - \mu_{P_W}}{2})^2}{2s_M}} \left(\frac{\mu_{P_M} - \mu_{P_W}}{2}\right) P_M}{S_M^{3/2}} \right) \quad (19)$$

If we fix  $s_W = s_M$ , the two exponential function are equals. The two terms inside the parenthesis are inverse of one another meaning that equation (19) is equal to zero.

$\mu_A^* = \frac{\mu_{P_M} - \mu_{P_W}}{2}$  is the expression of one singular strategy.



## 4 Analyses of the singular strategies when the foraging length evolves

Expression of the relative fitness function of a mutant and a resident with different foraging lengths  $s_{Am}$  and  $s_{Ar}$  is already quite complex:

$$\omega(\sigma_{A_m}, \sigma_{A_r}) = -\frac{\sigma_{A_r} \left( \frac{e^{-\frac{(\mu_A - \mu_{P_W})^2}{2s_{ArW}}} P_W}{\sqrt{s_{ArW}}} + \frac{e^{-\frac{(\mu_A - \mu_{P_M})^2}{2s_{ArM}}} P_M}{\sqrt{s_{ArM}}} \right)}{\sqrt{\pi} \sqrt{\sigma_{A_m}^2 + \sigma_{A_r}^2}} + \frac{e^{-\frac{(\mu_A - \mu_{P_W})^2}{2s_{AmW}}} P_W}{\sqrt{2\pi} \sqrt{s_{AmW}}} + \frac{e^{-\frac{(\mu_A - \mu_{P_M})^2}{2s_{AmM}}} P_M}{\sqrt{2\pi} \sqrt{s_{AmM}}} \quad (20)$$

with  $s_{ArW} = \sigma_{A_r}^2 + \sigma_{P_W}^2$ ,  $s_{AmW} = \sigma_{A_m}^2 + \sigma_{P_W}^2$ ,  $s_{ArM} = \sigma_{A_r}^2 + \sigma_{P_M}^2$ , and

$$s_{AmM} = \sigma_{A_m}^2 + \sigma_{P_M}^2.$$

Derivation with respect to  $\sigma_{Am}$  to express the fitness gradient gives:

$$\frac{\sigma_{A_m}}{2\sqrt{\pi}} \left( \frac{2P_W \sigma_{A_r} e^{-\frac{(\mu_A - \mu_{P_W})^2}{2s_{ArW}}}}{(\sigma_{A_m}^2 + \sigma_{A_r}^2)^{3/2} \sqrt{s_{ArW}}} + \frac{\sqrt{2} P_W e^{-\frac{(\mu_A - \mu_{P_W})^2}{2s_{AmW}}} ((\mu_A - \mu_{P_W})^2 - s_{AmW})}{(s_{AmW})^{5/2}} \right) + \frac{2P_M \sigma_{A_r} e^{-\frac{(\mu_A - \mu_{P_M})^2}{2s_{ArM}}}}{(\sigma_{A_m}^2 + \sigma_{A_r}^2)^{3/2} \sqrt{s_{ArM}}} + \frac{\sqrt{2} P_M e^{-\frac{(\mu_A - \mu_{P_M})^2}{2s_{AmM}}} ((\mu_A - \mu_{P_M})^2 - s_{AmM})}{(s_{AmM})^{5/2}} \quad (21)$$

## 5 The different flowering landscapes

As explained in the introduction we explore both the impact of an increased gap in the flowering season, and of an asymmetry between the two flowering lengths. We study the impact of the plant flowering phenology values on the analytical calculation. We also check our analytical prediction and explore coevolution processes with simulations, with different flowering phenologies and starting foraging phenologies. In the following we consider that one plant phenology is fixed, for example the human managed one  $P_M$ , and the other varies in both flowering mean and length with environmental changes. Both plants phenologies are represented on fig. 6, the blue curve corresponding to the flowering phenology of the managed species and the red curve to that of the wild one.

For each resource landscape we launch three simulations with pollinators with different starting mean foraging phenologies, one with a foraging peak early in the season (green curve in fig. 6), a second in between the two flowering peaks (orange curve in fig. 6) and a third late in the flowering season (purple curve in fig. 6). The foraging length at the beginning of the simulations are always identical and fixed at  $\sigma_A = 20$ . The value of the mean foraging day at the beginning of the simulation depending on the flowering landscape is calculated with the following formula:

$$\mu_{Aearly} = \mu_{P_M} - 2\sigma_{P_M}, \mu_{Amiddle} = \frac{\mu_{P_M} + \mu_{P_W}}{2}, \mu_{Alate} = \mu_{P_W} + 2\sigma_{P_W} \quad (22)$$

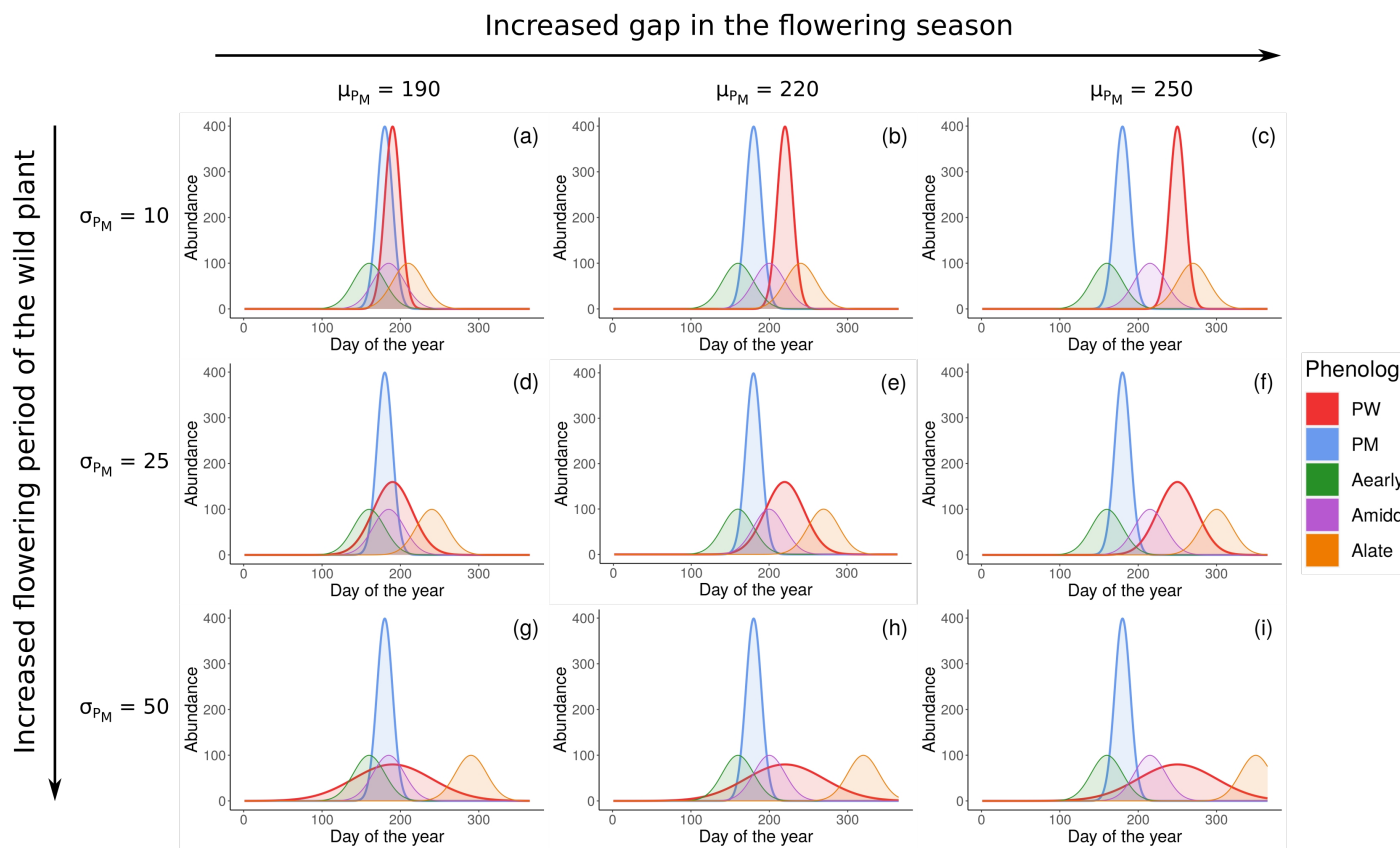


Figure 6: Different flowering landscapes tested via simulations. Bold curves correspond to the flowering phenologies of the managed and wild plants. Lighter curves correspond to the pollinator foraging phenologies alternatively tested as starting point for the simulation process. Note that while we plot three simulation situations on each graph, they are always launched separately, with only one foraging pollinator at the beginning. For all graphs, we

consider  $P_W = P_M = 10000$  and the starting abundance of the pollinator is always  $A_{early} = A_{middle} = A_{late} = 5000$ , and  $\mu_{PW} = 180$ ,  $\sigma_{PW} = 10$ ,  $\sigma_A = 20$  at the beginning and  $c_{base} = 0.1$ , as in the simulations.

### More simulations with the different flowering landscapes

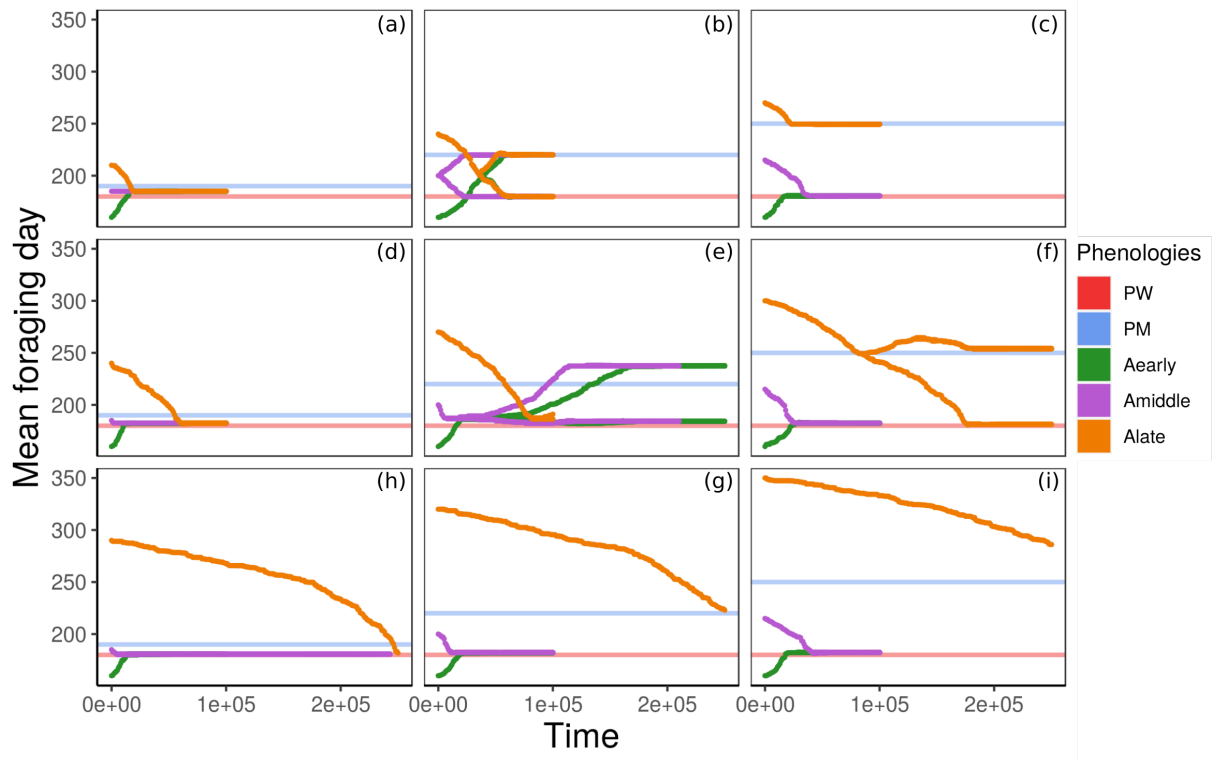


Figure 7: Simulations of the evolution of the pollinator mean foraging day in different flowering landscapes. The different flowering landscape are those represented on figure 6. Color coding is similar to figure 3. Note that simulations starting the later (orange lines) on panels (e), (g) and (i) are not at equilibrium yet.

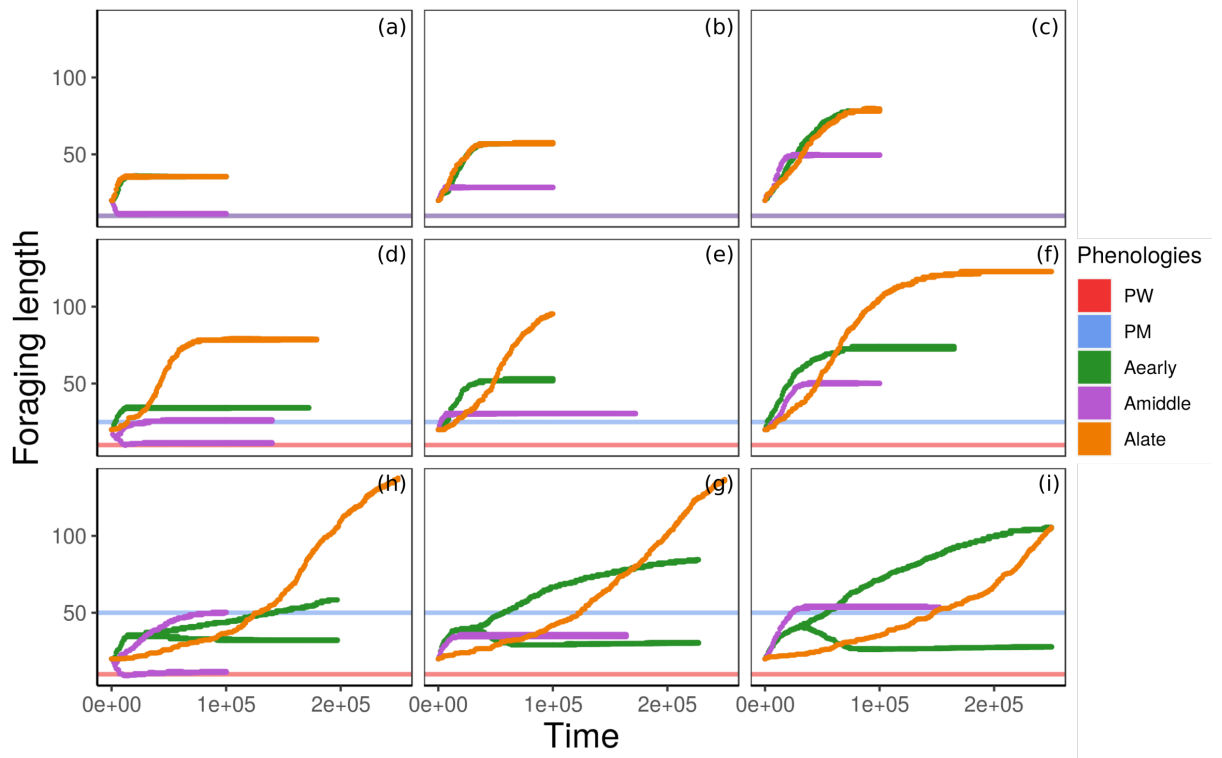


Figure 8: Simulations of the evolution of the pollinator foraging range in different flowering landscapes. The different flowering landscape are those represented on fig. 6. Colour coding is similar to figure 3. Note that simulations starting late (orange lines) on panels (e), (g), (h) and (i), and simulations starting early in the season (green lines) on panels (g), (h) and (i) and are not at equilibrium yet.

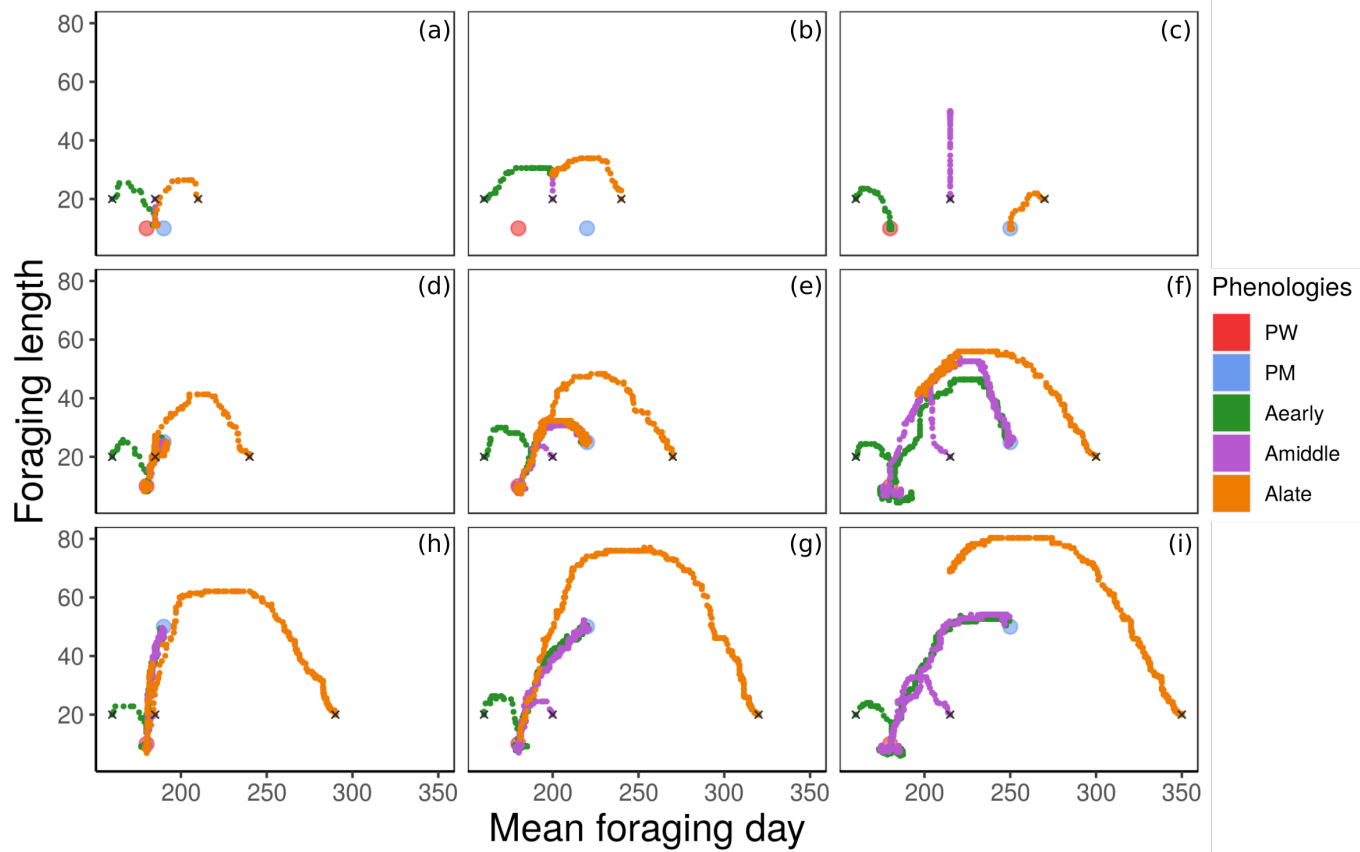


Figure 9: Simulations of the coevolution of the mean foraging day and foraging range of a pollinator in different flowering landscapes. The different flowering landscape are those represented on fig. 6. Color coding is similar to figure 3. The gray cross indicate the simulation starts, and the blue and red circle the values of the wild and managed species pool phenologies. Note that simulations starting late (or orange lines) on panels (f), (h) and (i) are not at equilibrium yet.

## Discussion

### 1 Response of different interaction types to environmental changes

Our three chapters consider three different interaction types in response to three environmental changes. While the first chapter models trophic interactions between species, the second one considers a mutualistic interaction. The third chapter investigates consumer-resource interactions which are commensal as the consumer benefits from the resources without affecting them. Among the results provided by our different models, the variety of interactions studied in this thesis thus allows us to discuss and compare the robustness of mutualistic and antagonistic interactions to differences in the environment resulting from global changes. In the following when we refer to the robustness or stability facing environmental changes, we mean that the considered population does not undergo a strong decline with this change, and does not go extinct. A robust and/or stable population can, however, respond via the selection of trait(s) that might help it cope with the new environment.

#### 1.1 Ecological feedbacks as a function of interaction types

Interaction types have been suggested to be differently robust to environmental changes, both from an ecological and eco-evolutionary perspective. Mutualistic and antagonistic (e.g. predation) pairs of species create different ecological feedbacks that will influence their response to environmental changes. As shown in the upper-left part of figure 15, the positive effect predation has on the consumer population is down-regulated by the negative effect it has on the resources. This negative feedback loop creates the very well-known oscillatory dynamics of the Lotka-Volterra model, also one of the first long-term demographical patterns observed in the wild (e.g. the famous hare-lynx dynamics, comprehensively studied by the ecologist community with data gathered by MacLulich (1937) and Elton and Nicholson (1942)). Via this regulatory mechanism, coexistence of the two partners is maintained in time and oscillatory dynamics depend on the strength of the trophic

interactions ((McCann et al., 1998)). On the contrary, if we consider a pair of consumer and resource species linked by a mutualistic interaction (e.g. a plant and a pollinator or mycorrhizal fungi, down-left part of figure 15) we observe a positive ecological feedback loop. An increase in one interactor density or abundance will increase the interaction and its benefits for the partner species, which will, in turn, increase its abundance or density, etc. This would theoretically drive the system to infinite growth. However, in reality, other environmental constraints (limited resources, conspicuousness to predators, sensitivity to diseases) will regulate the populations. Examples of those limits are mechanisms like pollen limitation (e.g. as in Kudo and Suzuki, (2002), or density-dependent disease e.g. on pollinated crops and wild plant (Burdon and Chilvers, 1982; Gilbert, 2002).

While it was not needed on our food web models, due to this down-regulation via the negative ecological feedback, the mutualistic model that we developed in chapter two required the addition of an extra parameter to avoid a runaway toward infinite growth of both partners. We therefore included a maximum level for the value of the resource investment in the mutualism (e.g. plant attractiveness in our model) below which stability is warranted. If we compare existing studies on ecological robustness to change, the response of antagonistic and mutualistic interactions to perturbations are often different, mutualistic systems showing abrupt collapses (e.g. Lever et al. 2014 and chapter 2) while perturbation effects are more gradual for antagonistic systems (e.g. chapter 1). Fussmann et al., (2014) even observed that an environmental change, temperature warming, actually stabilised the demographic oscillation observed in their predator-prey systems in relation to weaker trophic interaction strength. Looking at different types of networks in the same environment (food webs, parasitoid webs, seed dispersal and pollination networks) Pocock et al. (2012) show that network including pollinators seem to be particularly fragile to environmental changes, and that restoration focusing on one functional group was not often beneficial to its partner species from different network types. The current collapse of species and their partners is

indeed especially pronounced for mutualistic species like pollinators and their associated plants (e.g. Biesmeijer et al., 2006; Potts et al., 2010).

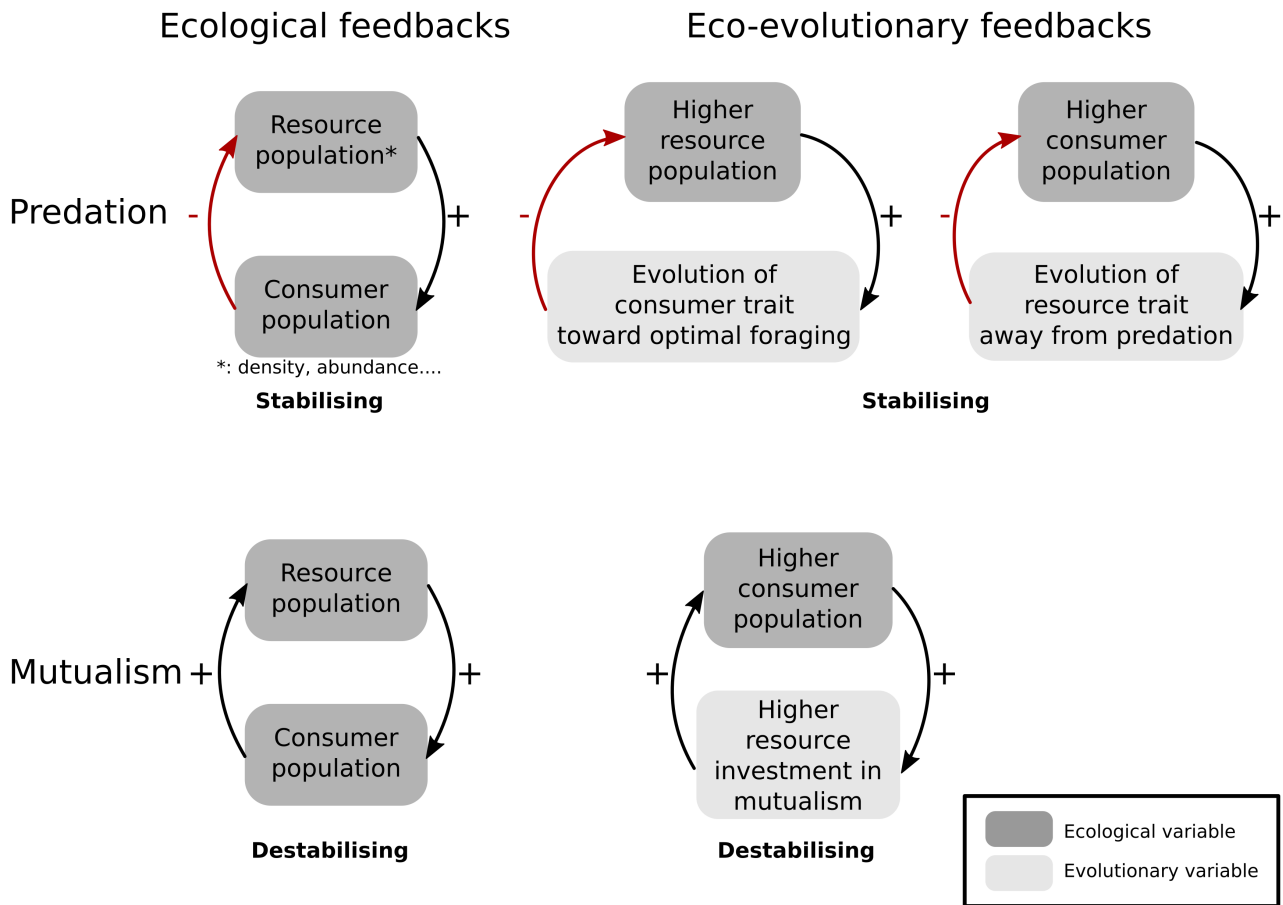


Figure 15: Comparison of the ecological and eco-evolutionary feedbacks observed in mutualistic and antagonistic interactions, and their destabilising or stabilising effects on the community. IN the main text, we present a mutualistic interaction that is a consumer-resource one but these feedbacks holds for any type of mutualism. Note that in that case, the resource can be e.g. a plant producing nectar, exudates, or special protecting structures, and the consumer a pollinator, ant, or fungi.

## 1.2 Eco-evolutionary feedbacks as a function of interaction type

On top of these ecological feedbacks, antagonistic and mutualistic interactions create eco-evolutionary feedback loops, the interactor demography impacting trait selection that in turn affects the intensity of the interaction, hence the demography of the populations.

For the predation interaction, this eco-evolutionary feedback can correspond to the adaptive foraging mechanism, which again helps stabilising the community. Ecological models without evolutionary regulations often exhibit the above-mentioned oscillatory patterns and chaotic



behaviour (Hastings and Powell, 1991). In principle, ecological complex food webs with a great number of interacting species should be highly unstable (May, 1973). And as explained before, the ecological feedback loop created by predation, by alternatively depleting the predator and prey populations, keeps the system relatively unstable. However, complex food webs and antagonistic interactions are massively found in nature and still seem to persist in time (Polis, 1991; Winemiller, 1990). One explanation for their maintenance in time is the adaptive foraging mechanism modelled in chapter 1 and studied in Kondoh (2003). A number of studies have shown that consumer behavioural or evolutionary adaptive foraging can explain food-web long-time stability (Loeuille, 2010b; Stephens and Krebs, 1986). Adaptive foraging can be defined (e.g. as in Loeuille 2010a) as the changes in a consumer exploitation of resources that results in a higher fitness compared to conspecific with another foraging strategy, and is therefore selected. Optimal foraging theory (i.e. the fact that evolution selects individuals with a fitness that maximises their foraging process) is an alternative view of the same stabilising effect (Pyke, 2016; Pyke et al., 1977). The upper right part of figure 15 illustrates this stabilising mechanism. A strong decrease in the resource demography following intense predation will deplete this resource for future predators, triggering the evolution of the consumer trait linked to predation efficiency, like body size in our first model. This evolution will both affect the internal rates of the consumer but also its foraging efficiency, to again optimally forage on the most abundant resource (different from the previously depleted one) allowing this previously overexploited resource to grow again. On the resource side, this depletion will also trigger the evolution of the resource (e.g. the resource body size in our more complex trophic network in chapter 1), away from the most eaten size to escape predation. This adjustment of the predation pressure maintains the equilibrium between populations (Thierry et al., 2011).

By being able to evolve their foraging strategies, antagonistic partners like predators can respond more freely to environmental changes. This is indeed what we see in our first model, especially for upper trophic predators that are less constrained in their foraging strategies. They are therefore

responding more strongly to temperature changes via the evolution of their body-size, maximising resource intake and minimising energetic losses. An experimental warming in a grassland food web reveals for example different evolving responses of predators to warming, allowing to maintain species interactions and the associated food web all along the thermal gradient (Barton, 2011). This, however, has still limitation and in our system we observe extinction of the top predators when overheated, their energy requirement and losses being too high to be compensated by adaptive foraging (e.g. as observed in experimental tri-trophic planktonic food web by Seifert et al. (2015) and in many empirical studies, as surveyed in this meta-analysis by Fussmann et al. (2014)).

Oppositely we observe positive eco-evolutionary feedback loops in many mutualistic systems that will also tend to destabilise a mutualistic community responding to environmental changes. If we consider a resource-consumer interaction as in our second chapter (e.g. with a plant and a pollinator, but this is valid for any type of mutualistic interaction) an increase in the consumer population selects for an increase in the mutualistic investment by the resource and, in return, increases the mutualistic exchange with the resource (lower right panel in figure 15). Again this never-ending increase is not biologically relevant, and often physical, metabolic (e.g. energetic limitation, size constraints) or external constraints will limit the investment in the interaction (Stang et al., 2006b). In our second model, we regulate this runaway via a trade-off between this mutualistic investment and the intrinsic growth rate of the individual (e.g. plant vegetative reproduction). Contrary to the case where the consumer increase, a decrease in the consumer population will lead to a disinvestment in the mutualistic interaction on the resource side, potentially up to the consumer disappearance. In our model, we observe this disinvestment when only one partner evolves, but this could also be the case if the other species had a lower evolving potential (long life cycle, small population, small mutation rate) as emphasised by Loeuille, (2019). If the mutualistic interaction is obligatory to the consumer, the evolutionary process rescuing the resource population from a consumer decrease (e.g. as in Carlson et al. (2014)) could lead the obligatory consumer to extinction

(evolutionary murder, defined in Parvinen (2005), and in chapter 2). This evolution toward disappearance of the mutualism is for example what we observe in some plant-arbuscular mycorrhizae symbioses. Using a comparative approach, Werner et al. (2018) detail 25 interaction breakdowns in this type of mutualisms and observe two possible outcomes: the plant switch to another symbiont partner or evolve a new mean of extracting the essential nutrient(s) from the environment. Indeed, in a comprehensive review, Toby Kiers et al. (2010) note three possible evolutionary outcomes for disturbed mutualisms aside from extinctions: mutualism switch to antagonism, partner change and mutualism abandonment. These mechanisms could play a part in the parallel biodiversity declines recently observed, especially for pollinators and their associated plants (Barnosky et al., 2011; Biesmeijer et al., 2006; Potts et al., 2010). A relatively recent review (Traveset and Richardson, 2014) also pointed out the fragility of mutualistic systems to invasion, probably because the traits often found in mutualistic species favour invasiveness (i.e. how well a species invade a novel system). As pointed out by Guimarães Jr et al. (2011), mutualistic systems often comprise generalist and even super-generalist interactors, that facilitate the invasion of alien species (Geslin et al., 2017; Traveset and Richardson, 2014). The above described positive feedback loop reinforces the invasion process and the integration of the new species to the system, often detrimentally to other species. Even simple Lotka-Volterra type models capture this difference in response between interaction types, showing that trophic interaction is more stable than mutualistic or competitive ones (Loeuille, 2010a).

### 1.3 Are antagonistic interactions indeed more robust than mutualistic ones to environmental changes?

Both these above references and our results tend to suggest that antagonistic interactions are more eco-evolutionary stables than mutualistic ones. Species engaged in mandatory mutualistic interactions might therefore be more sensitive to global changes. However, there are still a lot of mutualistic systems in nature. Are they really on the verge of a breakdown, weakened by many environmental changes as stated by Toby Kiers et al. (2010)? Frederickson (2017) begs to differ,

arguing especially that conditions under which mutualisms turn to antagonism are rarely found. While this view is supported by Sachs and Simms (2006), they also emphasise that there are still many mutualism breakdowns, but most frequently due to mutualism abandonment as in our second chapter. Mutualistic species are not isolated from the rest of the community, and while environmental changes might quickly affect their populations, there can also be direct coupling between mutualistic interaction and other negative feedbacks stabilising the species demography and evolution. This balancing effect has been observed and modelled several times (Mougi and Kondoh, 2012; Sauve et al., 2014) and has given rise to the interaction-type diversity hypothesis (Kondoh and Mougi 2015), which states that the stability is highest in ecological communities with multiple interaction types. An example of such coupling is the interspecific population regulation of the senita cactus *Pachycereus schottii* by the moth *Upiga virescens* via a combination of antagonistic (frugivory by the moth larvae) and mutualistic (pollination by the adult moth) interactions (Holland et al., 2004). In this modelled system, the equilibrium is reached via an energetic allocation trade-off between excess flowering and fruit abortion in the cactus side that modulates the two interaction types. To compensate for a strong increase in pollination by too numerous moths that could destabilise the mutualistic interaction, the plant produces even more flowers. This excess flowering results in greater fruit abortion that will deprive of food the next generation of larvae in excess, reducing the next pollination interaction. This strategy was proven convergent and resisted invasion by cheater plants, preserving the moth-cactus mutualism.

## 2 Impact of the degree of generalism on the response to environmental changes

The ecological and evolutionary responses of a population to an environmental change depend on the degree of generalism of the species. Some of this thesis works can give hints on the impact of the degree of generalism on the response of consumer-resource interactions to environmental changes. While the model presented in chapter 1 does not explicitly test for this, our current revised

version, not included in this thesis, exhibits interesting behaviour linked to the degree of generalism discussed in the following part. While generalism is a fixed parameter in this revised version of our first model, it can be indirectly drawn from the interpretation of chapter 2 parameter values (the investment into intrinsic growth, as developed later), and is a resulting pattern of the evolutionary process in our third model.

In general, we expect specialist interactors to be more vulnerable to environmental changes than generalists (Clavel et al., 2011; Ferrer and Negro, 2004), especially because they have a narrower resource niche by definition, hence less potential interactors to choose from. This is indeed a common pattern observed in nature. Biesmeijer et al. (2006) e.g. observed the strongest decline in pollinators (bees and hoverflies) that were specialist to a habitat or flower species, as well as univoltine and non-migrant species. As mentioned in our introduction, there are many possible ecological and evolutionary responses of a population facing an environmental change, which depend on species generalism degree as represented in figure 16.

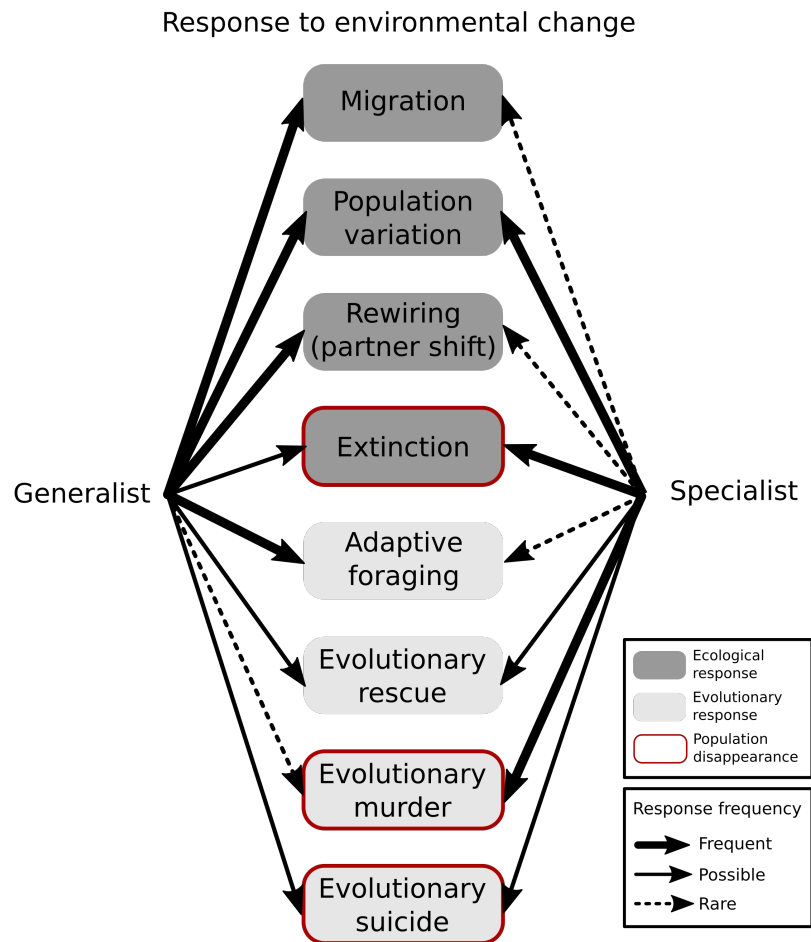


Figure 16: Different potential responses of a population facing environmental changes, and its frequency depending on the species degree of generalism.

The schematic view of the potential responses of generalists and specialists to environmental changes presented in figure 16 emphasises the fragilities of specialists, more likely to undergo deleterious processes. Different ecological and evolutionary responses are outlined in figure 2 and below in relation to their expected frequency depending on the degree of generalism (for mechanisms like evolutionary rescue or suicide, studies rarely focus on the degree of generalism of the species, we fixed the same frequency by lack of available knowledge).

### 2.1 Generalism degree and adaptive foraging or rewiring

Specialist species are expected to be less able to do rewiring than generalist because they have fewer species to choose from. Bartley et al., (2019) insist on this by showing the increased propensity of generalists for undergoing both topological rewiring (interacting with new species by

reaching new environment) and interaction strength rewiring (variation in the frequency of interaction with current partner, and indirect effect on their partner's partners). As studied by Ferrière et al., (2007) having alternative partners provides a stabilising mechanism through rewiring, especially for mutualistic system invaded by cheater (Ferriere et al., 2002; Yoder and Tiffin, 2017). In relation to this, specialists are also considered as less apt for migration because they are more likely to have fewer niches very similar to their own e.g. with similar resource species or resources they are able to alternatively eat in reachable distance (Bartley et al., 2019). Hints of this migration limitation to track their preferred niche start to be observed. Warren et al. (2001) e.g. showed that 89 % of British butterflies facing land-use degradation and climate warming declined in distribution size over the past 30 years, while half of the mobile and generalist species increased their habitat range over the same period.

We thus expect that specialists, being more constrained in their feeding range than generalists and less able to undergo rewiring on an ecological scale, or even adaptive foraging by evolving traits related to partner interaction, are more sensitive to environmental change. Indeed in the most recent version of our first model (not presented in this thesis but soon to be resubmitted), we can explicitly explore the impact of the degree of generalism value. We observe that the effect of warming on the evolution of body size is limited, especially at high trophic levels, when the consumers are more specialists. In the simple two-species model, the body size of a specialist consumer is almost unaffected by changes in temperature, whatever the resource type (inorganic chemostat or inorganic resource with logistic growth). This could be explained by the stronger feeding constraints that are exerted on specialist consumers. In our model, it then seems that when the consumer in the community are more generalist, they are more responsive to changes, and in general maintain higher biomass and diversity than a community of specialist consumers. Again this reduced evolutionary response of specialists compared to generalist could explain some of the current

decline of specialist species (Biesmeijer et al., 2006; Clavel et al., 2011; Ferrer and Negro, 2004; Potts et al., 2010).

However, it should be noted that adaptive foraging could be either viewed as a frequent outcome for generalist foragers, that have better abilities to switch partners, or as the mechanism creating these generalist profiles. On the contrary, rewiring, which is the ecological equivalent to adaptive foraging, is only possible if the switching partner can undergo other interactions (e.g. no morphological, coexistence or energetic constraints)(Bernays, 1998). In particular, the degree of generalism can itself result from the adaptive processes stimulated by environmental changes, e.g. if the evolution of adaptive foraging creates the generalist pattern. In our third chapter, the degree of generalism of a consumer species depends on the relative amount of energy obtained by interacting with one of the two resources compared to the total quantity of energy resulting from all interactions, and it is determined by the temporal overlap of the floral resources. We do not consider differences in preferences between the two floral resources, and including the evolution of this additional parameter could further improve our understanding of the evolution of the adaptations at stake. Another study, incorporating adaptive foraging and projecting via simulation the temporal dynamics of three empirical pollination webs, showed a positive impact of this evolutionary behaviour on the maintenance of specialist species in pollination networks (Valdovinos et al., 2016). Specialists were maintained in the networks via nestedness, the most abundant generalists foraging mainly on their most specialists interactors, preserving them from decline with environmental variations.

## 2.2 Evolutionary suicide, murder or rescue: does it depend on the generalism degree?

The degree of generalism also impacts the population resistance (maintenance or disappearance of the population) facing a perturbation. A population can disappear via various mechanisms, as shown in figure 16. If the change is too quick for the population or its mutation rate too small,



evolution can be hindered and, if too unfavourable, it will lead the population directly to extinction. However, even if the population does evolve in response to the change, it can still go extinct according to two evolutionary mechanisms, evolutionary suicide and evolutionary murder (Parvinen, 2005). There are so far few examples of evolutionary suicide in nature (Rankin and López Sepulcre, 2005). One famous is the selection of cod via intense fisheries, favouring faster maturing at small size cods (Conover and Munch, 2002). These fish, despite having a higher relative fitness than their slower maturing counterparts, still produce less offspring on average, leading to a strong decline in the current population abundance (Olsen et al., 2004). Whether specialists would be more affected than generalists by this evolutionary process remains to be investigated. Specialists are known to be more vulnerable to extinction, and Dakos and Bascompte (2014) even showed that specialist extinction is a good predictor of approaching tipping points. Extinction of specialist species is also more frequent as a secondary extinction after the loss of a partner species (Brodie et al., 2014).

Aside from secondary extinction, another possible outcome is when the partner does not decrease but undergo selection that restores its population (i.e. evolutionary rescue (Ferriere and Legendre, 2013)) by means of the interaction abandonment. This is what we observe in our second model for the evolving resource. We can indeed indirectly discuss the impact of the degree of generalism in this model. For the evolving resource, the intrinsic growth rate could be also viewed as an alternative energy sources for growth, for example provided by other interactors. It means that the bigger this parameter is, the less the consumer invests in the mutualistic interaction according to our trade-off, meaning the less it depends on the modelled mutualistic consumer for its growth and the less it is specialised on it. On the consumer side, its intrinsic growth parameter could also be indirectly considered as its degree of generalism. Indeed, the greater this intrinsic growth (i.e. the demographic growth that does not depend on the mutualistic interaction), the more this growth can be due to other food sources (e.g. other plants nectar and pollen, alternative sugar-laden or other

nutrient-rich foods). If we consider these parameters as the degree of specialisation into the mutualistic interaction of each partner, the observed potential evolutionary murder could be then seen as the extinction of a specialist species deprived of its sole interactor. This disinvestment could even be in favour of the emergence of new cheating interactors. In an experiment measuring selection in a constrained environment of interacting wild legume and rhizobium lineages, Porter and Simms, (2014) observed selection constantly favouring the emergence of rhizobium cheater, but never rescuing legume that provided less resources to rhizobium partner. This is an empirical proof of the emergence of antagonistic interactions via mutualism abandonment.

Note that this increased propensity toward decline with environmental changes of specialist does not always mean that they are generally decreasing under current changes. Indeed, while numerous studies mention a worldwid decline of specialist species some specialists species are thriving under current changing conditions. This is especially the case of specialist species that benefit from human activities. Humans produce resources that favour specialist commensals like the barn owl (Hindmarch and Elliott, 2015), and create new environments ( e.g. urban areas) where there is a released predator pressure (Rebolo-Ifrán et al., 2017).

### 3 Generally observed empirical evolutionary patterns associated with environmental changes

In these three chapters, we thoroughly explore the eco-evolutionary outcomes of our models in different environments. Below are summarised in a table the main evolutionary responses observed in these different consumer-resource systems to the three environmental changes studied. Some of our observed patterns have already been found in previous studies and are listed in the empirical evidence section (table 1).

Table 1: Most generally obtained evolutionary patterns with our three models and already published similar ones

Evolutionary trait(s)	Environmental pressure	Evolutionary response pattern	Some empirical evidences
Body size in a food web	Temperature differences, no impact of temperature on the consumers attack rate	No impact of temperature except a slight body size decrease for very high temperature <sup>a</sup>	No change of zooplankton size with warming (experiment) (Yvon-Durocher et al., 2011) <sup>b</sup>
	Temperature differences, consumers attack rate increases with temperature increase	Increase in body size with temperature increase <sup>a</sup>	(Huss et al., 2019) (Yom-Tov, 2003) <sup>b</sup>
	Temperature differences, consumers attack rate reach an maximum for intermediate temperature	Humped-shaped response, maximum body size for intermediate temperature <sup>a</sup>	Most observed outcome: body size decline with warming (Daufresne et al., 2009; Edeline et al., 2013; Sheridan and Bickford, 2011; Tseng et al., 2018) <sup>b</sup>
Investment in a mutualistic interaction (e.g. nectar and other nutrients production, number and size of flowers...)	Partner population increase	Increase in mutualism investment up to a fixed maximal limit, constrained by the trade-off between mutualism investment and intrinsic growth	No clear evidence. Lead: maybe via the effect of invasive and massively introduced managed species (MIMS) on their preferred interactors (Geslin et al., 2017; Holzschuh et al., 2016) <sup>b?</sup>
	Partner population decrease <sup>c</sup>	Disinvestment in mutualism, could enhance partner decline	Experiments only: (Bodbyl Roels and Kelly, 2011; Gervasi and Schiestl, 2017)
Consumer foraging phenology (mean foraging date and foraging length)	Hugh gap in the middle of the resource season	Only one consumer, specialised on the nearest peak <sup>d</sup>	One neglected early flowering pulse (Schmitt, 1983) <sup>b</sup> short foraging period corresponding to a flowering pulse (Riedinger et al., 2015) <sup>b</sup>
	Asymmetry in resources distribution	Diversification and emergence of two	Phenology is a major trait explaining niche

	(same quantity over a short peak or long period of time), not too overlapping	consumers more or less specialists (the most specialised one forage on the peaky resource) <sup>e</sup>	partitioning in plant-pollinators networks (Junker et al., 2013) . Alternative lead: comparing the effect of MIMS plants with peaky phenology and spread out wild plants phenologies on pollinators (Geslin et al., 2017) <sup>b</sup> ?
	Very strong overlap between resources	Only one consumer, generalist <sup>f</sup>	Lead: specialists switch to a generalist behaviour when the resource niche is too narrow (Miller-Struttman and Galen, 2014)

<sup>a</sup>: The observed evolutionary responses are similar between the two species and multi-trophic models.

<sup>b</sup>: There is not yet proof that these changes result from evolution.

<sup>c</sup>: Studied only for concave trade-offs.

<sup>d</sup> : As soon as the overlap increase due to resource peaks asymmetry we started observing diversification and two consumers on the two resources peak, especially in the case of traits coevolution.

<sup>e</sup>: No diversification is observed if the mean foraging date of the consumer at the start of the evolutionary process is very late compared to that of the nearest resource.

<sup>f</sup> : Especially when only the resource length evolved.

In our first chapter, while no changes in body size or even increase with warming have been observed in the wild (Huss et al., 2019), many empirical and experimental studies report a common decrease in body sizes with warming (Daufresne et al., 2009; Emmrich et al., 2014; Sheridan and

Bickford, 2011), claiming it to be one of the universal responses to warming. Here we only observe body size decrease when the attack rate has a thermal optimum and consumer species are in an overheated environment compared to that optimum. This could be an indication that current ecological communities are already overheated. Moreover, the chosen effect of temperature on attack rate is starting to be investigated with empirical data, and a recent study found that, in marine communities, maximal attack rates were observed at mid-latitude, corresponding to intermediate temperatures (Whalen et al., 2020), as in our third scenario with intermediate thermal optimum (see table 1 line 3). Nonetheless, they note that for terrestrial ones, an increase in temperature usually leads to an increase in the consumption rate (our second scenario in the first chapter, table 1 line 2). Using fish fossil records, another recent study also points out increased fish productivity with temperature, due to increased efficiency of energy transfer between trophic levels and increased primary productivity with temperature warming (Britten and Sibert, 2020). This is more in line with our second scenario of increasing attack rate with temperature. This increase in attack rate efficiency with temperature is also noted in Rall et al., (2012). Note that this global decreasing trend is not always true, and has been already questioned by Gardner et al. (2011) in a summarising paper. As these studies on attack rate show, there is not one consumer's attack rate response to warming, and our different scenarios could therefore cover different coexisting mechanisms that are species-dependent.

Our second chapter results are presented in table 1 at line 4 and 5. So far, there are few empirical studies explicitly studying the evolutionary disinvestment following partner decline, but some experimental studies already observed such mechanisms. Several studies did experimental evolution manipulating pollinator density (Bodbyl Roels and Kelly, 2011) and/or type (Gervasi and Schiestl, 2017) and followed the evolution of plant traits associated with their attractiveness to pollinators and traits linked to self-reproduction. These studies observe a disinvestment in the trait associated with sexual reproduction in plants and investment in mutualism (e.g. quantity of nectar, volatile

organic compounds, size of the flowers), and an increase in traits like the self-seed set. This evolutionary pattern is hard to catch in the wild, but could partly explain the current global decrease of a lot of species that strongly rely on mutualistic interactions when one of the interactors can grow and/or reproduce independently of the interaction. This could be the case for mutualistic species like specialist pollinators and angiosperms (Biesmeijer et al., 2006), or mycorrhizal fungi (Helgason et al., 2007), if they are interacting with a more generalist partner (a common feature of mutualistic networks, that are known to be very nested).

As presented for better clarity in our model and result sections of chapter 3, this third model could biologically be easily associated with pollinators or herbivores feeding on alternative plant resources with different phenologies. Such phenological data are more and more available (Kharouba et al., 2018; Leong et al., 2016). As pointed out e.g. by Kharouba et al., (2018) there is not one global response of the pollinators and plant phenologies facing global changes (Duchenne et al., 2020), as well as for other species engaged in consumer-resource interactions. Observed phenological patterns are not homogeneous and they are hard to associate with a specific global change, some phenologies switch to earlier dates and other to later ones (CaraDonna et al., 2014; Duchenne et al., 2020), and there is very few information about changes in the duration of the phenologies (CaraDonna et al., 2014; Hällfors et al., 2020), and even less about the evolutionary responses associated to a certain resource phenology distribution (but for modelling studies as in Bewick et al., (2016). Can these differences in switching phenological patterns be partly due to the new interactor's distribution as in our model? We further discuss the impact of explicit spatial distribution of resources on explaining the observed phenological patterns in the perspective part.

All this shows that the correspondence between our observations and previous studies is not always perfect, and there are still discrepancies between what we obtained and what is observed in natural and experimental communities, but our models are nonetheless helpful in explaining biological patterns. Our first model exhibits many different outcomes depending on the considered scenario of

temperature impact on the consumers attack rates, and only in some of the model's conditions do we find the most current observed natural patterns. The eco-evolutionary outcomes of our second model are very rarely observed in the wild. Measuring infield evolutionary processes, and correlating them clearly to a specific environmental change is not an easy task. Our model could suggest additional eco-evolutionary explanations for the ecological demographic patterns already observed (Biesmeijer et al., 2006; Potts et al., 2010). Our third model is yet to be completed by feedbacks between the different interactors, but already offers a variety of responses depending on the resources temporal distribution. Because there is not one general trend in the phenological changes observed today, our model could help explore these differences in responses depending on the resource phenological landscapes. All our models have different uses when comparing them to these pre-existing studies. They clarify the potential underlying mechanisms, pointing out extra evolutionary effects that could have been forgotten, or explore in greater detail the potential evolutionary outcomes of specific situations. While we could not compare directly our model to specific datasets in this thesis, our work still shows the usefulness of models in ecology and evolution. While our models are quite simple, we are still able to interpret them in terms of biological events and functioning, and these interpretations allow us to better challenge environmental questions. The usefulness of modelling in these fields is regularly questioned, and a nice summary of theoretical works relevance and potential improvements can be found in Otto and Rosales, (2020) and Servedio, (2020).

## 4 Perspectives: Modelling temporally explicit environmental changes

### 4.1 The intensity and duration of the perturbation

Our models, albeit simple, allowed us to explore in great details the impacts of different environmental conditions on various consumer-resource interactions and traits evolution. It would be interesting to extend our present models by introducing more explicit temporal scales of eco-evolutionary changes as well as of perturbations. So far our models give an overview of the end of

the evolutionary process (or the intermediate state in case of diversification event) but this is mostly a static view at eco-evolutionary equilibrium. It does not offer room for temporal variation within the system and real-time following the potential trait shifts, collapse and rescue events. Indeed, because we do not only follow the ecological dynamics of our system but also the evolution of some key traits that shape the species interactions, we could explicitly follow the role of evolution in accentuating some evolutionary patterns (e.g. even to the detriment of some of the species, leading to evolutionary suicide or murders (Parvinen, 2005)) or in restoring the growth of otherwise threatened species by allowing adaptation to the new environment (evolutionary rescue (Gomulkiewicz and Holt, 1995)). These key evolutionary mechanisms, presented in our introduction at the beginning of this thesis, can be easily tested with simulations of model build-up and temporal dynamics. This could be also a chance to highlight delayed mechanisms like extinction debts (Tilman et al., 1994) or time-lag in the adaptation process (Essl et al., 2015).

Moreover, while we only focused so far on the communities eco-evolutionary dynamics and equilibrium in different fixed environments, adding a temporal dimension to our models would allow us to make temporally explicit environmental changes. We can play around with the amplitude and duration of such changes and see their interferences with and responses of the system at the ecological and evolutionary levels.

Environmental perturbations are often categorised in two types: pulse and press perturbations. The former corresponds to an acute and quick change in the environment, which is rapidly restored to its previous state, but whose consequences can be long lasting on the communities it affects. Among very frequent environmental press perturbations are sudden enrichment in nutrient e.g. via one-off nitrogen release, heavy rainfall or even flood, or a sudden fire event. The latter is often a less pronounced perturbation (but not always, see Hansen et al., 2006) but that lasts for a longer period, is chronic or even increases in intensity with time. Major press perturbations are current global warming, land-use intensification, or sea-level rise. Some global changes can fall into both



categories. A drought can either be a pulse event, sudden and not long-lasting, as studied in our third model where it is responsible for a lack of resource in the middle of a foraging season, or be a press one if it results from long term warming and precipitation decrease or is a recurrent event in the considered system. The same is true for some previously mentioned environmental changes like rainfall or nutrient deposition that can continuously increase with time, or a brutal change in land-use activities. These lists show that both types of perturbations could be considered in these potential modelling projects, as they would be in line with those already tested in this thesis and would allow for a more realistic analysis of global change impacts.

A temporal version of a food web model, very similar to the one presented in chapter 1 has been added to this thesis appendix (Yacine et al., 2020). In this model, we explore temporally explicit changes in temperature, with or without a potential evolutionary rescue. The warming occurs once the system has reached an eco-evolutionary equilibrium and exhibits several (generally 4-5) trophic levels. In Yacine et al., (2020), we study mostly a press perturbation, as we increase the environmental temperature during the simulation process after a first eco-evolutionary equilibrium, and follow the simulation until the next equilibrium is reached. In one scenario we do more of a pulse perturbation by reversing the environmental temperature to its previous cool value after a switch to a warmer one.

If we add an explicit temporal scale to our phenological model (chapter 3), we could test some of the previously mentioned changes. So far we explored the impact of different fixed distribution of resources on the evolution of the consumer foraging phenology. Among other scenarios, we tested the impact of a resource gap in the middle of the season. By adding a temporal scale we could test the effect of a one time change in resource distribution (e.g. a sudden drought or fire in the middle of the season that create a punctual and more or less strong drop in the resource availability, or on the contrary a favourable climate that boosts plant growth), or a continuous increase in the resource gap with time (e.g. following projected climate changes and increased drought events in the middle of the season). The effect of asymmetry in resource temporal distribution can also be tested on an explicit temporal scale. A sudden change in the land-use practices could be embodied by a switch in

the phenological distribution of one or several resources, and the current effect of climate changes can be modelled by an increasing shift in the starting and end dates of the resource phenology.

Introducing this explicit temporal scale in our models changes the tools that we can apply to their analysis. The previously used analytical tools will not provide enough information and most of the analysis will have to be conducted via numerical simulation. A problem with this method is the potential lack of comprehensiveness regarding all the parameters conditions and simulation outcomes. We are never sure that what we observe and biologically interpret is representative of our model outcomes. Fortunately, some recent tools like OpenMOLE (<https://openmole.org/>) have been developed to ensure a comprehensive exploration of a parameter space and model sensitivity. Such a tool could be of great use if we further complement our models with this temporal complexity.

#### 4.2 The relative time scales of the perturbation compared to the ecological and evolutionary dynamics

As expressed earlier, adding this explicit time scale would also allow us to deepen the study of the different ecological and evolutionary responses of our systems. Are pulse perturbations triggering mostly ecological responses, while long term evolutionary responses are only significant in the case of press perturbation? Franks et al. (2007) observe a strong and long-term evolutionary response in plant flowering time with a very short pulse perturbation. The earlier shift they observe (from 1.9 to 8.6 days) in response to summer drought is visible in only a few generations. In Yacine et al. (2020) we test both type of perturbations, and always observe a strong evolutionary response. The chosen time scales will, of course, depend on the response variables we want to focus on in our analysis, but also on the goal of our study: exploration of the mechanical responses triggered by a certain environmental change via thorough analytical methods, or understanding of a specific real-life situation to produce management guidelines. Depending on the considered environmental perturbation and chosen study goal, its impact and the observed response will be at different time scales. The ecological response will be described by the species abundance and behaviour. The evolutionary response will depend on the generation time and the genetic diversity of the species.

If we focus on the phenological changes of our third models, they can be very rapid (e.g. land-use change) or take some time (e.g. floral distribution changes with climate change). As in Yacine et al. (2020), it could therefore be useful to play around with the evolutionary potential of the species, to compare the ecological and eco-evolutionary responses of the system. If our goal is to compare our outcomes with experimental or empirical results, and/or better understand them for futures more applied programs, we should bear in mind that the more complex model is not always the better in explaining a given biological situation (Otto and Rosales, 2020). We could also compare the short and long-term responses observed in our model. This is especially pertinent now that more and more long-term datasets are available for analysis (e.g. Duchenne et al. 2020) and could be used to challenge our results. A system initially highly disturbed by the environmental change will maybe stabilise on a longer term due to ecological and eco-evolutionary feedback loops. On the contrary, we could observe delayed negative responses following an environmental change, e.g. extinction debts in our systems (Essl et al., 2015; Tilman et al., 1994). This delayed response is especially important to bear in mind as we try to survey more and more comprehensively the impacts and potential management actions that could be undertaken facing current global changes.

#### 4.3 The potential eco-evolutionary responses of the community

When following the eco-evolutionary responses of the community to a given temporal environmental change, one of the first questions that arises is on the chosen metrics to characterize community eco-evolutionary responses.

If we choose to focus on the community stability, should we follow its resistance (capacity of our system to remain unchanged, e.g. in term of species and link diversity, after a perturbation) or resilience (capacity of our system to recover to its previous state after a perturbation) to environmental change (Allison and Martiny, 2008)? Is there a threshold in the perturbation intensity and duration above what the system cannot resist or recover? More generally, what type of stability do we consider in our analysis? There are nowadays many stability metrics available, with a more

or less clear biological interpretation. Some types of perturbations and responses are disregarded considering today's global changes potential implications. All this is pointed out in this summarising paper by Kéfi et al., (2019) on ecological stability. Adding evolution would require an even more careful choice of the metrics used to follow our systems response.

Evolutionary responses of the communities are also important to consider. As for the expected outcomes, our model could indeed help us to detect mechanisms like evolutionary rescue, evolutionary suicide, murder and extinction debts. The potential of evolution for rescuing or threatening species and their communities has been partially studied throughout this thesis (see in particular chapter 2), but more specifically in Yacine et al., (2020), presented in this thesis appendix. In this paper, we show that evolution can indeed restore biological diversity, but can also sometimes hinder its recovery. After some tipping-points, the selective pressure changes and restoring previous environmental conditions is not enough to recover the loss of declining species.

Community and species changes can also occur on different time scales. Interestingly, (Zee et al., 2017) show, in another temporally explicit model following rapid trait evolution in food webs and its stability following extinction events, that while their system responded strongly on a short time scale, a long-term response was almost absent. On a short time scale, they observe that a high evolutionary rate rescued low densities population from extinction, mostly via increased variations with mutation (standing variation was not sufficient to observe these evolutionary rescue events). However, on a longer time scale, it was not enough to prevent long-term extinction of some of the community's populations.

Lastly, Loeuille (2019) points out another phenomenon inherent in considering temporarily explicit evolutionary responses. In his paper, he shows that because interactors are responding at different speeds to an environmental change (here the ability to switch phenologies to an earlier date), the created mismatches can exacerbate the effect of the already suboptimal environment. This could sometimes go to the extent of one of the species disappearance, creating an evolutionary murder

(evolution of one species that rescues its population and is lethal to its interactor (Parvinen, 2005)). Such mismatches are more and more spotted in wild communities. Because of morphological, functional or conditional constraints, species do not respond uniformly to change (Parmesan, 2007; Petanidou et al., 2014; Thackeray et al., 2010; Visser and Gienapp, 2019). Whether or not it will always harm the studied community dynamics and persistence is yet to be determined...

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## Annexe

The present paper as just been accepted in *Journal of Animal ecology* and will soon be published

# 1 Collapse and rescue of evolutionary food webs 2 under global warming

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## 16 **Running headline**

17 Evolutionary rescue in food webs

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## 19 **Abstract**

- 20 1. Global warming is severely impacting ecosystems and threatening ecosystem  
21 services as well as human well-being. While some species face extinction risk,  
22 several studies suggest the possibility that fast evolution may allow species to  
23 adapt and survive in spite of environmental changes.
- 24 2. We assess how such evolutionary rescue extends to multitrophic communities  
25 and whether evolution systematically preserves biodiversity under global  
26 warming.
- 27 3. More precisely, we expose simulated trophic networks of co-evolving  
28 consumers to warming under different evolutionary scenarios, which allows us  
29 to assess the effect of evolution on diversity maintenance. We also investigate  
30 how the evolution of body mass and feeding preference affects coexistence  
31 within a simplified consumer-resource module.
- 32 4. Our simulations predict that the long-term diversity loss triggered by warming  
33 is considerably higher in scenarios where evolution is slowed down or switched  
34 off completely, indicating that eco-evolutionary feedback indeed helps to  
35 preserve biodiversity. However, even with fast evolution, food webs still  
36 experience vast disruptions in their structure and functioning. Reversing  
37 warming may thus not be sufficient to restore previous structures.
- 38 5. Our findings highlight how the interaction between evolutionary rescue and  
39 changes in trophic structures constrains ecosystem responses to warming with  
40 important implications for conservation and management policies.



## 41 **Keywords**

42 Adaptive Dynamics, Biodiversity conservation, Body mass evolution, Climate Change, Co-  
43 evolution, Consumer-Resource model, Eco-evolutionary tipping point, Evolutionary rescue,  
44 Trophic networks

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## 59 **Introduction**

60           The consequences of global change on biodiversity are now well-documented. They  
61 include the extinction of species (Barnosky et al., 2011), changes in species demography, ranges  
62 and phenologies (Parmesan & Yohe, 2003) and alterations of ecological interactions (Tylianakis  
63 et al., 2008). Significant ecological network reorganizations and changes in ecosystems  
64 functioning are therefore expected. In such a stressful context, it is unclear whether the  
65 evolution (or co-evolution) of species will have a net positive or negative effect on network  
66 maintenance and stability.

67           Existing models investigating ecosystem responses to global warming often ignore  
68 evolutionary processes and the interaction of species. This is particularly true for “niche” or  
69 “envelope” models (Colwell & Rangel, 2009) that link data of species occurrence with climatic  
70 variables to build a multivariate statistical representation of the species niche. Future  
71 distributions of species are then predicted according to different climate change scenarios (e.g.,  
72 Pearson et al., 2002) implicitly assuming that niches are fixed. Evolution, however, affects  
73 species’ fundamental niches while the reshuffling of species interactions can lead to changes in  
74 realized niches (Tylianakis et al., 2008). While envelope models are important first steps, they  
75 are thus limited in their ability to understand the effects of global warming, and to provide  
76 relevant conservation policies (Lavergne et al., 2010).

77           Ignoring evolution is based on the controversial assumption that ecological and  
78 evolutionary processes act on separate timescales. Recent studies, however, indicate that  
79 evolution may act within a few generations (Koch et al., 2014; Olsen et al., 2004), especially in  
80 a context of anthropogenic pressures and disturbances (Hendry, Farrugia, & Kinnison, 2008).  
81 For example, many empirical studies (e.g., Daufresne, Lengfellner, & Sommer, 2009) document  
82 warming-induced reductions in body size (reviewed in Sheridan & Bickford, 2011). While a  
83 clear identification of evolution vs other processes of phenotypic variations is often lacking,

84 these empirical variations suggest that global warming exerts strong selective pressures on body  
85 size. This is crucial because body size is a key biological trait influencing many ecological  
86 constraints (Brown et al., 2004), including trophic and competitive interactions. Therefore  
87 variations of body size are likely to affect the whole food web (e.g., O’Gorman et al., 2017).  
88 Next to body size, changes in foraging strategies have also been documented in the context of  
89 global change, potentially resulting in a rewiring of the corresponding community network.  
90 Several studies, for instance, documented contemporary evolution in the diet of native  
91 herbivores to include invasive plant species (e.g., Carroll et al., 2005). Another example is the  
92 butterfly *Aricia agestis* (UK), which widened its larval host range as a result of increased  
93 temperatures (Pateman et al., 2012). The associated genetic signature (Buckley, Butlin, &  
94 Bridle, 2012) strongly suggests this is a case of evolutionary adaptation, that has enabled the  
95 species to expand its range poleward.

96 In some situations, evolution enables species to survive environmental deterioration.  
97 Gomulkiewicz & Holt (1995) theorized this concept as “evolutionary rescue”: adaptive  
98 evolutionary change restores positive growth in declining populations and prevents extinction.  
99 The empirical evidence for evolutionary rescue, as well as the different factors involved, are  
100 discussed in detail in the review by Carlson, Cunningham, & Westley (2014). Effects of  
101 evolution are however not always positive for biodiversity. Environmental change can alter  
102 evolutionary dynamics so that a non-viable phenotype is selected given the new ecological  
103 conditions (“evolutionary trapping”, Ferriere & Legendre, 2012; empirical e.g., Singer &  
104 Parmesan, 2018). Negative effects of evolution on diversity also arise when the evolution of  
105 one species drives its interacting partners towards extinction (“evolutionary murder”, e.g.,  
106 Dieckmann, Marrow, & Law, 1995). Assessing both positive and negative effects of evolution  
107 is crucial to implement relevant conservation decisions (Stockwell, Hendry, & Kinnison, 2003).

108           The last example readily highlights how accounting for the community context is  
109 equally important, since the interplay between evolution and species interactions can lead to  
110 unexpected behaviors, as illustrated by the two following examples. Within a spatially explicit  
111 model of competitive communities, Norberg et al. (2012) demonstrated that evolution under  
112 climate change can create extinction debts long after climate stabilization, but only when  
113 competition is accounted for. Osmond, Otto, & Klausmeier (2017) showed that, surprisingly,  
114 the maximum environmental change rate an evolving prey population can support increases in  
115 the presence of predators. In some cases, the presence of a predator accelerates prey evolution,  
116 facilitating its persistence (e.g., selective predation on maladapted prey).

117           Within a network context, the conditions for and the mechanisms underlying  
118 evolutionary rescue can therefore be much more complex compared to monospecific systems.  
119 A focal species could be rescued by the evolution of another interacting species (“indirect  
120 evolutionary rescue”, Yamamichi & Miner, 2015). On the other hand, if evolutionary rescue  
121 happens for various species within the network, a focal species could still go extinct if its  
122 enemies’ (resp. positive interactors) recovery is too fast (resp. too slow) compared to its own  
123 (Loeuille, 2019). A key question is therefore whether evolutionary rescue, derived from a  
124 monospecific approach, can extend to ecological networks. Single or few species models  
125 represent important stepping stones to address this question, because they focus on essential  
126 key mechanisms. However, they provide limited insights into the complex indirect interactions  
127 occurring in diverse networks (Ellner & Becks, 2011). Although currently rare (but see Norberg  
128 et al. (2012)), models that consider evolutionary processes within multispecies communities are  
129 thus essential.

130           Here, we ask whether evolutionary rescue at the network scale can promote food web  
131 persistence under warming. We address this question using an evolutionary food web model  
132 that is based on body masses and feeding preferences. Starting from a single consumer

133 population feeding on a basal resource, the evolution of these two consumer traits leads to the  
134 emergence of complex multitrophic communities. Related models have been shown to share  
135 many features with empirical food webs (Allhoff et al., 2015; Loeuille & Loreau, 2005). Once  
136 the initial build-up is complete, we expose such simulated networks to warming events. We  
137 vary both the warming intensity and the mutation rate in order to investigate the interplay  
138 between warming, evolution and network diversity maintenance. While this simulation  
139 approach provides valuable insights into eco-evolutionary responses to warming at the  
140 community scale, it is admittedly difficult to unravel the underlying mechanisms governing  
141 these responses. We therefore complement our work by analytically investigating the processes  
142 by which evolution facilitates or constrains diversity maintenance within a simplified  
143 framework consisting of only one consumer and its resource.

144 The overarching goal of the present study is to expand existing knowledge from  
145 simplified mono-specific systems to complex multispecies networks. We show that with or  
146 without evolution, warming is responsible for considerable diversity losses. In line with both  
147 theoretical (Binzer et al., 2012; Weinbach et al., 2017) and experimental work (Petchey et al.,  
148 1999), we find these losses to be more frequent among upper trophic levels. Evolution has a  
149 positive effect on diversity maintenance. It notably enables diversity to progressively and  
150 partially recover after a transient collapse. Our results are globally in line with the expectations  
151 derived from evolutionary rescue theory (Gomulkiewicz & Holt, 1995).

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## 157 **Model**

### 158 **Ecological dynamics**

159 The trophic network consists of a set of primary producers providing energy to the whole  
 160 community (hereafter basal resource of (aggregated) biomass density  $B_0$ ) and consumer morphs  
 161  $i$ . Its dynamics follow:

$$\frac{dB_0}{dt} = r \left( 1 - \frac{B_0}{K} \right) B_0 - \sum_i a_{i0} B_0 B_i \quad (1)$$

$$\frac{dB_i}{dt} = \sum_{j=\text{ressource/prey}} e a_{ij} B_j B_i - \sum_{j=\text{predator}} a_{ji} B_j B_i - \sum_{j=\text{competitor}} c_{ij} B_j B_i - d_i B_i \quad (2)$$

162  
 163 The basal resource follows a logistic growth in the absence of higher trophic levels, with  
 164 intrinsic growth rate  $r$  and carrying capacity  $K$  (equation 1). Variations of biomass density  $B_i$   
 165 of a morph  $i$  (equation (2)) are composed of four terms: predation gain, predation loss, losses  
 166 due to interference competition, as well as intrinsic losses due to respiration and basic mortality  
 167 (hereafter respiration). A complete list of parameters and variables is provided in Table1.

Variables and parameters		Biological meaning	Default value	Unit
<i>Variables</i>	$B_i$	Biomass density of morph $i$		$kg.m^{-2}$
	$m_i$	Body mass of morph $i$		$kg$
	$f_i$	Feeding preference of morph $i$ (i.e., preferred prey size)		$kg$
<i>Temperature parameters</i>	$T$	Temperature	[275,320] (2-47 °C)	$K$
	$T_0$	Reference temperature	293 (20 °C)	$K$
	$E$	Activation energy	0.65	$eV$
	$k$	Boltzmann Constant	$8.61710^{-5}$	$eV.K^{-1}$

<i>Ecological parameters</i>	$r_0$	Growth rate at temperature $T_0$	1	$s^{-1}$
	$r(T)$	Intrinsic growth rate of basal resource		$s^{-1}$
	$K_0$	Carrying capacity at temperature $T_0$	10	$kg \cdot m^{-2}$
	$K(T)$	Carrying capacity of the basal resource		$kg \cdot m^{-2}$
	$d_0$	Respiration rate at temperature $T_0$	0.3	$kg^{0.25} \cdot s^{-1}$
	$d_i(T)$	Respiration rate of morph $i$		$s^{-1}$
	$e$	Conversion efficiency	0.85	1
	$c_0$	Intra-morph competition rate	0.15	$m^2 \cdot s^{-1}$
	$c_{ij}$	Competition rate between morph $i$ and morph $j$		$kg^{-1} \cdot m^2 \cdot s^{-1}$
	$a_{ij}$	Attack rate of morph $i$ on morph $j$		$kg^{-1} \cdot m^2 \cdot s^{-1}$
	$s$	Feeding range (width of consumption niche)	0.25	$kg$
	$\varepsilon$	Extinction threshold	$210^{-6}$	$kg \cdot m^{-2}$
<i>Evolutionary parameters</i>	$\mu$	Mutation rate	$(10^{-1}, 10^{-2}, 10^{-3})$	$s^{-1}$
	$\sigma$	Mutational amplitude	0.25	$kg$

169 **Table 1: Variables and parameters.** Dependence on temperature is explicitly indicated. The values given here  
 170 represent the standard parameter set used in our simulations, unless stated otherwise.

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## 180            **Temperature dependence**

181            Biochemical reactions and thus metabolic rates are known to grow exponentially with  
182            temperature. We therefore incorporate temperature dependency as an Arrhenius function in  
183            the resource growth rate  $r$  and the respiration rate  $d_i$  of consumer  $i$  following Brown et al.  
184            (2004):

$$r(T) = r_0 \exp\left(\frac{-E(T_0 - T)}{kTT_0}\right) \quad (3)$$

$$d_i(T) = d_i \exp\left(\frac{-E(T_0 - T)}{kTT_0}\right) \quad (4)$$

185  
186            We furthermore assume that the carrying capacity of the basal resource decreases exponentially  
187            with temperature as in Fussmann et al. (2014).

$$K(T) = K_0 \exp\left(\frac{E(T_0 - T)}{kTT_0}\right) \quad (5)$$

188  
189            Here,  $k$  is the Boltzmann constant,  $E$  the activation energy and  $T_0$  the reference temperature  
190            (Table 1). We assume these relationships to hold over the temperature range we consider here  
191            (275-300 K, 2-47 °C) (but see Discussion).

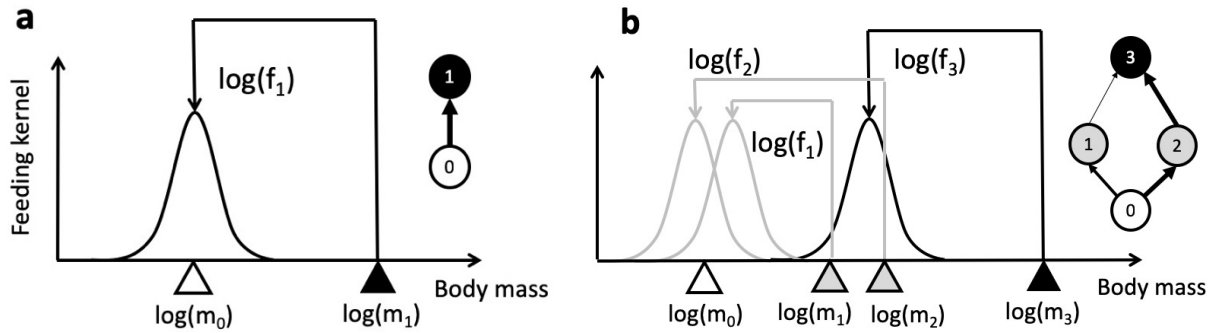
192

## 193            **Presentation of evolving traits**

194            Each consumer morph  $i$  has two adaptive traits: body mass  $m_i$  and feeding preference  
195             $f_i$ . Body mass is known to largely constrain trophic interactions (see for instance Woodward et  
196            al. (2005)). The basal resource has a body mass  $m_0$  that we assume fixed. The feeding  
197            preference  $f_i$  corresponds to the prey body mass allowing a maximal attack rate. Fig.1 illustrates  
198            how traits constrain trophic interactions.



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**Figure 1:** (Adapted from Allhoff et al., 2015). **a.** Consumer-Resource module. The consumer (▲) has a body mass  $m_1$  and feeds on the basal resource (△) with maximum attack rate (black curve) because its feeding preference  $f_1$  corresponds to the resource body mass  $m_0$ . Resulting trophic interaction on the right. **b.** Complex multitrophic network emerging by co-evolution. The snapshot here shows 3 morphs: morph 3 (▲) feeds on morph 1 and 2 (△) with respectively low and high attack rates, morph 1 and 2 feed on the basal resource (△) with respectively low and high attack rates. Resulting trophic module on the right. This is a snapshot view; the real networks are dynamic and typically have many more morphs.

Respiration and attack rates scale with body mass (Brown et al., 2004; Peters, 1983). In our model, attack rates depend on the relative differences between predators' feeding preferences and prey's body masses. Supporting our formulation, several empirical studies indicate that predation intensity is determined by predator-prey body mass ratios (Naisbit et al., 2011; Vucic-Pestic et al., 2010). Around a predator's feeding preference, attack rates are thus distributed right-skewed on an absolute scale, meaning higher predation on smaller prey (Aljetlawi, Sparrevik, & Leonardsson, 2004; Brose et al., 2008). We furthermore assume competition to increase for similar feeding preferences, due to niche overlap (MacArthur & Levins, 1967). The feeding niche width is denoted by  $s$  (Fig. 1) and  $c_0$  is a scaling constant for the interference competition.

$$d_i = m_i^{-0.25} d_0 \quad (6)$$

$$a_{ij} = \frac{m_i^{-0.25}}{\sqrt{2\pi}s} \exp\left(\frac{-\left(\log(f_i) - \log(m_j)\right)^2}{2s^2}\right) \quad (7)$$

220

$$c_{ij} = \frac{c_0}{\sqrt{2\pi s}} \exp\left(\frac{-(\log(f_i) - \log(f_j))^2}{4s^2}\right) \quad (8)$$

221

## 222 **Methods**

### 223 **Simulations**

224 Simulations start from a single ancestor morph ( $m_1 = 100$ ,  $f_1 = 1$ ) feeding on the basal  
225 resource ( $m_0 = 1$ ). The succession of mutation events (one mutation every  $\frac{1}{\mu}$  time steps) leads  
226 to the emergence of a multitrophic network with typically 30 to 40 morphs and 4 to 5 trophic  
227 levels (Allhoff et al., 2015; Loeuille & Loreau, 2005). Proportionally to population abundances,  
228 a parent morph is chosen randomly at each mutation event. Mutant traits are then drawn from  
229 log-normal distributions centered around the parent's traits. Occasional big mutational steps are  
230 allowed (details in Appendix S2.B). The mutant is initially very rare as its initial biomass  
231 density corresponds to the extinction threshold  $\varepsilon$  taken from the parent population.

232 To assess the role of evolution for the maintenance of diversity, we consider two  
233 evolutionary scenarios: with evolution (“scenario E”) and without evolution (“scenario NE”).  
234 Scenarios NE consist of the following sequence of events: (1) the network is built up with a  
235 mutation rate  $\mu$ ; (2) evolution stops ( $\mu = 0$ ) when a quasi-equilibrium is reached; (3) warming  
236 occurs; (4) simulation stops when a new quasi-equilibrium is reached. Scenarios E follow the  
237 same sequence except (2). We consider quasi-equilibrium situations to be reached when the  
238 relative trait diversity variability over time is below a critical value (see Appendix S2.B). We  
239 are thus not focusing on the transient state following perturbation but on the long-term response  
240 to warming, when a steady state is reached.

241 We ran a total of 420 simulations. For each of the two scenarios (with evolution E,  
242 without evolution NE), we ran simulations with all factorial combinations of  $\mu =$   
243  $10^{-1}, 10^{-2}, 10^{-3}$  and  $\Delta T = 0, 2, 4, 6, 8, 10, 20$  K or  $^{\circ}\text{C}$  (initial temperature is always 275K  
244 ( $2^{\circ}\text{C}$ )). We ran 10 replicates for each combination of parameters. We focus on the role of  $\mu$  and  
245  $\Delta T$ , because a well-supported expectation from evolutionary rescue theory is that evolution is  
246 less likely to save the species when the disturbance is high, or when the genetic variability (here  
247 brought by mutation) is low (Gomulkiewicz & Holt 1995, Carlson et al. 2014). We want to test  
248 whether these assumptions remain valid in a multispecies context.

249

## 250 **Evolutionary rescue at the multitrophic network scale**

251 Ferriere & Legendre (2012) propose a broad definition of evolutionary rescue that we  
252 adapt to our network context: “evolutionary rescue occurs when a population subject to  
253 environmental change ‘performs better’ under the operation of evolutionary processes than  
254 without these processes”. We measure the network performance as the diversity maintained  
255 after warming relative to the diversity that was present before (hereafter “persistence”, see  
256 appendix S2.B). Diversity is measured either as trait or species diversity. Trait diversity  
257 corresponds to the total number of morphs present at a given time. While this is certainly a  
258 valuable measure from a functional and structural point of view, a large focus exists in  
259 conservation biology on the preservation of species diversity. Because our model ignores  
260 genetic details and focuses on phenotypes, the definition of species is notoriously tricky. For  
261 lack of better criteria, we define species as clusters in the phenotypic space (Appendix S2.A).  
262 We used statistical models implemented in R-software to compare persistence across scenarios.  
263 For each mutation rate, we fitted two ANCOVAs to link trait or species diversity persistence  
264 with evolutionary scenarios (evolution E vs no evolution NE) and warming intensities (details  
265 in Appendix S2.C). The results of the statistical analysis are summarized in Table S2.

## 266 Identifying mechanisms in a simplified model

267 The Consumer-Resource (CR) module is derived from equations (1) and (2), assuming  
268 one consumer feeding on the resource and potentially its conspecifics (cannibalism).

$$\frac{dB_0}{dt} = r \left( 1 - \frac{B_0}{K} \right) B_0 - a_{10} B_1 B_0 \quad (9)$$

$$\frac{dB_1}{dt} = e a_{10} B_0 B_1 - (a_{11}(1 - e) + c_{11}) B_1^2 - d_1 B_1 \quad (10)$$

269

270 We use adaptive dynamics (Dieckmann & Law, 1996; Metz, Nisbet, & Geritz, 1992) to  
271 investigate how warming affects the eco-evolutionary dynamics. Two major assumptions are  
272 made: firstly, evolution occurs on longer timescales than ecology and, secondly, mutations are  
273 of small amplitude. Timescale separation allows the environment felt by the mutant to be clearly  
274 defined by the resident population at ecological equilibrium ( $B_0^*$ ,  $B_1^*$ ) (analytical expression in  
275 Appendix S1.A.1). When the analytical work indicates the system is supposed to go extinct, we  
276 assess the potential for evolutionary rescue as in Ferrière & Legendre (2012). More precisely,  
277 we undertake simulations to test whether fast evolution may prevent extinction.

278 For instance, considering trait  $m_1$  (body mass), the invasion fitness  $w(m_1^{mut}, m_1^{res})$  of  
279 a mutant corresponds to its relative growth rate in the resident population when rare. Positive  
280 values of  $w$  indicate that the mutant frequency increases, eventually replacing the resident.  
281 Evolutionary dynamics are captured by the sequence of trait substitutions, and can be  
282 approximated by the canonical equation of adaptive dynamics (Dieckmann & Law 1996). This  
283 equation (Appendix S1 B.1) indicates that the trait evolves through time proportionally to the  
284 selection gradient, a quantity that captures how the relative fitness  $w(m_1^{mut}, m_1^{res})$  varies with  
285 the mutant trait  $m_1^{mut}$  (Appendix S1 B.1). The values of the resident trait  $m_1^{res}$  where the  
286 selection gradient vanishes are evolutionary singularities. They are classified into Continuously

287 Stable Strategies (CSS, Eshel, 1983), Branching Points (BP, Geritz et al., 1997) and Repellers  
288 according to two properties: convergence and invasibility.

289 Convergence indicates that the trait evolves toward the singularity in its vicinity  
290 (convergent: CSS, BP; non-convergent: Repellor). Invasibility specifies whether the singularity  
291 may be invaded by nearby mutants (non-invasible: CSS; invasible: BP, Repellor). Branching  
292 points are particularly important in terms of diversity: they yield the emergence of a stable  
293 dimorphism in the population due to disruptive selection (e.g., the coexistence of two consumer  
294 populations with different body masses). Knowing the evolutionary singularities and their  
295 properties (Appendix S1 B.3.d) enables the full determination of the evolutionary dynamics of  
296 the consumer population within the CR module.

297

298 All in all, this simplified framework allows the eco-evolutionary dynamics of the  
299 consumer population confronted with warming to be more easily tractable. Such a thorough  
300 understanding allows to highlight key mechanisms that may also act at the co-evolving  
301 multitrophic scale. However, we keep in mind that the patterns observed within the CR module  
302 framework might not upscale straightforwardly to multitrophic networks due to non-trivial  
303 indirect interactions occurring in multispecies communities. In the main text, we study the  
304 evolution of the traits  $m_1$  and  $f_1$  separately, but we also tackle the co-evolution of the two traits  
305 in the supporting information (Fig. S2, Appendix S1.B.4).

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## 310 Results

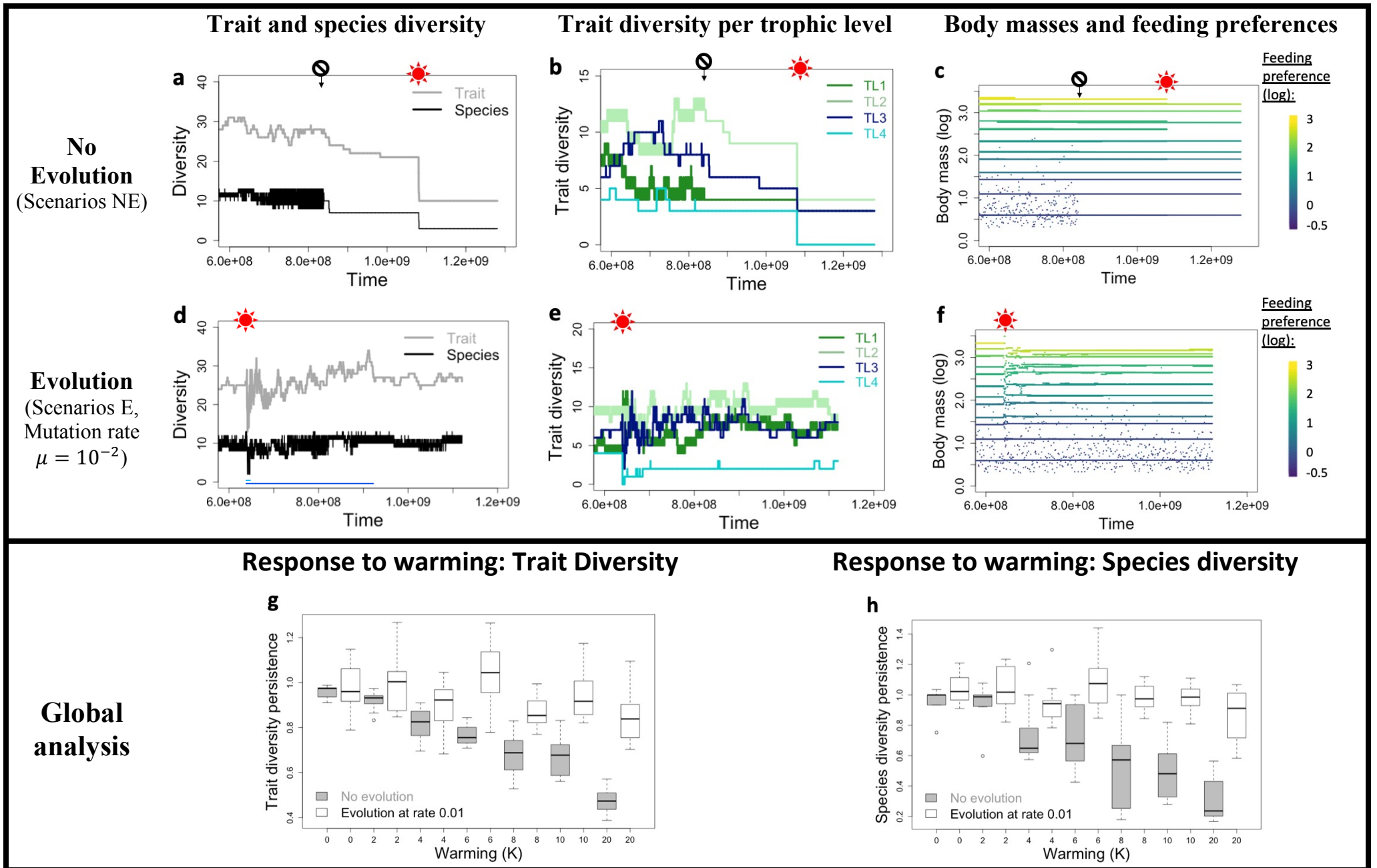
### 311 Warming induces diversity losses within trophic networks

312 Warming is responsible for considerable biodiversity losses within multitrophic networks.  
313 This is true with (Fig. 2d) or without evolution (Fig. 2a). Though diversity recovers fast when  
314 evolution is allowed, note that diversity collapses to half of its initial value (Fig. 2d). Long after  
315 the transient state, diversity stabilizes at smaller values than before warming for a vast majority  
316 of simulations, with and without evolution (Fig 2g&h). A warming of 8°C for instance leads to  
317 a significant loss of trait diversity (around 32% without evolution, 13% with evolution). For a  
318 mutation rate  $\mu = 10^{-2}$ , the statistical model fitted explains around two thirds of the observed  
319 variance, with warming explaining almost one third of it (Table S2.A). The model confirms the  
320 expected tendency revealed by Fig. 2g&h: stronger warming leads to higher diversity loss. The  
321 estimated coefficients governing the linear dependence of persistence on warming intensity are  
322 significantly negative without evolution ( $Warming_{Effect} = -0.024$ ,  $p_{value} < 2.10^{-16}$ ) or  
323 with evolution ( $Warming_{Effect} + Interaction_{Effect} = -0.007$ ,  $p_{value} < 10^{-3}$ ).

324 Diversity is lost because some consumer populations go extinct following the warming  
325 event. As temperature increases, less energy is available at the bottom of the trophic network  
326 (decline in basal resource's carrying capacity  $K(T)$ , equation 5), while the metabolic  
327 requirements increase (increase in respiration loss rate  $d_i(T)$ , equation 4). Despite an increase  
328 of plants productivity (basal resource's growth rate  $r(T)$ , equation 3), the ratio of ingestion to  
329 metabolic losses overall decreases with warming. In the CR framework, this decrease is driven  
330 by the ratio  $\frac{r}{K}$ :

$$\frac{Ingestion}{Metabolism} \stackrel{\text{def}}{=} \frac{ea_{10}B_0^*(T)}{d_1(T)} = \frac{\left[ a_{10} + \frac{r}{d_1} (a_{11}(1-e) + c_0) \right] ea_{10}}{\frac{r}{K} (a_{11}(1-e) + c_0) + ea_{10}^2} \quad (11)$$

331



**Figure 2: Diversity response to warming.** a-b-c: Diversity and evolutionary dynamics of a simulation where evolution has been stopped (prohibition symbol indicates stopping time) before warming from 275 K to 295 K (sun symbol); d-e-f: Same outputs with ongoing evolution at warming. g-h: Boxplots of trait and species diversity persistence according to different warming intensities for scenarios with or without evolution. Each box corresponds to 10 independent replicas. See Table 1 for parameter values.

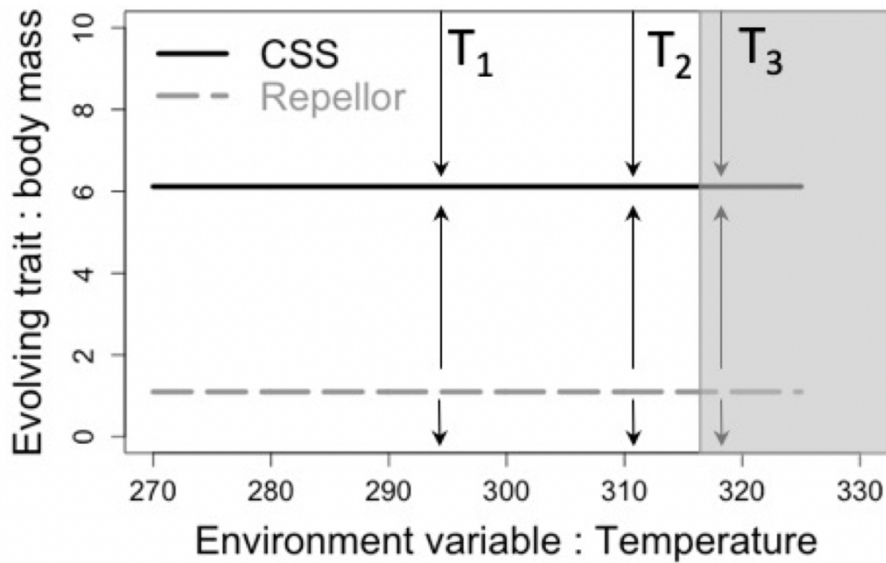
332 This ingestion ratio reaches the critical value of one at a critical temperature  $T_c(f_1)$ , above  
333 which a consumer with feeding preference  $f_1$  cannot survive (Appendix S1.A). Ingestion is  
334 maximal when the consumer's feeding preference matches exactly the basal resource  
335 phenotype. No consumer population can therefore survive above the limit temperature  $T_{lim} \stackrel{\text{def}}{=} T_c(f_1 = m_0)$   
336  $T_c(f_1 = m_0)$  (equation 12, Appendix S1.A).

$$T_c(f_1) \leq T_{lim} \stackrel{\text{def}}{=} \frac{2E}{\frac{2E}{T_0} + k \left( \ln \left( \frac{\sqrt{2\pi} s d_0}{e K_0} \right) \right)} \quad (12)$$

337  
338 The limit temperature  $T_{lim}$  being independent of the consumer's traits, even fast evolution  
339 would not allow any consumer population to survive higher temperatures. Fig. 3 for instance  
340 shows how evolved body mass depends on temperature. Above  $T_{lim}$  ( $\approx 316.4K$  here, grey  
341 area), no consumer phenotype is viable. Consumer survival depends on the intensity of  
342 warming: a warming from  $T_1$  to  $T_2$  would allow survival while a warming from  $T_1$  to  $T_3$  would  
343 lead to extinction. Note also that temperature does not impact evolved body mass in the CR  
344 module (analytical proof in appendix S1 B.2).



## Body mass evolution and temperature



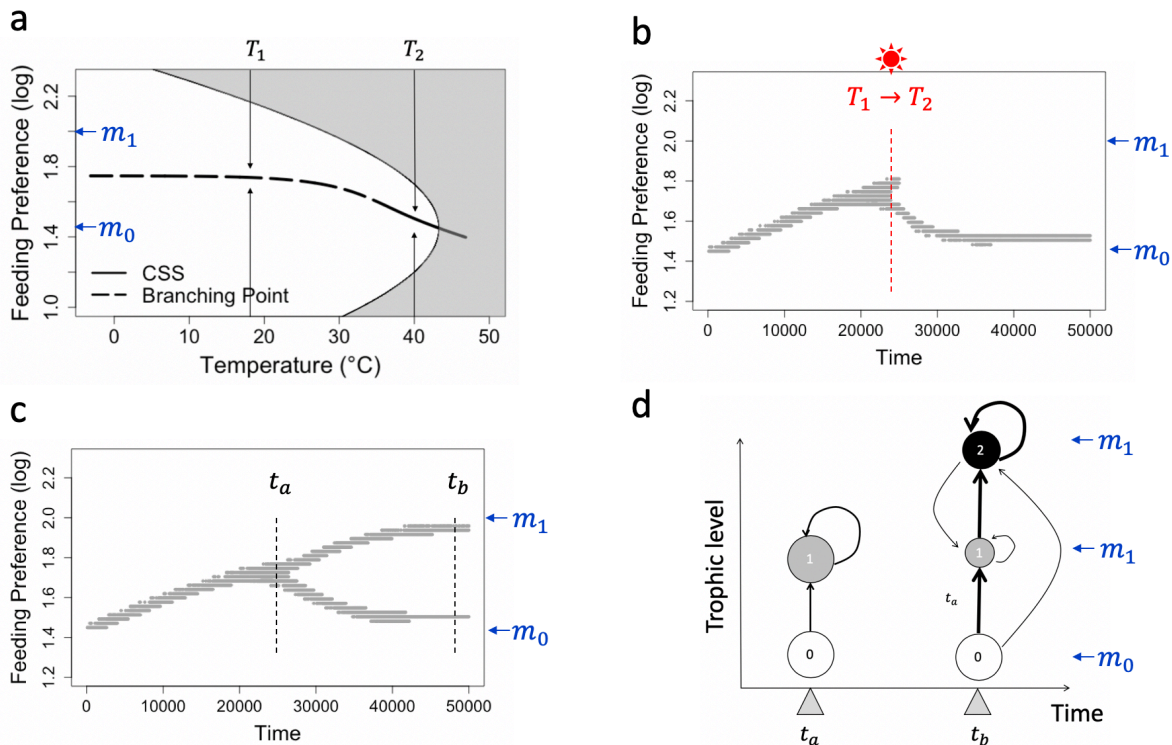
345

346 **Figure 3: Body mass evolution and temperature (E3 diagram).** Grey area cannot support the consumer. Arrows  
347 indicate the direction of evolutionary trajectories. Temperatures  $T_1, T_2, T_3$  show different warming scenarios.  
348 Parameters:  $f_1 = m_0$ . Other parameters as in Table 1.

349

350 Warming can also reduce long-term diversity by changing the selection regime from  
351 disruptive to stabilizing. Within the CR framework, such a pattern is observed in the case of  
352 feeding preference evolution, for intermediate consumer to resource body mass ratios (Fig. 4,  
353 details in Appendix S1 B.3.c). As temperature increases, the convergent singularity changes  
354 from an invisable BP to a non-invasible CSS (Fig. 4a). Diversification at branching yields the  
355 emergence of a stable dimorphism of contrasting feeding preferences ( $\approx (m_0, m_1)$ ), Fig. 4c).  
356 The initial 2-level food chain ( $t_a$ , Fig. 4d), consisting of a consumer population feeding equally  
357 on the basal resource and conspecifics (cannibalism), evolves into a 3-level food chain ( $t_b$ , Fig.  
358 4d). The intermediate level (Fig. 4d, 1) now primarily relies on basal resource consumption,  
359 making the upper trophic level (Fig. 4d, 2) viable despite being highly cannibalistic. As  
360 illustrated in Fig. 4b, a warming from  $T_1$  to  $T_2$  at branching ( $t_a$ ) completely changes the  
361 evolutionary dynamics. At  $T_2$ , the loss of the upper trophic level leads to a 2-level food chain

362 with a consumer population primarily feeding on the basal resource. Trait diversity is lost and  
 363 will not recover as selection is stabilizing at  $T_2$  (CSS, Fig. 4a). Long-term warming-induced  
 364 diversity losses can derive from a loss of diversification processes driven by warming.  
 365



366 **Fig. 4: Warming switches the selection regime from disruptive to stabilizing** (CR module, evolution of feeding  
 367 preference  $f_1$ ).  $m_1 = 100$ ,  $m_0 = 28.2$  **a.** Dependence of singularities on temperature. **b/c.** Evolutionary dynamics  
 368 (mutation rate  $\mu = 10^{-2}$ , mutation steps  $\pm 5\%$ ) at temperature  $T_1$  (**c**, Branching Point) or for a warming from  $T_1$   
 369 to  $T_2$  occurring at branching (**b**, sun symbol). **d.** Schematic view of the trophic network before ( $t_a$ ) and long after  
 370 branching ( $t_b$ ). Arrow thickness shows the intensity of trophic interactions. Circle size is proportional to the morph  
 371 density. Other parameters are as in Table 1.  
 372  
 373

374 In our simulated networks, upper trophic levels, corresponding to consumers with high  
 375 body masses and/or feeding on large prey (Fig. 2c&f), are most vulnerable to warming (Fig.  
 376 2b&e). This may be explained by three factors. Firstly, the analysis of the CR module reveals  
 377 that a higher body mass is responsible for a sharper decrease of the ingestion ratio with warming  
 378 (Fig. S1, Appendix S1 A.4). Secondly, in a multitrophic context, upper trophic levels suffer  
 379 from accumulated warming-induced energy losses happening at lower trophic levels. Thirdly,  
 380 a final reason for the vulnerability of upper trophic levels is their low population sizes. This

381 reduces their evolvability, thus their ability to adapt to new environmental conditions. Warmed  
382 trophic networks are consequently flatter. Warming-induced losses of diversifying processes  
383 that yield the emergence of upper trophic levels, such as the branching point in Fig. 4, could  
384 also contribute to the pattern observed.

385

## 386 **Evolution can mitigate warming-induced diversity losses**

387 Warming triggers diversity losses with or without evolution (Fig. 2a&d). However,  
388 recovery is possible when morphs can evolve (Fig. 2d), while it is not when evolution has been  
389 switched off (Fig. 2a). Such a recovery necessitates a considerable amount of time. In Fig. 2d,  
390 it took 200 000 mutation events/generations (light blue line) to reach pre-warming diversity  
391 levels and far more for diversity to be stable over time ( $2.8 \cdot 10^6$  mutation events/generations,  
392 dark blue line). The diversity eventually maintained in the trophic network is significantly  
393 higher in scenarios with evolution (Ancovas, Table S2). The results are quantitatively illustrated  
394 on trait diversity for a mutation rate  $\mu = 10^{-2}$  but remain consistent across the three mutation  
395 rates tested. Evolution has a positive effect on diversity persistence. This effect is both direct  
396 ( $Evolution_{Effect} = 0.06$ ,  $p_{value} = 0.0204$ ,  $Var_{explained} = 28.4\%$ ) and indirect, increasing  
397 in importance with warming ( $Interaction_{Effect} = 0.017$ ,  $p_{value} < 10^{-8}$ ,  $Var_{explained} =$   
398  $9.5\%$ ). This interactive effect is strong enough to totally offset the negative linear dependence  
399 of diversity persistence on warming in scenarios with evolution for the two other mutation rates  
400 tested ( $10^{-1}$ ,  $10^{-3}$ ). In these cases, trait diversity recovers totally after a long transient state.  
401 Due to the interaction term, the stronger the warming, the higher the diversity maintained thanks  
402 to ongoing evolution across the trophic network (Fig 2g&h). It reaches a maximum of almost  
403 40% at 20°C, with 48% of trait persistence in scenarios without evolution vs 85% in scenarios  
404 with evolution. Among evolutionary scenarios, we also tested the theoretically known  
405 association between faster evolution and better rescue by comparing diversity maintenance

406 across mutation rates (ANCOVA). Counterintuitively, no significant difference was found (but  
407 see discussion).

408 The analysis of the CR module highlights two processes that potentially explain how  
409 evolution contributes to preserve the diversity in multitrophic networks: evolutionary rescue  
410 and an indirect mechanism we label “diversity-mediated buffering effect”. These processes,  
411 which are illustrated in the case of feeding preference  $f_1$  evolution, are explained in detail  
412 further below.

413 It can be shown that the consumer’s evolved feeding preference  $f_1^*$  is necessarily between  
414 its own body mass ( $m_1$ ) and the body mass of the resource ( $m_0$ ) (Appendix S1 B.3). The study  
415 of feeding preference in this interval is thus sufficient. We define the consumer trait  $\alpha \stackrel{\text{def}}{=} \frac{\log(m_1/f_1)}{\log(m_1/m_0)}$   
416 describing the proportion of resource consumption on the total consumer regime.

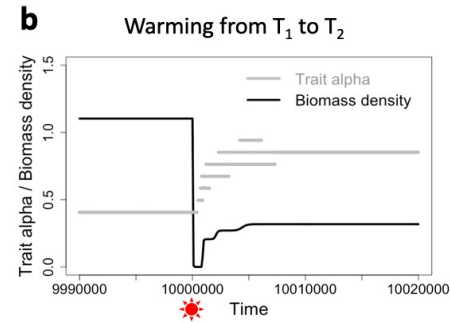
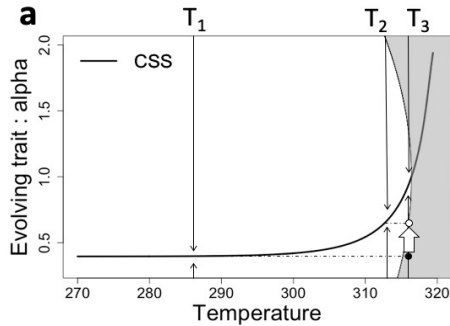
417 Strictly equivalent to feeding preference evolution, it is more convenient to study the evolution  
418 of  $\alpha$  that varies between two extreme scenarios: the consumer is essentially cannibalistic ( $\alpha =$   
419 0) or primarily relies on the basal resource ingestion ( $\alpha = 1$ ). The analysis of the CR module  
420 reveals that four qualitative outcomes, corresponding to four ecological scenarios, are possible  
421 (Appendix S1 B.3.c, Table S1). These scenarios are illustrated in Fig. 5. They differ in two key  
422 features: (1) the consumer to resource body mass ratio ( $L \stackrel{\text{def}}{=} \frac{\log(m_1/m_0)}{s}$ ) is either small (scenario  
423 A), intermediate (scenario B) or large; (2) for large ratios, whether the consumer body mass  
424 ( $m_1$ ) is small (scenario C) or big (scenario D). Note that dynamics presented earlier (Fig. 4a)  
425 correspond to scenario B (Fig. 5c).

426 Evolutionary rescue can never happen for temperatures above  $T_{lim}$  (equation 12), but is  
427 always possible if the final temperature remains below  $T_{lim}$  (Fig. 5). Consumers that adapt fast  
428 enough to the new conditions will avoid extinction, as figured by the white arrows in Fig. 5a-  
429 c-f-h. For instance, at small CR body mass ratios (scenario A, Fig. 5a), a warming from  $T_1$  to

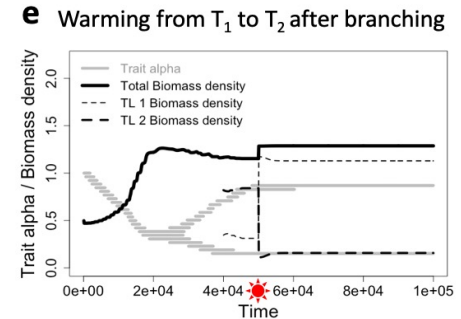
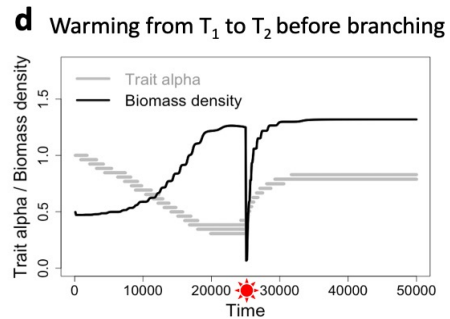
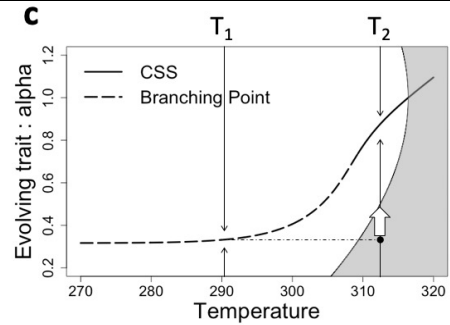
### E<sup>3</sup>-diagrams

### Examples of simulated Eco-Evolutionary dynamics

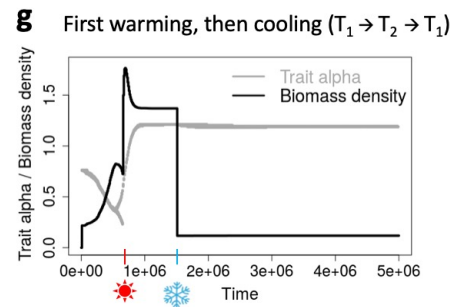
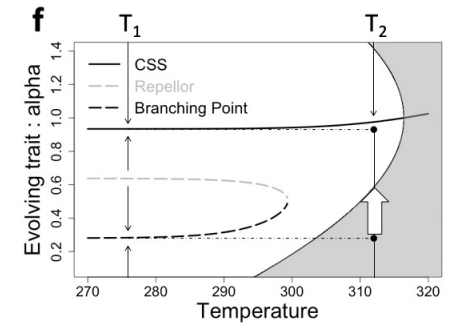
**Scenario A**  
Small  
consumer to  
resource  
mass ratio  
( $L = 1$ )



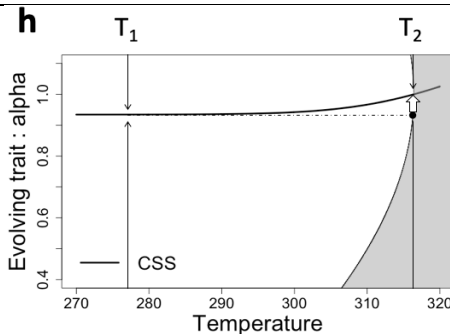
**Scenario B**  
Intermediate  
consumer to  
resource  
mass ratio  
( $L = 2.2$ )



**Scenario C**  
Big  
consumer to  
resource  
mass ratio  
( $L = 2.8$ )  
Small  
consumer  
body mass



**Scenario D**  
Big  
consumer to  
resource  
mass ratio  
( $L = 2.8$ )  
Big  
consumer  
body mass



**Figure 5: a-c-f-h E<sup>3</sup> diagrams** corresponding to scenarios A, B, C and D (Table S1). Grey areas are non-viability regions; the curves indicate the evolutionary singularities. Thin black arrows indicate the direction of evolution and the big white arrows indicate potential evolutionary rescues. **b-d-e Model simulations with evolutionary rescue occurring** (sun indicates warming time). Evolutionary rules:  $\mu = 10^{-2}$  and small mutational steps:  $5\%f_1$ . **g-** Model simulation with evolutionary hysteresis occurring (sun: warming; snowflake: cooling). Evolutionary rules:  $\mu = 10^{-2}$  and small mutational steps:  $1\%f_1$ . Parameter values are in Table 1.

430  $T_3$  leads the system to enter the non-viability area (black dot in grey area). The food chain can  
431 however persist if evolution is fast enough (white arrow), as larger values of  $\alpha$  are selected,  
432 outside the non-viability area. Such values imply higher intakes from the basal resource relative  
433 to cannibalism that enable the maintenance of a sufficient ingestion rate despite the deteriorated  
434 environmental conditions. The selection of higher intake from the basal resource relative to  
435 cannibalism seems consistent across scenarios (Fig. 5). Simulations confirm the possibility of  
436 evolutionary rescue (Fig. 5b). The consumer population collapses, but if  $\alpha$  evolves fast enough,  
437 the population recovers. Note that if warming is slow from  $T_1$  to  $T_2$  first and then from  $T_2$  to  $T_3$   
438 (Fig. 5a), the trait would remain close to the CSS curve, and the population would never be  
439 threatened. Progressive warming decreases extinction risk, in agreement with theoretical  
440 (Gomulkiewicz & Holt, 1995) and empirical work (Bell & Gonzalez, 2009).

441 When evolution allows the diversification of the consumer niches, warming is  
442 potentially less threatening as the different occupied niches are unlikely to be simultaneously  
443 destroyed. We propose to label this mechanism “diversity-mediated buffering effect”. This can  
444 be observed in scenarios where branching leads to a stable dimorphism among consumers  
445 (scenarios B&C) so that a three-level food chain emerges (Fig. 4). We simulated the eco-  
446 evolutionary dynamics following a warming from  $T_1$  to  $T_2$  affecting either the two-level food  
447 chain (Fig 4d, just before branching at time  $t_a$ ) or the three-level food chain (Fig 4d, long after  
448 branching at time  $t_b$ ). While warming at  $t_a$  largely threatens the population, the impact of  
449 warming is vastly reduced when temperature changes at  $t_b$  (Fig. 5d vs 5e). Note that while the  
450 top trophic level biomass still suffers from the disturbance, the intermediate consumer  
451 phenotype actually benefits from warming (Fig 5e). Total consumer biomass increases.  
452 Interestingly, the selected intermediate consumer’s trait  $\alpha$  pre-warming is close to the one  
453 selected under warmed conditions (Fig. 5e vs 5d).

454 Our simulated multitrophic networks emerge via successive branching events starting  
455 from a single consumer population initially. As a result, the consumer morphs occupy a wide  
456 diversity of niches (Fig. 2c&f) that ranges across 4 trophic levels (Fig. 2b&c). In other words,  
457 this “diversity-mediated buffering effect” is at play at the multitrophic network scale because  
458 multitrophic networks are the result of the consumer niche diversification.

459

## 460 **Evolution can also exacerbate the consequences of warming** 461 **on diversity**

462 While evolution often facilitates diversity maintenance in our simulated trophic networks,  
463 note that it cannot totally mitigate the negative effect of warming on diversity. Actually, in  
464 some cases we found that evolution can even exacerbate the negative consequences of  
465 warming-induced diversity losses. For instance, the analysis of the CR model suggests that  
466 warming can lead to eco-evolutionary tipping points that would severely depress persistence.  
467 Given scenario C, warming from  $T_1$  to  $T_2$  modifies the number of singularities (Fig. 5f). At  $T_1$ ,  
468 three singularities exist (CSS, Repellor and BP) while at  $T_2$  only the CSS remains.  
469 Consequently, starting from a resident consumer’s trait near branching, warming would be  
470 responsible for a reduction of diversity, as the system switches from selective pressures that  
471 allow stable polymorphism (BP) to a monomorphic situation (CSS). While similar to scenario  
472 B (Fig. 4), a major difference exists. Given the convergent properties of the CSS, decreasing  
473 temperature will not recover the initial diversity, as phenotypes remain at the selected CSS.  
474 This is a case of evolutionary hysteresis. Simulations confirm such dynamics (Fig. 5g). Starting  
475 near branching, we warm the system from  $T_1$  to  $T_2$  and observe the loss of the polymorphism.  
476 When the system is cooled back to  $T_1$ , the system remains monomorphic. Here, the initial  
477 diversity lost to warming cannot be recovered by reducing temperature because of the eco-  
478 evolutionary constraints on consumer’s evolution. This result raises the possibility that diversity

479 losses may be long-lasting and difficult to reverse, as a result of abrupt changes in selective  
480 regimes.

481

## 482 **Discussion**

483 Our investigation into the effect of warming within multitrophic networks shows that  
484 warming is responsible for important diversity losses across food webs. While evolution helps  
485 to maintain biodiversity, it is certainly not sufficient to totally mitigate diversity losses.  
486 Evolution acts in at least two complementary ways. (1) By producing diversified ecological  
487 niches, as a result of disruptive selection, it leads to trophic networks that are more resistant to  
488 warming. (2) After warming, evolutionary rescue processes across the network lead to gradual  
489 and partial recovery. Evolution can however also exacerbate the negative consequences of  
490 warming, for instance by making them last longer (hysteresis), due to the crossing of eco-  
491 evolutionary tipping points. The consistency and coherence of the picture obtained by  
492 combining two complementary frameworks, with different scales and complexities, gives  
493 confidence on the robustness of our work. Our key results, as discussed in more detail below,  
494 have potential implications for the preservation of biodiversity in the context of current  
495 warming.

496

497 Warming induces important diversity losses within trophic networks. As experimentally  
498 observed (Rall et al., 2010), the ratio of ingestion to metabolic losses decreases because less  
499 energy is available at the bottom of the food web (primary producers) in a context of increasing  
500 metabolic expenditures. As a result, several consumer morphs go extinct. These extinctions are  
501 more likely to happen high in the food web. This result seems firmly grounded as several studies  
502 using a large diversity of approaches found a similar pattern (Petchey et al., 1999; Pounds,



503 Fogden, & Campbell, 1999; Binzer et al., 2012). Potential explanations combine a sharper  
504 decrease of the ingestion ratio for morphs that are closer to their viable minimum; the bottom-  
505 up accumulation of deleterious consequences and the low evolvability associated with smaller  
506 population sizes and longer generation times. Warming also reduces diversity by altering  
507 evolutionary processes. Our CR framework shows that it can modify the selection regime from  
508 disruptive to stabilizing (scenario B&C). Altering diversity patterns through such modifications  
509 of selection regimes has deeper implications. Such effects are likely to last longer and be more  
510 difficult to reverse because of the additional constraints they entail (e.g. hysteresis). Our results  
511 support the idea that conservation ecology should focus more on preserving the processes  
512 facilitating and maintaining diversity rather than diversity patterns per se (Smith, Bruford, &  
513 Wayne, 1993).

514

515 Evolution partly mitigates warming-induced diversity losses within multitrophic  
516 networks, as shown by our statistical analysis (Table S2). Two complementary mechanisms are  
517 likely at play. First, evolution reduces diversity losses through a “diversity-mediated buffering  
518 effect”. This relies upon two observations: evolution (disruptive selection) leads to the  
519 diversification of the consumer niche (successive branching events) that allows the emergence  
520 of multitrophic networks; the greater the diversity of occupied niches at warming, the more  
521 robust is the food web because of the increased likelihood of some strategies being resistant  
522 (Fig. 5 d&e). This mechanism is akin to the “insurance hypothesis” proposed to explain the  
523 resilience of diverse systems (Yachi & Loreau, 1999). Second, evolution allows diversity to  
524 progressively recover through evolutionary rescue processes. In our CR framework,  
525 evolutionary rescue is indeed often possible when evolutionary changes in foraging strategies  
526 allow higher energy acquisition or when evolution of body sizes reduces energy requirements.  
527 Such changes in either body size or foraging strategy in response to warming have been

528 documented in nature. The metaanalysis of Daufresne et al. (2009) for instance shows a  
529 significant decrease in the size of ectothermic aquatic organisms in response to climate change.  
530 In the United Kingdom, Pateman et al. (2012) showed that the butterfly *Aricia agestis*,  
531 originally a specialist of *Helianthemum nummularium* as a larval host plant, has been able to  
532 widen its foraging strategy, allowing its expansion in the face of climate change. It now also  
533 largely uses *Geranium mole* which is more abundant in warmer climates.

534 In our simulated multitrophic networks, evolutionary rescue likely happens for low and  
535 intermediate trophic levels (Fig 2f), which evolve faster due to larger population sizes. It is  
536 facilitated by occasional mutations with large phenotypic effects. Top trophic levels recover  
537 eventually from intermediate trophic level populations that evolve higher body masses and  
538 feeding preferences until occupying the niche freed by the extinction of top trophic levels. The  
539 recovery of the network's diversity is however partial as lower biomass is available from  
540 primary production. Surprisingly, we found that higher mutation rates, associated with faster  
541 evolution, are not systematically associated with higher diversity persistence. A possible  
542 explanation is that, in addition to the intensity of selection, network recovery depends on the  
543 variability on which selection can act. Eventually, more frequent mutations do not yield more  
544 variability, but redundant phenotypes. This idea is in line with experimental results by Fugère  
545 et al. (2020) which clearly highlight that past a certain genetic variability, no improvement is  
546 observed in the rescue process. The work of Fugère et al. (2020) additionally illustrates how  
547 experimental evolution in microcosms or mesocosms offer promising opportunities for the  
548 critical empirical investigations into evolutionary rescue, especially at the multitrophic scale.

549  
550 Evolution can however exacerbate the negative consequences of warming. Evolutionary  
551 hysteresis for instance makes them difficult to reverse, lasting longer. It implies strong and  
552 possibly irreversible shifts between alternative states corresponding to tipping points (Suding

553 & Hobbs, 2009). In line with previous studies (Dakos et al., 2019), our work emphasizes the  
554 importance of considering both evolution and ecological dynamics to understand tipping points,  
555 especially in the context of global changes where selective pressures are likely strong.  
556 Observed in a simple food chain (CR, Fig. 5g), eco-evolutionary tipping points might also exist  
557 within complex multitrophic networks but such an investigation goes beyond the scope of the  
558 present paper. We simply note here that the transient state's considerable duration following  
559 warming (e.g. Fig. 2d) potentially offers opportunities for hysteresis arising from the co-  
560 evolution of traits and interactions we did not consider here. What is more, the overall  
561 vulnerability of the small populations during the transient state raises additional challenges.  
562 Demographic stochasticity or drift could dampen or impede progressive recovery. Important  
563 ecosystem services are likely to be degraded for a great period on a human timescale. However,  
564 we note that a recent study of the Cretaceous–Paleogene mass extinction suggests that  
565 functional recovery may happen much faster than diversity recovery (Alvarez et al., 2019).

566

567 Our parametrization relies, as much as possible, on available empirical data. Yet, our  
568 models are of course a crude simplification focused on a question, making many simplifying  
569 assumptions. For instance, we assume the carrying capacity of the basal resource to decrease  
570 exponentially with temperature based on the empirical data analyzed by Fussmann et al. (2014).  
571 This relationship is however debated and likely context-dependent, varying with the explicit  
572 limiting nutrient dynamics (Uszko et al., 2017). Moreover, while there is evidence for an  
573 increase of attack rates with temperature (Rall et al., 2010), available data suggest this effect is  
574 rather weak (Binzer et al., 2012; Rall et al., 2012). A hump-shaped relationship also seems  
575 more realistic when considering wide temperature ranges (Englund et al., 2011). Because it is  
576 not the focus of the present work (but see Weinbach et al., 2017 for an analysis of this question  
577 on the present model), the lack of a large scientific consensus led us to choose constant attack

578 rates. Likewise, conversion efficiencies show large variations in nature and may depend on  
579 trophic positions (Lindeman, 1942). Herbivores (TL1) feeding on primary producers (TL0)  
580 typically have lower conversion efficiencies (Yodzis & Innes, 1992). We investigated the  
581 robustness of our results by varying this parameter in the CR module (Appendix S1.B.3). At  
582 lower efficiencies, we no longer observe evolutionary hysteresis, but typically have  
583 evolutionary rescue happening. Hysteresis is thus associated with high conversion efficiencies  
584 characteristic of higher trophic level (carnivores, Yodzis & Innes, 1992), which can be  
585 interpreted as additional evidence that higher trophic levels are more vulnerable to warming  
586 (Binzer et al., 2012). Overall, while lower conversion efficiencies certainly imply lower energy  
587 flows resulting in more vulnerable networks, there is no obvious reason to think the positive  
588 effects of evolution on diversity maintenance would change.

589

590         The concept of evolutionary rescue, originally formulated within a monospecific  
591 framework (Gomulkiewicz & Holt, 1995b), seems to extend to the community scale as our  
592 work suggests that multitrophic networks confronted with warming perform better when  
593 evolution is at play (Ferriere & Legendre, 2012). Among these processes, the evolutionary  
594 rescue of low and intermediate trophic levels, that facilitates the recovery of higher trophic  
595 levels, is key. The diversification of ecological niches ensuing from disruptive selection is  
596 equally important as our work unravels a diversity-mediated buffering effect. As a result, all  
597 measures favoring evolvability, such as spatial or temporal variability or the presence of micro-  
598 habitat, are likely to make the community more resistant to warming. Likewise, all measures  
599 targeting the key factors for evolutionary rescue, as presented in the review by Carlson et al.  
600 (2014), should favor trophic networks' persistence and resilience.

601         Yet, evolutionary processes are not sufficient to preserve biodiversity in the context of  
602 global change. Indeed, our work highlights important diversity losses for considerable amounts

603 of time before a partial recovery can potentially happen. Specifically, the transient collapse may  
604 severely affect ecosystem services sustained by ecological networks, with large impacts from a  
605 management point of view. What is more, several mechanisms we do not consider here could  
606 dampen or even prevent the recovery. Low population size may induce adverse ecological  
607 (demographic stochasticity, Allee effects) or evolutionary effects (genetic drift) impeding  
608 persistence. We also did not model the evolution of primary producers under warming, which  
609 may mostly affect other traits than body size (Parmesan, 2006). Empirical evidence highlights  
610 for instance temporal mismatches between plants and herbivores resulting from heterogenous  
611 phenological shifts in response to climate warming (Visser & Gienapp, 2019). The consecutive  
612 energy losses further threaten the maintenance of diversity within multitrophic networks.

613 In summary, while evolution has a positive effect on biodiversity maintenance within  
614 trophic networks confronted with warming, the impact of warming is nevertheless expected to  
615 be dramatic and long lasting, with severe consequences for human populations. Conservation  
616 and biodiversity management policies should better integrate evolutionary components to  
617 properly address the issues raised by global change.

618

## 619 **Supporting Information:**

620

621 Additional Supporting Information may be found in the online version of this article:

622

623 **Table S1.** Warming impacts the CR evolutionary dynamics: the 4 possible scenarios

624 **Table S2.** Diversity persistence in the complex multitrophic networks: statistical analysis summary

625 **Fig. S1.** The decrease of the ingestion ratio with temperature depends on body mass

626 **Fig. S2.** Consumer Resource module: the two-trait co-evolution scenario

627 **Appendix S1.** Eco-evolutionary dynamics of the Consumer-Resource module

628 **Appendix S2.** Complex multitrophic network model

629 **Appendix S3.** Simulation code

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632

633

634

635

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641

642

## 643 **Author's contributions statement:**

644  
645 NL, KTA and YY conceived the ideas and designed the methodology. The analysis was  
646 conducted by AW (body mass evolution) and YY (feeding preference evolution and co-  
647 evolution). As for the simulated complex multitrophic networks, KTA developed the code,  
648 which was later adapted by YY to do the simulations. Results analysis was done by NL, KTA  
649 and YY. YY wrote the first draft of the manuscript that has been subsequently reviewed and  
650 edited by NL and KTA. All authors contributed critically to the drafts and gave final approval  
651 for publication.

652

## 653 **Data Accessibility Statement:**

654  
655 The code used for the simulations (programming language C) is available in the supporting  
656 information (Appendix S3).

657

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# 1 **Supporting Information**

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74 **Table S1:** Warming impacts the CR evolutionary dynamics: the 4 possible  
 75 scenarios

76  
 77

Scenario	CR body mass ratio	Consumer body mass	Mathematical significance	Qualitative outcomes (evolution of $\alpha$ )
A	Small	Any	$L \ll L^c(M_1)$	<ul style="list-style-type: none"> <li>One singularity: a CSS that increases with temperature (higher resource consumption)</li> </ul>
B	Intermediate	Any	$L < L^c(M_1)$ $L \approx L^c(M_1)$	<ul style="list-style-type: none"> <li>One singularity whose value increases with warming (higher resource consumption)</li> <li>Warming switches the selection regime from disruptive (BP) to stabilizing (CSS) (loss of polymorphism)</li> </ul>
C	Big	Small	$L > L^c(M_1)$	<ul style="list-style-type: none"> <li>Three singularities (CSS, Repellor and BP) for low temperatures and only one (CSS) for high temperatures (evolutionary hysteresis)</li> </ul>
D		Big		<ul style="list-style-type: none"> <li>One singularity: a CSS that increases with warming (increased resource consumption)</li> </ul>

78 **Table S1:** The four possible scenarios with their biological and mathematical significances.  $L^c(m_1)$  is the value  
 79 of  $L$ , determined numerically and  $m_1$ -dependent, at which important features of equation (H) change, leading to  
 80 different evolutionary dynamics.

81  
 82  
 83  
 84  
 85

86 **Table S2: Diversity persistence in the complex multitrophic networks: statistical**  
 87 **analysis summary for trait diversity (A) and species diversity (B)**

88  
 89

Mutation rate	Direct effect of evolution		Effect of warming intensity		Interaction term		Adjusted R <sup>2</sup>
	$\delta_2$	Effect size	$\beta$	Effect size	$\gamma_2$	Effect size	
$\mu = 10^{-1}$	0.051	32.3%	-0.029***	11.5%	0.031***	15.6%	58.6 %
$\mu = 10^{-2}$	0.060*	28.4%	-0.024***	30.3%	0.017***	9.5%	67.6%
$\mu = 10^{-3}$	0.062**	39.8%	-0.019***	18.5%	0.017***	13.1%	70.7%

90 **Table S2 (A): Trait diversity persistence.** Outputs of the 3 ANCOVAs. Index 1 corresponds to the level « No  
 91 evolution », which serves as a reference ( $\delta_1 = \mathbf{0}$ ,  $\gamma_1 = \mathbf{0}$ ), while index 2 corresponds to the level « Evolution »  
 92 ( $\delta_2$ ,  $\gamma_2$ ). All fitted ANCOVAs have a p-value below  $2 \cdot 10^{-16}$ . Significance code:  $<10^{-3}$  \*\*\*,  $<10^{-2}$  \*\*,  $<0.05$  \*

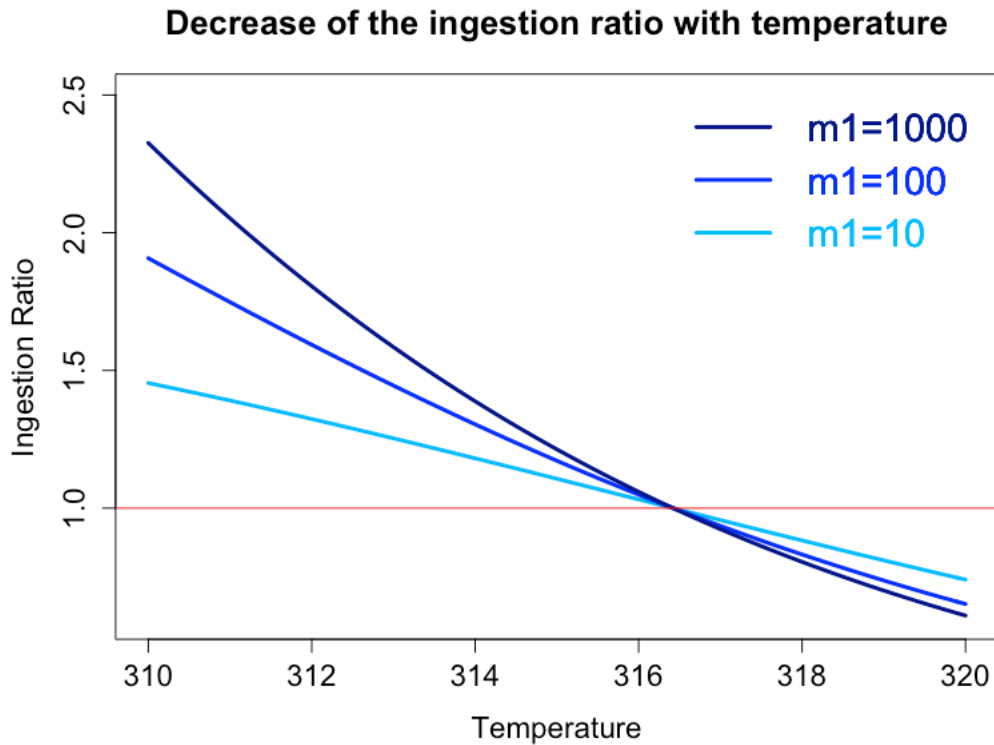
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Mutation rate	Direct effect of evolution		Effect of warming intensity		Interaction term		Adjusted R <sup>2</sup>
	$\delta_2$	Effect size	$\beta$	Effect size	$\gamma_2$	Effect size	
$\mu = 10^{-1}$	-0.026	27.1%	-0.037***	27.9%	0.036***	24.8%	79.4%
$\mu = 10^{-2}$	0.126**	33.4%	-0.035***	22.6%	0.027***	8.9%	64.1%
$\mu = 10^{-3}$	0.196***	37.3%	-0.029***	12.2%	0.023***	5.8%	54.4%

96 **Table S2 (B): Species diversity persistence.** Outputs of the 3 ANCOVAs. Index 1 corresponds to the level « No  
 97 evolution », which serves as a reference ( $\delta_1 = \mathbf{0}$ ,  $\gamma_1 = \mathbf{0}$ ), while index 2 corresponds to the level « Evolution »  
 98 ( $\delta_2$ ,  $\gamma_2$ ). All fitted ANCOVAs have a p-value below  $2 \cdot 10^{-16}$ . Significance code:  $<10^{-3}$  \*\*\*,  $<10^{-2}$  \*\*,  $<0.05$  \*

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 105

106 **Fig. S1:** The decrease of the ingestion ratio with temperature depends on body  
107 mass



108  
109 **Figure S1:** The ingestion ratio (equation (11)) decreases with temperature. Values above one (resp. below) indicate  
110 a net energy gain (resp. loss). The bigger the consumer body mass  $m_1$ , the stronger the decrease. Note that the  
111 critical temperature  $T_c(f_1)$  above which a consumer with feeding preference  $f_1$  cannot survive is independent of  
112 its body mass  $m_1$ . Here, we chose  $f_1 = m_0 = 1$ . All other parameters as in **Table 1**.

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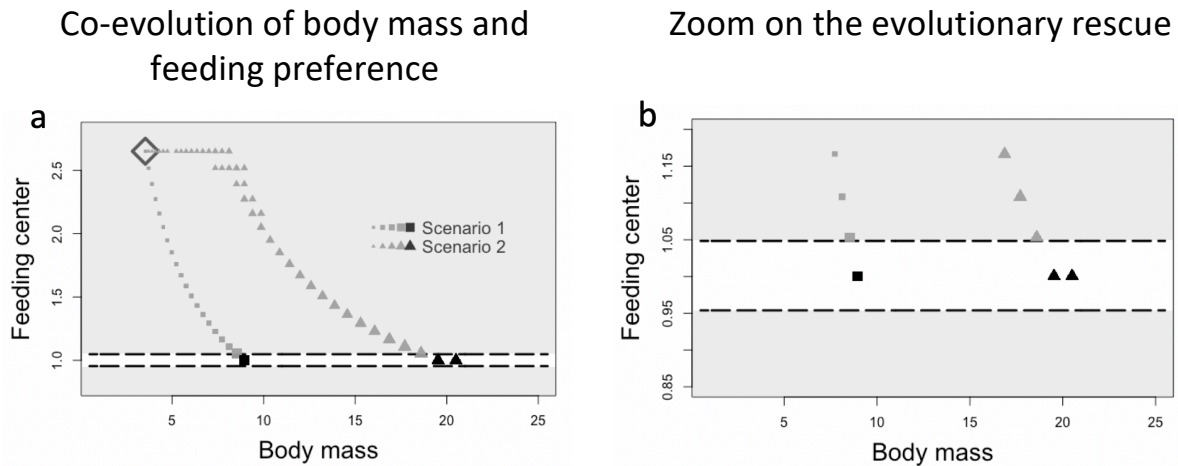
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125 **Fig. S2:** Consumer Resource module: the two-trait co-evolution scenario

126



127 **Figure S2: a.** Co-evolution of body mass and feeding preference under two scenarios. **Scenario 1:** body mass and  
128 feeding preference evolve at rate  $\mu = 10^{-2}$  (squares). **Scenario 2:** body mass evolves at  $\mu = 10^{-2}$  while feeding  
129 preference evolves at  $\mu = 10^{-3}$  (triangles). Unfilled grey diamond: initial conditions. The simulations started at  
130 280 K and the increase in symbol size indicates the direction of time. The biggest grey symbols thus correspond  
131 to the long-term selected phenotypes at 280 K. Once such a stable evolutionary state is reached, a warming to  
132 316.4 K (almost maximal sustainable temperature) occurs. The consumer body mass and feeding preference, which  
133 were within the non-viability area at 316.4 K (light grey), evolve in response to warming. The newly selected  
134 phenotypes (black symbols) are within the viability area at 316.4 K (white), which indicates an evolutionary rescue  
135 process. **b.** Zoom (y-axis) to see the evolutionary rescue consecutive to warming. Note that the selected phenotypes  
136 at 280 K were one mutation away from being viable at 316.4 K. Parameter values are in **table 1**.

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# 150 **Appendix S1: Eco-evolutionary dynamics of the** 151 **Consumer-Resource module**

152  
 153 This document is dedicated to present the analytical work supporting the results  
 154 presented in the main document on the CR module. The main equations (main document) are  
 155 indexed as in the main document while new important ones are indexed by a letter, in order to  
 156 avoid confusion. The same applies for figures or tables. This document also serves to present  
 157 some complementary side results we feel improve the understanding of our work.

158

## 159 **A. Ecological dynamics:**

160

161 Population dynamics are given by the following equations:

162

$$\frac{dB_0}{dt} = r \left(1 - \frac{B_0}{K}\right) B_0 - a_{10} B_1 B_0 \quad (9)$$

$$\frac{dB_1}{dt} = e a_{10} B_0 B_1 - (a_{11}(1 - e) + c_{11}) B_1^2 - d_1 B_1 \quad (10)$$

163

### 164 **1. Ecological equilibria:**

165

166 Ecological equilibria are given by resolving  $\frac{dB_0}{dt} = 0$  and  $\frac{dB_1}{dt} = 0$  which leads to 4 possible  
 167 solutions:

168

$$\{B_0^* = 0 ; B_1^* = 0\}$$

169

$$\{B_0^* = K ; B_1^* = 0\}$$

170

$$\left\{ B_0^* = 0 ; B_1^* = \frac{-d_1}{(a_{11}(1 - e) + c_{11})} \right\}$$

171

$$\left\{ B_0^* = K \left( 1 - \frac{a_{10} \left( e a_{10} - \frac{d_1}{K} \right)}{\frac{r}{K} (a_{11}(1 - e) + c_0) + e a_{10}^2} \right) ; B_1^* = \frac{r \left( e a_{10} - \frac{d_1}{K} \right)}{\frac{r}{K} (a_{11}(1 - e) + c_0) + e a_{10}^2} \right\}$$

172

173 The third equilibrium is not reachable because  $B_1^* < 0$ . The fourth equilibrium is called the  
 174 coexistence equilibrium.



## 175 2. Ingestion ratio and coexistence:

176

177 The coexistence equilibrium is possible when  $B_0^* \geq 0$  and  $B_1^* \geq 0$ .

178 First, we demonstrate:  $\forall T \geq 0, B_0^* \geq 0$  at the coexistence equilibrium.

179

$$180 \quad B_0^* > 0 \Leftrightarrow \frac{r}{K} (a_{11}(1-e) + c_{11}) + ea_{10}^2 - a_{10} \left( ea_{10} - \frac{d_1}{K} \right) > 0$$

$$181 \quad \Leftrightarrow \frac{r}{K} (a_{11}(1-e) + c_{11}) + a_{10} \frac{d_1}{K} > 0$$

182

183 The last relation is always true which ends the proof.

184

185 The flux of biomass providing energy from resource to consumer ( $ea_{10}B_0^*(T)$ ) divided by the

186 flux of biomass lost due to metabolic expenditures ( $d_1(T)$ ) corresponds to the ingestion ratio

187  $IR$ .

188

$$189 \quad IR \stackrel{\text{def}}{=} \frac{\text{Ingestion}}{\text{Metabolism}} \stackrel{\text{def}}{=} \frac{ea_{10}B_0^*(T)}{d_1(T)}$$

190 But

$$191 \quad B_0^* = K \left( 1 - \frac{a_{10} \left( ea_{10} - \frac{d_1}{K} \right)}{\frac{r}{K} (a_{11}(1-e) + c_0) + ea_{10}^2} \right) = \frac{r(a_{11}(1-e) + c_0) + a_{10}d_1}{\frac{r}{K} (a_{11}(1-e) + c_0) + ea_{10}^2}$$

192 So that:

193

$$IR = \frac{\left[ a_{10} + \frac{r}{d_1} (a_{11}(1-e) + c_0) \right] ea_{10}}{\frac{r}{K} (a_{11}(1-e) + c_0) + ea_{10}^2} \quad (11)$$

194

195 Now, we show that the consumer population is viable if and only if its ingestion rate is above

196 one.

197

198 We have:

$$199 \quad 0 = \frac{dB_1}{dt} = ea_{10}B_0^*B_1^* - d_1B_1^* - (a_{11}(1-e) + c_{11})B_1^{*2}$$

200 Which implies:

$$201 \quad ea_{10}B_0^*B_1^* - d_1B_1^* > 0$$

202 Now:

$$203 \quad B_1^* > 0 \Leftrightarrow ea_{10}B_0^*(T) > d_1(T) \Leftrightarrow \text{Ingestion} > \text{Metabolism} \Leftrightarrow IR > 1$$

204

### 205 3. Critical and limit temperature:

206 We now prove that the ingestion ratio reaches a value of one at a critical temperature above  
 207 which, according to the previous section, no consumer population can survive. For  
 208 convenience, we introduce the following notations:

209

210 We define  $M_0, M_1, F_1$  by  $M_1 \stackrel{\text{def}}{=} \log_{10}(m_1)$   $F_1 \stackrel{\text{def}}{=} \log_{10}(f_1)$

$$211 \quad IR \geq 1 \Leftrightarrow B_1^* \geq 0 \Leftrightarrow ea_{10} \geq \frac{d_1}{K} \Leftrightarrow \frac{e}{\sqrt{2\pi}s} \exp\left(-\frac{(F_1 - M_0)^2}{2s^2}\right) \geq \frac{d_0}{K_0} \exp\left(\frac{-2E(T_0 - T)}{kTT_0}\right)$$

$$212 \quad \Leftrightarrow \frac{(F_1 - M_0)^2}{2s^2} \leq \ln\left(\frac{eK_0}{\sqrt{2\pi}s d_0}\right) + \frac{2E(T_0 - T)}{kTT_0}$$

213

$$214 \quad \Leftrightarrow T \leq \frac{2E}{\frac{2E}{T_0} + k \left[ \frac{(F_1 - M_0)^2}{2s^2} + \ln\left(\frac{\sqrt{2\pi}s d_0}{eK_0}\right) \right]} \stackrel{\text{def}}{=} T_c(F_1)$$

215

216  $T_c(F_1)$  is maximal when its denominator is minimal, that is to say when  $F_1 = M_0$ . Note that  
 217 this is the parametrization used in the case of body mass evolution, feeding center being fixed.

218 It leads to equation (12):

219

$$220 \quad T_c(f_1) \leq T_{lim} \stackrel{\text{def}}{=} \frac{2E}{\frac{2E}{T_0} + k \left( \ln\left(\frac{\sqrt{2\pi}s d_0}{eK_0}\right) \right)} \quad (12)$$

220

221 With the standard parameter values presented in table 1,  $T_{lim} \approx 316.4$  K.

222

223 In the case of feeding preference evolution, the convenient way to express the condition for  
 224 coexistence ( $B_1^* \geq 0$ ), is the following (used for the viability areas in the E3 diagrams **Fig. 3**).

225

$$226 \quad \frac{(F_1 - M_0)^2}{2s^2} \leq \ln\left(\frac{eK_0}{\sqrt{2\pi}sd_0}\right) + \frac{2E(T_0 - T)}{kTT_0}$$

$$227 \quad \Leftrightarrow \left( \begin{array}{c} \ln\left(\frac{eK_0}{\sqrt{2\pi}sd_0}\right) + \frac{2E(T_0 - T)}{kTT_0} \geq 0 \\ -\sqrt{2s^2 \left[ \ln\left(\frac{eK_0}{\sqrt{2\pi}sd_0}\right) + \frac{2E(T_0 - T)}{kTT_0} \right]} \leq F_1 - M_0 \leq \sqrt{2s^2 \left[ \ln\left(\frac{eK_0}{\sqrt{2\pi}sd_0}\right) + \frac{2E(T_0 - T)}{kTT_0} \right]} \end{array} \right)$$

$$229 \quad \left( \begin{array}{c} T \leq \frac{2E}{\frac{2E}{T_0} + k \left( \ln\left(\frac{\sqrt{2\pi}sd_0}{eK_0}\right) \right)} \stackrel{\text{def}}{=} T_{lim} \\ -\sqrt{2s^2 \left[ \ln\left(\frac{eK_0}{\sqrt{2\pi}sd_0}\right) + \frac{2E(T_0 - T)}{kTT_0} \right]} \leq F_1 - M_0 \leq \sqrt{2s^2 \left[ \ln\left(\frac{eK_0}{\sqrt{2\pi}sd_0}\right) + \frac{2E(T_0 - T)}{kTT_0} \right]} \end{array} \right) \quad (A)$$

230

#### 231 4. Ingestion ratio and body mass:

232 We have:

$$233 \quad IR = \frac{\left[ a_{10} + \frac{r}{d_1} (a_{11}(1 - e) + c_0) \right] e a_{10}}{\frac{r}{K} (a_{11}(1 - e) + c_0) + e a_{10}^2} \quad (11)$$

234

234 The only remaining dependence of temperature is due to the relative productivity  $\frac{r}{K}$  of the pool

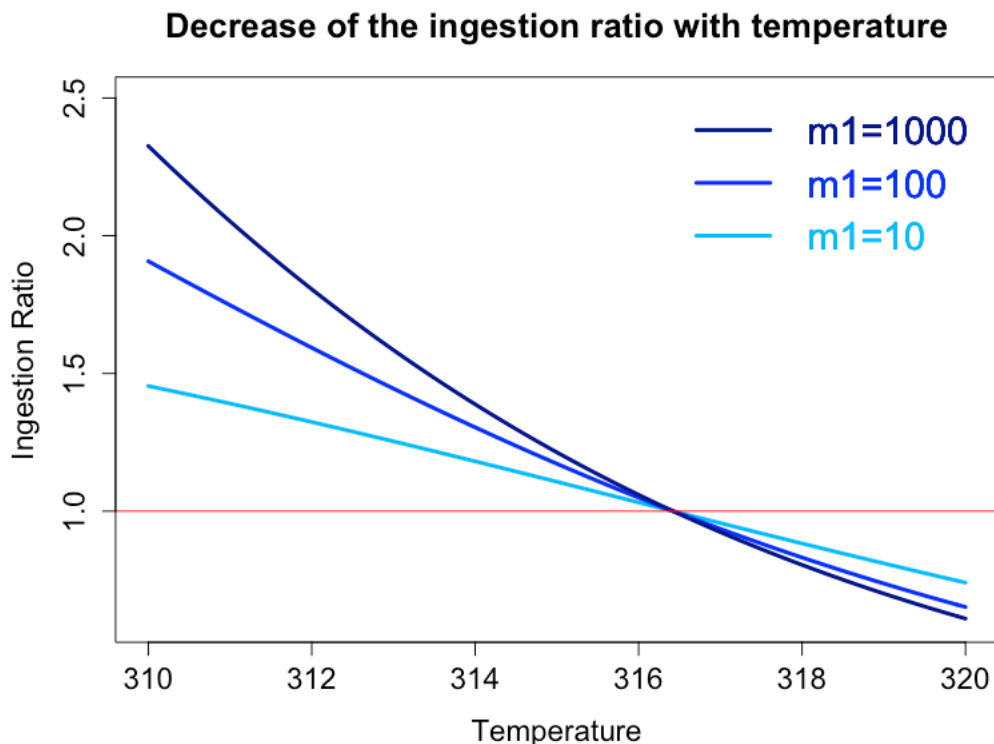
235 of plants forming the basal resource. It increases exponentially with temperature ( $\frac{r}{K} =$

236  $\frac{r_0}{K_0} \exp\left(\frac{-2E(T_0 - T)}{kTT_0}\right)$ ) and explains that the ingestion ratio decreases with temperature. It is

237 interesting to investigate this relationship for different consumer body masses  $m_1$  as bigger

238 body masses are expected as one goes up the trophic network. **Fig. S1** shows that the ingestion

239 ratio exhibits a sharper decrease with temperature as the consumer body mass increases.



240

241 **Figure S1:** The ingestion ratio (equation (11)) decreases with temperature. Values above one (resp. below) indicate  
242 a net energy gain (resp. loss). The bigger the consumer body mass  $m_1$ , the stronger the decrease. Note that the  
243 critical temperature  $T_c(f_1)$  above which a consumer with feeding preference  $f_1$  cannot survive is independent of  
244 its body mass  $m_1$ . Here, we chose  $f_1 = m_0 = 1$ . All other parameters as in **Table 1**.

245

246 This result indicates that upper trophic levels, that are associated with bigger sizes (**Fig. 2c&f**),  
247 are likely to suffer more from warming than lower trophic levels. We would like to point out  
248 that the ranking of ingestion ratios with body masses observed in the CR module  
249 ( $IR(m_1 = 1000) > IR(m_1 = 100) > IR(m_1 = 10)$ ) do not contradict the fact that upper  
250 trophic levels are likely to be initially closer to their critical ingestion ratio. Indeed, the  
251 argument relies on the trophic distance from the basal resource, each trophic interaction being  
252 associated with losses ( $e < 1$ ). Here (**Fig. S1**), the three consumer populations differ in body  
253 mass but have the same trophic level (= 1).

254

## 255 **B. Evolutionary dynamics:**

256

### 257 **1. The adaptive dynamics framework**

258 In the case of body mass ( $m_1$ ) evolution, the invasion fitness  $w(m_1^{mut}, m_1^{res})$  of a rare  
 259 mutant corresponds to its relative growth rate in the resident population:

$$w(m_1^{mut}, m_1^{res}) = \left[ \frac{1}{B_1^{mut}} \frac{dB_1^{mut}}{dt} \right]_{B_0^*, B_1^*, B_1^{mut} \ll B_1^*} \quad (\text{B})$$

260 The sequence of trait substitutions describes the evolutionary dynamics of the system and can  
 261 be approximated by the canonical equation (Dieckmann & Law, 1996) that links the trait  
 262 dynamics to the selection gradient:

$$\frac{dm_1}{dt} = CN_1^* \mu \sigma^2 \underbrace{\left[ \frac{\partial w(m_1^{mut}, m_1^{res})}{\partial m_1^{mut}} \right]_{m_1^{mut} = m_1^{res} = m_1}}_{\text{selection gradient}} \quad (\text{C})$$

263 where  $C, N_1^*, \mu, \sigma$  are respectively a homogenizing constant, the equilibrium resident population  
 264 density, the mutation rate and the amplitude of mutations. The zeros of equation (C) are  
 265 evolutionary singularities,  $m_1^*$ , satisfying:

$$\left[ \frac{\partial w(m_1^{mut}, m_1^{res})}{\partial m_1^{mut}} \right]_{m_1^{mut} = m_1^{res} = m_1} = 0 \quad (\text{D})$$

266  
 267 The convergence and invasibility properties of an evolutionary singularity are determined via  
 268 the second derivatives of the invasion fitness function as detailed in section B.2.d.

269

## 270 2. How does the selected body mass depend on temperature?

271 Reminder: we define  $M_0, M_1, F_1$  by  $M_1 \stackrel{\text{def}}{=} \log_{10}(m_1)$   $F_1 \stackrel{\text{def}}{=} \log_{10}(f_1)$

### 272 a. Fitness of invasion

273 Here, we expose the whole approach to determine the invasion fitness function in the adaptive  
 274 dynamics' framework:

275 We consider a rare mutant 1' appearing in the resident population 1, given the population  
 276 dynamics equations, we have:

277

$$278 \quad \frac{1}{B_{1'}} \frac{dB_{1'}}{dt} = \underbrace{ea_{1'0}B_0}_{\text{ressource}} - \overbrace{(c_{1'1'}B_{1'} + c_{1'1}B_1)}^{\text{competition}} + \underbrace{(ea_{1'1}B_1 - a_{11'}B_1 - (1-e)a_{1'1'}B_{1'})}_{\text{consumption interaction between 1 and 1'}} - d_{1'}$$

279

280

281 Given 1 and 1' have the same feeding preference, we have  $c_{1'1'} = c_{1'1} = c_0$  and  $a_{11'} = a_{1'1'}$ .

282 Also,  $B_{1'} \ll B_1$  (rare mutant). Hence:  $c_{1'1'}B_{1'} \ll c_{1'1}B_1$  and  $(1-e)a_{1'1'}B_{1'} \ll a_{11'}B_1$

283 All in all, we deduce:

$$284 \quad \frac{1}{B_{1'}} \frac{dB_{1'}}{dt} = ea_{1'0}B_0 - c_0B_1 - a_{11'}B_1 + ea_{1'1}B_1 - d_{1'}$$

285 Which leads to:

286

$$287 \quad w(M_{1'}, M_1) \stackrel{\text{def}}{=} \left[ \frac{1}{B_{1'}} \frac{dB_{1'}}{dt} \right]_{\substack{B_{1'} \ll B_1 \\ B_0^*, B_1^*}} = ea_{1'0}B_0^* - c_0B_1^* - a_{11'}B_1^* + ea_{1'1}B_1^* - d_{1'}$$

288

### 289 b. Evolutionary singularities

290 We first need to determine the derivative of the fitness invasion function with respect to the

291 mutant body mass (first variable):

292

$$293 \quad \frac{\partial w(M_{1'}, M_1)}{\partial M_{1'}} = eB_0^* \frac{\partial a_{1'0}}{\partial M_{1'}} - \underbrace{\frac{\partial c_0 B_1^*}{\partial M_{1'}}}_0 - B_1^* \frac{\partial a_{11'}}{\partial M_{1'}} + eB_1^* \frac{\partial a_{1'1}}{\partial M_{1'}} - \frac{\partial d_{1'}}{\partial M_{1'}}$$

$$294 \quad = -\frac{\ln(10)}{4} ea_{1'0}B_0^* - \frac{(F_1 - M_{1'})}{s^2} a_{11'} - \frac{\ln(10)}{4} ea_{1'1}B_1^* - \frac{\ln(10)}{4} d_{1'}$$

295

296 Thus:

$$297 \quad \left[ \frac{\partial w(M_{1'}, M_1)}{\partial M_{1'}} \right]_{M_{1'}=M_1} = -\frac{\ln(10)}{4} (ea_{1'0}B_0^* + ea_{11'}B_1^* - d_{1'}) - \frac{(F_1 - M_1)}{s^2} a_{11'}B_1^*$$

298

299 At ecological equilibrium  $\frac{dB_1}{dt} = 0$  gives  $ea_{1'0}B_0^* + ea_{11'}B_1^* - d_{1'} = c_0B_1^* + a_{11'}B_1^*$  and hence:

300

$$301 \quad \left[ \frac{\partial w(M_{1'}, M_1)}{\partial M_{1'}} \right]_{M_{1'}=M_1} = B_1^* \left( -\frac{\ln(10)}{4} (c_0 + a_{11'}) - \frac{(F_1 - M_1)}{s^2} a_{11'} \right)$$

302

303 Evolutionary singularities occur when the selection gradient vanishes:

304

$$305 \quad \left[ \frac{\partial w(M_{1'}, M_1)}{\partial M_{1'}} \right]_{M_{1'}=M_1} = 0 \Leftrightarrow -\frac{\ln(10)}{4} (c_0 + a_{11}) - \frac{(F_1 - M_1^*)}{s^2} a_{11} = 0$$

$$306 \quad \Leftrightarrow c_0 + a_{11} \left( 1 - \frac{4(M_1 - F_1)}{s^2 \ln(10)} \right) = 0$$

307 Noting explicitly the dependence of  $a_{11}$  on  $M_1$ , we deduce evolutionary singularities  $M_1^*$  verify:

308

$$c_0 + a_{11}(M_1^*) * \left( 1 - \frac{4(M_1^* - F_1)}{s^2 \ln(10)} \right) = 0 \quad (E)$$

309

310 Temperature does not influence any parameter of equation (E) indicating that warming has no  
311 effect on the evolutionary dynamics of body mass here.

312

### 313 3. How does the selected feeding preference depend on temperature?

#### 314 a. Fitness of invasion

315

316 Here, the evolving trait is  $f_1$  or equivalently  $F_1$ . As we did before, we consider the appearance  
317 of a new morph 1' issued from 1 by a random small mutation.

318 Given our model, its biomass follows the equation (note that  $d_1 = d_{1'}$ ):

319

$$320 \quad \frac{1}{B_{1'}} \frac{dB_{1'}}{dt} = ea_{1'0}B_0 + ea_{1'1}B_1 - (1 - e)a_{1'1'}B_{1'} - a_{11'}B_1 - c_{1'1'}B_{1'} - c_{11'}B_1 - d_1$$

321

322 Using  $B_{1'} \ll B_1$  and  $F_1 \approx F_{1'}$  (small mutation hypothesis), we find:

323

$$324 \quad \frac{1}{B_{1'}} \frac{dB_{1'}}{dt} = ea_{1'0}B_0 + (ea_{1'1} - a_{11'})B_1 - c_{11'}B_1 - d_1$$

325

326 When considered at ecological equilibrium, the previous expression gives the invasion fitness  
327 function:

328

$$329 \quad w(F_{1'}, F_1) \stackrel{\text{def}}{=} \left[ \frac{1}{B_{1'}} \frac{dB_{1'}}{dt} \right]_{\substack{B_{1'} \ll B_1 \\ B_0^*, B_1^*}} = ea_{1'0}B_0^* + (ea_{1'1} - a_{11'})B_1^* - c_{11'}B_1^* - d_1$$

330

331 *b. Evolutionary singularities:*

332 When the selection gradient vanishes:

333

$$334 \quad \left[ \frac{\partial w(F_{1'}, F_1)}{\partial F_{1'}} \right]_{F_{1'}=F_1} = 0 \Leftrightarrow \left[ eB_0^* \frac{\partial a_{1'0}}{\partial F_{1'}} + eB_1^* \frac{\partial a_{1'1}}{\partial F_{1'}} - B_1^* \underbrace{\frac{\partial a_{11'}}{\partial F_{1'}}}_0 - B_1^* \frac{\partial c_{11'}}{\partial F_{1'}} - \underbrace{\frac{\partial d_1}{\partial F_{1'}}}_0 \right]_{F_{1'}=F_1} = 0$$

$$335 \quad \Leftrightarrow \frac{-eB_0^*}{s^2} a_{10}(F_1 - M_0) - \frac{eB_1^*}{s^2} a_{11}(F_1 - M_1) + \frac{B_1^*}{2s^2} \underbrace{(F_1 - F_1)}_0 c_0 = 0$$

336

337

338 So that evolutionary singularities  $F_1^*$  satisfy:

339

$$(M_1 - F_1^*)a_{11}B_1^* - (F_1^* - M_0)a_{10}B_0^* = 0 \quad (\text{F})$$

340

341

342 *Proof of the existence of at least one singularity:*

343

344 Here, we prove that equation (F) has at least one solution and that all solutions  $F_1^*$  verify:  $M_0 <$

345  $F_1^* < M_1$ . For convenience we define:

$$346 \quad \alpha \text{ such as : } F_1 = \alpha M_0 + (1 - \alpha)M_1 \quad \text{ie: } \alpha \stackrel{\text{def}}{=} \frac{M_1 - F_1}{M_1 - M_0}$$

347

$$348 \quad L \stackrel{\text{def}}{=} \frac{M_1 - M_0}{s}$$

349 Equation (F) can be rewritten with these new notations, by noting that  $M_1 - M_0 > 0$

350 (hypothesis of the model):

$$\alpha \exp\left(\frac{-\alpha^2 L^2}{2}\right) B_1^*(\alpha, T, M_1, L) - (1 - \alpha) \exp\left(\frac{-(1 - \alpha)^2 L^2}{2}\right) B_0^*(\alpha, T, M_1, L) = 0 \quad (\text{G})$$

351 We define:

$$352 \quad z(\alpha, T, M_1, L) \stackrel{\text{def}}{=} \alpha \exp\left(\frac{-\alpha^2 L^2}{2}\right) B_1^*(\alpha, T, M_1, L) - (1 - \alpha) \exp\left(\frac{-(1 - \alpha)^2 L^2}{2}\right) B_0^*(\alpha, T, M_1, L)$$



353

354 We have,  $z(0, T, M_1, L) < 0, z(1, T, M_1, L) > 0$  and, given  $T, M_1, L$   $z_\alpha : \alpha \rightarrow z(\alpha, T, M_1, L)$   
 355 is a continuous function. So, by the Intermediate Value Theorem, there exists  $\alpha^*$  such that  
 356  $z_\alpha(\alpha^*) = z(\alpha, T, M_1, L) = 0$ . This is equivalent to say that equation (D) or (16) has at least one  
 357 solution. Moreover, under coexistence (i.e.  $B_0^* > 0$  and  $B_1^* > 0$ ), if  $\alpha \leq$   
 358  $0$  then  $z(\alpha, T, M_1, L) < 0$  and if  $\alpha \geq 1$  then  $z(\alpha, T, M_1, L) > 0$  so that we have necessarily  
 359  $0 < \alpha^* < 1$ . This is equivalent to  $M_0 < F_1^* < M_1$ . This ends the proof.

360

361 *c. Effect of warming on feeding preference evolution and emergence of 4*  
 362 *scenarios:*

363

364 Since  $B_0^*(T)$  and  $B_1^*(T)$  do depend on the temperature, equation (F) indicates temperature  
 365 has an impact on the singularities and consequently on evolutionary dynamics. In order to go  
 366 further, we rewrite (F) replacing  $B_0^*$  and  $B_1^*$  by their explicit expressions and isolating the  
 367 temperature from the evolutionary singularity:

368 equation (F)  $\Leftrightarrow$  equation (G)  $\Leftrightarrow \frac{B_1^*(\alpha, T, M_1, L)}{B_0^*(\alpha, T, M_1, L)} = \frac{(1 - \alpha) \exp\left(\frac{-(1 - \alpha)^2 L^2}{2}\right)}{\alpha \exp\left(\frac{-\alpha^2 L^2}{2}\right)}$

369  $\Leftrightarrow \frac{ea_{10} - \frac{d_\infty 10^{-\frac{M_1}{4}}}{K_\infty} \exp\left(\frac{-2E}{kT}\right)}{a_{11}(1 - e) + c_0 + \frac{d_\infty 10^{-\frac{M_1}{4}}}{R_\infty} a_{10}} = \frac{(1 - \alpha) \exp\left(\frac{-(1 - \alpha)^2 L^2}{2}\right)}{\alpha \exp\left(\frac{-\alpha^2 L^2}{2}\right)}$

370  $\Leftrightarrow e \exp\left(\frac{-(1 - \alpha)^2 L^2}{2}\right)$

371  $-\frac{\sqrt{2\pi} s d_\infty}{K_\infty} \exp\left(\frac{-2E}{kT}\right)$

372  $= \left[ (1 - \alpha) \exp\left(\frac{-\alpha^2 L^2}{2}\right) + \sqrt{2\pi} s c_0 10^{\frac{M_1}{4}} \right.$

373  $\left. + \frac{d_\infty 10^{-\frac{M_1}{4}}}{R_\infty} \exp\left(\frac{-(1 - \alpha)^2 L^2}{2}\right) \right] \left[ \frac{(1 - \alpha) \exp\left(\frac{-(1 - \alpha)^2 L^2}{2}\right)}{\alpha \exp\left(\frac{-\alpha^2 L^2}{2}\right)} \right]$

374

$$\begin{aligned}
 375 \quad & \Leftrightarrow e \exp\left(\frac{-(1-\alpha)^2 L^2}{2}\right) - \frac{\sqrt{2\pi} s d_\infty}{K_\infty} \exp\left(\frac{-2E}{kT}\right) \\
 376 \quad & = (1-e) \frac{(1-\alpha)}{\alpha} \exp\left(\frac{-(1-\alpha)^2 L^2}{2}\right) + \sqrt{2\pi} s c_0 10^{\frac{M_1}{4}} \frac{(1-\alpha)}{\alpha} \exp\left(\frac{-(1-2\alpha)L^2}{2}\right) \\
 377 \quad & + \frac{(1-\alpha) d_\infty 10^{\frac{-M_1}{4}}}{R_\infty} \exp\left(\frac{-(2(1-\alpha)^2 - \alpha^2)L^2}{2}\right)
 \end{aligned}$$

378

379 We define  $C(M_1) = \sqrt{2\pi} s c_0 10^{\frac{M_1}{4}}$  and have the equivalence with:

$$\begin{aligned}
 380 \quad & \frac{\sqrt{2\pi} s d_\infty}{K_\infty} \exp\left(\frac{-2E}{kT}\right) \\
 381 \quad & = \frac{-1}{\alpha} \left[ (1-\alpha) C(M_1) \exp\left(\frac{-(1-2\alpha)L^2}{2}\right) \right. \\
 382 \quad & \left. + (1-\alpha) \frac{d_\infty 10^{\frac{-M_1}{4}}}{R_\infty} \exp\left(\frac{-(2(1-\alpha)^2 - \alpha^2)L^2}{2}\right) \right. \\
 383 \quad & \left. + \left[ (-\alpha e + (1-e)(1-\alpha)) \exp\left(\frac{-(1-\alpha)^2 L^2}{2}\right) \right] \right]
 \end{aligned}$$

384

$$\begin{aligned}
 385 \quad & \Leftrightarrow \frac{\sqrt{2\pi} s d_\infty}{K_\infty} \exp\left(\frac{-2E}{kT}\right) \\
 386 \quad & = \frac{-1}{\alpha} \left[ (1-\alpha) C(M_1) \exp\left(\frac{-(1-2\alpha)L^2}{2}\right) + (1-e-\alpha) \exp\left(\frac{-(1-\alpha)^2 L^2}{2}\right) + (1 \right. \\
 387 \quad & \left. - \alpha) \frac{d_\infty 10^{\frac{-M_1}{4}}}{R_\infty} \exp\left(\frac{-(2(1-\alpha)^2 - \alpha^2)L^2}{2}\right) \right]
 \end{aligned}$$

388

$\Leftrightarrow Q(T) = G(\alpha, M_1, L)$ <span style="float: right;">(H)</span>
---

389

390 Where the functions  $Q(T)$  and  $G(\alpha, M_1, L)$  are defined by:

391

$$392 \quad Q(T) \stackrel{\text{def}}{=} \frac{\sqrt{2\pi} s d_\infty}{K_\infty} \exp\left(\frac{-2E}{kT}\right)$$

393

$$G(\alpha, M_1, L) \stackrel{\text{def}}{=} \frac{-1}{\alpha} \left[ (1 - \alpha) C(M_1) \exp\left(\frac{-(1 - 2\alpha)L^2}{2}\right) + (1 - e - \alpha) \exp\left(\frac{-(1 - \alpha)^2 L^2}{2}\right) + (1 - \alpha) \frac{d_\infty 10^{-\frac{M_1}{4}}}{R_\infty} \exp\left(\frac{-(2(1 - \alpha)^2 - \alpha^2)L^2}{2}\right) \right]$$

396

397 To investigate the effect of temperature on the evolutionary dynamics, we analyze the  
398 functions:

$$\begin{aligned} 399 \quad & T \rightarrow Q(T) \\ 400 \quad & \alpha \rightarrow G(\alpha, M_1, L) \end{aligned}$$

401

402 Q captures the temperature component of selection while G captures the biotic components of  
403 selection that depend on the consumer feeding preference ( $\alpha$ ), body mass ( $M_1$ ) and consumer  
404 to resource body mass ratio (L).

405

406 Study of Q as a function of T:

407 Q is increasing with the temperature T and has the following variation table:

408

T	0	$+\infty$
Q(T)	0	$\frac{\sqrt{2\pi}sd_\infty}{K_\infty}$

409 **Table A:** Table of variation of  $Q(T)$ . Note that  $Q(T)$  is always positive.

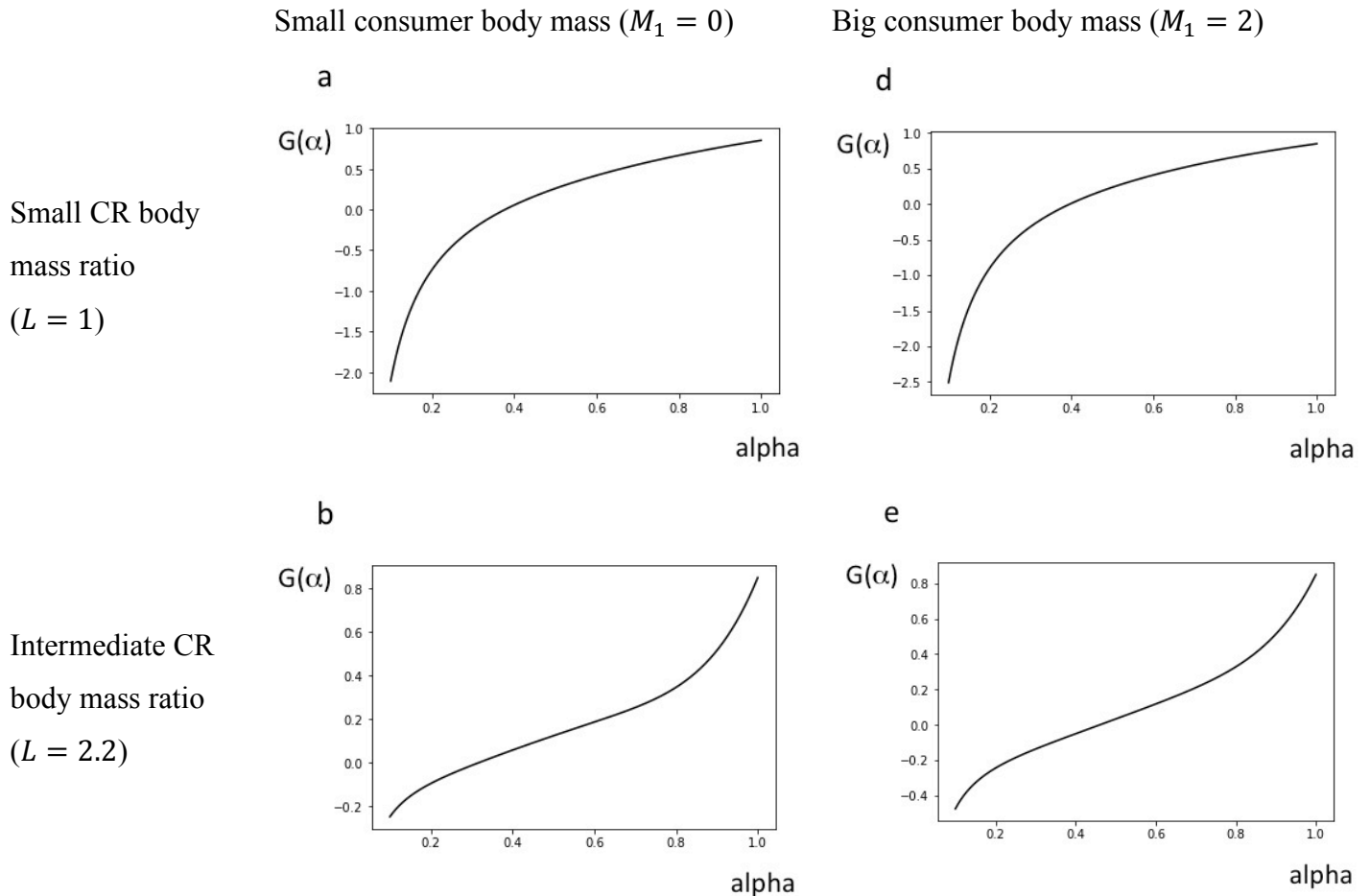
410

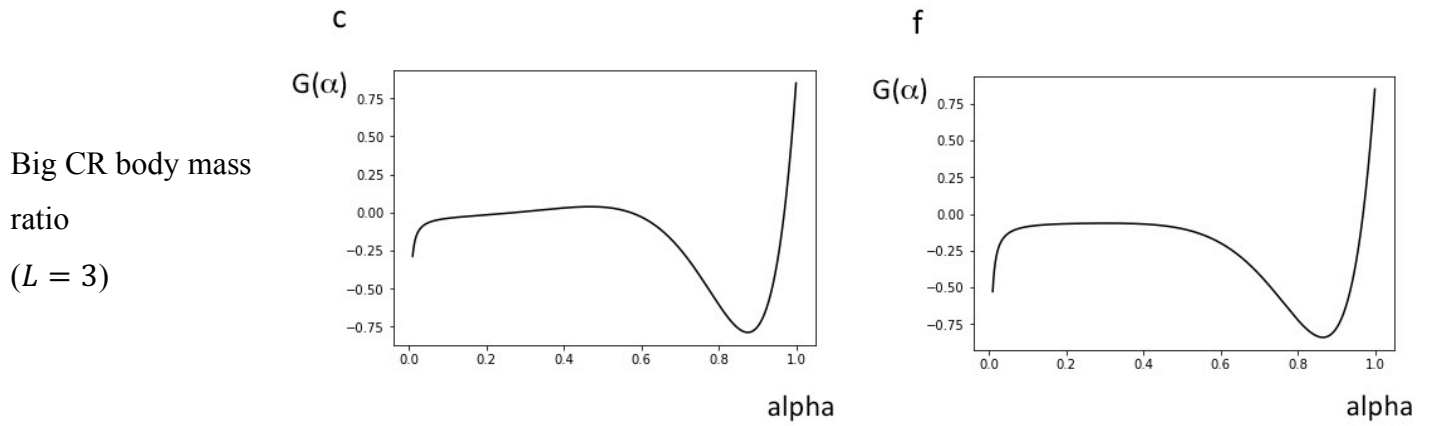
411

412 Study of G as a function of  $\alpha$ ,  $M_1$  and L seen as parameters:

413 Analytically we cannot determine all the possible behaviors of G. Thus, we used the  
414 software Python to investigate its variation. **Fig. B** shows the shape of G for different values  
415 of Consumer to Resource (CR) body mass ratios.

416 For small CR body mass ratios,  $G$  is increasing with  $\alpha$  (**Fig. B a&d**). For big CR body  
 417 mass ratios,  $G$  is not monotonous anymore (**Fig. B c&f**). There is a value of the parameter  $L$ ,  
 418  $M_1$ -dependant, we refer to as  $L^c(M_1)$ , around which the switch of behavior from monotonous  
 419 to not monotonous occurs. We can show by studying the derivative  $\frac{\partial G}{\partial \alpha}$  that  $\forall M_1 \in \mathbb{R}, L^c(M_1) \geq$   
 420  $\sqrt{2}$ . Its value is around 2.2 for the values of  $M_1$  we investigated ( $M_1 = 0$  and  $M_1 = 2$ ). In  
 421 addition, just before the change of behavior occurs, the curvature of  $G$  changes (**Fig. B b&e**)  
 422 meaning its second derivative switches sign. This can have consequences on the nature of the  
 423 singularities as this nature depends on the second derivatives of the fitness gradient. This led us  
 424 to consider scenarios with an intermediate CR body masses ratio.  
 425  
 426  
 427





428 **Fig. B:** Plots of  $G(\alpha)$  for various values of  $L$  and  $M_1$ .

429 From the previous analysis, we deduce the following table of variation for  $G$ :

430

Case	$\alpha$	0	$\alpha_1(M_1, L)$	$\alpha_2(M_1, L)$	1
$L \leq L^*(M_1)$	$G(\alpha)$				
$L > L^*(M_1)$	$G(\alpha)$				

431 **Table B:** Variation table of function  $G$  according to the value of  $L$

432 If the consumer to resource body mass ratio is small,  $G$  is strictly increasing with  $\alpha$  so that there  
 433 is necessarily only one singularity.

434 If the ratio between consumer and resource body mass is big, the behavior of  $G$  indicates  
 435 the existence of up to three singularities. The coexistence condition on temperature ( $T_{lim}$ )  
 436 implies  $Q(T) < e$  so that it is impossible to have two singularities (except one degenerate case)  
 437 Hence, in this case, there is one or three singularities, depending on  
 438  $G(\alpha_1(M_1, L))$ ,  $G(\alpha_2(M_1, L))$  and  $T$ .

439 Finally, while there is no qualitative difference between the case of a small consumer  
 440 body mass and a big one when the CR body mass ratio is either small (**Fig. A a&d**) or  
 441 intermediate (**Fig. A b&e**), there is one in the case it is big. In that case, when the consumer

442 body mass is small,  $G(\alpha_1) > 0$  (**Fig. A e**), while when the consumer body mass is big,  $G(\alpha_1) <$   
 443  $0$  (**Fig. A f**). This is important since  $Q(T)$  is always positive (see Table A). This means there  
 444 can potentially be 3 singularities in the case of a small consumer body mass while there is only  
 445 one in the case of a big consumer body mass.

446  
 447 All this analysis of equation (H) leads to distinguish 4 scenarios that differ in the impact  
 448 of warming on feeding preference evolution: small CR body mass ratio (**scenario A**),  
 449 intermediate CR body mass ratio (**scenario B**), big CR body mass ratio and small consumer  
 450 body mass (**scenario C**), big CR body mass ratio and big consumer body mass (**scenario D**).  
 451 These scenarios emerge through the technical analysis of the classical equation of adaptive  
 452 dynamics (equation D) but are ecologically consistent as they differ in parameters known to be  
 453 important for trophic interactions, namely body masses and body mass ratios ( $M_1, L = \frac{M_1 - M_0}{s}$   
 454  $\frac{M_1 - M_0}{s}$ ). These scenarios are presented in the following **table S1**, with their ecological meaning  
 455 and evolutionary dynamics.

456

457 Warming impacts the CR evolutionary dynamics: the 4 possible scenarios

458

459

Scenario	CR body mass ratio	Consumer body mass	Mathematical significance	Qualitative outcomes (evolution of $\alpha$ )
A	Small	Any	$L \ll L^c(M_1)$	<ul style="list-style-type: none"> <li>One singularity: a CSS that increases with temperature (higher resource consumption)</li> </ul>
B	Intermediate	Any	$L < L^c(M_1)$ $L \approx L^c(M_1)$	<ul style="list-style-type: none"> <li>One singularity whose value increases with warming (higher resource consumption)</li> <li>Warming switches the selection regime from disruptive (BP) to stabilizing (CSS) (loss of polymorphism)</li> </ul>

C	Big	Small	$L > L^c(M_1)$	<ul style="list-style-type: none"> <li>Three singularities (CSS, Repellor and BP) for low temperatures and only one (CSS) for high temperatures (evolutionary hysteresis)</li> </ul>
D		Big		<ul style="list-style-type: none"> <li>One singularity: a CSS that increases with warming (increased resource consumption)</li> </ul>

460 **Table S1:** The four possible scenarios with their biological and mathematical significances.  $L^c(M_1)$  is the value  
461 of  $L$ , determined numerically and  $M_1$ -dependent, around which important features of equation (H) change, leading  
462 to different evolutionary dynamics.

463

464 d. Nature of the evolutionary singularities

465

466 Let  $F_1^*$  be the evolutionary singularity.

467 Non-invasibility corresponds mathematically to:

468

469 
$$\left[ \frac{\partial w(F_{1'}, F_1)}{\partial F_{1'}} \right]_{F_{1'}=F_1=F_1^*} < 0$$

470 Moreover, we have the following expression obtained by derivation:

471

472 
$$\left[ \frac{\partial w(F_{1'}, F_1)}{\partial F_{1'}} \right]_{F_{1'}=F_1} = \frac{e}{s^2} a_{10} B_0^* ((1 - \alpha)^2 L^2 - 1) + \frac{e}{s^2} a_{11} B_1^* (\alpha^2 L^2 - 1) + \frac{B_1^* c_{11}}{2s^2}$$

473 We used this expression to determine numerically trough Python software the invasibility  
474 properties.

475

476 Convergence corresponds mathematically to:

477 
$$\left[ \frac{d}{dF_1} \left[ \frac{\partial w(F_{1'}, F_1)}{\partial F_{1'}} \right]_{F_{1'}=F_1} \right]_{F_1=F_1^*} < 0$$

478 In the case of one singularity  $F_1^*$ , it can be shown without calculation that the singularity will  
479 be convergent stable.

480 Proof:

481 Let  $F < M_0$  and  $0 < \varepsilon < \frac{M_0 - F}{2}$ , we have  $w(F + \varepsilon, F) > 0$  because the mutant with trait ( $F +$   
 482  $\varepsilon$ ) has better attack rates on both the resource and the resident  $F$  and experiences less  
 483 competition with the resident  $F$  than experienced by the resident ( $c_{11} = c_0$ ).

484 Hence,  $\left[ \frac{\partial w(F_{1'}, F_1)}{\partial F_{1'}} \right]_{F_{1'}=F_1, F_1=F} > 0$ .

485 In the same way, we have:  $\forall F > M_1, \left[ \frac{\partial w(F_{1'}, F_1)}{\partial F_{1'}} \right]_{F_{1'}=F_1, F_1=F} < 0$

486 Moreover, the function:

487 
$$\mathbb{R} \rightarrow \mathbb{R}$$

488 
$$F_1 \mapsto \left[ \frac{\partial w(F_{1'}, F_1)}{\partial F_{1'}} \right]_{F_{1'}=F_1}$$

489

490 is continuous and only vanishes at  $F = F_1^* \in ]M_0, M_1[$ .

491 Hence,  $\forall F < F_1^*, \left[ \frac{\partial w(F_{1'}, F_1)}{\partial F_{1'}} \right]_{F_{1'}=F_1, F_1=F} > 0$ ,  $\forall F > F_1^*, \left[ \frac{\partial w(F_{1'}, F_1)}{\partial F_{1'}} \right]_{F_{1'}=F_1, F_1=F} < 0$  and

492 
$$\left[ \frac{\partial w(F_{1'}, F_1)}{\partial F_{1'}} \right]_{F_{1'}=F_1, F_1=F_1^*} = 0 \text{ thus: } \left[ \frac{d}{dF_1} \left[ \frac{\partial w(F_{1'}, F_1)}{\partial F_{1'}} \right]_{F_{1'}=F_1} \right]_{F_1=F_1^*} < 0$$

493

494 In the case of three singularities  $F_1^* < F_2^* < F_3^*$ , with the same kind of arguments, we know at  
 495 least one singularity is convergent stable. It appears numerically that  $F_1^*$  and  $F_3^*$  are convergent  
 496 stable while  $F_2^*$  is not. This analysis gives the qualitative outcomes of warming for each scenario  
 497 presented in **Table S1**.

498

499

500 *e. Robustness check: variation of the conversion efficiency*

501

502 The conversion efficiency is likely to vary with the feeding mode, with overall smaller values  
 503 for herbivores and larger values for carnivores, as estimated by (Yodzis & Innes, 1992). We  
 504 propose here to investigate the effect of warming on the consumer's evolutionary dynamics  
 505 (trait  $\alpha$ ) for a value of conversion efficiency that corresponds to herbivory ( $e = 0.45$ ).

506

507 Value of  $T_{lim}$ :

508



509 The critical temperature value above which the consumer population cannot survive anymore  
 510 increases with the conversion efficiency as indicated by equation (B).

511

Conversion efficiency	Limit Temperature
$e = 0.85$	$T_{lim} = 316.4$
$e = 0.45$	$T_{lim} = 312.3$

512

513 Evolutionary dynamics:

514 Fig. B (akin Fig. 3) shows the evolutionary dynamics of the trait  $\alpha$  according to temperature  
 515 for the four scenarios (Table 1).

516

517

	<b>E<sup>3</sup>-diagrams</b>	<b>Comparison with Fig. 3</b>
<p><b>Scenario A</b>                      Small consumer to resource mass ratio (<math>L = 1</math>)</p>		<p>Similar to Scenario A presented in Fig. 3 a</p>
<p><b>Scenario B</b>                      Intermediate consumer to resource mass ratio (<math>L = 2.2</math>)</p>		<p>Different from Scenario B presented in Fig. 3 c:   <i>Branching does not occur anymore for low temperature values (Fig. 3c)</i></p>
<p><b>Scenario C</b>                      Big consumer to resource mass ratio (<math>L = 2.8</math>)                      Small consumer body mass (<math>m_1 = 1</math>)</p>		<p>Different from Scenario C presented in Fig. 3 f:   <i>We do not have two additionnal singularities (Branching Point and Repellor) for low temperature values. Consequently,</i></p>

		<i>evolutionary hysteresis is no longer possible.</i>
<p><b>Scenario D</b></p> <p>Big consumer to resource mass ratio (<math>L = 2.8</math>)</p> <p>Big consumer body mass (<math>m_1 = 100</math>)</p>		<p>Similar to Scenario D presented in Fig.3 h</p>

518 **Figure C:**  $E^3$  diagrams corresponding respectively to scenarios A, B, C and D (**Table S1**). Grey areas are non-  
519 viability regions; the curves indicate the evolutionary singularities with the type of lines indicating their nature. **a.**  
520 Thin black arrows indicate the direction of evolution and the big white arrow indicates potential evolutionary  
521 rescue. Note that there is potential for evolutionary rescue in all scenarios although it is illustrated only in **a.**

522 This analysis reveals that some of the results observed for a higher value of conversion  
523 efficiency hold while others do not.

<b>Consistent results</b>	<b>Non-consistent results</b>
<ul style="list-style-type: none"> <li>• All scenarios are characterized by an increasing CSS with warming: in order to cope with higher metabolic demands, the consumer population has to increase its attack rate on the basal resource. The ingestion ratio has to stay above the critical value of one.</li> <li>• Above a critical temperature <math>T_{lim}</math>, the consumer population cannot survive anymore whatever the trait <math>\alpha</math>.</li> <li>• For temperature below <math>T_{lim}</math>, <b>evolutionary rescue is always</b></li> </ul>	<ul style="list-style-type: none"> <li>• The four scenarios do not differ in their evolutionary dynamics anymore.</li> <li>• Whatever the scenario and the temperature, branching is not possible any more. Consequently, we do not observe warming reducing polymorphism (scenario B) nor evolutionary hysteresis (scenario C).</li> </ul>

<b>possible</b> as illustrated by the white arrow in <b>Fig. C a.</b>	
---	--

524

525 All in all, this robustness check confirms that evolutionary rescue is a potential mechanism by  
526 which evolution can impede the consumer population extinction given the temperature stays  
527 below a critical value  $T_{lim}$ . However, some of our results, such as the potential for warming to  
528 dampen diversification processes (Scenario B, Fig. 3) seem to only apply for higher value of  
529 conversion efficiency. This can be interpreted as additional evidence that higher trophic levels  
530 are more vulnerable to warming (e.g. Binzer et al., 2012).

531

532

#### 533 4. The co-evolution of body mass and feeding preference

534 The separation between body mass and feeding preference evolution implemented so far  
535 may only be justified if one trait evolves much faster than the other (e.g. asymmetries in  
536 heritabilities). In other conditions, the two traits coevolve. We simulated two co-evolutionary  
537 scenarios that differ in mutation rates ( $10^{-2}$  for both traits in scenario 1 and  $10^{-2}$  (resp.  $10^{-3}$ )  
538 for body mass (resp. feeding preference) in scenario 2). Warming goes from 280 to 316.4K  
539 (from 7 to 43°C, slightly below  $T_{lim}$ ). Evolutionary trajectories are shown on **Fig. S**.  
540 Evolutionary rescue occurs and enables food chain persistence. Note two important results.  
541 First, the two scenarios yield different evolutionary trajectories. The relative speed of evolution  
542 between the two evolving traits therefore affect evolutionary dynamics, possibly constraining  
543 evolutionary rescue. Second, while warming does not affect body mass when only body mass  
544 is allowed to evolve (equation (E), **Fig. 3**), it does under co-evolution. Here, warming exerts a  
545 selective pressure on the consumer feeding preference (see equation E) whose evolution, in  
546 turn, exerts a selective pressure on the consumer body mass. Consequently, both body mass and  
547 feeding preference are affected by warming (squares and triangles trajectories in **Fig. S1a**).  
548 Evolutionary rescue trajectories (**Fig. S1b**) then involve the effective evolution of both traits.

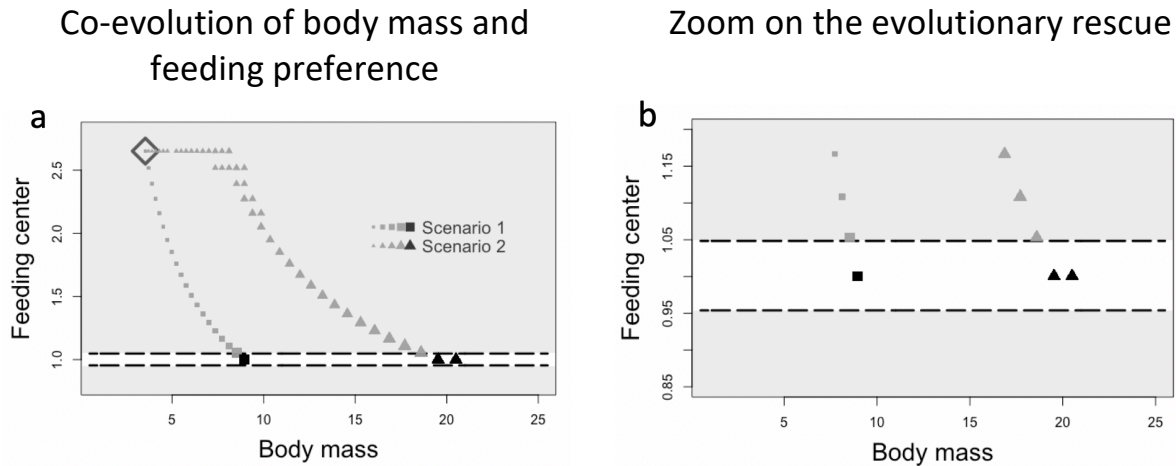
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554 **Figure S2: a.** Co-evolution of body mass and feeding preference under two scenarios. **Scenario 1:** body mass and  
555 feeding preference evolve at rate  $\mu = 10^{-2}$  (squares). **Scenario 2:** body mass evolves at  $\mu = 10^{-2}$  while feeding  
556 preference evolves at  $\mu = 10^{-3}$  (triangles). Unfilled grey diamond: initial conditions. The simulations started at  
557 280 K and the increase in symbol size indicates the direction of time. The biggest grey symbols thus correspond  
558 to the long-term selected phenotypes at 280 K. Once such a stable evolutionary state is reached, a warming to  
559 316.4 K (almost maximal sustainable temperature) occurs. The consumer body mass and feeding preference, which  
560 were within the non-viability area at 316.4 K (light grey), evolve in response to warming. The newly selected  
561 phenotypes (black symbols) are within the viability area at 316.4 K (white), which indicates an evolutionary rescue  
562 process. **b.** Zoom (y-axis) to see the evolutionary rescue consecutive to warming. Note that the selected phenotypes  
563 at 280 K were one mutation away from being viable at 316.4 K. Parameter values are in **table 1**.

564

565 This result indicates that the eco-evolutionary dynamics within the complex multi-trophic  
566 network, where both traits coevolve, is likely to exhibit complex patterns not captured within  
567 the CR module. This complexity arises from the indirect interactions at play. Indirect  
568 interactions correspond for instance to interactions between the two evolving traits, as  
569 illustrated in this section. The many indirect ecological interactions occurring at the network  
570 scales also explain this additional complexity.

571

## 572 **References:**

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576

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579

## 580 **Appendix S2: Complex multitrophic network model**

581

582 Our community evolution model starts with a consumer feeding on the basal resource.  
583 The evolution of the consumer body mass and feeding preference follows a mutation/selection  
584 process leading to the emergence of a complex multi-trophic network of approximately 30 to  
585 40 morphs and 4 to 5 trophic levels. A morph corresponds to an adaptive phenotype, that is to  
586 say, a couple (*body mass, feeding preference*).

587

### 588 **A. Definition of species diversity:**

589

590 At first, we only have one straightforward diversity measure: the trait diversity (i.e. the  
591 number of morphs in the trophic network at a given time). Because our model ignores genetic  
592 details and focuses on phenotypes, the definition of species is notoriously tricky. For lack of  
593 better criteria, we define species as clusters in the phenotypic space. The silhouette method  
594 (Rousseeuw, 1987) is used to determine the best number of clusters on the k-means clustering  
595 algorithm applied on the set of body masses and feeding preferences ( $m_i, f_i$ ) corresponding to  
596 the trait diversity. The number of clusters gives what we define as species diversity.

597

598 We consider a set of observations and a clustering. For each observation  $i$ , we note  $C_i$   
599 the cluster to which  $i$  is affected. For each observation  $i$ , the silhouette width  $S(i)$  is a measure  
600 of how much the observation is close to its cluster  $C_i$  in comparison with other clusters. It is  
601 defined as follow:

$$602 \quad S(i) = \frac{b(i) - a(i)}{\max(a(i), b(i))}$$

603 Where:

604

- 605 •  $a(i)$  is the average dissimilarity between  $i$  and the other observations in  $C_i$
- 606 •  $b(i)$  is the average dissimilarity between  $i$  and the observations in the closest cluster to  
607  $i$ ,  $C$ , with  $C \neq C_i$  (ie  $b(i) = \min_C d(i, C)$ )

608

609  $S(i)$  is between -1 and 1 and the more it is close to 1, the better is the affectation of  $i$  in the  
610 clustering. We use  $\text{mean}_i S(i)$  as a measure of the performance of a given clustering. We  
611 compare the different clustering obtained by the k-means algorithm for different values of  $k$ .

612

613 We implemented the algorithm in R-software using the packages “Cluster” by Martin  
614 Maechler, Peter Rousseeuw Anja Struyf, Mia Hubert, Kurt Hornik, Pierre Roudier, Juan  
615 Gonzalez (2017).

616

## 617 **B. Simulations:**

### 618 **Random draw of mutant’s traits**

619 Proportionally to the population densities distribution, a parent morph is chosen  
620 randomly at each mutation event. Mutant traits are then drawn from log-normal distributions  
621 centered on the parent’s traits. More precisely, mutant  $j$ ’s traits  $\log_{10}(m_j)$  (resp.  $\log_{10}(f_j)$ ) are  
622 randomly selected from a normal distribution of mean  $\log_{10}(m_i)$  (resp.  $\log_{10}(f_i)$ ) and variance  
623  $\sigma^2$ . The value of  $\sigma$  (0.25) allows occasional big mutational steps: 5% of the mutations result in  
624  $m_j < \frac{m_i}{3}$  or  $m_j > 3m_i$ .

625

### 626 **Transition criterion**

627 According to the scenario, each simulation follows a sequence of events.

628

- 629 • Scenarios NE: (1) the network is built up with a mutation rate  $\mu$ ; (2) evolution stops  
630 ( $\mu = 0$ ); (3) warming occurs; (4) simulation stops.
- 631
- 632 • Scenarios E: (1) the network is built up with a mutation rate  $\mu$ ; (2) warming occurs; (3)  
633 simulation stops.

634

635 Each transition is triggered once the transient dynamics are over. We consider these transient  
636 dynamics to be over when the ratio between the trait diversity standard deviation and mean  
637 (coefficient of variation) over a time window of  $2 \cdot 10^6$  mutation events is below 0.045.

638 This translates into:

639

$$640 \text{ Coefficient of Variation over time} \stackrel{\text{def}}{=} \frac{\sigma_{\text{trait diversity}}}{\varphi_{\text{trait diversity}}} < 0.045$$

641

642 Where  $\sigma_{\text{trait diversity}}$  is the standard deviation of the trait diversity over a time window of  $2 \cdot 10^6$   
643 mutation events and  $\varphi_{\text{trait diversity}}$  is the trait diversity mean over the same time period. Such  
644 a criterion allows for at least 95% of the observed trait diversity over this time window to be  
645 within the range of  $\pm 10\%$  of the observed trait diversity mean over the same period.

646

### 647 **Diversity before and after warming (persistence):**

648 Due to the constant mutation/extinction events, diversity is subject to stochastic  
649 variation while we would like to have exactly one measure of diversity before and after  
650 warming to assess performance. Therefore, we take the diversity before (resp. after) as the  
651 average diversity over the time window of  $2 \cdot 10^6$  mutation events that satisfied the transition  
652 criterion before (resp. after) warming ( $\varphi_{\text{trait diversity}}$ ). Each simulation gives a diversity  
653 maintenance measure we call “persistence”, either calculated for trait or species diversity.

654

$$655 \quad \text{DiversityPersistence} = \frac{\varphi_{\text{diversity}}(\text{after warming})}{\varphi_{\text{diversity}}(\text{before warming})}$$

656

657

### 658 **C. Statistical analysis:**

659 We want to compare the diversity response to warming within our multi-trophic network  
660 with and without evolution.

661

662 For trait and species diversity, three models were fitted ( $\mu = 10^{-1}, 10^{-2}, 10^{-3}$ ) in order  
663 to contrast diversity persistence for different evolutionary scenarios (scenario E  $\mu$  against  
664 scenario NE  $\mu$ ). 6 ANCOVAs were fitted with evolution as factor (two levels: “evolution”  
665 versus “no evolution”) and intensity of warming as quantitative variable (0, 2, 4, 6, 8, 10, 20K).  
666 The model is written as follows:

667

$$668 \quad \text{Model: DiversityPersistence}_{ij} = \mu + \delta_i + (\beta + \gamma_i) * \text{WarmingIntensity}_{ij} + \varepsilon_{ij}$$

669 As indicated in **table S2**, index 1 (resp. index 2) corresponds to the level “no evolution” (resp.  
670 “evolution”). The level “no evolution” serves as a reference ( $\delta_1 = 0, \gamma_1 = 0$ ). Therefore,  $\delta_2$   
671 corresponds to the direct effect of evolution, while  $\gamma_2$  corresponds to the interaction term  
672 between evolution and warming or indirect effect of evolution.  $\beta$  describes the direct effect of  
673 warming.

Mutation rate	Direct effect of evolution		Effect of warming intensity		Interaction term		Adjusted R <sup>2</sup>
	$\delta_2$	Effect size	$\beta$	Effect size	$\gamma_2$	Effect size	
$\mu = 10^{-1}$	0.051	32.3%	-0.029***	11.5%	0.031***	15.6%	58.6 %
$\mu = 10^{-2}$	0.060*	28.4%	-0.024***	30.3%	0.017***	9.5%	67.6%
$\mu = 10^{-3}$	0.062**	39.8%	-0.019***	18.5%	0.017***	13.1%	70.7%

674 **Table S2 (A): Trait diversity persistence.** Outputs of the 3 ANCOVAs. Index 1 corresponds to the level « No  
675 evolution », which serves as a reference ( $\delta_1 = \mathbf{0}$ ,  $\gamma_1 = \mathbf{0}$ ), while index 2 corresponds to the level « Evolution »  
676 ( $\delta_2$ ,  $\gamma_2$ ). All fitted ANCOVAs have a p-value below  $2 \cdot 10^{-16}$ . Significance code:  $<10^{-3}$  '\*\*\*',  $<10^{-2}$  '\*\*',  $<0.05$  '\*'

677  
678  
679

Mutation rate	Direct effect of evolution		Effect of warming intensity		Interaction term		Adjusted R <sup>2</sup>
	$\delta_2$	Effect size	$\beta$	Effect size	$\gamma_2$	Effect size	
$\mu = 10^{-1}$	-0.026	27.1%	-0.037***	27.9%	0.036***	24.8%	79.4%
$\mu = 10^{-2}$	0.126**	33.4%	-0.035***	22.6%	0.027***	8.9%	64.1%
$\mu = 10^{-3}$	0.196***	37.3%	-0.029***	12.2%	0.023***	5.8%	54.4%

680 **Table S2 (B): Species diversity persistence.** Outputs of the 3 ANCOVAs. Index 1 corresponds to the level « No  
681 evolution », which serves as a reference ( $\delta_1 = \mathbf{0}$ ,  $\gamma_1 = \mathbf{0}$ ), while index 2 corresponds to the level « Evolution »  
682 ( $\delta_2$ ,  $\gamma_2$ ). All fitted ANCOVAs have a p-value below  $2 \cdot 10^{-16}$ . Significance code:  $<10^{-3}$  '\*\*\*',  $<10^{-2}$  '\*\*',  $<0.05$  '\*'

683

684 An additional ANCOVA was fitted in order to compare the diversity persistence  
685 according to the mutation rate  $\mu$ . Here, diversity persistence is explained by the mutation rate  
686 ( $\mu = 10^{-1}, 10^{-2}, 10^{-3}$ ) as a three-level factor and the intensity of warming (0, 2, 4, 6, 8, 10,  
687 20 K) as a quantitative variable. The model is written as follows (but results are not shown  
688 because not significant):

689

690 Model:  $DiversityPersistence_{ij} = \mu + \delta_i + (\beta + \gamma_i) * WarmingIntensity_{ij} + \varepsilon_{ij}$



691           A graphical visualization showed all hypothesis for ANCOVA were verified for each  
692 fitted model. All statistical analyses were conducted using R-software (version 3.5.2). The  
693 “Anova” function of the R-package “car” was also used.

694

695 **References:**

696 Rousseeuw, P. J. (1987). Silhouettes: A graphical aid to the interpretation and validation of  
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## 721 **Appendix S3: Simulation code**

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723 The C code given as supporting information (file: SimulationCode.c) corresponds to the  
724 code simulating complex multi-trophic networks for scenarios NE (i.e. without evolution). In  
725 order for the code to work, the folder where it is launched has to contain a folder with a correct  
726 path (see variable “path” L75 & input data L 149). In addition to this variable “path”, 3 other  
727 inputs are necessary (see L 149-152 of the code): a seed, a new temperature and a deltaTm (i.e.  
728  $1/\mu$ ,  $\mu$  being the mutation rate).

729

730 In order to simulate scenarios E (with evolution), the following 2 changes are necessary:

731

732 (1): L 301: **while** (t<tend && S<Smax && S>0 && state<3)

733

734 Has to be replaced by:

735

736 **while** (t<tend && S<Smax && S>0 && state<2)

737

738

739 (2) L341-344:

740

741 **if**(state==1)

742 {

743 pattern=0;

744 }

745

746 Has to be replaced by:

747

748 **if**(state==1)

749 {

750 temperature=newtemperature;

751 }

752

753

754

755

## **Dynamiques éco-évolutives dans différents environnements: implications pour la structure et le maintien des communautés écologiques**

### **Résumé**

Les changements environnementaux actuels affectent les espèces, mais aussi leurs interactions au sein des communautés. Leur réponse écologique et évolutive dépend en partie de traits phénotypiques qui affectent le type et l'intensité des interactions. Dans cette thèse, nous explorons l'impact de différents environnements sur les communautés antagonistes (e.g. réseaux trophiques) ou mutualistes (e.g. réseaux plantes-pollinisateurs). Nous suivons l'effet de paramètres environnementaux comme la température, l'abondance et la distribution temporelle d'un ou plusieurs interacteurs sur la réponse de ses partenaires. Nous étudions ainsi les boucles de rétroaction éco-évolutives concernant la taille corporelle, l'investissement dans l'interaction mutualiste ou encore la phénologie de recherche de nourriture. Les interactions antagonistes semblent plus stables que les interactions mutualistes grâce à des boucles de rétroaction éco-évolutives négatives. Les espèces les plus spécialistes sont aussi plus fragiles, souffrant souvent d'un déclin démographique et d'une réponse évolutive réduite aux changements environnementaux. Sous certaines conditions, nous observons des réponses évolutives en accord avec certains patrons empiriques (e.g., déclin des tailles corporelles avec l'augmentation des températures, désinvestissement dans les interactions mutualistes quand l'un des partenaires décline). Modéliser explicitement la durée et l'amplitude des perturbations environnementales pourrait apporter des précisions sur les capacités de résistance et résilience des différentes communautés étudiées.

Mots clés : ecologie des communautés, dynamique adaptative, modélisation, interactions antagonistes et mutualistes, changements globaux,

**Eco-evolutionary dynamics in different environments: implication for the maintenance and structure of ecological communities**

## Abstract

Environmental changes affect species but also the interaction connecting them within a community. Their ecological and evolutionary responses partly depend on biological traits affecting the type and strength of these interactions. In this thesis we use models to explore the impact of different environments on resource-consumer communities, either antagonistic (e.g. food webs) or mutualistic (e.g. plant-pollinator webs). We follow the impact of environmental parameters like temperature, abundance, and temporal distribution of interactors on their partner species. We study potential eco-evolutionary feedbacks, following the evolution of traits affecting the interaction like body size, investment in mutualism, or foraging time. Antagonistic interactions seem more stable than mutualistic ones via negative eco-evolutionary feedbacks. The more specialist species are also more fragile, often declining or being less able to evolve with environmental changes. Under specific modelling conditions we observe evolutionary responses previously reported in the literature e.g. decreased body size with warming, disinvestment in the mutualistic interaction when the partner population declines). Explicit modelling of the length and amplitude of the considered environmental perturbations could help explore the stability of the studied communities.

Keywords : community ecology, adaptive dynamics, modelling, antagonistic and mutualistic interaction, Global change impacts