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Enigma Evolution Project: Report of an Internship at the University of California Merced

1 Introduction

Ecosystems are typically large and complex, though the forces that give rise to these qualities are poorly understood. One prominent avenue of research is the study of the role of species interactions - both antagonistic¹⁻³ and mutualistic⁴⁻⁶ - in driving the emergence of complexity and diversity. Especially the macroevolutionary perspective is of high interest here and provides a rich field of open questions^{7,8}. Given the extensive time span in question, data availability is limited and sparse. Thus, theoretical approaches utilizing mathematical models and simulations can be expected to be crucial for the advancement of the field.

Network theory has proven to be particularly useful here as network models are capable of condensing the complexity of the real world to something manageable while retaining enough descriptive power and biological meaning to serve as effective tools for the investigation of the complex dynamics of ecosystems⁹⁻¹¹. There is a large variety of network models with different levels of details and focal points that allow for the study of both structure and dynamics of ecosystems. While models incorporating population dynamics and the flow of energy are of great use for the investigation of ecological interactions, we argue that they are often prohibitively complex for exploring macroevolutionary - scale questions at the level of the community. Therefore, we propose a boolean adaptive network model focusing on the dynamics of structure on interaction networks where species are nodes and their various interactions links.

At this level, three main processes shape the structure of communities: Migration, extinction and evolution. Adaptive network models, which dynamically introduce and remove nodes and links in interaction with the dynamics in the system¹², have been used extensively in the study of all three¹³⁻¹⁶. Many of these models can be sorted into two categories each of which focuses on one primary mechanism through which diversity emerges in ecosystems:

- (1) Community assembly models, originating in island biogeography¹⁷, investigate how community structure is shaped by the interplay of migration and local extinctions.
- (2) Evolutionary models study how evolution and extinctions work together to create diversity, often on much longer timescales.

While both approaches yield networks that closely align with realistic ones across key aspects, evolutionary models often have the great benefit of combining ecological dynamics that govern the co-existence and extinction of species with evolutionary dynamics¹⁵. This holds great relevance as it has become increasingly evident over the last decades that many aspects of community structure can

only be understood as a product of ecoevolutionary dynamics^{18,19}. While there has been substantial progress in understanding the intertwined role of microevolution and ecology^{7,20}, the vast temporal scale inherent in macroevolutionary processes still presents challenges when integrating them with ecological dynamics^{7,8,21}.

While many models only consider interactions of one specific type, both, trophic^{2,3} as well as non-trophic¹ interactions and especially mutualisms⁴⁻⁶ are central to fueling the evolution of complexity and diversity in ecosystems. Because dynamic outcomes such as stability and resilience²² depend on the structure of these diverse interaction types in combination^{23,24}, to what extent they contribute to changes across macroevolutionary timescales must also be considered. A primary challenge is then to integrate these ingredients into a model of sufficient but not overwhelming complexity where their combined effects can be explored.

Here, we extend the interaction framework introduced by Yeakel et al.²⁵ to include macroevolutionary dynamics in order to investigate the influence of multi-type interactions on the eco-evolutionary dynamics of community structure. The resulting model is an ecological community assembly model that also features macroevolutionary dynamics and trophic as well as non-trophic interactions. We show that this framework is capable of generating complex and diverse ecological networks that can be simulated over macroevolutionary timescales. This makes it a promising candidate for the study of eco-evolutionary questions focusing on the impact of biotic factors in the form of species interactions.

Due to the time limitations of this project, we did not delve into these questions though. Instead, we further investigated the data that was produced for the test of the usability of the generated networks. Specifically, we studied the impact of eco-evolutionary rates on the evolving diversity and complexity of ecosystems. Eco-evolutionary rates, such as speciation and extinction rates, are widely regarded as influential elements shaping diversity patterns^{26,27}. For instance, a declining speciation rate that eventually fell below extinction rates decreased dinosaur diversity and, thus, their resilience against disturbances for tens of million years before their final demise in the Cretaceous–Paleogene mass extinction event²⁸. We observe that competitive exclusion, which underlies one type of extinctions in our framework, needs to be sufficiently slow to allow for the development of complex ecosystems. Furthermore, we see a decreasing species richness for rising speciation rates that we attribute to an increasing similarity of the extant species.

2 Methods - The model

The foundation of our studies is the ENIgMa-Model, originally developed by Yeakel et al. in [25], which we modified and extended to fit our purposes. The scenario it describes is that of an initially uninhabited island that over the course of time is populated by species that migrate there. An ecosystem assembles; species compete over resources, some go extinct from the island and might or might not remigrate, others replace them and so on. On top of these ecological dynamics we add macroevolutionary processes that come into play over longer time scales (see section 2.2). Here we continue with a description of the original model.

2.1 The original ENIgMa-model.

2.1.1 The general structure. The ENIgMa-model is a rather minimalist network approach to the modeling of the assembly of an ecosystem in which ecological entities are the nodes and their interactions the links. Here, an ecological entity can be one of three things: A basal resource that is considered to be always present, the population of a species or a so called modifier that is created by some species and changes its environment. In nature we find a multitude of possible interactions these entities could have. The model aims to describe a broad range of those by defining four basic types of interactions modeled as directed links that give it its name: E: eat, N: need, Ig: ignore and Ma: make interactions. Eat interactions describe all direct trophic interactions. This could, for instance, be predators eating their prey, autotrophs receiving their energy from the sun or insects feeding on pollen. Need interactions describe the relationship of a species to another ecological entity that provides some non-trophic service to it that it relies on. The classic example would be a plant needing a pollinator for procreation, but it could also describe a liana needing another plant to reach direct sunlight. Make interactions indicate that a modifier is made by a species. Finally, ignore interactions symbolize that two ecological entities do not significantly interact in any way described by the previous three interaction types and are modeled as the absence of a link. This does not mean, however, that there is no interaction at all between the two entities as many types of interactions we observe in nature would be described by motifs consisting of more than one link in the ENIgMa-model. Two predators, for instance, might ignore each other in the sense of the model but interact indirectly as they compete over a prey they share. The interaction links of the model are, thus, just the basic components that combined in a network form the complex interactions we see in nature.

This describes the internal structure of the networks we work with, but how are they established? As mentioned before, we assume that the island is uninhabited at first. Consequently, the only nodes it initially contains are the basal resources. It is then populated from a so called "species pool". This pool is not to be understood as any specific ecosystem but more as a collection of all species that could potentially invade the island's ecosystem. They could in principle live in a multitude of ecosystems on other islands or continents. This species pool is generated before every simulation as described in the following section.

2.1.2 The generation of the pool. The abstract nature of our model makes direct comparisons with real life networks and species rather uninformative and imprecise. Thus, we do not try to translate existing networks into our model but rather generate our pool networks randomly. Not wanting to impose a special structure, we try to put as little input into the pool network as possible and only set the fraction of all possible interactions that are realized and the initial size of the network. With this information we sample our networks from a uniform distribution of all networks with these properties.

More precisely, we define the number of basal resources, the number of species, the average number of modifiers a species creates and for eat and need interactions the fraction of all links that

are of this type. Using that information, we compute the total amount of make interactions and create as many modifiers. The resulting network is somewhat similar to an Erdős-Rényi random network. It is different though as it has different types of nodes and links and not all links can point from every type of node to every other: Eat and need interactions always point from a species to another node, while make interactions always point from a species to a modifier. This means that there are no non-ignore links in the subnetwork of basal resources and modifiers.

To avoid species that have no food source, we then modify our network such that we give species that got no eat interaction in the generation process a random basal resource as food source. This creates a bias towards more primary producers which we think to be acceptable, though. Contrary to that, modifiers that are not created by any species are eliminated from the pool.

2.1.3 The assembly process. Given the species pool, the community on the island is assembled from it. This assembly of the community network is the heart of the simulation. A key part of it are the ecological dynamics in the community that determine if a species can survive on the island. There are two aspects to that in the ENIgMa-model. First, a species has to be structurally supported which we define to mean that at least one of its food-sources has to be present on the island as well as all entities it has a need interaction with. This constitutes a fundamental difference between need and eat interactions in the ENIgMa-model. Need interactions are designed to be mandatory, making them a strong structural constraint, whereas eat interactions are less restrictive, since it suffices to have one of your foodsources available. The second mechanism in the model that controls the survival of species is based on the principle of competitive exclusion. It states that two species that compete over the same limiting resources can not coexist with static abundances as one of them will always outcompete the other²⁹. The model translates that to the requirement that every species has to be the strongest competitor for at least one of its resources. The competitive strength of a species is here determined by the interactions it has and is, therefore, the same for all its foodsources. More precisely, every link a species has grants it a bonus or penalty on its competitive strength based on the type of the link. Reflecting the pressure a predator puts on a prey's population, species that get eaten by others get a penalty on their competitive strength³⁰. The same is true for predators, which get a penalty for each of their food sources to model the advantage of trophic specialists compared to generalists³¹⁻³⁴. Need interactions, which are the building blocks of mutualisms, give the species receiving the service a competitive advantage³⁵. Ecosystem engineers get a bonus on their competitive strength for each modifier they make as we consider them to be niche constructors³⁶.

The actual assembly process is then, as in the original ENIgMa-model, realized by defining a set of event types that can happen under certain circumstances. Each of those has an exponentially distributed waiting time with an expected value specific to the type of event. Those can be seen as rates at which a possible event occurs statistically. The original model knew four types of events: Colonizations, two types of local extinctions and the disappearance of modifiers.

Colonization events describe successful invasions of the island's ecosystem by a species from the pool. To be a candidate for such an event, a species has to be structurally supported by the island network as explained above. If an ecosystem engineer colonizes, it always introduces all modifiers it creates to the island.

The two types of local extinctions are based on the two conditions a species has to fulfill in order to be able to survive on the island. If a species is not the strongest competitor for at least one of its food sources, it is a candidate for a so called primary extinction event. If a species is not structurally supported by the island network, it is queued for secondary extinction. This name stems from the fact that all species have to be structurally supported in order to be able to establish themselves on the island. Thus, they

can only be a candidate for secondary extinction if at least one other species or modifier goes extinct first. We call both of these types of extinctions local as the species is only removed from the community on the island but remains in the species pool and can potentially remigrate to the island later.

When an ecosystem engineer goes extinct, the modifiers it creates do not disappear at the same time. This property of engineered modifiers to have a legacy and remain in an ecosystem even after their engineers have gone extinct is considered to be typical for engineers³⁷. A modifier that is not engineered by any species is, however, queued for disappearance.

2.2 The ENIgMa-model - evolved. While the original focus of the ENIgMa-model was to shine a light onto the structural influence of ecosystem engineers on ecosystem assembly, the model's capability to span vast time scales makes it a promising candidate for the study of the interplay of macroevolution and ecology. To make that possible we introduced two new types of events: Evolutions and global extinctions.

2.2.1 Evolutionary Events. As the model is focused on interactions and their structure disregarding varying interaction strengths, it is natural to model evolutions by changing the type of interactions. Concisely, we model an evolutionary event in three steps. First, a random species from the local community is picked. Secondly, a random interactant is drawn that could be any ecological entity currently present in the community. Finally, the type of their interaction is changed. In the case of a species-species interaction this could affect either the incoming or the outgoing interaction. All types of feasible interactions have the same chance to become the new interaction. We chose this completely random approach, deciding against favoring some mutations over others, to be as unbiased as possible because the level of abstraction of the model makes it extremely hard to justify any preferences. On the other hand, we usually set our initial parameters such that most interactions are non-interactions. Thus, most evolutionary events will turn non-interactions into interactions and, consequently, evolution has the effect to increase the mean degree of the network on a short time scale. The long term impact could be different though. For instance, highly connected species could have a higher risk to go extinct because they have too many needs or a too low competitive strength as a result of too many food sources.

2.2.2 Evolutionary events - cladogenesis vs. anagenesis. Another fundamental decision to be made about the evolutionary process is if it is divergent. By divergent we mean that both the original species and the evolved version coexist after the evolutionary event, so a cladogenesis. Alternatively the evolved species could replace its parent, an anagenesis. We decided to keep both possibilities but used divergent evolution in all our simulations. In any case, we would want to have some selection process ensuring that the way we model evolution somehow favours species that are better adapted to the system. In the case of a non-divergent evolution, where only one of the two species is kept, we decided to actually not always keep the evolved species but the species with the higher competitive strength. The divergent case, where the original species and its mutated version are kept, allows for an explicit modeling of the selection process. The system's dynamics decide whether both species are able to coexist in the long run or only one and if so which of the two.

A short consideration of the divergent case shows that the two options might often result in a similar situation in the long run: As the original species and the evolved one only differ by one interaction, they will be direct competitors of each other in many cases. This will often lead to one of them being a candidate for primary extinction immediately. If, for example, an ignore interaction becomes a need interaction, both species will have the same food sources and the evolved species will be a stronger competitor as

it gets a competitive bonus from the new need interaction. Therefore, the original species will be queued for extinction and in many cases go extinct shortly thereafter. In those cases, the result of the selection process is the same as in the non-divergent evolutionary process. In this sense, it could be said that the non-divergent evolution is a simplified, shortcut version of the divergent evolution. In other cases, the competitive strength is a less meaningful predictor of a species ability to survive in the system. For example, consider the case where the new interaction is an eat interaction. The evolved species will have a lower competitive strength because of the penalty associated with the additional food source. On the other hand, the new food source could have no or only weaker competing consumers, which would enable the new species to survive in its own niche. To allow for such situations, was one of the main reasons to use the divergent approach in our simulations.

The divergent evolution creates some challenges however: If we actually were to not change any other relationships to the evolved species but the one to the interactant chosen in the evolutionary process, an additional constraint is created for all species that need the parent. For instance, a plant that needs a pollinator would need the original pollinator and all its potential descendants. This means it would likely go extinct if only one of the pollinators went extinct. That seemed to be a hardly justifiable side effect of an evolutionary event. Thus, we decided to not inherit those incoming needs. The plant in our example would still only need the original pollinator and ignore its descendants. It could be argued that the need for pollination should actually be fulfilled if only one or a portion of the pollinators are present, but that would mean a fundamental change of the model with its mandatory needs. Therefore, we decided against this option and it is not unjustifiable to model it the way we do. It is not necessarily the case, that an evolved species fulfills all the functions in an ecosystem that its predecessors fulfil. The breakdown of mutualisms is a well known phenomenon³⁸. In our example the pollinator would become a parasite and the mutualism a predation. Such processes are well documented³⁹⁻⁴¹ although they are empirically rarer than many theoretical considerations suggest⁴².

2.2.3 Global extinctions. Another implication of the divergent approach is that each evolutionary event creates a new species, thus, the overall amount of species in the pool grows indefinitely. In order to counteract that, we introduced another type of event, global extinctions, that permanently eliminate a random species from the whole pool. Here we again had multiple options. One would be to really randomly pick the species to go extinct from the whole pool. This could be interpreted as a random disturbance independent of any ecological features of the species to go extinct. While that is a simple option, it seems to be more reasonable to somehow use the ecological features of the species to ensure that well adapted ones are less likely to go extinct globally. To achieve this, the species chosen for global extinction are exclusively drawn from the pool of species currently absent in the local community. This approach acknowledges the tendency of well-adapted species to exhibit longer stays within the community.

2.2.4 Multiple basal resources. The original ENIgMa-model features one basal resource, that could for example be considered to be the sun. But in order to get sufficiently complex networks it was important to have more than one species on the lowest trophic level, consuming the basal resource. This made it necessary to somehow change the competition over the basal resource, which was achieved by artificially protecting autotrophs from primary extinction. While it served its purpose in the original model, it was not the most elegant solution to begin with. Having introduced evolution, this special rule proved to be problematic. As autotrophs could not go extinct (unless they developed a need interaction to something that could), there was a growing number of autotrophs evolving and the developing networks tended to be pretty simple and had very low average trophic levels. Sometimes the network

Table 1 The different event rates and their labels

Rate label	corresponding event
r_c	colonization
r_{1°	primary extinction
r_{2°	secondary extinction
r_{oe}	object disappearance
r_{evo}	evolution
r_g	global extinction

consisted mostly of autotrophs with needs for each other that kept multiplying, a hardly justifiable situation created by the absence of competition or other regulating factors.

To solve this problem, we decided to abolish the special treatment of autotrophs and instead introduced more than one basal resource to ensure that there can be more than one species on the lowest trophic level. One way to interpret those basal resources is to see them as some sort of microhabitats. They could stand for different soil conditions or availability of water or sunlight for example.

3 Results and Discussion

3.1 Reasonable parameter spaces - varying r_{1° . Having decided on the details of the model, the first question we had to answer was if the model is capable of producing networks that are ecologically reasonable and at the same time sufficiently complex to be of interest. To that end, we explored our parameter space to find feasible subspaces. More specifically, the parameters we investigated were the rates at which different events occur and their influence on certain key properties of the community network. For an overview of the labels of the different event rates, see Table 1. As the absolute value of the rates simply gauges the timescale, only their relative values are of interest and we could fix one of them to an arbitrary value. We chose the colonization rate.

We used four attributes of the simulated networks to assess if they are ecologically feasible and of interest: The species richness, the maximal trophic level and the mean degree of the subnetworks consisting of only need and only eat interactions, respectively.

3.1.1 The species richness as a function of r_{1° . The first attribute we investigated was the species richness of the island community which we employed as a measure of its diversity. While the species richness is variable in time, it has to be bounded i.e., it can not grow indefinitely, as that would be ecologically impossible. Theoretically, our framework allows networks to grow indefinitely as no principally limiting factor like energy is modeled explicitly. Thus, the model has to be tweaked to find a balance by other means. Our approach to achieve that was to compensate the species adding processes of colonization and evolution with the different species removing extinction types. Keeping the additive rates and global extinction at fixed values, we began by varying the primary and secondary extinction rates independently. The results show that too low extinction rates lead to an approximately linearly increasing species richness over time which appears to be unbounded. We assume that this ecologically unreasonable behaviour is due to evolution producing new species faster than they can go extinct even though they are queued for extinction.

This behaviour changes at some point when we increase the extinction rates. We get bounded species richnesses that eventually only fluctuate around a mean. This is a phenomenon we utilized a lot in our analysis when it occurred: After an initial burn-in phase, the network reaches a settled state in which many of its properties, while they are not constant, only fluctuate around a mean. That allows us to disregard the explicit temporal evolution of the networks and only look at averaged attributes. Here, we use this approach to study the mean of the species richness yet again averaged over 50 replicates as a function of the primary extinction

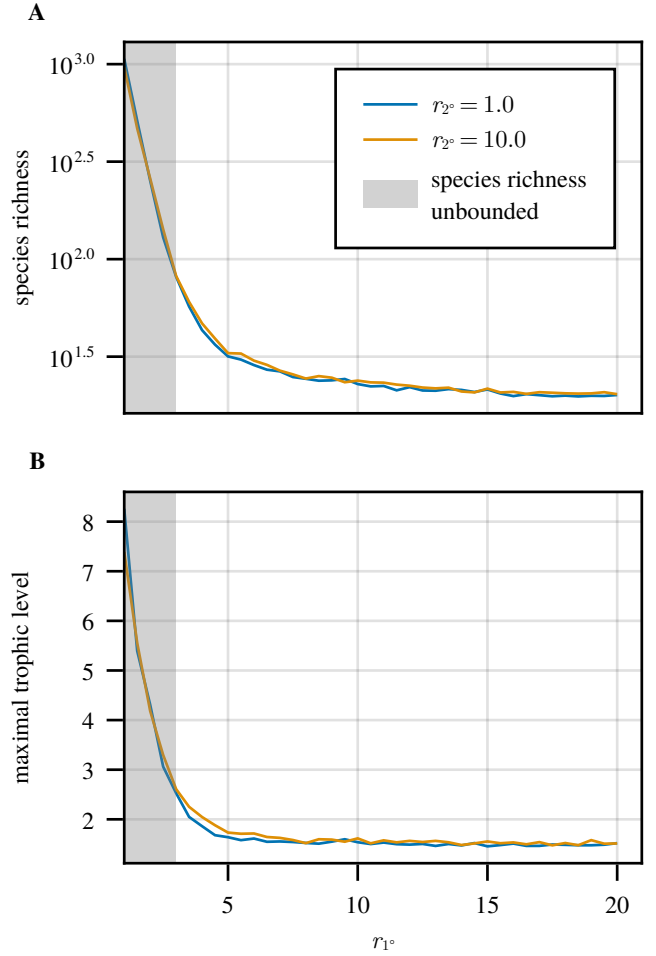


Fig. 1 Community species richness (A) and maximal trophic level (B) as functions of the primary extinction rate.

The results are computed after an initial burn-in phase in which we assume the communities properties to stabilize. We then average the properties over the last 2000 iterations of the simulation. This mean is again averaged over 50 repetitions of our simulation with identical parameter settings. In the greyed out area, the species richness is not bounded which is ecologically unreasonable and impedes the interpretability of the means.

rate. This situation is depicted in panel A of Figure 1 for two exemplary secondary extinction rates. We find that this averaged mean decreases faster than exponentially with growing r_{1° (Note the logarithmic scale of the vertical axis). For medium to high primary extinction rates the species richness is so low that the systems might not be of interest for further analysis. A big part of the higher species richness for low r_{1° is due to an increased amount of species that are queued for primary extinction but survive longer in an unstable state. There is a significant portion of the surplus of species, though, that consists of long term stable species which we assume had the opportunity to adjust before they went extinct. Concerning the secondary extinction rate, we observe that it has no significant influence on the species richness in the parameter range we tested.

3.1.2 The maximal trophic level as a function of r_{1° . Our next objective was to verify that the generated networks exhibit a sufficient level of structural complexity to be of interest. The main metric we used to measure structural complexity is the maximal trophic level, which we computed using the 'TrophInd' function of the R package 'NetIndices'⁴³. Again varying over the primary and secondary extinction rates, we found that while r_{2° has an impact

on the maximal trophic level it is rather small compared to the one of r_1° . One reason for this small impact of r_2° is probably that species that are not connected to a basal resource via a series of eat interactions are not considered for the computation of trophic levels. Which means that all species that are queued for secondary extinction because they lack a food source are ignored here. Thus, increasing r_2° might have an impact on the network by faster removing disconnected species from the community, but that has no effect on the maximal trophic level.

Similar to the mean species richness the mean of the maximal trophic level decreases faster than exponentially with increasing primary extinction rate. Panel B of Figure 1 shows the mean of the maximal trophic level yet again averaged over 50 replicates as a function of r_1° for $r_2^\circ \in \{1; 10\}$. Already at rather low primary extinction rates in the order of the colonization rate, we get really low maximal trophic levels below 2 where most species are primary producers. At this point there is still a great amount of primary extinction candidates in the communities. As for the species richness, this indicates that we have to allow species to persevere for quite some time although they are weaker than their competitors to enable the development of complex communities.

3.1.3 Competitive exclusion vs. neutral theory. To interpret these last observations we want to take a closer look at primary extinctions. The competitive exclusion principle, the underlying concept based on which primary extinctions are modeled in our framework, is well known not to be a strict law but rather a tendency of nature to favours fitter species. Competition is a long-standing candidate to explain patterns of diversity in ecosystems that has been challenged and complemented by other concepts most famously neutral theory. The Neutral Theory of Biodiversity and Biogeography states that community structure is mainly shaped by random processes, while interactions such as competition play a minor role. It is to some extent designed to be the counterpart to ever more complex niche models and follows the idea of Occam's Razor^{44,45}. Currently it is assumed that both processes have a meaningful impact on the structure of communities⁴⁶. In our model, the conflict between the rather deterministic niche theory and the fundamentally stochastic neutral theory is to some extent encapsulated in the primary extinction rate r_1° . With high primary extinction rates the competitive exclusion principle is essentially modeled deterministically as outcompeted species will go extinct very fast without a realistic chance for survival or adaption. The lower r_1° , the more it becomes a matter of chance if an outcompeted species survives for longer times and might even be able to adapt. In this context it is noteworthy that our model only generates complex networks if competitively weaker species are allowed to survive for longer times. It suggests that the necessity of stochastic processes for the assembly of complex communities may already be inherent in the foundational aspects of ecosystems captured in our simplified structural model.

3.1.4 The mean number of eat interactions as a function of r_1° . The degree distribution is another important property of the network that we wanted to track. Especially the mean degrees of the subnetworks consisting of only eat and only need interactions, respectively. Analogous to the plots before, panel A of Figure 2 depicts the mean of the mean eat degree i.e., the mean number of food sources a species has, as a function of r_1° . We again see very high values for low primary extinction rates where the species richness is unbounded and a faster than exponential decline for increasing r_1° . This decline is in line with the negative effect of eat interactions on the competitive strength. Higher primary extinction rates make this competitive disadvantage more significant for a species survival. Changing r_2° from 1 to 10 has approximately the same effect as a change of r_1° from 5 to 20. This is somewhat surprising as more food sources should give a species a higher chance not to become structurally unstable and be a candidate for secondary extinction. Overall, the attained values of the mean

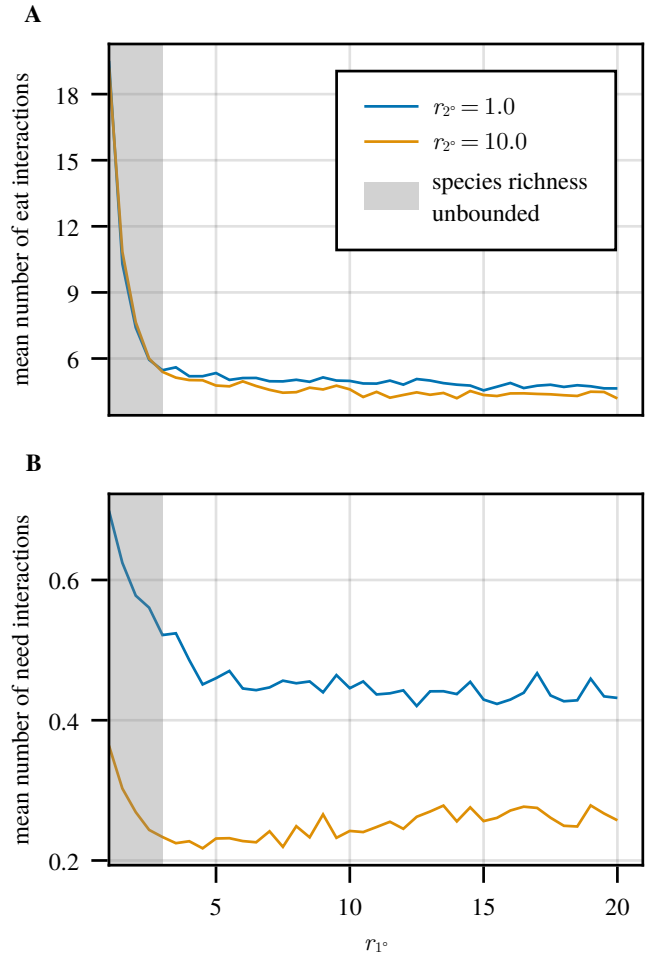


Fig. 2 Mean degree of the subnetworks of only eat (A) and only need (B) interactions as functions of the primary extinction rate. Again, the results are computed after an initial burn-in phase in which we assume the communities properties to stabilize. We then average the properties over the last 2000 iterations of the simulation. This mean is again averaged over 50 repetitions of our simulation with identical parameter settings. In the greyed out area, the species richness is not bounded which is ecologically unreasonable and impedes the interpretability of the means.

number of food sources is ecologically reasonable for all values of r_1° where the species richness is bounded.

3.1.5 The mean number of need interactions as a function of r_1° . Similarly, we looked at the mean degree of the subnetwork of all need interactions (see panel B of Figure 2). First of all, the relative difference between the results for high and low values of r_2° is a lot bigger. This can likely be explained by the high risk of secondary extinction that need interactions entail, which is made more severe if those extinctions are more frequent. As before, we see very high values and a steep decline in the areas where the species richness is unbounded. In the bounded area we see a new behaviour. In the case of a high secondary extinction rate, after attaining a minimum, the mean number of needs increases again for higher primary extinction rates. This can likely be attributed to the opposing affects of need interactions on species. While, as mentioned, they entail a high risk of secondary extinction, they also grant a big competitive advantage. Thus, for parameter ranges where secondary extinction is dominant, need interactions are highly discouraged, but when primary extinctions become more frequent the bonus in competitive strength becomes more and more relevant allowing more species with need inter-

actions to stay in the community. In the case of a low r_{2° , the suppression of need interactions is not so strong and we do not see an increase but rather a stagnation for higher values of r_{1° . Again, the mean number of need interactions is ecologically reasonable for all values of r_{1° where the species richness is bounded.

3.2 Reasonable parameter spaces - varying r_{evo} . Having explored the parameter space along the axes of r_{1° and r_{2° for a fixed r_g and r_{evo} , we wanted to vary the evolutionary rate. As we decided to model evolution with diversification, each evolutionary event creates an additional species. As explained above, this growth in species richness is somewhat balanced by global extinctions. Thus, we decided to vary r_{evo} and r_g simultaneously. More precisely, we fixed the the following relationship:

$$r_{evo} = 2r_g.$$

Furthermore, we set $r_{1^\circ} = 3.5$, an intermediate value that allows for reasonable and interesting results.

3.2.1 The species richness as a function of r_{evo} . Panel A of Figure 3 shows the species richness of the community as a function of r_{evo} for a high and a low value of r_{2° . Note that both axes are in a logarithmic scale. In the case of a high secondary extinction rate, we get an almost constant if slightly decreasing species richness for about two orders of magnitude in r_{evo} . When r_{evo} comes within an order of magnitude of r_{1° the species richness begins to grow simultaneously with some portion of the simulations not leading to a bounded species richness. At this point, the evolutionary process probably produces species faster than they could go extinct locally in the community. Consequently, they are not available to global extinction and the overall number of species would keep growing indefinitely. The same happens for low values of r_{2° . The effect is much stronger though, creating rapidly growing networks, none of which appear to be of a bounded size for high values of r_{evo} . This is in accordance with our expectations as the local extinction is even slower in this case.

The initial decline of the stable species richness over almost two orders of magnitude of r_{evo} for the low value of r_{2° was more surprising. The first intuition might be that a higher evolutionary rate means a faster addition of new species and that that should lead to a higher species richness. While it is true that more species are created, the new species apparently do not lead to a higher species richness in the long run. One possible explanation that came to mind was that the species in the community become more similar to each other with higher evolutionary rates and similar species tend to be direct competitors of each other. Thus, it is understandable that a network with a higher average similarity of its species is less stable and will become smaller. While we could not exactly and mechanistically explain how this increased similarity and competition lead to smaller networks on the level of our model, we could show that the species do become more similar with increasing evolutionary rate. More than that, there is a correlation between low species richness and a higher similarity of the species in the network even for constant parameters.

3.2.2 Similarity and species richness. To quantify the similarity of species, we used the Sørensen-Dice coefficient. This statistical tool, also known as Dice similarity coefficient (DSC), was developed to measure the similarity of two statistical samples⁴⁷. It is defined as:

$$DSC(X, Y) = \frac{2|X \cap Y|}{|X| + |Y|} \quad (1)$$

where X and Y could be any finite sets. It ranges from 0 to 1 and attains 1 if and only if the two samples are identical. In our case we calculated the similarity of two species as the Sørensen-Dice coefficient of the sets of their interactants, that is, their neighbours in the network. We modified the coefficient, though, to differentiate

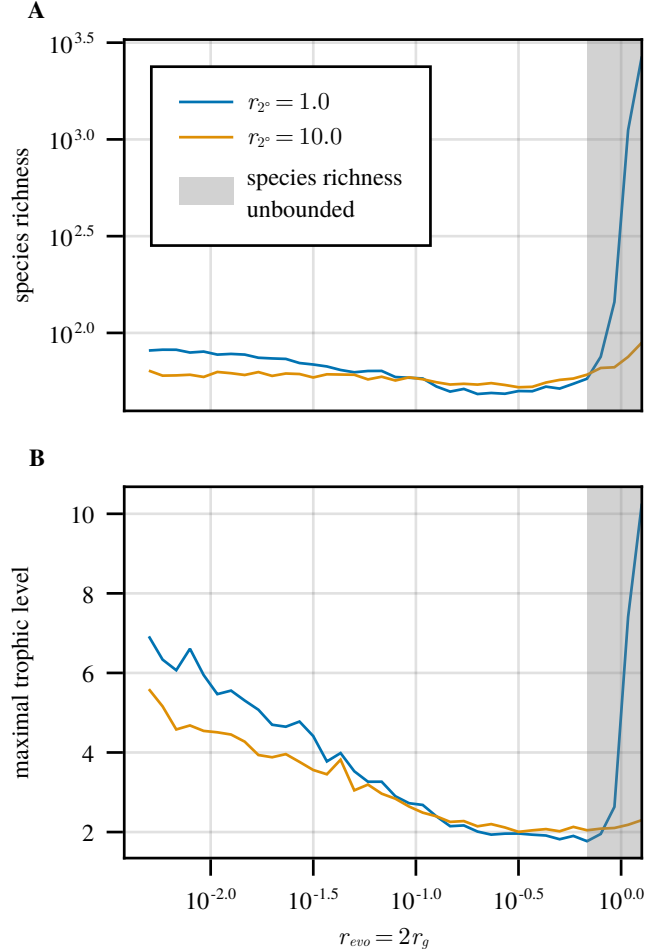


Fig. 3 Community species richness (A) and maximal trophic level (B) as functions of the evolutionary rate. Again, the results are computed after an initial burn-in phase in which we assume the communities properties to stabilize. We then average the properties over the last 2000 iterations of the simulation. This mean is again averaged over 50 repetitions of our simulation with identical parameter settings. In the greyed out area, the species richness is not bounded which is ecologically unreasonable and impedes the interpretability of the means.

between types of interactants i.e., if two species both interact with a third but one of them eats it while the other needs it, this is not considered to increase their similarity. Put in a formula, we defined the similarity of two species A and B as:

$$DSC(A, B) = \frac{2(|A_{eat} \cup B_{eat}| + |A_{need} \cup B_{need}|)}{|A_{eat}| + |A_{need}| + |B_{eat}| + |B_{need}|}. \quad (2)$$

Here, A_{eat} and A_{need} are the sets of all species that A eats and needs, respectively. Looking only at outgoing neighbours, we decided to ignore predators, and make interactions where not used in our simulations anyways.

Using this definition, we computed the pairwise similarity of all species in the community network. The mean value of those similarities is plotted as a function of the evolutionary rate in panel A of Figure 4. The resulting graph is clearly increasing as we suspected. This supports our hypothesis that the decreasing species richness in the community for an increasing evolutionary rate might in part be caused by an increasing similarity of the species in the network.

Additionally, we studied the correlation between the species richness and our similarity measure for the 50 replicates we had for each parameter configuration. Panel C of Figure 4 shows a scatter plot for fixed parameters with the mean pairwise similarity on the vertical axis and the species richness on the horizontal axis. Panel B shows the Pearson correlation coefficient of those two variables as a function of the evolutionary rate. We see an evidently negative correlation over all parameter values that mostly produced bounded species richnesses. This, again, backs our hypothesis.

3.2.3 The maximal trophic level as a function of r_{evo} . Panel B of Figure 3 shows the maximal trophic level, again as a function of r_{evo} coupled with r_g for a low and a high secondary extinction rate. Here, only the horizontal axis is in a logarithmic scale. For low and intermediate values of r_{evo} and r_g , we see approximately exponentially declining maximal trophic levels. For the low value of r_{2° , this decline is faster but starts from a higher value. In absolute terms, we see that for high evolutionary rates the systems might be too simple to be of greater interest for further analysis. For lower to medium values of r_{evo} , a quite wide parameter space, we get maximal trophic levels that could be found in empirical networks though.

4 Summary and outlook

The framework developed in this report is a powerful tool to tackle eco-evolutionary questions. We could show its ability to simulate ecosystems over macroevolutionary timescales and generate networks that are complex and compatible with empirical ones. We used it to study the influence of eco-evolutionary rates on the structure and especially complexity of the generated networks. Notably, we observe that with extinctions modeled based on the principle of competitive exclusion a degree of stochasticity in their timing becomes necessary to allow for the development of complex networks. This indicates that the importance of stochasticity in forming complexity in ecosystems is already inherent in the basic structure of the networks captured in our model. Changing the speciation rate we find that more new species do not necessarily lead to more species overall. Indeed, higher speciation rates lead to a decreasing species richness over some orders of magnitude of the speciation rate. We contribute this at least partly to the increasing similarity of the extent species. To what extent this effect might be mitigated or even nullified by the introduction of a spatial component and, thus, the chance to avoid competition would be an interesting avenue for further research.

Also within the boundaries of the framework as it is, its capacity to simulate ecosystems over macroevolutionary timescales makes it a strong candidate for further investigations into the dynamics of the structure of ecological interaction networks. A worthwhile opportunity for future research might be provided by the extinction

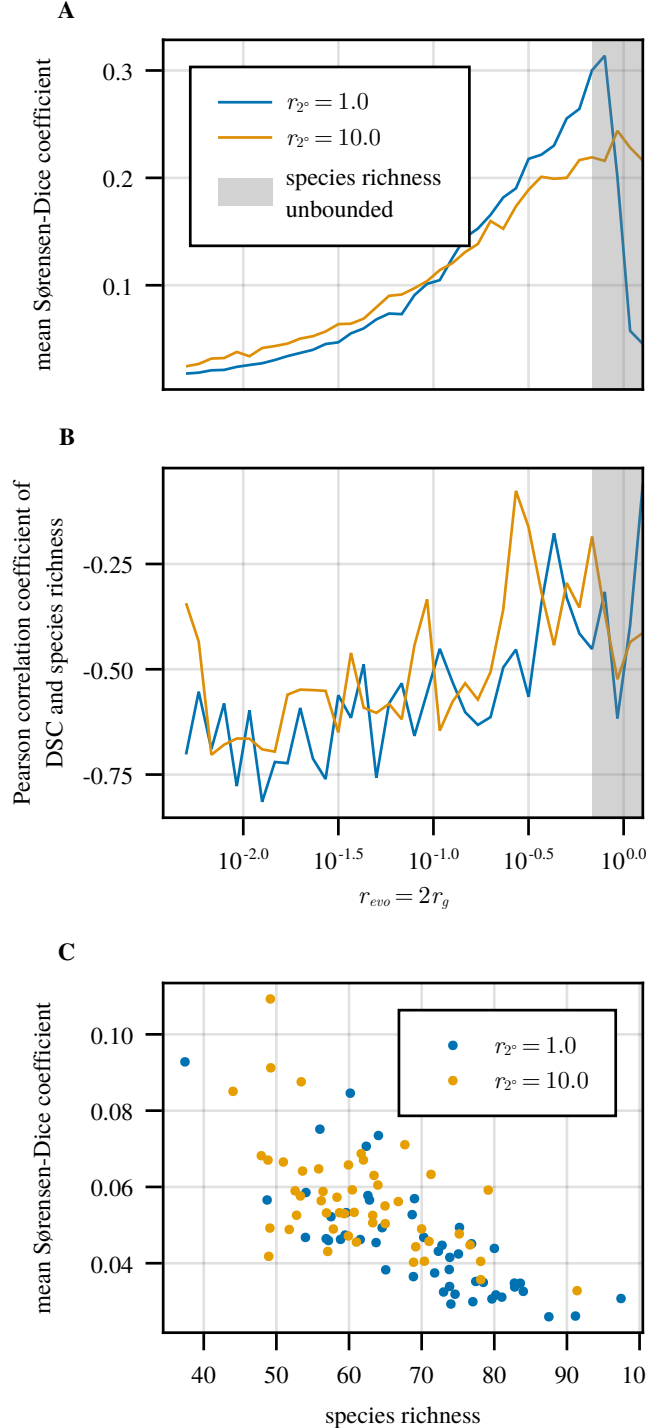


Fig. 4 Mean Sørensen-Dice coefficient of species in the community (A) and the Pearson correlation coefficient of the mean Sørensen-Dice coefficient and the species richness in the community (B) as functions of the evolutionary rate. The Sørensen-Dice coefficient or DSC of two species defined in Eq. (2) is a measure of the species' similarity. Panel A shows the mean of the pairwise DSC of all species in the community at the end of our simulations. Here, it is only averaged over the 50 replicates with identical parameters. Panel B shows the Pearson correlation coefficient of the mean DSC and the species richness in the community. The relationship of those two parameters is exemplary depicted in a scatter plot in Panel C for $r_{evo} = 0.027$.

cascades commonly observed in our simulations. What triggers them? Are specific motifs relevant for their occurrence. Are certain network structures more susceptible to them? Do the networks exhibit different structural properties before and after large extinction cascades?

References

- Medina, I., Kilner, R. M. & Langmore, N. E. From micro- to macroevolution: brood parasitism as a driver of phenotypic diversity in birds. en. *Current Zoology* **66** (ed Muñoz, M.) 515–526. issn: 2396-9814. <https://academic.oup.com/cz/article/66/5/515/5866979> (2023) (Oct. 2020).
- Brodersen, J., Post, D. M. & Seehausen, O. Upward Adaptive Radiation Cascades: Predator Diversification Induced by Prey Diversification. en. *Trends in Ecology & Evolution* **33**, 59–70. issn: 01695347. <https://linkinghub.elsevier.com/retrieve/pii/S0169534717302598> (2023) (Jan. 2018).
- Gorzela, P., Salamon, M. A. & Baumiller, T. K. Predator-induced macroevolutionary trends in Mesozoic crinoids. en. *Proceedings of the National Academy of Sciences* **109**, 7004–7007. issn: 0027-8424, 1091-6490. <https://pnas.org/doi/full/10.1073/pnas.1201573109> (2023) (May 2012).
- Bastolla, U. *et al.* The architecture of mutualistic networks minimizes competition and increases biodiversity. en. *Nature* **458**, 1018–1020. issn: 0028-0836, 1476-4687. <https://www.nature.com/articles/nature07950> (2023) (Apr. 2009).
- Weber, M. G. & Agrawal, A. A. Defense mutualisms enhance plant diversification. en. *Proceedings of the National Academy of Sciences* **111**, 16442–16447. issn: 0027-8424, 1091-6490. <https://pnas.org/doi/full/10.1073/pnas.1413253111> (2023) (Nov. 2014).
- Chomicki, G., Weber, M., Antonelli, A., Bascompte, J. & Kiers, E. T. The Impact of Mutualisms on Species Richness. en. *Trends in Ecology & Evolution* **34**, 698–711. issn: 01695347. <https://linkinghub.elsevier.com/retrieve/pii/S0169534719300837> (2023) (Aug. 2019).
- Weber, M. G., Wagner, C. E., Best, R. J., Harmon, L. J. & Matthews, B. Evolution in a Community Context: On Integrating Ecological Interactions and Macroevolution. *Trends in Ecology & Evolution* **32**, 291–304. issn: 0169-5347. <https://www.sciencedirect.com/science/article/pii/S0169534717300162> (2017).
- Hembry, D. H. & Weber, M. G. Ecological Interactions and Macroevolution: A New Field with Old Roots. *Annual Review of Ecology, Evolution, and Systematics* **51**, 215–243. eprint: <https://doi.org/10.1146/annurev-ecolsys-011720-121505>. <https://doi.org/10.1146/annurev-ecolsys-011720-121505> (2020).
- May, R. M. Will a Large Complex System be Stable? *Nature* **238**, 413–414 (1972).
- Gross, T., Rudolf, L., Levin, S. A. & Dieckmann, U. Generalized Models Reveal Stabilizing Factors in Food Webs. *Science* **325**, 747–750. eprint: <https://www.science.org/doi/pdf/10.1126/science.1173536>. <https://www.science.org/doi/abs/10.1126/science.1173536> (2009).
- Allesina, S. & Tang, S. Stability criteria for complex ecosystems. *Nature* **483**, 205–208. issn: 1476-4687. <https://doi.org/10.1038/nature10832> (Mar. 2012).
- Gross, T. & Sayama, H. in *Adaptive Networks: Theory, Models and Applications* (eds Gross, T. & Sayama, H.) 1–8 (Springer Berlin Heidelberg, Berlin, Heidelberg, 2009). isbn: 978-3-642-01284-6. https://doi.org/10.1007/978-3-642-01284-6_1.
- Dieckmann, U. & Doebeli, M. On the origin of species by sympatric speciation. en. *Nature* **400**, 354–357. issn: 0028-0836, 1476-4687. <https://www.nature.com/articles/22521> (2023) (July 1999).
- Drossel, B., Higgs, P. G. & McKane, A. J. The Influence of Predator–Prey Population Dynamics on the Long-term Evolution of Food Web Structure. en. *Journal of Theoretical Biology* **208**, 91–107. issn: 00225193. <https://linkinghub.elsevier.com/retrieve/pii/S0022519300922033> (2023) (Jan. 2001).
- Drossel, B. & McKane, A. J. in *Handbook of Graphs and Networks* 218–247 (John Wiley Sons, Ltd, 2002). isbn: 9783527602759. eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1002/3527602755.ch10>. <https://onlinelibrary.wiley.com/doi/abs/10.1002/3527602755.ch10>.
- Bascompte, J. & Stouffer, D. B. The assembly and disassembly of ecological networks. en. *Philosophical Transactions of the Royal Society B: Biological Sciences* **364**, 1781–1787. issn: 0962-8436, 1471-2970. <https://royalsocietypublishing.org/doi/10.1098/rstb.2008.0226> (2023) (June 2009).
- MacArthur, R. H. & Wilson, E. O. *The theory of island biogeography* (Princeton university press, 2001).
- Pelletier, F., Garant, D. & Hendry, A. Eco-evolutionary dynamics. en. *Philosophical Transactions of the Royal Society B: Biological Sciences* **364**, 1483–1489. issn: 0962-8436, 1471-2970. <https://royalsocietypublishing.org/doi/10.1098/rstb.2009.0027> (2023) (June 2009).
- Hendry, A. P. *Eco-evolutionary Dynamics* isbn: 978-1-4008-8308-0. <https://www.degruyter.com/document/doi/10.1515/9781400883080/html> (2023) (Princeton University Press, Princeton, Dec. 2017).
- Johnson, M. T. & Stinchcombe, J. R. An emerging synthesis between community ecology and evolutionary biology. en. *Trends in Ecology & Evolution* **22**, 250–257. issn: 01695347. <https://linkinghub.elsevier.com/retrieve/pii/S0169534707000341> (2023) (May 2007).
- Hendry, A. P. in *Eco-evolutionary Dynamics* 304–318 (Princeton University Press, Princeton, 2017). isbn: 9781400883080. <https://doi.org/10.1515/9781400883080-013>.
- Kéfi, S., Miele, V., Wieters, E. A., Navarrete, S. A. & Berlow, E. L. How Structured Is the Entangled Bank? The Surprisingly Simple Organization of Multiplex Ecological Networks Leads to Increased Persistence and Resilience. *PLOS Biology* **14**, 1–21. <https://doi.org/10.1371/journal.pbio.1002527> (Aug. 2016).
- Kéfi, S. *et al.* Network structure beyond food webs: mapping non-trophic and trophic interactions on Chilean rocky shores. *Ecology* **96**, 291–303. eprint: <https://esajournals.onlinelibrary.wiley.com/doi/pdf/10.1890/13-1424.1>. <https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1890/13-1424.1> (2015).
- Pilosof, S., Porter, M. A., Pascual, M. & Kéfi, S. The multilayer nature of ecological networks. en. *Nature Ecology & Evolution* **1**, 0101. issn: 2397-334X. <https://www.nature.com/articles/s41559-017-0101> (2023) (Mar. 2017).
- Yeakel, J. D. *et al.* Diverse interactions and ecosystem engineering can stabilize community assembly. *Nature Communications* **11**, 3307 (2020).
- Schluter, D. & Pennell, M. W. Speciation gradients and the distribution of biodiversity. *Nature* **546**, 48–55. issn: 1476-4687. <https://doi.org/10.1038/nature22897> (June 2017).
- López-Estrada, E. K., Sanmartín, I., García-París, M. & Zaldívar-Riverón, A. High extinction rates and non-adaptive radiation explains patterns of low diversity and extreme morphological disparity in North American blister beetles (Coleoptera, Meloidae). *Molecular Phylogenetics and Evolution* **130**, 156–168. issn: 1055-7903. <https://www.sciencedirect.com/science/article/pii/S1055790318300903> (2019).
- Sakamoto, M., Benton, M. J. & Venditti, C. Dinosaurs in decline tens of millions of years before their final extinction. *Proceedings of the National Academy of Sciences* **113**, 5036–5040. eprint: <https://www.pnas.org/doi/pdf/10.1073/pnas.1521478113>. <https://www.pnas.org/doi/abs/10.1073/pnas.1521478113> (2016).
- Barnett, V. in *Encyclopedia of Animal Cognition and Behavior* (eds Vonk, J. & Shackelford, T.) 1–6 (Springer International Publishing, Cham, 2020). isbn: 978-3-319-47829-6. https://doi.org/10.1007/978-3-319-47829-6_2100-1.
- S. Brown, J., Kotler, B. P. & Valone, T. J. Foraging Under Predation - a Comparison of Energetic and Predation Costs in Rodent Communities of the Negev and Sonoran Deserts. *Australian Journal of Zoology* **42**, 435–448. <https://api.semanticscholar.org/CorpusID:83937891> (1994).
- MacArthur, R. & Levins, R. COMPETITION, HABITAT SELECTION, AND CHARACTER DISPLACEMENT IN A PATCHY ENVIRONMENT. *Proceedings of the National Academy of Sciences* **51**, 1207–1210. eprint: <https://www.pnas.org/doi/pdf/10.1073/pnas.51.6.1207>. <https://www.pnas.org/doi/abs/10.1073/pnas.51.6.1207> (1964).
- Dykhuizen, D. & Davies, M. An Experimental Model: Bacterial Specialists and Generalists Competing in Chemostats. *Ecology* **61**, 1213–1227. eprint: <https://esajournals.onlinelibrary.wiley.com/doi/pdf/10.2307/1936839>. <https://esajournals.onlinelibrary.wiley.com/doi/abs/10.2307/1936839> (1980).
- Futuyma, D. J. & Moreno, G. The Evolution of Ecological Specialization. *Annual Review of Ecology and Systematics* **19**, 207–233. issn: 00664162. <http://www.jstor.org/stable/2097153> (2023) (1988).
- Costa, A. *et al.* Generalisation within specialization: inter-individual diet variation in the only specialized salamander in the world. *Scientific Reports* **5**, 13260. issn: 2045-2322. <https://doi.org/10.1038/srep13260> (Aug. 2015).
- Bronstein, J. L. Conditional outcomes in mutualistic interactions. *Trends in Ecology & Evolution* **9**, 214–217. issn: 0169-5347. <https://www.sciencedirect.com/science/article/pii/S0169534794902461> (1994).
- Krakauer, D. C., Page, K. M. & Erwin, D. H. Diversity, Dilemmas, and Monopolies of Niche Construction. *The American Naturalist* **173**, PMID: 19061421, 26–40. eprint: <https://doi.org/10.1086/593707>. <https://doi.org/10.1086/593707> (2009).
- Hastings, A. *et al.* Ecosystem engineering in space and time. *Ecology Letters* **10**, 153–164. eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1461-0248.2006.00997.x>. <https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1461-0248.2006.00997.x> (2007).
- Sachs, J. L. & Simms, E. L. Pathways to mutualism breakdown. *Trends in Ecology & Evolution* **21**. Publisher: Elsevier, 585–592. issn: 0169-5347. <https://doi.org/10.1016/j.tree.2006.06.018> (2023) (Oct. 2006).
- Pellmyr, O., Leebens-Mack, J. & Huth, C. J. Non-mutualistic yucca moths and their evolutionary consequences. en. *Nature* **380**, 155–156. issn: 0028-0836, 1476-4687. <https://www.nature.com/articles/380155a0> (2023) (Mar. 1996).
- Machado, C. A., Jousset, E., Kjellberg, F., Compton, S. G. & Herre, E. A. Phylogenetic relationships, historical biogeography and character evolution of fig-pollinating wasps. en. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **268**, 685–694. issn: 0962-8452, 1471-2954. <https://royalsocietypublishing.org/doi/10.1098/rspb.2000.1418> (2023) (Apr. 2001).

41. Als, T. D. *et al.* The evolution of alternative parasitic life histories in large blue butterflies. en. *Nature* **432**, 386–390. issn: 0028-0836, 1476-4687. <https://www.nature.com/articles/nature03020> (2023) (Nov. 2004).
42. Frederickson, M. E. Mutualisms Are Not on the Verge of Breakdown. en. *Trends in Ecology & Evolution* **32**, 727–734. issn: 01695347. <https://linkinghub.elsevier.com/retrieve/pii/S0169534717301763> (2023) (Oct. 2017).
43. Kones, J. K., Soetaert, K., van Oevelen, D. & Owino, J. Are network indices robust indicators of food web functioning? a Monte Carlo approach. *Ecological Modelling* **220**, 370–382 (2009).
44. Hubbell, S. P. *The Unified Neutral Theory of Biodiversity and Biogeography (MPB-32)* isbn: 9780691021287. <http://www.jstor.org/stable/j.ctt7rj8w> (2023) (Princeton University Press, 2001).
45. Hubbell, S. P. Neutral Theory in Community Ecology and the Hypothesis of Functional Equivalence. *Functional Ecology* **19**, 166–172. issn: 02698463, 13652435. <http://www.jstor.org/stable/3599285> (2023) (2005).
46. Real, R., Báez, J. C., Fa, J. E., Olivero, J. & Acevedo, P. Making the competitive exclusion principle operational at the biogeographical scale using fuzzy logic. *Frontiers in Ecology and Evolution* **10**. issn: 2296-701X. <https://www.frontiersin.org/articles/10.3389/fevo.2022.991344> (2022).
47. Dice, L. R. Measures of the Amount of Ecologic Association Between Species. *Ecology* **26**, 297–302. issn: 00129658, 19399170. <http://www.jstor.org/stable/1932409> (2023) (1945).