Fitness landscapes of biotic interactions shape the ecological and evolutionary dynamics of biodiversity

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Abstract

Biotic interactions promote, maintain or reduce diversity within and between species. Ecologists and evolutionary biologists have thus long studied links between biotic interactions and biodiversity dynamics. Yet theoretical and empirical research on these links are still separated by a substantial gap. This gap arises because empiricists rarely quantify the fitness consequences of interactions whereas theoreticians often describe these consequences in a simplistic manner. To bridge this gap, we introduce the concept of 'fitness landscapes of biotic interactions' (FLINTs). These landscapes relate the fitness consequence of an interaction for a focal organism to traits of both the focal organism and the interaction partner. FLINTs are an important extension of classical fitness landscape theory since they resolve how biotic environments alter fitness landscapes. We summarize current knowledge about FLINTs and show that their topography can strongly deviate from simplistic trait-matching landscapes implicitly assumed in many theoretical studies. We then illustrate how FLINT topography shapes biodiversity dynamics using an example of co-evolutionary diversification in plants and

flower-visiting insects. This leads us to outline a research agenda that measures real-world FLINTs and analyses their consequences for biodiversity dynamics. In summary, FLINTs are a novel framework that fosters integration of theoretical and empirical research on how biotic interactions shape biodiversity dynamics.

Abstract

Antagonism; competition; eco-evolutionary model; mechanisms of biotic interactions; mutualism; natural selection.

Introduction

Two fundamental properties of life are that organisms are diverse and that organisms interact with each other. Biodiversity dynamics and biotic interactions are tightly connected since interactions promote, maintain or reduce diversity within and between species through both ecological and evolutionary processes (Vellend 2016). In particular, biodiversity dynamics depend on the properties of biotic interactions, notably on their type (antagonistic, mutualistic or competitive), strength, and degree of specialisation. This holds both for the evolutionary (Ehrlich & Raven 1964, Futuyma & Agrawal 2009, van der Niet et al. 2014) and ecological dynamics of biodiversity (Chesson 2000, Chesson & Kuang 2008, Qian & Akçay 2020). Due to the fundamental impact of biotic interactions on the evolutionary and ecological dynamics of biodiversity, their interdependence has long been a focus of theoretical and empirical research.

There is, however, still a substantial gap between theoretical and empirical research addressing the impact of biotic interactions on biodiversity dynamics. We argue that this has three reasons. First, theory development usually focuses on simplistic situations. For example, theoretical models commonly assume that fitness consequences of an interaction for both partners are strongest when the partners have matching trait values (Loeuille & Loreau 2005; Becker et al. 2022; Allhoff et al. 2015), whereas empirical research can reveal substantially more complex trait dependencies (e.g. Brose et al. 2005; Irwin et al. 2010). This limits the application of theory to real-world systems. Secondly, empirical research rarely quantifies how biotic interactions affect the fitness of interaction partners *sensu stricto* (see Glossary) and instead only measures fitness components (such as individual growth rates of caterpillars and seed set of their host plants). Yet, fitness ultimately determines the ecological and evolutionary dynamics of biodiversity both within and between species (Vellend 2016; Hendry et al. 2018). Thirdly, we argue that theoreticians and empiricists lack a common conceptual framework to jointly develop a deeper understanding of the relationships between biotic interactions and biodiversity dynamics.

To close this gap, we propose the fitness landscape of biotic interactions (FLINT) as a conceptual framework that links the phenotypes of interacting organisms to the fitness consequences of their interaction and to emergent biodiversity dynamics, such as community dynamics, microevolutionary dynamics within interacting species, and macroevolutionary diversification. These FLINTs describe the ‘ecological theatre’ (Hutchinson 1965) in which the ecological and evolutionary dynamics of biodiversity play out. The FLINT framework provides a common language for theorists and empiricists and should foster closer integration of theoretical and empirical research across a variety of interaction types and study systems. In the following, we first outline the FLINT concept and summarize current knowledge about the FLINT topography. We then illustrate how the FLINT topography shapes biodiversity dynamics using an example of co-evolutionary diversification in plants and flower visitors. This leads us to outline a research agenda that measures real-world FLINTs and analyses their consequences for biodiversity dynamics.

Fitness landscapes of biotic interactions (FLINTs)

We define FLINTs as maps that relate the per-capita effect of an interaction partner on the fitness of a focal organism (see Glossary) to traits of both the focal organism and the interaction partner (Fig. 1). FLINTs build upon classical phenotypic fitness landscapes, which describe how an organism’s fitness depends on the organism’s traits (Lande & Arnold 1983). Fitness landscapes are extensively studied in evolutionary biology (e.g. Fragata et al. 2019, Papkou et al. 2023) and start to be applied in community ecology (Munoz et al. 2023). However, the fitness of an organism depends not only on the traits of the organism itself (as described by phenotypic fitness landscapes) but also on traits of its interaction partners (e.g. Munoz et al. 2023). FLINTs explicitly describe this dependence on traits of both the focal organism and the interaction partner (Fig. 1), thereby extending the classical fitness landscape concept (Fig. 2). The FLINT concept thus responds to recent calls to include biotic interactions into the study of ‘extended phenotypes’ in evolutionary theory (Edelaar et al. 2023) and fitness landscapes in community ecology (Munoz et al. 2023), and to explicitly reveal the role of biotic interactions and functional traits for macroevolutionary diversification in ‘evolutionary arenas’ (Nürk et al. 2020).

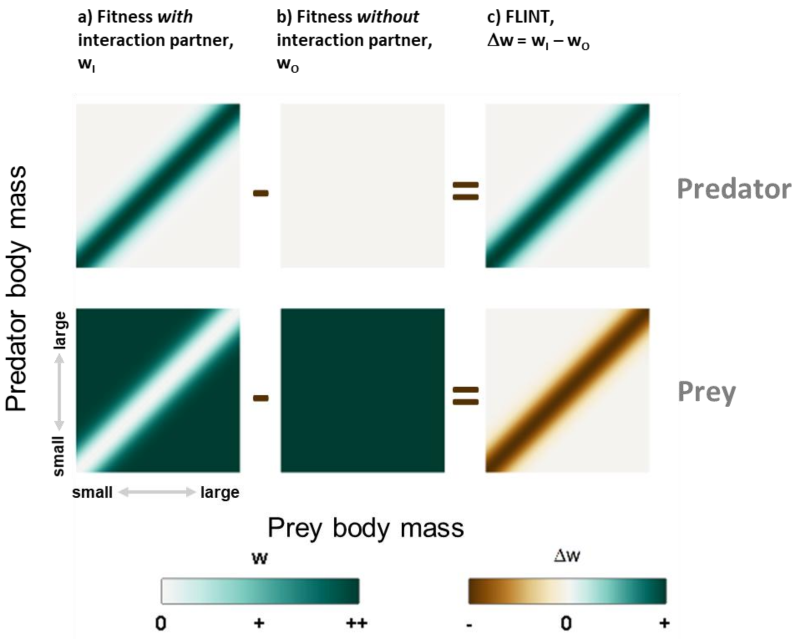

Figure 1 Fitness landscapes of biotic interaction (FLINTs) for the example of a predator-prey interaction driven by simple trait matching. For both predators (top row) and prey (bottom row), the panels show how traits of predators and prey affect (a) fitness in the presence of one interacting individual (w_I), (b) fitness in the absence of interaction partners (w_O) and (c) the per-capita fitness consequence of the interaction ($\Delta w = w_I - w_O$). (a) In the presence of a prey individual, a predator has maximal fitness when its own body mass matches the body mass of the prey. On the contrary, prey fitness in the presence of a predator is minimal when predator and prey mass match. (b) In the absence of the interaction partner, the predator has zero fitness whereas the prey has maximal fitness. Note that these 'intrinsic fitness landscapes' (Munoz et al. 2023) are by definition independent of traits of the interaction partner and in this example they are also independent of traits of the focal organism. (c) FLINTs map how the per-capita fitness consequence of an interaction for a focal organism depends on traits of both the focal organism and the interaction partner.

We illustrate the FLINT concept with a simple example of a predator-prey interaction. In this example, a predator has maximal fitness when its own body mass matches the body mass of the prey individual multiplied by a fixed factor, whereas predator fitness declines when the prey is either too small or too large for the predator (Fig. 1a). From this fitness map in the presence of one prey individual, we subtract the predator's 'intrinsic fitness landscape' (Munoz et al. 2023) in the absence of prey (in Fig. 1b this intrinsic fitness landscape is assumed to be flat at zero fitness). This subtraction yields the predator's FLINT, which describes how the effect of one prey individual on predator fitness depends on predator and prey mass (Fig. 1c). Accordingly, one can calculate the prey's FLINT (Fig. 1). This example represents simple trait matching where the fitness consequences for both partners are strongest when their trait values match (Fig. 1c). Note that trait matching for mutualistic interactions results in similar landscapes, except that the fitness consequences are positive for both partners. Such simple trait matching is commonly assumed in ecological and evolutionary models for the dynamics of interaction networks (e.g. Loeuille & Loreau 2005, Brännström et al. 2011; Allhoff et al. 2015; Becker et al. 2022; Metz et al. 2023). Crucially, however, FLINTs are not limited to such simple relationships but can have substantially more complex topographies.

The explicit consideration of interaction partners leads to three important differences between FLINTs (Fig. 2a) and classical fitness landscapes (Fig. 2c): (1) in a fitness landscape, an organism is represented by a single point, whereas in a FLINT each interaction between partners with distinct trait values is represented by a single point (Fig. 2a, b). (2) Fitness landscapes map total fitness whereas FLINTs map the per-capita effect of an interaction partner on fitness of the focal organism (Fig. 2a, c). (3) A peak in the fitness landscape does not necessarily correspond to a peak in the FLINT (Fig. 2).

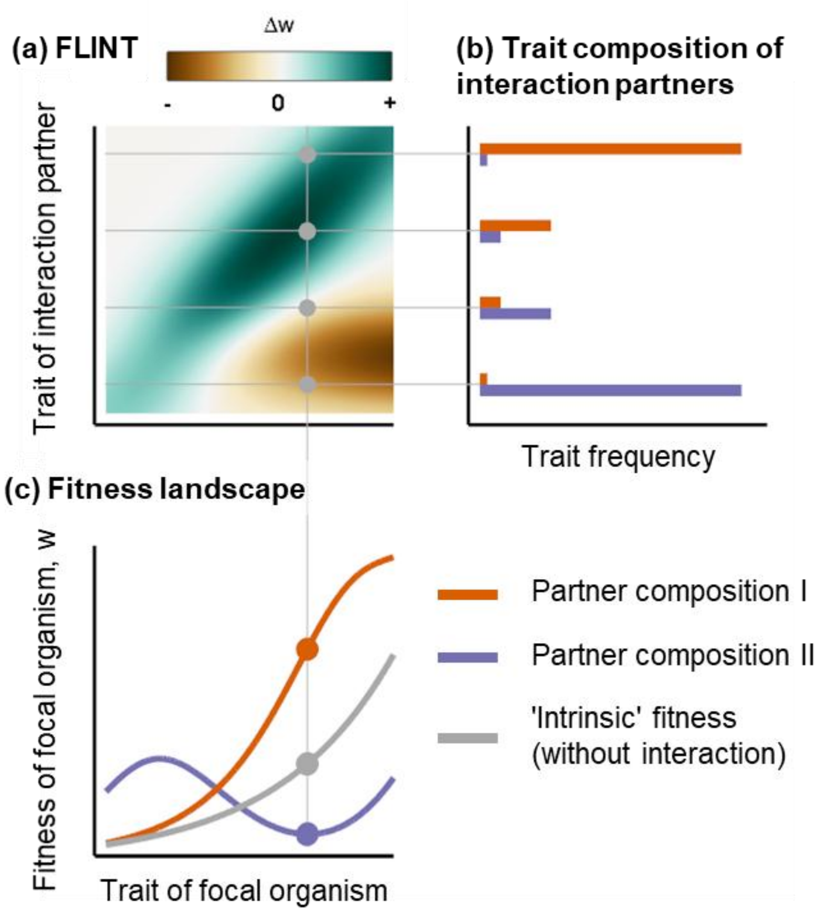

Figure 2 Links and differences between (a) the fitness landscape of biotic interactions (FLINT), (b) the trait composition of interaction partners and (c) classical fitness landscapes. The fitness landscape relates an organism's fitness to its trait(s) so that a given phenotype is represented by a single point in the fitness landscape. In a FLINT, the same organism is represented by multiple points that represent interactions with phenotypically distinct interaction partners. The FLINT determines how different trait compositions of interaction partners (orange vs. blue histograms in (b)), alter the focal organism's fitness relative to its intrinsic fitness without the interaction. Depending on FLINT topography, changes in the

trait composition of interaction partners can strongly alter the fitness landscape. Changes in the biotic environment thus alter the fitness landscape but not the FLINT.

In the classical fitness landscape paradigm, effects of the biotic environment on an organism's fitness are interpreted as 'noise' around the expected 'intrinsic' fitness without biotic interactions (Fig. 2c). FLINTs go beyond this by explicitly resolving how interactions modify an organism's intrinsic fitness (Fig. 2a). These fitness impacts result from the interaction landscape, the trait frequency distribution of the interaction partners and the numerical response (which specifies how the fitness impacts of multiple partner individuals combine; Solomon 1949; Andrén & Liberg 2023). Depending on FLINT topography, shifts in the trait frequency of interaction partners can strongly alter fitness landscapes (Fig. 2). This illustrates the value of the FLINT concept: as the biotic environment changes, the FLINT remains constant, determining changes in the fitness landscape and hence the direction of selection within and between species.

FLINTs provide a general framework for analysing the ecological and evolutionary dynamics of diversity in interacting organisms (Fig. 3). For a given set of interaction partners and their trait values, the FLINT (Fig. 3a) predicts a matrix of pairwise interaction coefficients (termed the 'interaction matrix' in ecology; Novak et al. 2016; Fig. 3b). This matrix determines biodiversity dynamics within and/or between species (Fig. 3c), which in turn alter the frequency distribution of interaction-relevant trait values (Fig. 3d). By characterizing the mechanisms through which biotic interactions impact fitness, FLINTs thus describe the invariant part of the 'ecological theatre' (sensu Hutchinson 1965) in which coevolutionary and community dynamics play out.

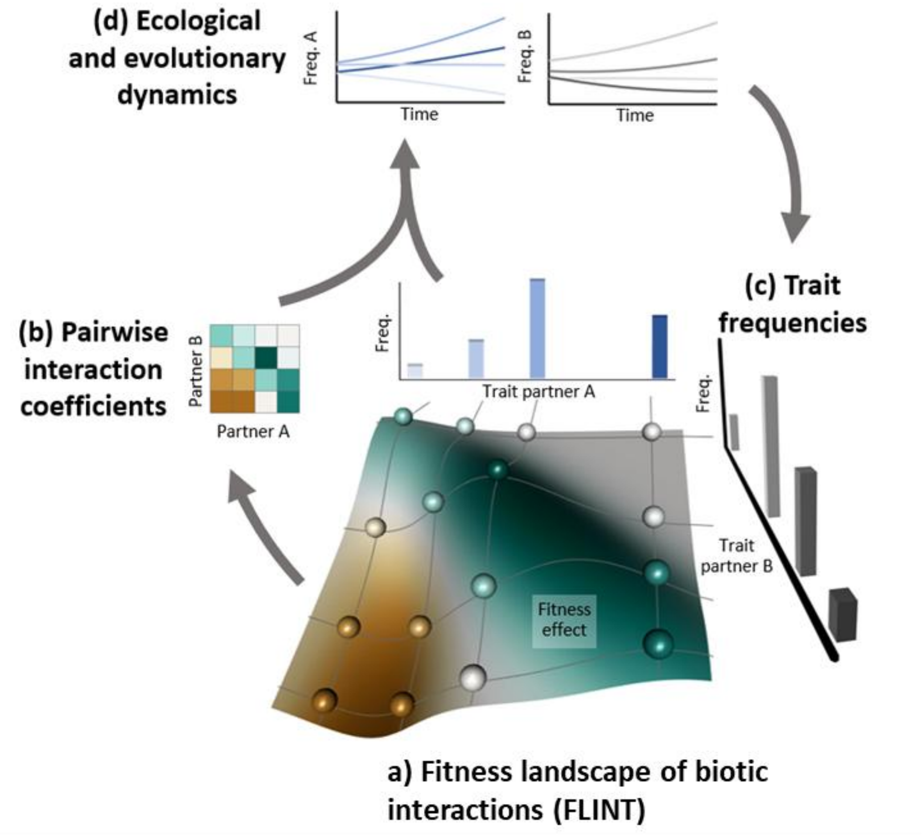

Figure 3 Fitness landscapes of biotic interactions (FLINTs) form the 'Hutchinsonian theatre' for the ecological and evolutionary dynamics of interacting organisms. For a given combination of trait values of interaction partner A and interaction partner B, FLINTs (a) predict a set of pairwise interaction coefficients (b) that is termed the 'interaction matrix' in community ecology. Based on the current frequency distribution of interaction-relevant trait values (c), this matrix determines biodiversity dynamics within and/or between species (d). These dynamics in turn alter the trait frequency distribution (c). For the sake of simplicity, (a) and (b) only show the FLINT and the interaction matrix for interaction partner B.

What we know about real-world FLINTs

There is limited quantitative knowledge about the topography of real-world FLINTs. While a few relevant data sets exist, e.g. from competition experiments with plants (e.g. Kraft et al. 2015) or from experiments measuring the fitness consequences of bacteria-phage interactions (e.g. Doud et al. 2024), they have not yet been presented as FLINTs. Given the scarcity of quantitative information about FLINT topographies, we discuss qualitatively how interaction mechanisms shape FLINTS. We structure this by the type of interaction, starting with interactions within a group of organisms (competition and/or facilitation), before moving to interactions between groups (mutualism and/or antagonism).

Classical ecological theory assumes that competition intensity increases with trait similarity of the competitors (MacArthur & Levins 1967), which implies trait-matching landscapes (Fig. 4a). In fact, trait matching is at the heart of niche differentiation as the classical mechanism stabilizing species coexistence (Chesson 2000, Levine 2016). However, there is limited empirical evidence for trait-dependent niche differentiation (Levine et al. 2025) that would lead to competitive trait-matching landscapes. In contrast, hierarchical competition seems to be more common (e.g. Tilman 1982, Purves et al. 2008, Levine et al. 2025). For instance, in a long-term competition experiment Dybzinski & Tilman (2007) found that prairie plant species with lower requirements for both soil nitrate and light (R^* and I^*) outcompeted their respective competitors. Such hierarchical competition gives rise to triangular landscapes (Fig. 4b) that differ substantially from diagonal trait-matching landscapes (Fig. 4a). Even more complex competitive landscapes would be expected under non-hierarchical (intransitive) competition in which competitors are not arranged in a competition hierarchy but rather form a loop of rock-paper-scissor-like interactions (Soliveres & Allan 2018). Intransitive competition can in principle arise from single-trait competition landscapes, for instance when different tropical plant species sharing a common pollinator flower at different times throughout the year (Stiles 1977) and when pollinators prefer plant species they encountered previously (flower constancy; Waser 1986; Fig. 4c). However, most mechanisms of intransitive competition involve hierarchical competitive effects of multiple traits and thus lead to more high-dimensional interaction landscapes. As an example, intransitive competition among genotypes of the bacterium *Escherichia coli* arises when toxin-insensitive cells outcompete toxin-producing cells, which kill toxin-sensitive cells, which in turn outcompete toxin-insensitive cells (Kerr et al. 2002).

Traits also determine when interactions shift from competitive to facilitative (Butterfield & Callaway 2013). In experimental *Arabidopsis thaliana* populations exposed to moderate salt stress, salt-sensitive genotypes were facilitated by neighbouring plants whereas salt-tolerant genotypes tended to experience competition. Simultaneously, salt-sensitive genotypes had stronger facilitative effects on their neighbours (Zhang & Tielbörger 2019). Such trait-dependence of interaction effects and responses again yields complex FLINT topographies (Fig. 4d).

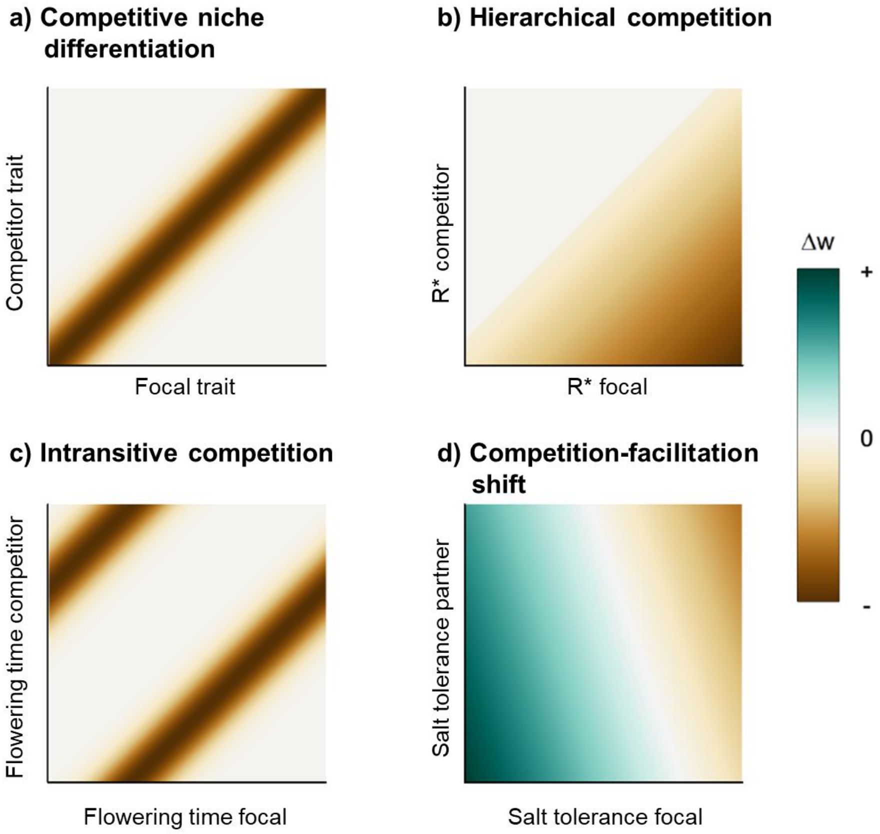

Figure 4 Examples of within-group fitness landscapes of biotic interactions (FLINTs). (a) Competitive trait-matching FLINTs result from trait-dependent niche differentiation. (b)Triangular FLINTs arise from hierarchical competition, e.g. when plant species with lower nutrient requirements (R*) outcompete species with higher R* (Dybzinski & Tilman 2007). (c) More unusual FLINTs may be generated by trait-dependent intransitive competition, e.g. when tropical plant species that differ in year-round flowering phenology (Stiles 1977) compete for pollinators showing flower constancy (Waser 1986). (d) Within-group FLINTs can also describe shifts between competition and facilitation that were, for instance, found between *Arabidopsis thaliana* genotypes with different salt tolerance (Zhang & Tielbörger 2019). Note that these within-group FLINTs differ from between-group FLINTs (Fig. 1) in that the same landscape applies to both interaction partners and that the same trait appears on the x- and y-axis.

Evidence for mutualistic trait-matching FLINTs comes from plant-pollinator interactions (Garibaldi et al. 2016). For instance, Anderson & Johnson (2007) showed that the proboscis length of the fly *Prosoeca ganglbaueri* and the corolla tube length of its primary floral food plant *Zaluzianskya microsiphon* were strongly correlated across sites and that short-tubed plants transplanted to sites with long-tubed plants and long-proboscid flies had reduced seed set. In another specialized pollination system, however, Nattero et al. (2010) found no evidence for morphological trait matching but rather a consistently higher fitness of plants with bigger flowers irrespective of pollinator traits. Moreover, traits of interaction partners can determine when interactions switch from mutualism to antagonism. An intensively studied example are ‘primary nectar robbers’ - flower visitors who damage flowers with concealed nectar to remove the nectar without contacting the plant's reproductive organs (Irwin et al. 2010). For example, the bumblebee *Bombus occidentalis* has a short proboscis that does not allow it to legitimately pollinate the tubular flowers of *Ipomopsis aggregata* (Irwin & Brody 1998). Instead, it damages the flower, which lowers seed set. The cheating behaviour of this nectar robber can thus profoundly modify FLINTs of plants and flower visitors, causing an antagonistic depression to appear next to the mutualistic, trait-matching ridge (Fig. 5a).

Antagonistic predator-prey interactions are often characterized by a rather narrow range of predator-prey body mass ratios (Brose et al. 2005). This can be explained mechanistically since predators of a given mass can only capture and handle prey up to a certain maximum mass and do not gain sufficient energy from prey below a certain minimum mass (Portalier et al. 2018). Net energy gain for predators is thus maximal at a given predator-prey body mass ratio (Portalier et al. 2019), giving rise to a trait-matching antagonistic FLINT (Fig. 1). Narrow consumer-resource body mass ratios that may indicate trait-matching FLINTs are, however, not universal in predator-prey interactions (see e.g. baleen whales feeding on zooplankton) and they are typically not found for host-parasite, host-pathogen or plant-herbivore interactions (Brose et al. 2005). For instance, in the interaction between the parasitic fungus *Metschnikowia bicuspidate* and its daphniid hosts, fungal genotypes with small spores mostly infect hosts with small gut diameters, whereas larger-spored genotypes infect all hosts, irrespective of their gut diameter (Sun et al. 2023). The fitness consequences of plant-herbivore interactions often depend less on size than on plant defences and the ability of herbivores to cope with them. Notably, plant toxin production has a negative fitness effect on generalist herbivores and limits negative fitness consequences for plants (Hopkins et al. 2008; Steppuhn & Baldwin 2007; Fig. 5b). However, some specialised herbivores incorporate high amounts of plant toxins into their body tissues for their own defence, a phenomenon termed sequestration (Beran & Petschenka 2022). For example, the Eurasian milkweed bug *Spilostethus saxatilis* is obligatorily associated with autumn crocus (*Colchicum autumnale*) from which it sequesters high amounts of colchicine alkaloids (Petschenka et al. 2022). In comparison to generalist herbivory, such toxin sequestration by specialist herbivores can revert the fitness effects of toxin production for both plants and herbivores and fundamentally alter their FLINTs (Fig. 5b).

In summary, many interaction mechanisms cause FLINTs to be more complex than the commonly assumed simple trait-matching landscapes. Hence, there is a need to assess how more complex FLINTs affect biodiversity dynamics.

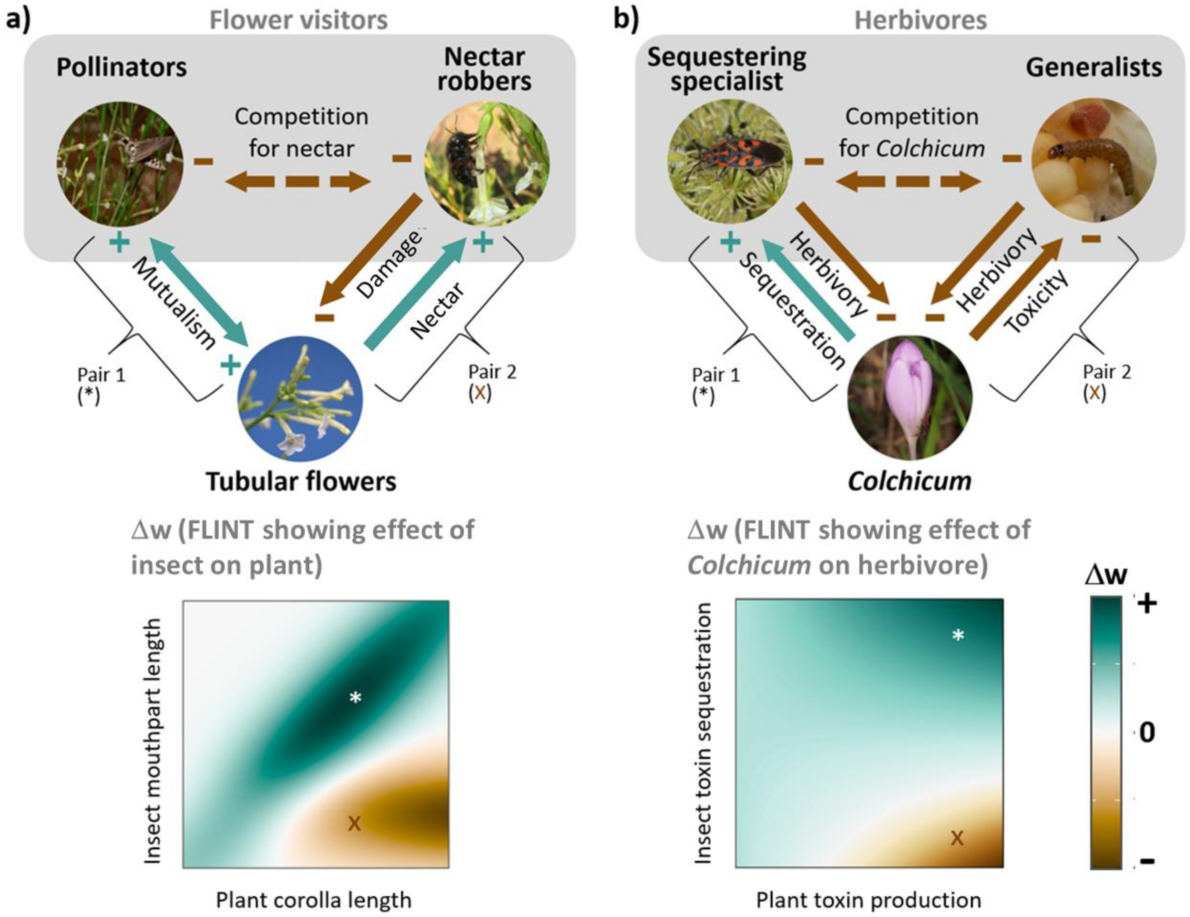

Figure 5 Examples of plant-animal interactions expected to cause complex FLINT topographies (only one FLINT per interaction shown). (a) Plant-flower-visitor interactions in which tubular flowers are pollinated by insects with matching traits (e.g. hawk moths with a long proboscis) while nectar is robbed by insects with non-matching traits (e.g. carpenter bees with short mouthparts). (b) Plant-herbivore interactions in which specialist herbivores that can sequester defensive plant toxins (e.g. colchicine sequestering seed bugs) for their own defense, while generalist herbivores suffer from the plant's toxicity. The marked points in the FLINTs depict specific plant-animal interactions that have positive (*) vs. negative (x) fitness outcomes. Photographs in a) © Danny Kessler and in b) © Georg Petschenka.

FLINTs shape biodiversity dynamics

We illustrate the importance of FLINTs for biodiversity dynamics by applying the FLINT framework to interactions between plants and flower-visiting insects (Box 1). First, we consider a simple mutualistic trait-matching landscape that is identical for both plants and insects (Fig. 6a). Starting with a single plant and a single insect variant, both the plant and the insect trait first evolve towards the peak of the interaction landscape, where the fitness effects of the mutualistic interaction are strongest. This almost gradual trait evolution arises from many consecutive replacements of resident variants by better adapted mutant variants (Fig. 6a, Box1). Subsequently, both the animals and the plants split up almost simultaneously into two separate variants each. This ‘branching’ arises since competition is strongest among individuals with similar trait values, which explains why sub-populations subsequently differentiate: mutant variants that have less similar traits benefit from reduced competition and outperform the residents. The system then continues to diversify via consecutive branching events (Fig. 7a; Fig. 8a). Similar dynamics of evolutionary emergence of interaction networks have been reported for both mutualistic and antagonistic interactions governed by simple trait matching (Loeuille & Loreau 2005; Brännström et al. 2011; Allhoff & Drossel 2013; Allhoff et al. 2015; Maliet et al. 2020).

Qualitatively different biodiversity dynamics arise (Fig. 7b) for a more complex FLINT in which both legitimate pollination and nectar robbing are possible. For the same parameter values and initial conditions, we find fewer branching events leading to a reduced diversification rate (Fig. 8b). This reduced diversification is combined with a trend towards plants evolving smaller trait values that avoid antagonism and animals following the trait evolution in plants (Fig. 7b). Consequently, the more complex FLINT results in a reduced network size (Fig. 7b).

In the example model, new variants appear through modification of resident variants (via mutation or speciation; Step 4 in Box 1). However, the function generating new variants could also represent immigration from an external variant pool via gene flow or dispersal (cf. Becker et al. 2022; Metz et al. 2023). Since immigrants typically show more trait variation than residents, this should lead to a more exhaustive exploration of the entire FLINT. It is also possible to not introduce any new variants, as in the case of classical ecological models used to study species coexistence (Chesson 2000).

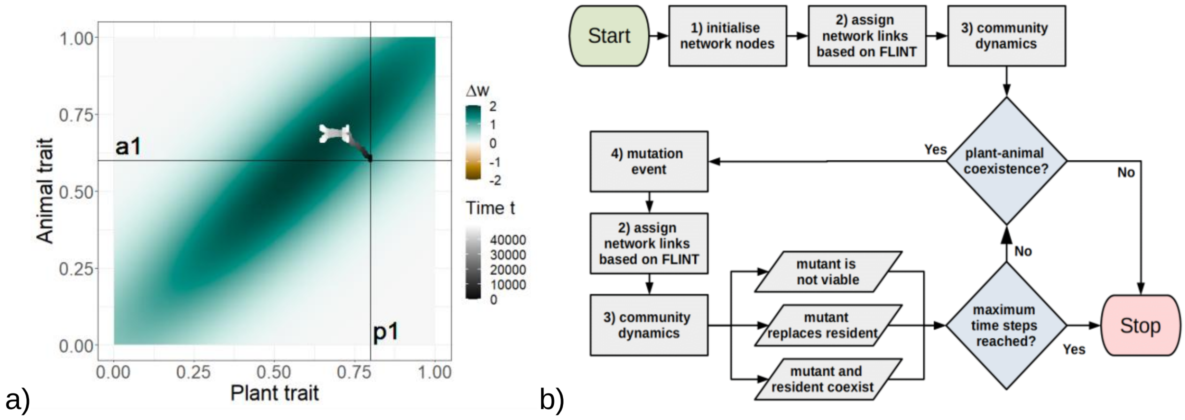

Figure 6 Overview of model components using the example of simple trait matching. (a) A FLINT capturing the per-capita fitness effects of a mutualistic plant-pollinator interaction. For simplicity, we assume that animals and plants have the same FLINT. Plant and animal traits (p_1 and a_1 r, respectively) represent the initial situation at simulation start. Also shown is the initial eco-evolutionary trajectory (in greyscale) that visualises the direction of adaptive changes in trait values over the first 250 mutation events. The full trajectory is shown in Fig 7a. (b) Flowchart of the eco-evolutionary algorithm, as explained in Box 1.

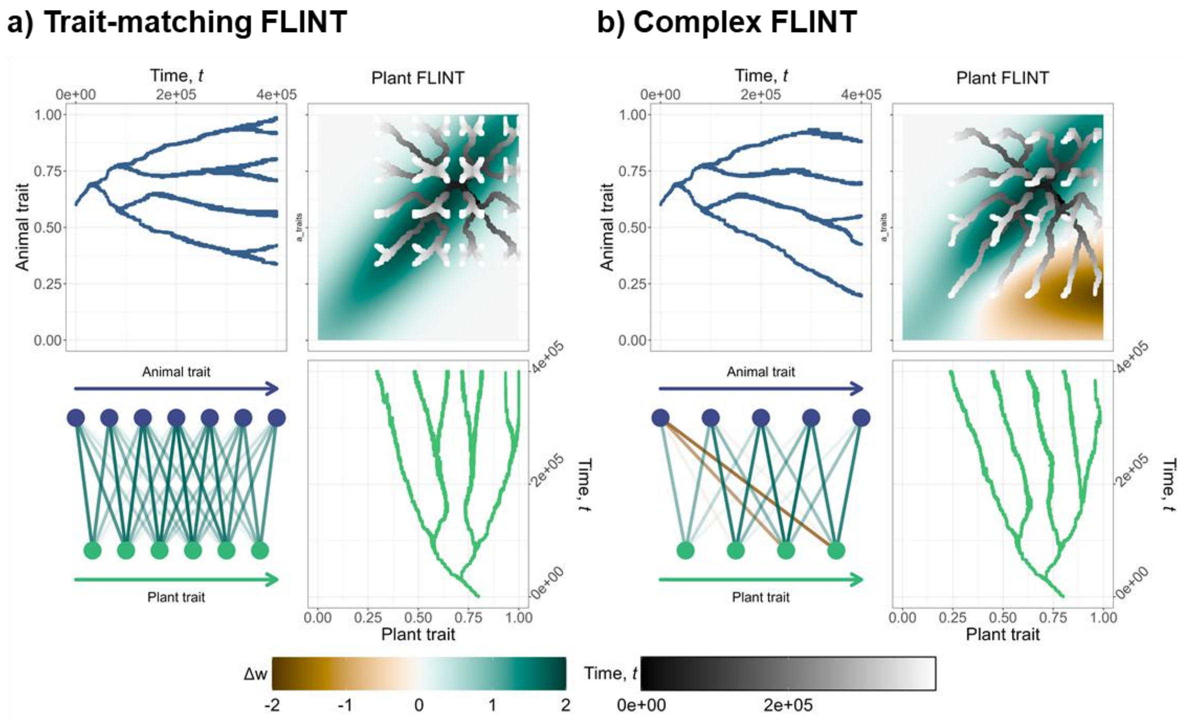

Figure 7 Fitness landscapes of biotic interactions (FLINTs) shape biodiversity dynamics. The figure contrasts eco-evolutionary dynamics obtained (a) for a simple mutualistic trait-matching FLINT, and (b) for a more complex FLINT that combines mutualistic trait matching with an antagonistic region representing nectar robbing (see Fig. 5a). For simplicity, only the plant FLINTs are shown. Overlaid over these FLINTs is the evolutionary trajectory over 400,000 time steps (corresponding to 2,000 mutation steps). Additional panels show the evolutionary branching of animals (top left) and plants

(bottom right), as well as the resulting network after 400,000 time steps (bottom left). The colour of network links indicates the interaction effect on the plant.

Box 1: An application of the FLINT framework to plants and flower-visiting insects

To illustrate how FLINTs shape biodiversity dynamics, we embed them into a model for the eco-evolutionary emergence of complex interaction networks. This model comprises four steps (Fig 6b) and we apply it to an example of flowering plants that interact with flower-visiting animals. In our example, plant variants (species or genotypes) differ in floral tube length p and animal variants differ in proboscis length a.

Step 1: Initialise plant and animal communities. Our example simulations start with a single plant and a single animal population (Fig 6a).

Step 2: Assign network links based on the FLINT. For a given plant population, the plant FLINT determines the fitness consequences (Δw) of interactions with a given animal population. Accordingly, the animal FLINT the fitness consequences for animals. These fitness consequences can be represented as links in the interaction network. For the simple mutualistic trait-matching with identical FLINTs for animals and plants, the starting trait values shown in Fig. 6a result in weak mutualism.

Step 3: Community dynamics. Fitness consequences of biotic interactions translate into changing population densities over time. We model the dynamics of these interacting populations with a set of coupled differential equations that (a) describe trait-dependent competition among plants and animals, respectively, and (b) describe plant-animal interactions with a Beddington-DeAngelis type numerical (and functional) response (Beddington 1975; DeAngelis et al. 1975). The interaction coefficients describing plant-animal interactions in the Beddington-deAngelis functions are the fitness consequences (Δw) determined in Step 2. We integrate this dynamical system for 200 time steps.

Step 4: Introduce new variants (via mutation). For each mutation event, we choose one of the available interaction partners as resident and add a very small mutant population to the system, inspired by the mathematical framework of Adaptive Dynamics (Geritz et al. 1997, Geritz et al. 1998, see Dieckmann & Ferrière 2004 or Brännström et al. 2013 for a review). In contrast to Adaptive Dynamics, we do not assume a strict separation of ecological and evolutionary time scales. Instead, we simply perform mutation events with a fixed frequency. The mutant trait value is chosen from a narrow normal distribution around the resident's trait.

Plant-animal coevolution. The simulation algorithm initially goes through the first three steps, before entering a loop in which step 4, 2 and 3 are executed repeatedly (Fig 6b). The traits of a new mutant population (step 4) determine how it interacts with the other variants already present in the system (step 2) and the updated dynamical system capturing the community dynamics (step 3) then determines its fate. The mutant might (a) replace the resident if it is better adapted to the current environment created by the other populations, (b) quickly go extinct in case it is not or (c) coexist with the resident. The latter outcome is known as evolutionary branching (Geritz et al. 1998). Multiple consecutive branching events describe the diversification of phenotypic traits (Fig. 8) and the emergence of interaction networks (Fig. 7).

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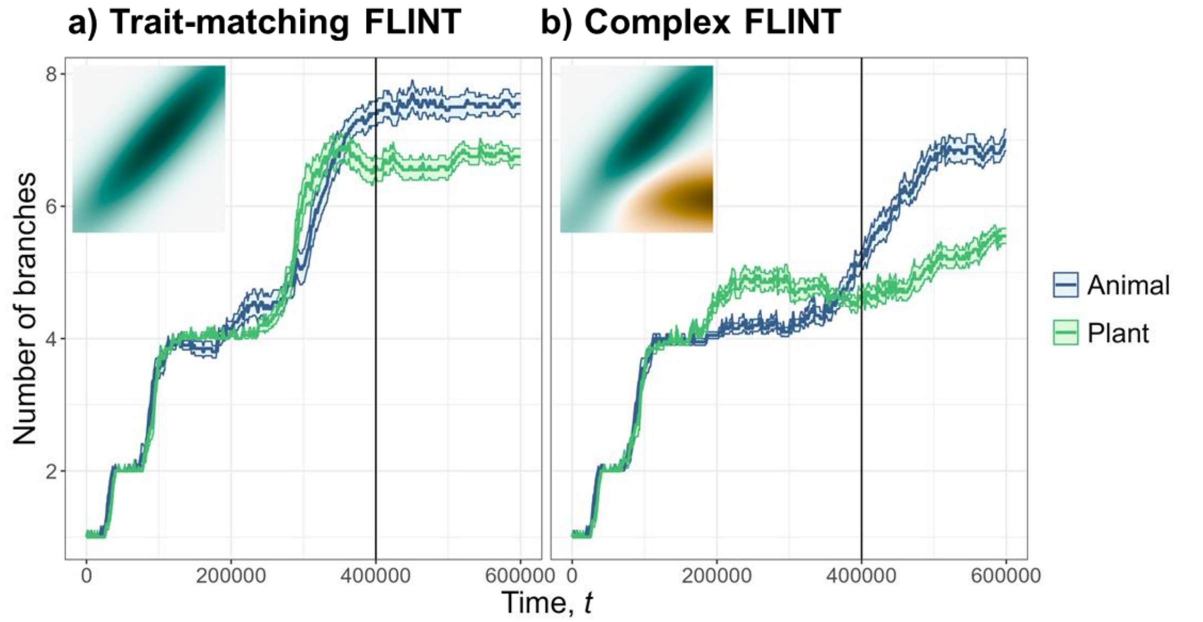

Figure 8 Diversification dynamics simulated (a) for a simple mutualistic trait-matching FLINT and (b) for a more complex FLINT in which antagonistic nectar robbing is possible. Vertical lines at t=400,000 correspond to the networks shown in Fig.7. Solid lines represent the number of branches for animals and plants, averaged over 20 simulations, respectively. Shaded areas represent standard errors.

Measuring FLINTs

Application of the FLINT framework to real-world interactions requires the quantification of (1) FLINTs describing how per-capita fitness effects of the interaction depend on the traits of the interaction partners (Fig. 1c), (2) the numerical response, which describes how total interaction effects on fitness scale with the densities of the interaction partners, and (3) intrinsic fitness landscapes (Munoz et al. 2023) describing the effect of the organisms' functional traits on their fitness in the absence of the interaction (Fig. 1b). In some cases, this interaction-independent fitness can be derived from first principles (e.g. herbivore fitness is 0 in the absence of plants, Fig. 1b). Otherwise, it needs to be obtained from measurements of fitness in absence of the interaction partner. We will not further elaborate on how one can measure numerical responses as this is discussed elsewhere (e.g. Andrén & Liberg 2023), but discuss below how one can overcome two major challenges for quantifying trait-fitness relationships. These challenges concern the measurement of fitness and the identification of interaction- and fitness-relevant traits.

The first challenge is the actual measurement of fitness (both in the presence and absence of interaction partners). For some organisms, fitness can be easily measured, such as for microorganisms (e.g. Papkou et al. 2023) or annual plants (e.g. Kraft et al. 2015). The challenge of measuring fitness is, however, particularly pronounced for organisms that are mobile, long-lived and/or have inaccessible life stages. Below, we discuss approaches for overcoming these challenges.

For mobile organisms, mesocosms (experimental enclosures of intermediate size; Stewart et al. 2013) provide a useful tool for quantifying fitness of small to medium-sized organisms under controlled yet semi-natural conditions in both the presence and absence of biotic interactions. For instance, Hart et al. (2019) used pond mesocosms to study how interactions between floating aquatic plants affect their population dynamics. Brendel et al. (2023) used mesocosms to prevent seed immigration and emigration in their study of fitness of 40 alien and native Asteraceae species, in both the presence and absence of biotic interactions with a native plant community. Mesocosms further allow studying fitness consequences of plant-pollinator interactions, such as the effects of interactions with one vs. many plant species on multiple fitness components across the life cycle of the wild bee *Osmia bicornis* (number of larvae, cocoons, hatched and surviving individuals; Klaus et al. 2021). For larger and more mobile organisms, mesocosm experiments are, however, not suitable. A key challenge for these organisms is to follow individuals for long enough so that fitness components - and biotic interactions with other organisms - can be reliably quantified. This can be achieved through classical methods such as bird ringing (e.g. Schmoll et al. 2007). Increasingly, however, automated tracking systems generate high-quality movement data at regional to global scales that improve the measurement of fitness components (Nathan et al. 2022).

For organisms that are more long-lived than the typical research funding cycle, fitness can be quantified by integrating measurements of fitness components with demographic life cycle models, such as integral projection models (IPMs; Merow et al. 2014; Ellner et al. 2016). IPMs quantify population growth rate and/or fitness from a description of how an organism’s vital rates (survival, growth, reproduction) depend on continuous traits such as size or age. Struckmann et al. (2019) used an IPM to model how herbivory and three plant functional traits affect fitness of the long-lived perennial *Asclepias syriaca* by impacting sexual reproduction, survival and clonal growth. Such an approach could be expanded by including herbivore traits to quantify FLINTs for both the plant and herbivore. In cases where a biotic interaction only affects a single fitness component or if interaction effects on certain fitness components cannot be measured (i.e. some life cycle stages are inaccessible), demographic life cycle models are also helpful. For instance, plant-pollinator interactions affect seed set but may not impact growth, survival or recruitment of plants. To predict the trait-dependence of fitness, a demographic life cycle model can integrate effects of both plant and pollinator traits on seed set with interaction-independent trait effects for the remaining fitness components (such as per-seed establishment rate, which determines the relationships between seed set and fitness, Treurnicht et al. 2021).

When the direct measurement of certain fitness components is not feasible (e.g. because the respective life cycle stages are inaccessible), an alternative approach is to infer the fitness component from molecular marker polymorphisms, for example by parentage analysis based on genotyping of sampled recruits (Schmoll et al. 2007). Recent advances in high-throughput sequencing technologies facilitate cost-effective parentage analysis, which only requires genotyping at a relatively small number of genetic markers (see Flanagan & Jones 2018). If the genetic basis of interaction-relevant traits is known (see Van der Niet & al. 2023 for pollination-relevant floral traits), high-throughput sequencing can furthermore be used to examine allele frequency shifts in the genes determining fitness-relevant traits. Ultimately, high-throughput sequencing even makes it possible to directly relate fitness consequences of an interaction to the genotypes of the interaction partners (Doud et al. 2024). This will make it possible to map genotypic FLINTs.

A further challenge lies in the identification of fitness-relevant functional traits of the focal organism and its interaction partner. While prior knowledge of the study system should suggest a selection of candidate traits, preliminary studies may be necessary to identify which and how many traits (e.g. Eklöf et al. 2013) are needed to quantify FLINTs. For some study systems, trait selection is easier than in others, for instance in aquatic food webs body mass may suffice, because other traits allometrically scale with body mass (Hudson & Reuman 2013). In other systems, the proportion of explained variance in fitness (R^2) should help to infer the appropriate number of traits needed to reliably explain fitness. It may also be possible to reduce the dimensionality of FLINTs by combining multiple traits into mechanistically derived ‘process-informed metrics’ (Levine et al. 2025). To obtain informative fitness landscapes, a gradient sampling approach (Kreyling et al. 2018) should then be used whereby fitness is measured across a broad range of trait values of the focal organisms and its interaction partner.

The measurement of FLINTs is clearly challenging for many study systems. However, the above overview shows that a wide range of techniques are available for overcoming these challenges. Moreover, this is worthwhile since FLINTs - which are measured in the universal ‘currencies’ of fitness and functional traits - are a useful tool for synthesis on the functional causes and consequences of biotic interactions. Such synthesis could for instance address whether FLINT topographies are constant across different abiotic environments, organisational levels (within vs between species) and taxonomic community compositions. In other words, to what extent is the ecological theatre in which interactions play out universal?

Theoretical research agenda

The example of coevolution between plants and flower visitors (Box 1) shows that FLINT topographies can impact biodiversity dynamics by altering diversification rates, long-term species richness, functional community composition and the structure of interaction networks. There is thus ample scope for future research analysing how the size, shape and arrangement of mutualistic, antagonistic and competitive FLINT regions impact biodiversity dynamics. For instance, Fig. 8 shows that the addition of an antagonistic region to a mutualistic FLINT hampers diversification, even though Maliet et al. (2020) found diversification to be higher under pure antagonism than under pure mutualism. The FLINT concept provides a general framework for exploring and reconciling such seeming contradictions between theoretical models.

FLINTs can also be used to study the long-term dynamics of ecological networks comprising multiple interaction types (Fontaine et al. 2011). A number of questions arise in this context: do these networks show ongoing fluctuations in size and structure (as in Allhoff et al. 2015)? Or do they become non-invasible, so that new variants cannot establish and the networks reach stable trait diversity (as in Loeuille & Loreau 2005)? Under which conditions are networks dominated by antagonism, mutualism or a mixture of both interaction types? Moreover, existing eco-evolutionary models for biodiversity dynamics in antagonistic and/or mutualistic FLINTs assume trait-matching competition within groups (e.g. Loeuille & Loreau 2005; Maliet et al. 2020; Box 1). How do biodiversity dynamics change if within-group interaction are instead described by more complex competition FLINTs (Fig. 4b-d)?

‘Rugged’ fitness landscapes with many peaks and valleys received much attention in evolutionary biology (and more recently in ecology; Munoz et al. 2023). FLINTs make it explicit that such rugged fitness landscapes can arise from biotic interactions: in the example shown in Fig. 2, a fitness valley is created by a high frequency of potential nectar robbers that selects against flowers in a certain size spectrum. Evolutionary and ecological dynamics in rugged fitness landscapes depend on whether trajectories can cross valleys separating two adaptive peaks (e.g. Bank 2022). The FLINT concept clarifies that such fitness valleys can be filled due to changes in the trait composition of interaction partners (Fig. 2; see Doud et al. 2024 for an empirical example in competing viral strains). This raises the question when FLINTs favour changes in partner composition that fill fitness valleys and when FLINTs trigger shifts in partner composition that deepen existing fitness valleys. It should, however, be noted that the challenge of crossing fitness valleys may be largely restricted to low-dimensional fitness landscapes: a high-dimensional fitness landscape is likely to have ‘bypasses’ of high fitness that link the peaks (Gavrilets 1997). It remains to be explored whether FLINT dimensionality (the number of fitness-relevant traits of the focal organism and its interaction partner) has similar effects.

FLINT-based biodiversity models may not only address a number of questions in theoretical ecology and evolutionary biology, they also predict a wide range of biological phenomena that can be quantified empirically (Figs. 3, 7). This includes the distribution of focal traits within communities, the structure of interaction networks, and properties of phylogenies. The statistical integration of FLINT-based models with these diverse data types (e.g. via Approximate Bayesian Computation) might thus be used for inverse model parameterization. More generally, however, FLINT-based biodiversity models have the potential to quantitatively integrate seemingly disparate empirical data in order to improve our understanding of biodiversity dynamics.

Conclusion

The ecological and evolutionary dynamics of biodiversity are driven by a rich set of biotic interactions that extend far beyond simple trait matching. Fitness landscapes of biotic interactions (FLINTs) capture this richness of biotic interactions by describing how the fitness effects of a biotic interaction depend on traits of both interaction partners. The FLINT concept thus enables a comprehensive analysis of how biotic interactions shape ecological and evolutionary dynamics. Our own experience as a diverse team of scientists makes us hopeful that the FLINT concept will facilitate communication between ecologists and evolutionary biologists, theoreticians and empiricists about the mechanisms and consequences of biotic interactions.

Glossary

Diversification: the process by which the diversity of organisms changes over time, including within-species diversification (through microevolution) and between-species diversification (through macroevolution). The net rate of between-species diversification is the difference between speciation and extinction rates (Wiens 2011; Tietje et al. 2022).

Fitness: here used as absolute fitness, the expected number of descendants after one full iteration of the life cycle, that is the expected number of adult offspring of an adult (Rousset 2004). When evaluated at species level, it is equivalent to the species' per-capita population growth rate (Vellend 2016).

Fitness landscape: phenotypic fitness landscapes map an organism's fitness to the organism's phenotypic traits (Lande & Arnold 1983). Phenotypic fitness landscapes build on the older concept of genotypic fitness landscapes which map an organism's fitness to its genotype (Wright 1932).

(Functional) Trait: a trait is a well-defined, measurable property of organisms, usually measured at the individual level and used comparatively across species. A functional trait is a trait that strongly influences organismal performance (McGill et al. 2006).

Interaction network (or ecological network): a representation of the biotic interactions within a community in which interacting organisms (network nodes representing species or individuals) are connected by pairwise interactions (links). In the case of weighted networks, information on the interaction frequency among nodes is included (Bascompte & Jordano 2007).

Interaction type: a set of biotic interactions that has the same qualitative (positive or negative) effect on the fitness of the interacting organisms. The three major interaction types are competition (-/-), antagonism (+/-) and mutualism (+/+).

Trait matching: matching of trait states of interacting partners in terms of morphology, appearance, chemistry, or phenology (Stang et al. 2009, Junker et al. 2013, Schleuning et al. 2015).

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