



The effect of mutualistic interactions on diversity patterns in island biogeography

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ABSTRACT

Islands are often regarded as “natural laboratories” for biology, and this applies also to ecological interactions between species that co-occur on islands. Mutualistic interactions, the association between organisms of two different species in which each benefits, should have important effects on the ability of species to establish, speciate or persist on islands. However, while island biogeography models increasingly incorporate the dynamics of biotic interactions in island ecosystems, current approaches do not consider the complexities introduced by mutualistic relationships, e.g., mutualism-driven immigration, cospeciation between mutualistic partners, dynamic formation and loss of mutualistic links. Here we present a new simulation model of island biogeography that explicitly includes mutualistic interactions and their influence on biodiversity at macroevolutionary scales. With this approach, we aim to better understand the effect of mutualism on insular diversity patterns over macroevolutionary time. Our model shows how mutualism influences species immigration, diversification and persistence through its effects on species-level processes. Strong mutualism is associated with higher species richness and more connected communities, while networks with weak or absent mutualism remain fragmented, with many species failing to establish interactions. By extending classical island biogeography to include ecological interaction networks, our study offers a new theoretical lens on how mutualism can influence biodiversity patterns and network structures in insular systems over evolutionary timescales.

1. Introduction

Scientists have often turned to islands to test fundamental principles that govern ecological and evolutionary processes in larger, more complex systems (Simberloff and Wilson, 1969; Warren et al., 2015; Massol et al., 2017). The relative isolation, dynamic geographies and limited resources of islands have provided invaluable insights into ecological interactions and the mechanisms driving evolutionary change, ranging from Darwin’s finches (Grant et al., 1976; Grant and Grant, 2006) and Caribbean lizards (Meiri, 2007), to Hawaiian silverswords (Baldwin et al., 1998). The development of MacArthur and Wilson (1963)’s classic island biogeography theory inspired island-based research (Simberloff, 1974; Whittaker et al., 2008; Valente et al., 2020). Since then, islands have continued to serve as ideal natural laboratories to explore macroevolutionary dynamics (Román-Palacios and Wiens, 2018), community assembly (Simberloff and Abele, 1976; Piechnik et al., 2008), species diversity (Ricklefs and Renner, 2012; Dupont et al., 2003; Olesen et al., 2002) and metapopulation dynamics (Ojanen et al., 2013).

Theoretical models, including both verbal and quantitative simulation models, have been crucial for the development of the field of island biogeography. The classical model of MacArthur and Wilson (1963) described insular biota as a balance between colonization and extinction. The general dynamic model (GDM) of oceanic island biogeography (Whittaker et al., 2008) additionally integrated island ontogeny, capturing how community assembly (including speciation) evolves over time in response to geological dynamics such as island formation and erosion. Furthermore, the DAISIE model (Valente et al., 2015) can simulate phylogenetic trees for entire insular communities under various dynamic scenarios. These models were originally developed to explain patterns of biodiversity, endemism and diversification in a range of islands. Despite their contributions, they do not explicitly consider how ecological interactions might alter island biota composition, affect species richness and biogeographical processes. To address this, Gravel et al. (2011) introduced the Trophic Theory of Island Biogeography (TTIB), which incorporates trophic, functional and local adaptation information into an island biogeography framework. This extension improves our ability to explain and predict species richness, community

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composition, and ecosystem stability on islands. However, TTIB focuses only on food web interactions and excludes speciation - a fundamental process, particularly on large isolated islands where high endemism arises from unique ecological conditions, as well as reduced gene flow from the mainland, driving both anagenetic and cladogenetic speciation (Valente et al., 2020).

Species in ecological communities are embedded in networks of interacting species and these ecological networks play a crucial role in shaping biodiversity. Advances in this field have illuminated how ecological interactions influence the geographical distribution of organisms (Wisiz et al., 2013), the assembly of communities (Qian and Akçay, 2020), as well as the evolutionary trajectories of populations (Pellmyr, 2003; Nuismer et al., 2013; Olesen et al., 2007). Although competition (antagonism) has historically dominated ecological research (Simberloff, 1982; Cooper, 1993; Silvestro et al., 2015), growing empirical and theoretical evidence highlights the importance of mutualistic interactions in promoting coexistence, fostering species diversity, and stabilizing community dynamics (Bascompte et al., 2003; Hale et al., 2020). In mutualistic interactions (e.g., plant-pollinator, plant-seed disperser, mycorrhizal symbiosis Fortuna and Bascompte, 2006; Sauve et al., 2016; Delavaux et al., 2019), species provide each other with resources, protection or other services (Lopez-Vaamonde et al., 2001). These interactions are essential to ecosystem functioning and may influence long-term evolutionary patterns by affecting species persistence, colonization success, and opportunities for diversification. For example, species engaged in mutualistic relationships might experience reduced extinction risk due to the additional resources or protection provided by partners, potentially allowing them to persist longer in dynamic or resource-limited environments (Gómez and Verdú, 2012; Weber and Agrawal, 2014). Mutualistic species may also be more successful colonizers if their interactions promote establishment probability upon arrival in new habitats (Schrader et al., 2021). Over evolutionary timescales, mutualism could create ecological opportunities that facilitate niche differentiation and drive cladogenetic speciation, or alternatively, strong dependence on specific partners might constrain diversification under certain conditions (Anderson and Johnson, 2008; Guimarães et al., 2011; Nathan et al., 2023). Moreover, even when the effects of mutualistic interactions on macroevolutionary processes such as immigration, extinction, and speciation are assumed to be known, the question is how all these effects will together influence community composition.

Plant-animal mutualistic interactions are perhaps the most widely studied in the context of ecological networks on islands. As reviewed in (Bascompte and Jordano, 2007), at ecological time scales, these interactions contribute to dispersal and establishment in new habitats. At evolutionary time scales, research has focused mainly on the genetic and phenotypic changes that occur in mutualistic partners over time (Kiers et al., 2003; Heath and Stinchcombe, 2014). Various hypotheses regarding the relationship between mutualism and diversification dynamics have been put forward, leading to different points of view on the long-term consequences of mutualism (Crepet, 1984). While some studies report links between mutualism (or associated traits) and net diversification rates (Lengyel et al., 2009; Gómez and Verdú, 2012), others find limited or no such pattern (Aslan et al., 2014), reflecting the complex and context-dependent nature of these relationships. A key challenge is therefore to disentangle how mutualistic interactions shape patterns of biodiversity and network structure within islands. Indeed, mutualism may influence different facets of biodiversity through its effects on the strength and structure of biotic interactions. Mutualistic relationships may affect not only the total number of species in a system (Peet, 1974; Magurran, 2013), but also key characteristics of ecological networks, such as network connectance, species degree and network components. Network connectance is a measure of the number of realized links over all possible links between species from different guilds, reflecting overall interaction density (Delmas et al., 2019). Species degree refers to the number of interaction partners a species has (e.g., how many animal species a plant species mutualistically interacts with), offering insight

into species-level roles within the network. Components are subgroups within a network in which all species are connected. The aforementioned metrics offer quantifiable insights into how mutualism affects community assembly and evolutionary dynamics. For example, mutualism may promote higher connectance and the emergence of large, cohesive network components under certain evolutionary scenarios, while its absence may lead to fragmented, species-poor networks. Although structural differences in mutualistic networks between mainland and island systems have been documented (Traveset and Richardson, 2014), the extent to which such patterns emerge through macroevolutionary processes remains underexplored. Addressing this gap requires integrative models that link ecological interactions with diversification, extinction, and dispersal dynamics over evolutionary time.

Theoretical models and empirical studies have increasingly investigated the relationship between mutualism and macroevolution (Oliver et al., 2008; Poisot et al., 2011; Hembry et al., 2014). Key questions include whether mutualistic interactions promote or constrain species diversification (Weber and Agrawal, 2014; Sachs et al., 2013), and whether mutualism buffers against species extinction events (Larson-Johnson, 2016; Afkhami et al., 2014). Coevolution between mutualistic partners may be crucial for the emergence of new species (Kay and Schemske, 2003; Kay et al., 2005; Kay and Sargent, 2009). Despite these advances, the role of mutualistic interactions in shaping biodiversity on islands remains understudied.

In this study, we develop a new macroevolutionary model of island biogeography that includes mutualistic interactions inspired by plant-animal interactions such as pollination. Our model incorporates assumptions of the effect of mutualism on the key processes of island colonization, speciation (both anagenesis and cladogenesis), extinction, and coevolution (between animals and plants) while also accounting for the gain and loss of links in networks. We explore how these processes interact with varying levels of mutualism under different macroevolutionary scenarios to shape community assembly, and particularly phylogenetic relationships between the emerging species. Specifically, we address the following main questions: i) How does the presence and strength of mutualism affect species richness, endemism, and diversity accumulation on an island over time? (ii) In what ways do mutualistic interactions influence the formation and fragmentation of ecological networks, including the emergence of generalists and ecologically isolated species? (iii) How do macroevolutionary rates – particularly cladogenesis, immigration, and extinction – modulate the effects of mutualism on network structure, connectivity, fragmentation and species diversity?

2. Methods

2.1. Macroevo-lutionary processes

We present a new dynamic stochastic model of island biogeography that includes mutualistic interactions. Our model considers an island (our focal geographical unit) and a fixed mainland source pool representing an ecologically plausible regional assemblage of animal and plant species that are subject to mutualistic interactions (e.g., pollination). These interactions are assumed to promote the survival and establishment of partners. However, not all species interact with each other. At any time t , the state of the island community is defined by (i) the presence or absence of each plant species and each animal species on the island, and (ii) the interaction network among co-occurring species.

The simulation begins with an empty island. The first (stochastic) event that can occur, is immigration, where a plant or an animal species colonizes the island from the mainland (Fig. 1). Once on the island, the following events may take place: (1) extinction of a species on the island; (2) speciation via anagenesis, where a mainland species present on the island becomes endemic to the island without lineage splitting; (3) speciation via cladogenesis, where one island species splits into two new endemic species; in both anagenesis and cladogenesis, the parental

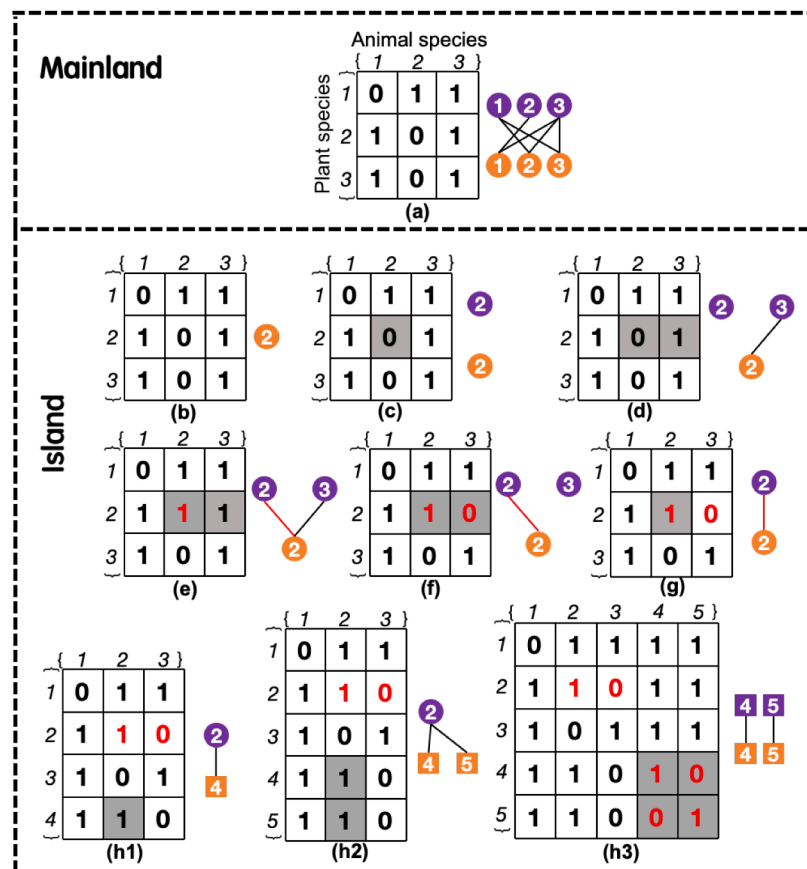


Fig. 1. Example of a mutualistic network on an island subject to macroevolutionary processes. (a) The mainland network consists of three plant species and three animal species. Species are connected by a mutualistic link if the corresponding element in the interaction matrix equals 1. Numbers above columns and to the left of rows correspond to the species of animal (columns) and plant (rows) that make up the community. The island network panels (a-h) show different hypothetical evolutionary events that can take place. Grey shades indicate the network on the island. To the right of each panel, a diagram of the existing network on the island is shown, where orange circles represent plant species and purple circles represent animal species. Lines connecting species represent mutualistic links. Endemic species are indicated by squares. (b) Plant species 2 colonizes the island. (c) Animal species 2 colonizes the island, and because it is not connected to plant species 2 on the mainland, it does not establish a link with that species yet. (d) Animal species 3 colonizes the island, immediately establishing a link with plant species 2 because they have a link on the mainland. (e) A link is stochastically gained between plant 2 and animal 2 (denoted in red). (f) A link is stochastically lost between plant 2 and animal 3. (g) Animal species 3 goes extinct. The three (h) panels show the three types of speciation events that can occur from panel (g) (they do not occur sequentially). (h1) Anagenesis - plant species 2 gives rise to a new island endemic species 4. The new species inherits the links from its parental species. (h2) Cladogenesis - plant species 2 splits into two new endemic species 4 and 5, which replace the parent species and inherit its links. (h3) Cospeciation - cospeciation occurs between plant 2 and animal 2, leading to two new species of plant and two new species of animal, each replacing their parent species. The daughter species split their parents' links, resulting in plant 4 linking to animal 4, and plant 5 linking to animal 5.

species is replaced and no longer persist; (4) cospeciation where two members of a mutualistic pair speciate simultaneously (see section on cospeciation below); (5) loss or acquisition of mutualistic links; (6) additional immigration by the same species or a different species. In the model, only one event can occur at a time, and links that exist on the mainland are automatically established when a species immigrates and its mutualistic partner is present on the island. The rates at which these events occur depend on the plant and animal species that are already present on the island, and on the interaction matrix. The equations and parameters that describe each of these processes are provided in Section 2.3. We first provide a verbal overview.

Immigration can occur multiple times by the same mainland species, but only the latest colonization time is kept, overwriting previous occurrences. We assume that the presence of mutualistic partners on the island can promote the long-term persistence of the interacting species, e.g., leading to higher immigration rates and lower extinction rates (Fig. 2a & d). Intrinsic rates for immigration, extinction and other processes are defined for each species, with immigration and cladogenesis rates exhibiting diversity dependence (these rates decline as the number of

species on the island increases, as available niche space becomes filled). Anagenesis is assumed to depend mostly on isolation (i.e. limited gene flow) rather than the presence of other species, and is thus unaffected by species richness on the island (Valente et al., 2020). However, it is influenced by differences in mutualistic partners-immigrated species may lose or gain links compared to their mainland ancestors, and once sufficiently different they may undergo anagenesis (Fig. 2b). We assume that cospeciation can occur between a pair of connected species, influenced by the availability of ecological opportunity defined by both plant and animal species (Fig. 2c) and exclusively by mutualism. Other processes such as antagonism (e.g., predator-prey dynamics Brockhurst and Koskella, 2013) and parasitism (e.g., host-parasite interaction Paterson and Gray, 1997) may also drive cospeciation, but we do not consider these here. In addition, in the model, species that have mutualistic links in the mainland community automatically keep these links when they co-occur on the island. These links may be lost on the island with the rate q_{loss} . Island species that have no links can gain new mutualistic links at a rate q_{gain} . When a speciation event occurs, daughter species inherit the link from their parental species.

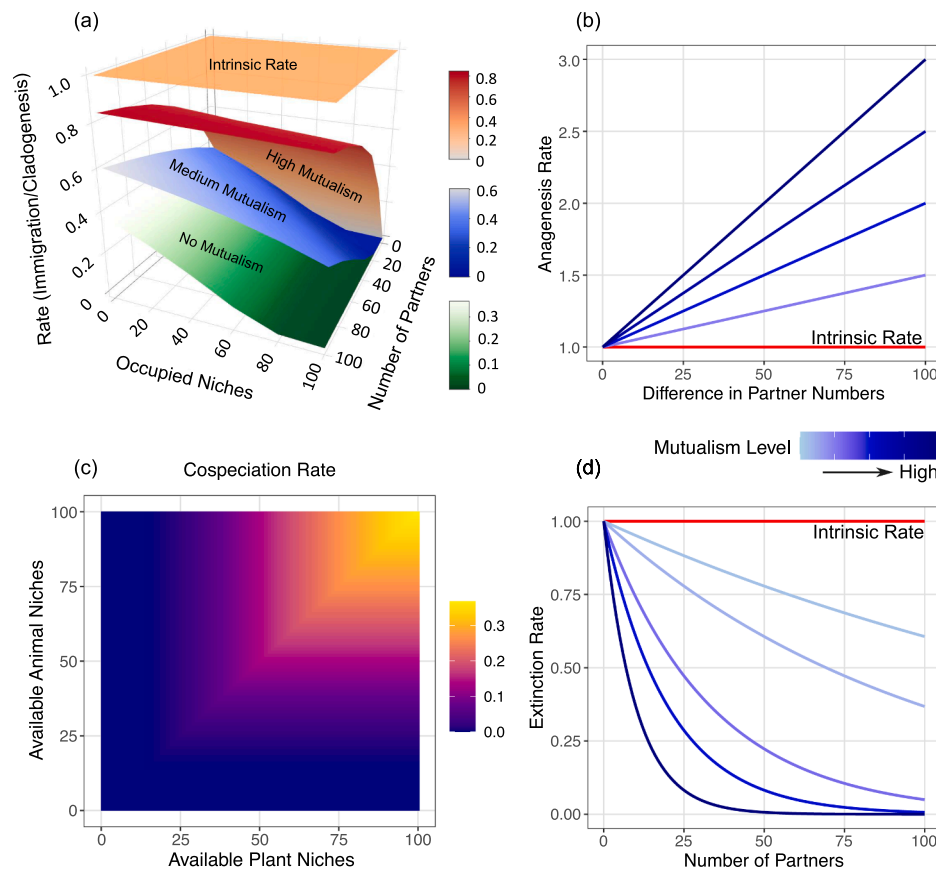


Fig. 2. Impact of mutualistic interactions on island biogeography parameters in our model. (a) The rate of immigration (or cladogenesis) increases with the number of mutualistic partners present on the island but declines with the total number of occupied species on the island. The top orange surface shows the intrinsic rate dynamics without mutualism. (b) The rate of anagenesis rates increases with increasing differences of the number of mutualistic partners and with increasing strength of mutualism. The red line marks the intrinsic anagenesis rate, set to 1.0 in this example. (c) The rate of cospeciation increases with the sum of available plant and animal niches. Note that in this model, cospeciation occurs exclusively due to mutualism. (d) The rate of extinction declines with increasing number of mutualistic partners present on the island and with increasing strength of mutualism. The red line is the intrinsic extinction rate, set to 1.0 in this example.

2.2. Mainland matrix construction

Using network theory to study ecological networks offers several advantages that make it a powerful and effective approach for understanding complex ecological interactions (Dormann and Strauss, 2014; Gu-seva et al., 2022). In our model, a mutualistic network is composed of two guilds, e.g., plant and animal species, forming a bipartite network with n_p plant species and n_A animal species. The interaction between these guilds is represented as a binary matrix m_{ij} , where an element equals 1 if plant species i and animal species j interact and $m_{ij} = 0$ otherwise. We employed a methodology inspired by Santamaría and Rodríguez-Gironé (2007), to generate the matrix on the mainland. According to their framework, the most effective approach is a “mixed model” that combines rules linking mutualistic partners whose trait ranges overlap (complementarity models) and whose traits are below a specific barrier value (barrier models). The mixed model provides a biologically realistic structure for mutualistic interactions, serving as a robust foundation for simulating ecological and evolutionary dynamics on islands. Applying the approach of Santamaría et al. to assemble the interaction matrix, and after removing plant and animal species that do not have any interactions, our final network in the mainland consists of $n_p = 135$ and $n_A = 612$ (for detailed mainland matrix information, see Table 1 and Appendix A.1).

2.3. Equations describing the model processes

Traditional diversity-dependence models typically assume a linear decline with increasing species richness. For instance, for immigration,

Table 1

Properties of the species interaction network of the mainland (m_{ij}) used in the simulations.

Species richness	Species degree	Connectance	Number of components	Largest component size
$n_p = 135$	$d_p = 16$	0.026	1	747
$n_A = 612$	$d_A = 3$			

Note: Species degree is the average value for plant and animal species, respectively.

this is:

$$\gamma = \begin{cases} \gamma_0 \left(1 - \frac{N}{K}\right) & \text{if } K - N > 0 \\ 0 & \text{otherwise} \end{cases} \quad (1)$$

Here, K represents total carrying capacity and N is the number of species (which can be interpreted as occupied ecological opportunity) on the island, and γ_0 is the maximum immigration rate when the island is empty. However, we argue that the rate of immigration should not be limited by diversity itself, but by the niche space still available, $K - N$. Replacing the term $1 - \frac{N}{K}$ by $K - N$ solves this problem but creates another one, namely that the immigration rate can become very large when K is large. Because in our model mutualism acts to increase the carrying capacity during the dynamics, this has unwanted consequences. To

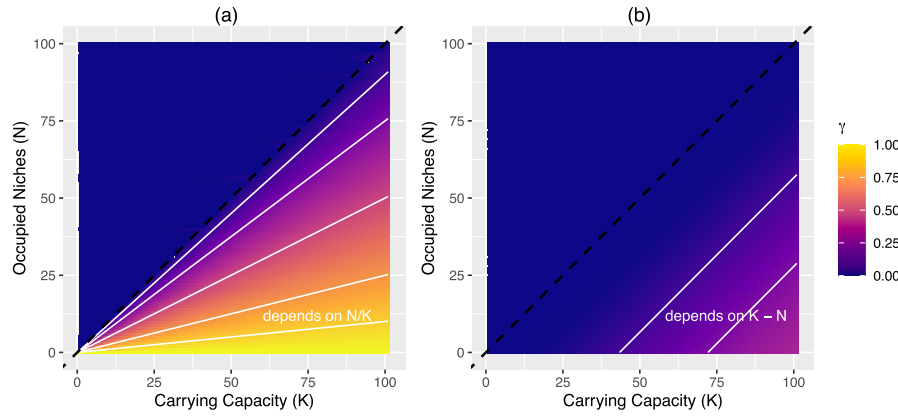


Fig. 3. Comparison of (a) linear and (b) exponential diversity-dependence in immigration model varying carrying capacity K and occupied niches N . Colors indicate immigration rate, and white contour lines connect combinations of K and N that yield equal values. $\alpha = 100$ and $\gamma_0 = 1.0$ in the example. The carrying capacity K varies from 1 to 101 in increments of 1 and N varies from 0 to 100 in increments of 1.

remedy this, we propose an alternative formulation:

$$\gamma = \begin{cases} \gamma_0 \exp\left(-\frac{\alpha}{K-N}\right) & \text{if } K - N > 0 \\ 0 & \text{otherwise} \end{cases} \quad (2)$$

where α controls the effect of the limited niche space on immigration. For infinite K we see that the immigration rate is γ_0 . We graphically show the difference between these two formulations in Fig. 3. We use this formulation to model diversity-dependent immigration, cladogenesis, and coevolutionary processes in our framework.

Immigration

We define the immigration rates for plant species γ_{P_i} , and animal species γ_{A_j} as follows:

$$\gamma_{P_i} = \begin{cases} \gamma_{P0} \exp\left(-\frac{\alpha}{K_{P_i} - N_P}\right) & \text{if } K_{P_i} > N_P \\ 0 & \text{if } K_{P_i} \leq N_P \end{cases} \quad (3)$$

$$\gamma_{A_j} = \begin{cases} \gamma_{A0} \exp\left(-\frac{\alpha}{K_{A_j} - N_A}\right) & \text{if } K_{A_j} > N_A \\ 0 & \text{if } K_{A_j} \leq N_A \end{cases} \quad (4)$$

Here, γ_{P0} is the intrinsic immigration rate for all plant species when there are no interacting animal species on the island. Likewise, γ_{A0} is the intrinsic immigration rate for all animal species without any interacting plant species being present on the island. K_{P_i} and K_{A_j} represent species-specific effective carrying capacities for plant species i and animal species j , respectively, where

$$K_{P_i} = K_{P0} + K_{P1} \sum_{j=1}^{N_A} M_{ij} A_j \quad (5)$$

and

$$K_{A_j} = K_{A0} + K_{A1} \sum_{i=1}^{N_P} M_{ji} P_i \quad (6)$$

We thus assume that the carrying capacity on the island includes two components, one which we term the “baseline” and the other the “interaction” component. K_{P0} and K_{A0} are the baseline components for plants and animals respectively, which refer to available ecological opportunity independent of mutualistic interactions. The interaction components $K_{P1} \sum_{j=1}^{N_A} M_{ij} A_j$ and $K_{A1} \sum_{i=1}^{N_P} M_{ji} P_i$ increase the ecological opportunity accessible to species that have mutualistic partners already present on the island. Importantly, species still experience shared crowding pressure within their guild, represented by the total number of

species currently present on the island (N_P and N_A). Thus, mutualism does not directly generate independent niche spaces for each species; rather, it modifies how much more of the shared ecological opportunity is accessible to a focal species. This phenomenological interaction-dependent increase can be interpreted as greater access to resources or services leading to improved establishment in otherwise unsuitable environments. K_{P1} and K_{A1} are thus scaling factors mediating the effects of mutualism. Low values of K_{P1} and K_{A1} indicate a modest mutualism level while high values indicate a strong mutualism level. $\sum_{j=1}^{N_A} M_{ij} A_j$ represents the number of animal partners of plant species i while $\sum_{i=1}^{N_P} M_{ji} P_i$ is the number of plant partners of animal species j . M_{ij} (M_{ji}) is the interaction between plant species i (animal species j) and animal species j (plant species i) on the island. P_i (A_j) indicate whether plant species i (animal species j) is present on the island, $P_i = 1$ ($A_j = 1$), or is absent from the island, $P_i = 0$ ($A_j = 0$). The parameter α mediates the immigration rate for plant species i (and animal species j). These expressions guarantee that the immigration rate for plant species i (or animal species j) does not exceed γ_{P0} (or γ_{A0} , Fig. 2a) and increases with the ecological availability on the island. Furthermore, it guarantees the following realistic assumptions: (i) When the overall carrying capacity is extremely small and there are no species on the island yet, the initial immigration rate should be very small as well (Fig. 3b). In linear models incorporating diversity dependence (e.g., Valente et al., 2015), this value is instead the maximum intrinsic rate (Fig. 3a). (ii) It gives the same value when the availability for new species is the same, as intended.

Extinction

The extinction rates μ_{P_i} , for plants, and μ_{A_j} , for animals, are modeled as:

$$\mu_{P_i} = \mu_{P0} \exp\left(-\mu_{P1} \sum_{j=1}^{N_A} M_{ij} A_j\right) \quad (7)$$

$$\mu_{A_j} = \mu_{A0} \exp\left(-\mu_{A1} \sum_{i=1}^{N_P} M_{ji} P_i\right) \quad (8)$$

We assume here that the rates of extinction are related to the number of mutualistic partners (Fig. 2d): species have access to more resources when they have more mutualistic partners co-occurring with them geographically, thus they are less likely to go extinct compared to those who have fewer partners to interact with. μ_{P0} and μ_{A0} are the intrinsic extinction rates for species without any mutualistic partners and extinction declines as the number of partners increases with a mutualism-related coefficient determined by μ_{P1} or μ_{A1} . Large values of μ_{P1} and μ_{A1} are

indicative of a pronounced mutualistic relationship, whereas small values suggest a reduction in mutualistic strength.

Speciation

Species can evolve into a new species without lineage splitting or into two new species with lineage splitting (Valente et al., 2015) on the island. For cladogenesis, we consider diversity dependence in rates, because there is a limit to the number of species, and thus the more species there are, the lower the chances of additional new species being formed. For cladogenesis rates, we assume, analogous to equations for the immigration rates:

$$\lambda_{P_i}^c = \begin{cases} \lambda_{P_0}^c \exp\left(-\frac{\alpha}{K_{P_i} - N_P}\right) & \text{if } K_{P_i} > N_P \\ 0 & \text{if } K_{P_i} \leq N_P \end{cases} \quad (9)$$

$$\lambda_{A_j}^c = \begin{cases} \lambda_{A_0}^c \exp\left(-\frac{\alpha}{K_{A_j} - N_A}\right) & \text{if } K_{A_j} > N_A \\ 0, & \text{if } K_{A_j} \leq N_A \end{cases} \quad (10)$$

where $\lambda_{P_0}^c$ and $\lambda_{A_0}^c$ are the intrinsic cladogenesis rates for plant species and animal species, respectively. Other terms have the same meaning as in Eqs. (3) and (4).

In anagenesis, a species gradually evolves into a new species over time. For the anagenesis rates, $\lambda_{P_i}^a$ for plants, and $\lambda_{A_j}^a$ for animals, we have:

$$\lambda_{P_i}^a = \lambda_{P_0}^a + \lambda_{P_1}^a \sum_{j=1}^{N_A} |M_{ij} - m_{ij}| A_j \quad (11)$$

$$\lambda_{A_j}^a = \lambda_{A_0}^a + \lambda_{A_1}^a \sum_{i=1}^{N_P} |M_{ji} - m_{ji}| P_i \quad (12)$$

where $\lambda_{P_0}^a$ is the intrinsic anagenesis rate for plant species when no mutual animal partners are on the island. Likewise, $\lambda_{A_0}^a$ is the intrinsic anagenesis rate for animal species when there are no mutual plant partners on the island. $\lambda_{P_1}^a$ and $\lambda_{A_1}^a$ are parameters mediating mutualism levels. We assume anagenesis depends primarily on isolation (i.e., limited gene flow), and interaction differences act as a proxy for ecological divergence between island and mainland environments. Immigrated species may encounter a different set of potential mutualistic partners on the island than on the mainland, because some partners may be absent while others may become available. The model therefore measures the difference between the interaction partners of a species on the mainland ($m_{ij} A_j$) and those available on the island ($M_{ij} A_j$). The larger the difference in mutualistic partners between the two environments, the more likely the species will undergo anagenesis on the island and thus eventually become a distinct species. m_{ij} (m_{ji}) is the mainland species interaction matrix. In the model, anagenesis itself does not directly alter interaction links; instead, links are stochastically lost or gained by the gain and loss processes described below.

Cospeciation

Cospeciation is a process by which two species speciate in parallel, resulting in new lineages that maintain their ancestors' ecological associations with each other (Kawakita and Kato, 2017). In the model we consider cospeciation taking place between animal and plant parent species of a mutualistic pair, resulting in two new animal daughter species and two new plant daughter species. Given that we assume a limit to the number of niches on the island, diversity dependence is applied. A pair of interacting species can undergo cospeciation depending on the minimal space for either plants or animals (Fig. 2c).

$$\lambda_{ij}^{\text{cospec}} = \begin{cases} \lambda_0 M_{ij} P_i A_j \exp\left(-\frac{\alpha}{\min(K_{P_0} - N_P, K_{A_0} - N_A)}\right) \\ 0, \text{ if } K_{P_0} \leq N_P \text{ or } K_{A_0} \leq N_A \end{cases} \quad (13)$$

Species that are both present on the island ($P_i = 1$ and $A_j = 1$) and interact with each other ($M_{ij} = 1$) can undergo cospeciation. In this model, we specifically assume that cospeciation is completely due to mutualism, hence ignoring other causes, for example, parasitism. λ_0 is the parameter that determines the level of cospeciation due to mutualism; hence when λ_0 is 0, there is no cospeciation. Low values of λ_0 indicate a modest effect of mutualism on cospeciation while high values indicate a strong effect of mutualism on cospeciation. Other parameters are the same as in Eqs. (3) and (4).

Gain and loss

Species that are present on the island can lose or gain mutualistic links. These gains and losses are crucial drivers for evolutionary change. We have gain and loss rates:

$$Q_{ij}^{\text{gain}} = q_{\text{gain}} (1 - M_{ij}) P_i A_j \quad (14)$$

$$Q_{ij}^{\text{loss}} = q_{\text{loss}} M_{ij} (P_i A_j + (1 - P_i) A_j + P_i (1 - A_j)) \quad (15)$$

The species present on the island ($P_i = 1$ and $A_j = 1$) that do not share any links ($M_{ij} = 0$) can evolve new links. In addition, species that have mutualistic links ($M_{ij} = 1$) can stochastically lose them if they are both present on the island, or one of the partners is absent ($P_i = 0$ or $A_j = 0$). q_{gain} is the per capita rate for a pair of species to gain a link. q_{loss} is the per capita rate for a pair of species to lose a link. P_i (A_j) indicates whether plant i (animal j) is on the island.

2.4. Stochastic simulation

We used the Doob-Gillespie algorithm (Gillespie, 1976) to simulate the model. This algorithm allows for stochastic process-based simulations in continuous time. The time until the next event is determined by sampling from an exponential distribution with the sum of the event rates as a parameter. Which event occurs is then sampled based on the rates of each event relative to the sum of all rates. The mainland species pool consists of 135 plant and 612 animal species (see Table 1). We conducted simulations across different parameter settings, each with 100 replicates. We set high and low values for the intrinsic rates of colonization, extinction, anagenesis, and cladogenesis to explore a broad parameter space (see Table 2). In addition, to assess the impact of mutualism, we defined three levels of mutualism effect strength: K_1 , μ_1 , λ_1^a and λ_0 are 0 for no effect of mutualism on the rates, $K_1 = 50$, $\mu_1 = 0.005$, $\lambda_1^a = 0.005$ and $\lambda_0 = 0.25$ for a medium mutualism level, and $K_1 = 100$, $\mu_1 = 0.01$, $\lambda_1^a = 0.01$ and $\lambda_0 = 0.5$ for a high mutualism level. We kept the following parameters constant for both plant and animal species: per capita rate of gaining and losing a link q_{gain} and q_{loss} , the adjustment parameter α , and the intrinsic carrying capacity K_0 . For each combination of high and low values of λ_0^c , μ_0 , γ_0 , and λ_0^a , we ran scenarios with no, medium, and high mutualism effect levels. In total, we ran $2^4 \times 3 \times 100 = 4800$ replicates. We consider a symmetrical system for plant and animal species, i.e., all parameter changes apply equally to both plant and animal species. We thus did not investigate how asymmetries in the rates between animals and plants would affect the results.

2.5. Simulation analysis

To assess the dynamics of species diversity and network connectivity under our different simulated scenarios, we computed the following set of metrics based on the simulated island datasets:

- Species richness. This refers to the total number of species on the island, a common measure of biodiversity (Magurran, 2013). In the context of this study, species richness was quantified for both plant and animal species separately, allowing us to examine patterns of biodiversity across different taxonomic groups. We quantified species richness (plant, animal or both) by counting the total number of species present on the island through time from the start until the end of the simulation.

Table 2

Parameter values used in the simulations. (A) The intrinsic immigration, extinction, speciation rates (including anagenesis and cladogenesis) and carrying capacity for both plant and animal species, which result in 16 parameter combinations. Numbers separated by commas are low and high values, respectively. (B) Three levels of the effect of mutualism on carrying capacity, extinction, anagenesis and cospeciation (The effects of carrying capacity will further affect immigration and cladogenesis). There are zero, medium, and high values for each of them, separated by commas. (C) Values of parameters that are kept fixed.

	Parameter	Values	Description
(A)	λ_0^c	0.3, 0.6	intrinsic cladogenesis rate
	μ_0	0.05, 0.2	intrinsic extinction rate
	γ_0	0.04, 0.08	intrinsic immigration rate
	λ_0^a	0.5, 1.0	intrinsic anagenesis rate
	K_0	50	intrinsic carrying capacity
(B)	K_1	0, 50, 100	Carrying capacity-mediated coefficient
	μ_1	0, 0.005, 0.01	Extinction-mediated coefficient
	λ_1^a	0, 0.005, 0.01	Anagenesis-mediated coefficient
	λ_0	0, 0.25, 0.5	Cospeciation-mediated coefficient
(C)	q_{gain}	0.001	Rate of gaining a link
	q_{loss}	0.001	Rate of losing a link
	α	100	Adjustment parameter

Note: $\lambda_0^c = \lambda_{p0}^c = \lambda_{a0}^c$, $\mu_0 = \mu_{p0} = \mu_{a0}$, $\gamma_0 = \gamma_{p0} = \gamma_{a0}$, $\lambda_0^a = \lambda_{p0}^a = \lambda_{a0}^a$, $K_1 = K_{p1} = K_{a1}$, $\lambda_1^a = \lambda_{p1}^a = \lambda_{a1}^a$, $\lambda_0 = \lambda_{p0} = \lambda_{a0}$, $K_0 = K_{p0} = K_{a0}$. For detailed definitions, please refer to Section 2.3.

- ii) Proportion of unconnected species. Within an island, there may be species that are not embedded in the network. We considered unconnected species to be those that exhibit no links with other species.
- iii) Connectance. This is defined as the proportion of realized links relative to all possible links within the network. This provides a network-wide metric of how connected species are.
- iv) Species degree. The degree of a species in a network is a network metric used to quantify the number of mutualistic links that a species in the community has (Newman, 2003; Williams, 2011). We tracked the distribution of species degree across all simulation runs, and analyzed how degree was related to species richness. Specifically, we investigated whether higher-degree species (i.e., generalists) exhibited greater species richness than lower-degree species (i.e., specialists).
- v) Number of network components. A network component is essentially a cluster of connected species within the network (Newman, 2003; Proulx et al., 2005). The largest component refers to the largest group of species that are connected to each other in the network. In a highly integrated group, most species within the component are mutually connected. The number of components refers to how many separate groups of connected species exist in the network. If there are many components, this indicates that the network is fragmented with many isolated groups of species.
- vi) Size of the largest network component. This is the number of species in the largest network component for each island. Component number and size were computed using the R package igraph.

We did not consider commonly used network statistics such as nestedness and modularity, because these are not well-defined for a community that may consist of several unconnected networks.

For each of the above-mentioned metrics, we examined their relationship with macroevolutionary parameters (see Table 2) and levels of the effect of mutualism (absent, medium, and high). All simulations and statistical analyses were conducted in R (version 4.4.2). The code is available on <https://doi.org/10.5281/zenodo.17158356>.

3. Results

3.1. Species diversity

We find that stronger mutualistic effects are associated with higher species richness on islands within the model framework (Figs. 4, A.1, A.2). This is evidently unsurprising because the effect of mutualism is modeled to increase the amount of niche space available. But we were mostly interested in how the various processes and corresponding parameters influence this diversity increase and also the network structure. Notably, under high intrinsic cladogenesis or immigration rates, species richness increased more substantially in medium and high mutualism effect scenarios, while the no mutualism effect scenario shows relatively little change. This is because increased rates of speciation or colonization amplify the effect of interaction-dependent ecological opportunity. An additional pattern visible is the increased variability among simulated communities under high cladogenesis rates, particularly when immigration rates are low. In these scenarios, island assembly becomes increasingly driven by in situ diversification rather than repeated immigration from the mainland. Intrinsic anagenesis rates generally (λ_0^a) contribute very little to changes in the total richness, as anagenesis reflects evolutionary change within lineages, without directly causing increase of diversity within the island. However, anagenesis does play a crucial role in the formation of endemic species (Fig. A.4). Note that there are more animal species than plant species on the island, which results from the larger source pool of animal species ($n_A = 612$) than plant species ($n_P = 135$) on the mainland (Fig. A.3).

3.2. Network connectivity

Our results show that network connectivity can be strongly influenced by intrinsic rates and mutualism levels (Fig. 5). A key finding of our simulations is that many species on the island are not part of the island network, that is, they are not connected to any other species on the island at the end of the simulation. This is particularly the case under the no effect of mutualism on the rates, where a consistently high proportion of species remain unconnected, regardless of the intrinsic macroevolutionary rates (Fig. 5a). This pattern is mirrored in the network connectance (Fig. 5b), which is clearly higher under the high mutualism effect level and exhibits little variation across parameter sets under no mutualism effect. When mutualism is introduced in the simulation, the proportion of unconnected species decreases sharply, reflecting both increased link persistence and higher probabilities of co-occurrence among interacting partners. Notably, islands with high cladogenesis rates (λ_0^c) have more connected networks than those simulated under low cladogenesis rates. In particular, higher cladogenesis rates are associated with lower proportions of isolated species and higher connectance among interacting species, consistent with the propagation of interactions through lineages via inheritance during speciation. The most tightly connected networks emerge under conditions of high cladogenesis and immigration, and low intrinsic extinction, particularly under the high mutualistic level (Fig. 5a). In contrast, when cladogenesis and immigration rates are low and the extinction rate is high, species remain largely unconnected and the existing networks are only loosely connected. Even under strong mutualism effects, low immigration limits network connectivity, emphasizing immigration's role in providing opportunities for species to establish links. Finally, we found a negative correlation between total species richness on the island and the proportion of unconnected species (Fig. 5c), suggesting that as biodiversity increases, the possibility of species remaining isolated declines. This relationship is strengthened under mutualistic effects, where increased co-occurrence and interaction persistence further reduce isolation.

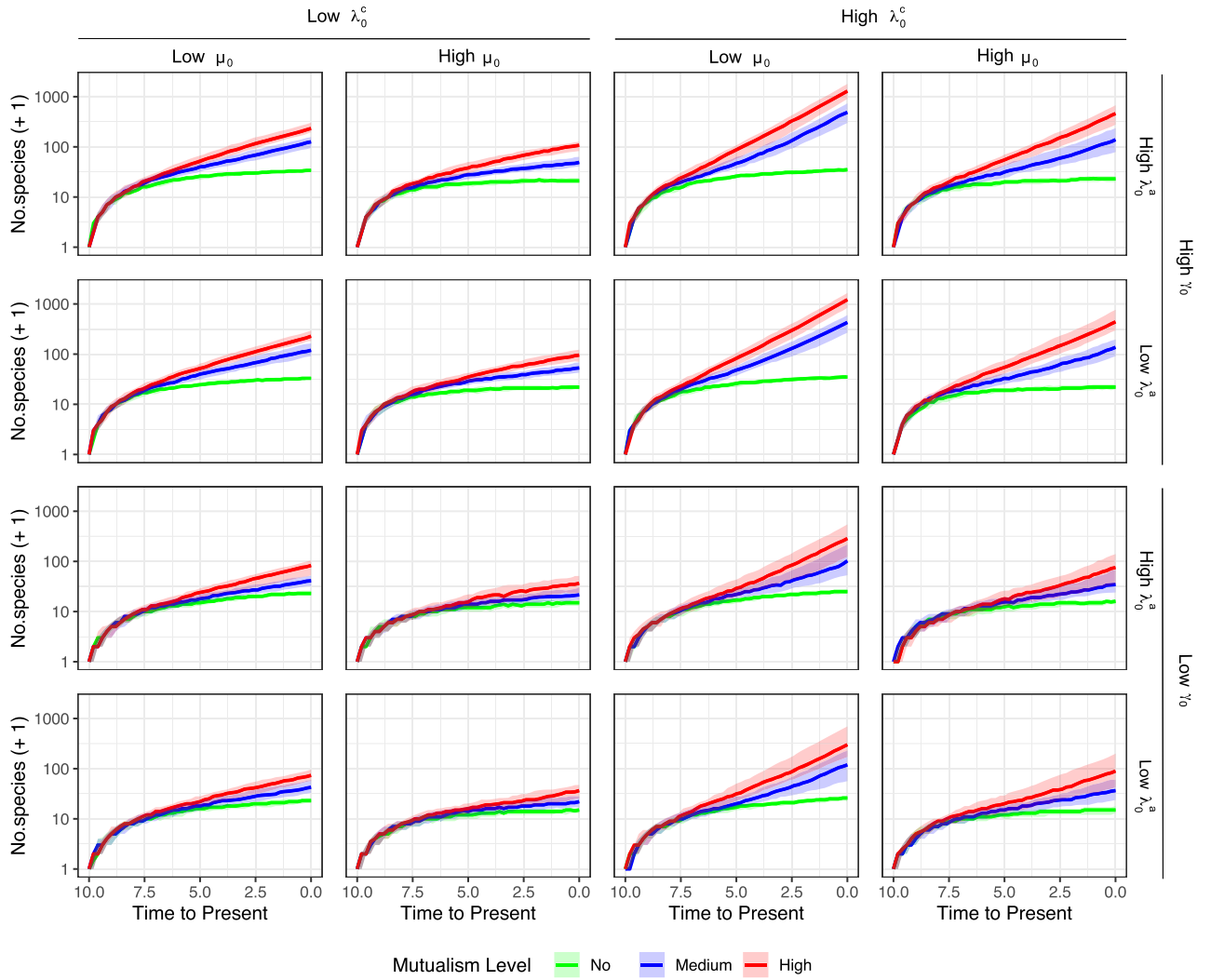


Fig. 4. Species richness through time under different levels of mutualism and parameter combinations. Species richness is defined as the number of species present on the island. The x-axis denotes evolutionary time from 10 million years ago to the present, and the y-axis shows the number of species (logarithmic scale), adjusted by adding one to prevent undefined $\log(0)$. Solid lines represent the median across 100 replicates, with shaded areas indicating the 25th (bottom) and 75th (top) quantiles. Mutualism effect levels are represented by colors: green (No), blue (Medium), and red (High). Each plot is a combination of different parameter values indicated in the outer axes. The exact values used as low and high parameter values are given in Table 2. λ_0^c , the intrinsic cladogenesis rate, μ_0 , the intrinsic extinction rate, γ_0 , the intrinsic immigration rate, λ_0^a , the intrinsic anagenesis rate. All intrinsic rates are symmetrically applied to both plant and animal species (e.g. $\gamma_{P0} = \gamma_{A0}$).

3.3. Species degree within network

Our simulations show that a strong mutualism effect on the assembly rates is associated with higher species diversity and a greater proportion of species with higher degrees within the network (Figs. 6 and A.5). This pattern reflects both increased interaction persistence and the accumulation of links under mutualistic effects, rather than an explicit shift in species' interaction strategies. Under no mutualism effect, the vast majority of species exhibit low degree ranges (they are each connected to a low number of species), with most species having degrees below 9, and unconnected species (with degree of 0) constituting the largest proportion. In contrast, in scenarios with medium or high mutualism effect, island communities are generally dominated by species with higher degrees, i.e. the majority of species exhibit a medium to high number of mutualistic links. When the rate of cladogenesis is low, the maximum degrees typically fall within the range of 33 to 64, except in scenarios characterized by high intrinsic immigration combined with low intrinsic extinction. When the intrinsic cladogenesis rates are high, networks tend to yield broader degree distributions. Under these

conditions, maximum degree values increase substantially when extinction rates are low but decrease markedly under high extinction rates, indicating that extinction constrains the accumulation and persistence of interaction links. Simulations with a high level of mutualism effect appear to be less affected by intrinsic extinction rates, but are influenced by intrinsic immigration rates.

The positive relationship between species degree and richness becomes notably more pronounced under elevated intrinsic cladogenesis rates (λ_0^c). This pattern arises because interaction links are inherited during cladogenesis, leading to phylogenetic autocorrelation in network structure, where lineages descending from highly connected ancestors tend to retain higher connectivity. As a result, the association between degree and richness reflects interaction inheritance and lineage diversification. Additionally, high extinction substantially reduces the proportion of lower-degree species but has less severe impacts on highly connected species under the high mutualism effect scenario. Intrinsic immigration rates (γ_0) further modulate this pattern by enabling the continued arrival and co-occurrence of interacting species, especially under medium to high mutualism effect levels, suggesting immigration plays a

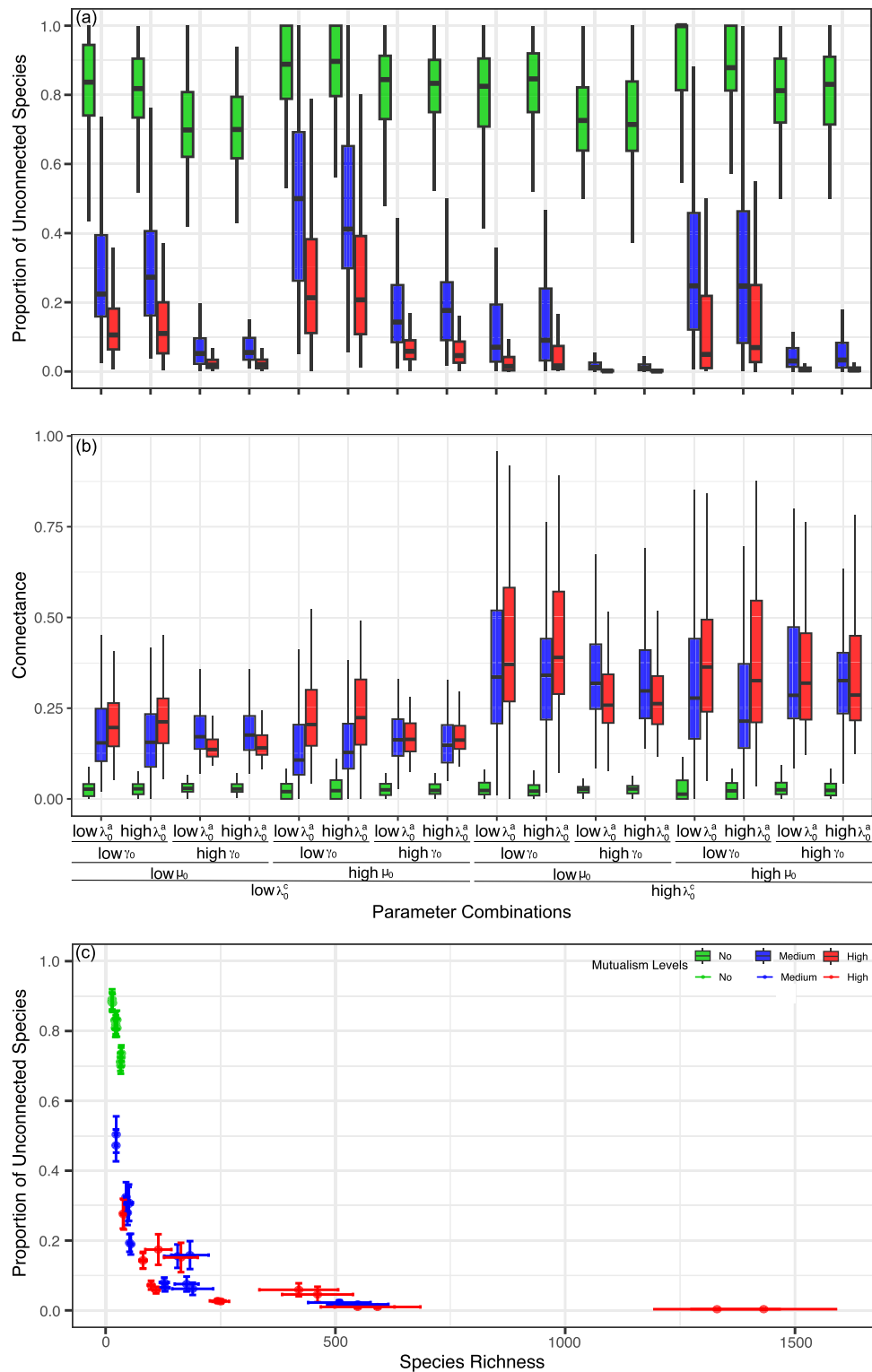


Fig. 5. Impact of mutualism effect levels and macroevolutionary parameters on network connectivity. (a) Proportion of species in the community that are unconnected across different parameter combinations (same x-axis as panel b). (b) Network connectance across different parameter combinations. Parameter details are provided in Table 2. (c) Relationship between species richness and the proportion of unconnected species. Each point represents the average values of a unique parameter combination, with bars showing 95% confidence intervals for both axes. All intrinsic rates are symmetrically applied to plant and animal species. Results for each parameter set represent values obtained across 100 replicates.

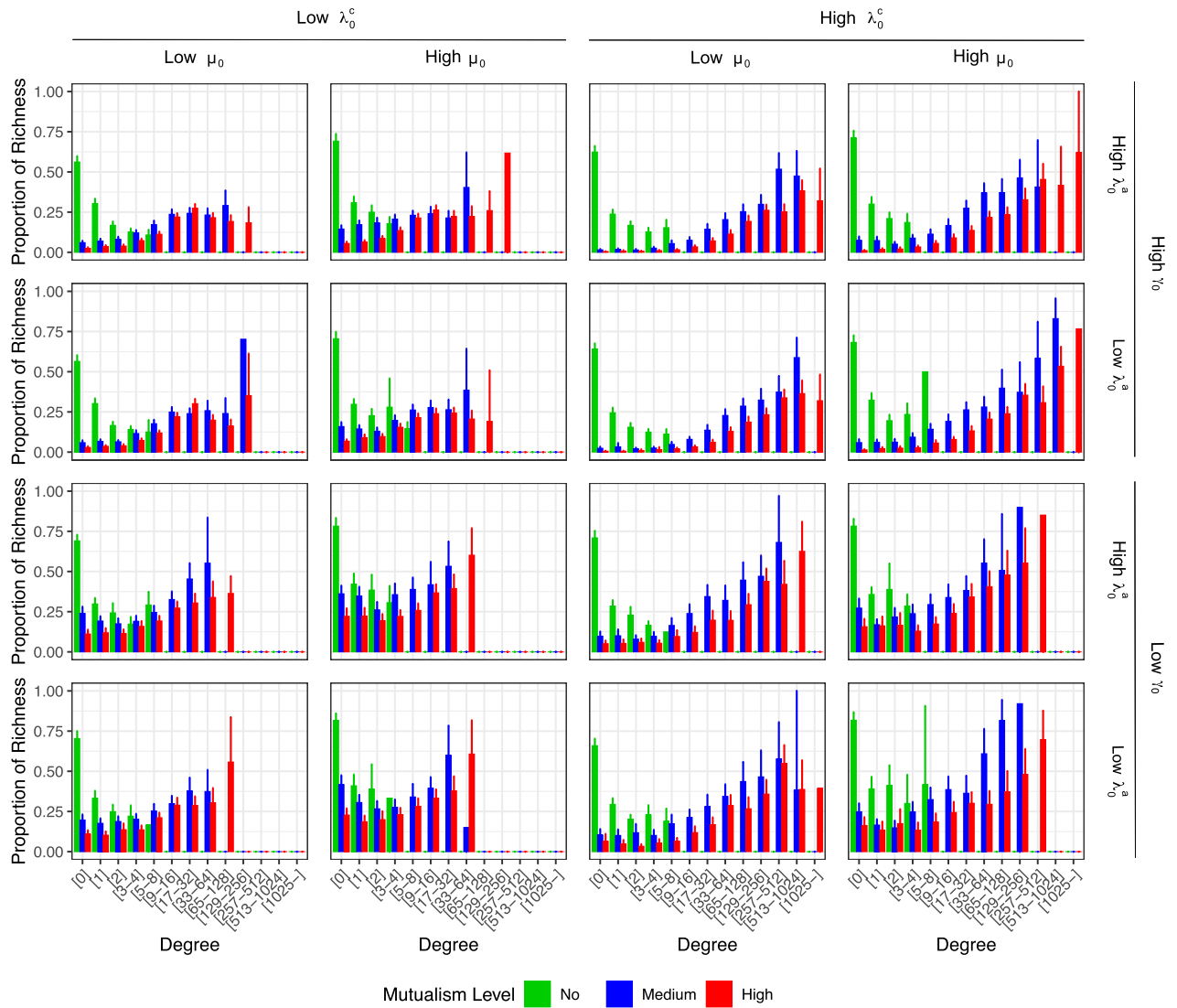


Fig. 6. Proportion of plant species richness in each degree range under different intrinsic macroevolutionary rates across different levels of mutualism effect. Degree is defined as the number of mutualistic links a plant species has with animal species. The x-axis represents different degree ranges on a logarithmic scale. The y-axis shows the average proportion of the total number of plant species with 95% confidence intervals across 100 simulation replicates that have a corresponding degree. Mutualism effect levels are represented by colors: green (No), blue (Medium), and red (High). Each plot is a combination of different parameter values indicated in the outer axes. The exact values used as low and high parameter values are given in Table 2. λ_0^c , the intrinsic cladogenesis rate, μ_0 , the intrinsic immigration rate, λ_0^a , the intrinsic anagenesis rate. All intrinsic rates are symmetrically applied to both plant and animal species (e.g., $\gamma_{P0} = \gamma_{A0}$).

key role in replenishing and maintaining mutualistic networks. Finally, the intrinsic anagenesis rate (λ_0^a), while generally exhibiting only subtle effects, nonetheless contributes meaningfully to increasing richness among higher-degree species when paired with high cladogenesis and mutualism effect levels.

3.4. Network components

Our simulations reveal that network fragmentation varies systematically with both connectance and model parameters, including mutualism levels (Figs. 7, A.6). Across all parameter combinations, networks with no mutualism effect exhibit high fragmentation, characterized by numerous small components. In contrast, medium and high levels of mutualism effect are linked to greater connectivity, reducing the number of components and substantially increasing the size of the largest connected group. As expected from network topology, the number of components is strongly and inversely related to connectance,

with more densely connected networks forming fewer, larger components (Fig. A.6). When examined as a function of connectance, much of the reduction in fragmentation under mutualism can be explained by its effect on increasing link density. Under no mutualism effect, networks typically form a small number of components (Table A.1), and the largest component rarely exceeds 10 species—indicating sparse connectivity. Medium mutualism effect gives rise to higher cohesion, with networks generally forming fewer components and the largest component often reaching several hundred species. Under strong mutualism, networks frequently consolidate into fewer components and often form a dominant component that includes most species. However, comparisons within overlapping connectance ranges (Fig. A.6) indicate that networks generated under different mutualism levels exhibit broadly similar fragmentation patterns once connectance is accounted for, suggesting that fragmentation is largely determined by link density rather than an independent structural effect of mutualism. Macroevolutionary dynamics further modulate these patterns. High cladogenesis (λ_0^c) and

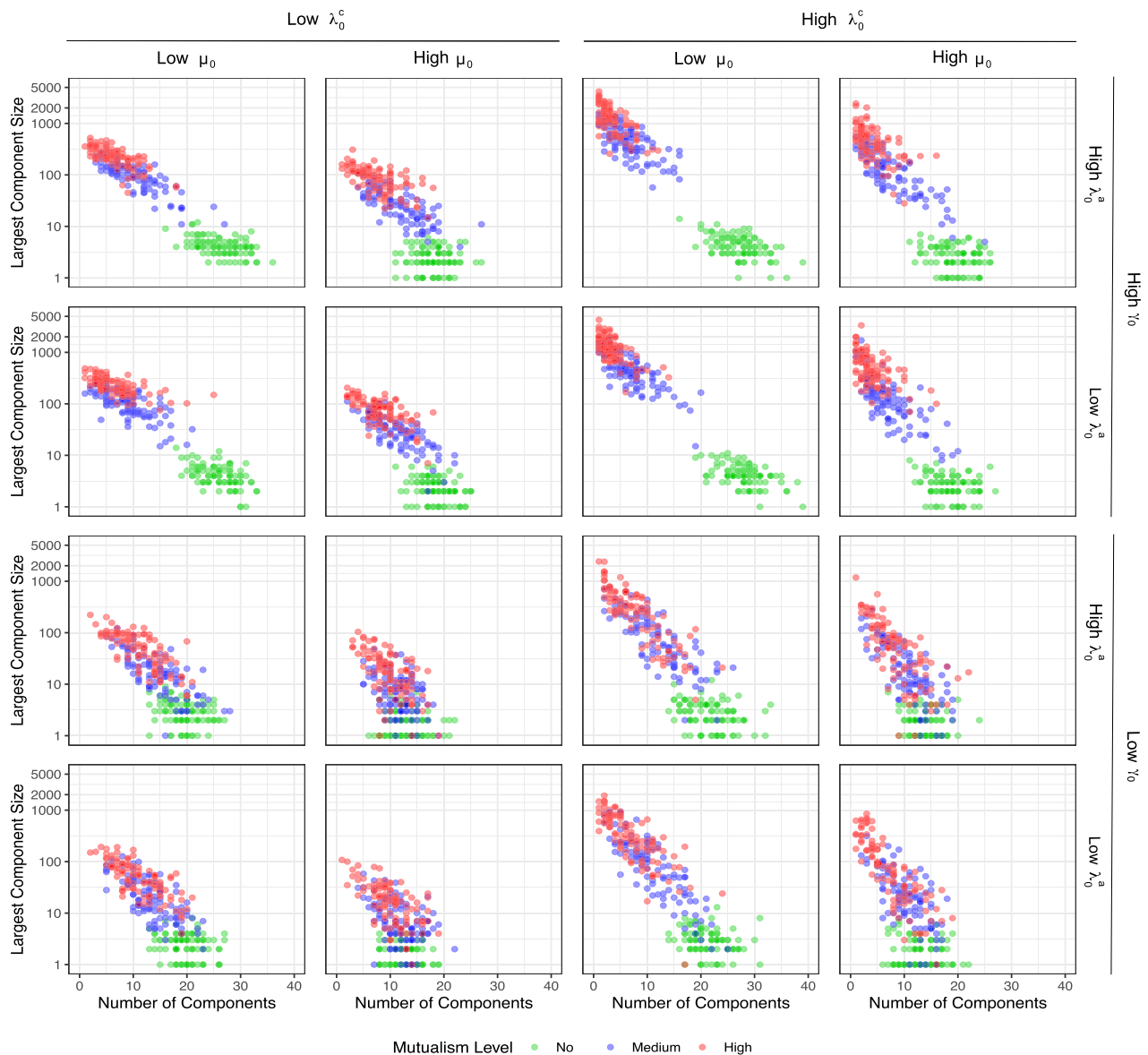


Fig. 7. Relationship between the number of components and the size of the largest component under different levels of mutualism effect and different parameter combinations. A component is defined as a group of species that are connected to each other. The x-axis represents the total number of components in the networks, and the y-axis shows the size of the largest component (log scale). Each dot represents a single simulation. Mutualism effect levels are represented by colors: green (No), blue (Medium), and red (High). Each plot is a combination of different parameter values indicated in the outer axes. The exact values used as low and high parameter values are given in Table 2. λ_0^c , the intrinsic cladogenesis rate, μ_0 , the intrinsic extinction rate, γ_0 , the intrinsic immigration rate, λ_0^a , the intrinsic anagenesis rate. All intrinsic rates are symmetrically applied to both plant and animal species (e.g., $\gamma_{P0} = \gamma_{A0}$).

immigration rates (γ_0) tend to promote network connectivity, particularly under mutualism. In such cases, networks often form a dominant component encompassing a large fraction of the species. Conversely, low cladogenesis or immigration, especially when coupled with high extinction (μ_0), limits component size and results in more fragmented networks, regardless of mutualism effect levels. This is most pronounced when the mutualism effect is absent, where interaction loss and limited co-occurrence constrain connectance, leading to persistently fragmented networks even under elevated cladogenesis rates.

4. Discussion

In this study, we bridge ecology and macroevolution by exploring how mutualistic networks – particularly plant-animal pollination interactions – influence macroevolutionary processes within an insular con-

text. Within the model, mutualistic interactions increase the effective ecological opportunity available to species by modifying immigration, extinction, and speciation rates, consistent with previous empirical and theoretical work (Gómez and Verdú, 2012; Litsios et al., 2012; Bascompte, 2019). The number of species on the island is much higher than in the system without mutualism effect (Fig. 4), especially when immigration and cladogenesis rates are high while extinction rate is low. Rather than representing a purely direct effect, differences in richness arise from the interaction between mutualism and macroevolutionary processes governing island assembly. Notably, under high intrinsic rates of cladogenesis or immigration, even a moderate mutualistic effect produces richness levels comparable to those under strong mutualism. This suggests that the impact of interaction-dependent ecological opportunity is amplified in high-turnover systems, where ecological opportunity and rapid lineage accumulation amplify its effects. Conversely, high

extinction rates reduce overall richness across all scenarios by limiting species persistence. These results highlight the uneven benefits of mutualism across species: generalists with more interactions gain resilience and diversification opportunities, while specialists or isolated species remain more vulnerable. This pattern is consistent with empirical observations that species embedded in more connected interaction networks tend to exhibit greater persistence (Bascompte et al., 2003; Vázquez et al., 2007), although in the present model this arises from interaction inheritance and network structure rather than an explicit fitness advantage tied to degree. Differences among species in persistence and diversification outcomes reflect both their interaction structure and the stochastic assembly of the network, rather than a direct increase in speciation probability with interaction degree. Our model further demonstrates that immigration and cladogenesis jointly shape both species richness and network structure, with higher rates promoting the emergence of larger and more connected network components. Notably, a high cladogenesis rate coupled with a low immigration rate may drive in situ diversification, resulting in greater variability in species richness across simulations. These patterns arise from the interaction of stochastic assembly processes, diversification, and interaction inheritance, rather than from mutualism alone.

Despite the overall rise in species richness, our model shows that many species remain unconnected, especially under low mutualism or weak macroevolutionary input. This indicates that diversification alone is not sufficient to generate network cohesion, as interaction structure depends not only on species accumulation but also on the co-occurrence of compatible partners and the persistence of links. In the absence of mutualism, species can still form links through two mechanisms: links present on the mainland are automatically realised when both interacting species co-occur on the island, and new links may also arise stochastically through the gain process between plant-animal pairs. However, because species colonize independently and suitable partners are often initially absent, networks in the no mutualism scenario tend to remain sparse and fragmented. When an effect of mutualism on the assembly rates is introduced, increased link persistence and higher probabilities of partner co-occurrence can partially counteract this tendency, but only under parameter combinations that support sufficient species turnover and co-occurrence – particularly high cladogenesis or immigration and low extinction. This finding aligns with the idea that mutualistic networks require not just ecological opportunity but also temporal overlap and partner compatibility (Olesen et al., 2008; Encinas-Viso et al., 2012). It also emphasizes the distinction between species accumulation and interaction structure: a species-rich community can still be structurally fragmented and functionally weak if the interactions fail to form.

Species with higher degrees – those forming many mutualistic links – tend to exhibit greater richness, especially under scenarios with strong or moderate mutualism. This association reflects the inheritance of interaction links during cladogenesis and the resulting phylogenetic autocorrelation in network structure, whereby lineages descending from highly connected ancestors tend to retain higher connectivity and accumulate more descendant species. Degree ranges expand markedly in simulations with strong immigration or cladogenesis, indicating that rapid lineage turnover facilitates the formation of new interactions. In particular, cladogenesis propagates existing interactions through lineage splitting, while immigration increases the likelihood of co-occurrence among compatible partners, together contributing to broader degree distributions. Conversely, high extinction rates disproportionately affect low-degree species, which lack the interaction redundancy to persist. In terms of network structure, networks with stronger mutualistic effects tend to exhibit lower fragmentation and larger dominant components. Without mutualism effect, networks remain highly fragmented with small, isolated clusters; under strong mutualism effect, however, components can grow to include thousands of species. These shifts in component size therefore primarily reflect changes in link density, together with the cumulative effects of macroevolutionary processes that promote co-occurrence and interaction persistence over time. Importantly,

immigration appears to be a key “producer” of network cohesion, providing the new colonists with the potential to connect across guilds and reinforce structural integrity.

We presented the model with plant-animal pollination networks in mind as a representation of mutualism, but other types of mutualistic interactions are also crucial for ecosystems, e.g. mycorrhizal associations between plants and fungi (Reddy et al., 2024), gut microbiota mutualism (Groussin et al., 2020) in animals, and ant-plant mutualism (Heil and McKey, 2003) where ants provide protection. In addition, in the current model, mutualism is implemented exclusively through positive effects on demographic and diversification rates, without explicitly incorporating costs, saturation effects, or trade-offs. This means that mutualism operates as a unidirectional force increasing ecological opportunity, and therefore some outcomes (e.g., increased richness or connectivity) are partly driven by model structure rather than emerging from opposing processes. Future extensions could incorporate antagonistic interactions, costs of maintaining interactions, or saturating benefits to better capture the balance of ecological forces. Our model relies on a binary network on the mainland, where interactions are either present or absent. This simplification helps us understand whether mutualism impacts the macroevolutionary processes, e.g. diversification. Nevertheless, interaction strengths have been found to influence the stability and dynamics of ecological networks (Laska and Wootton, 1998; Tang et al., 2014). Taking interaction strength into account (e.g. $0 \leq M_{ij} \leq 1$) will provide a more comprehensive understanding of how mutualism affects the species diversity on island through macroevolutionary processes. Our simulations consistently show the presence of unconnected species within the mutualistic network, even under moderate or strong mutualism effect levels. Rather than excluding these species, we retained them in the network analysis to better capture the structural consequences of interaction assembly. Their persistence highlights the fact that, under certain conditions—such as low immigration or high extinction—species may accumulate without establishing mutualistic ties. As a result, a community can be species-rich yet structurally fragmented, particularly when connectance remains low. These unconnected species may represent recent arrivals, ecological mismatches, or lineages awaiting integration, and their dynamics highlight a key limitation in empirical studies, where low sampling intensity may lead to the removal of unconnected species in network analysis. Such exclusions may not only overlook the ecological significance of these species but also misrepresent the true structure of the network. We acknowledge the difficulties in field collection work, and therefore call for a better analytical approach that can capture the full spectrum of species interactions.

Our model incorporates the role of mutualism in macroevolutionary processes by linking interaction structure to immigration, extinction, and diversification dynamics, while explicitly representing how interaction persistence, co-occurrence, and diversity dependence jointly shape community assembly. Such an integrative approach can provide valuable insights into the mechanisms shaping biodiversity patterns and the resilience of ecological communities in the face of ongoing environmental changes. For example, it can be applied to the emergence and subsequent development of new species in environments analogous to islands, where isolation and interaction dynamics play a critical role. More broadly, our results highlight the importance of considering both species-level processes and interaction structure when studying biodiversity dynamics, while also underscoring the need for future models to incorporate additional ecological mechanisms – such as interaction costs, trade-offs, and alternative interaction types – to capture the full complexity of natural ecosystems.

Declaration of generative AI and AI-assisted technologies in the manuscript preparation process

During the preparation of this work, the first author used ChatGPT (OpenAI) to improve language clarity and structure. After using

this tool, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the published article.

CRediT authorship contribution statement

Yang Shen: Writing – original draft, Formal analysis; **Luis Valente:** Writing – review & editing, Supervision, Conceptualization; **Rampal S. Etienne:** Writing – review & editing, Supervision, Conceptualization.

Declaration of competing interest

We declare that we have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Appendix

A.1. Mainland matrix construction

Following [Santamaría and Rodríguez-Gironé \(2007\)](#), the binary mainland species interaction network is constructed using a mixed model with a two-narrow-complementarity model and a two-barrier model. The mainland matrix M_0 is constructed as plant species (indicated by i) as rows and animal species (indicated by j) as columns (Note: we used the transpose of the matrix in the paper). The interaction matrix is given by:

$$M_{ij} = \begin{cases} 1 & \text{if } (|V_i^k - W_j^k| < 0.5 \cdot (\delta V_i^k + \delta W_j^k) \text{ for } k = 1, 2) \\ & \text{and } (V_i^k > W_j^k \text{ for } k = 3, 4) \\ 0 & \text{otherwise} \end{cases}$$

Here, V_i^k and W_j^k represent the central trait values for plant species i and animal species j , respectively. In the complementary model, a pair of species interact if their traits overlap. The traits $k = 1, 2$ are considered complementary. The terms δV_i^k and δW_j^k are independent random variables uniformly distributed in the interval $(0, 0.25)$. For barrier traits $k = 3, 4$, animal species j interact with plant species i if the trait value V_i^k is greater than W_j^k . We derived the number of animal species A from the equation given by [Santamaría and Rodríguez-Gironé \(2007\)](#): $A = 45.573 - 0.8082 \cdot P + 0.047 \cdot P^2$, where P is the number of plant species.

A.2. Effects on species richness

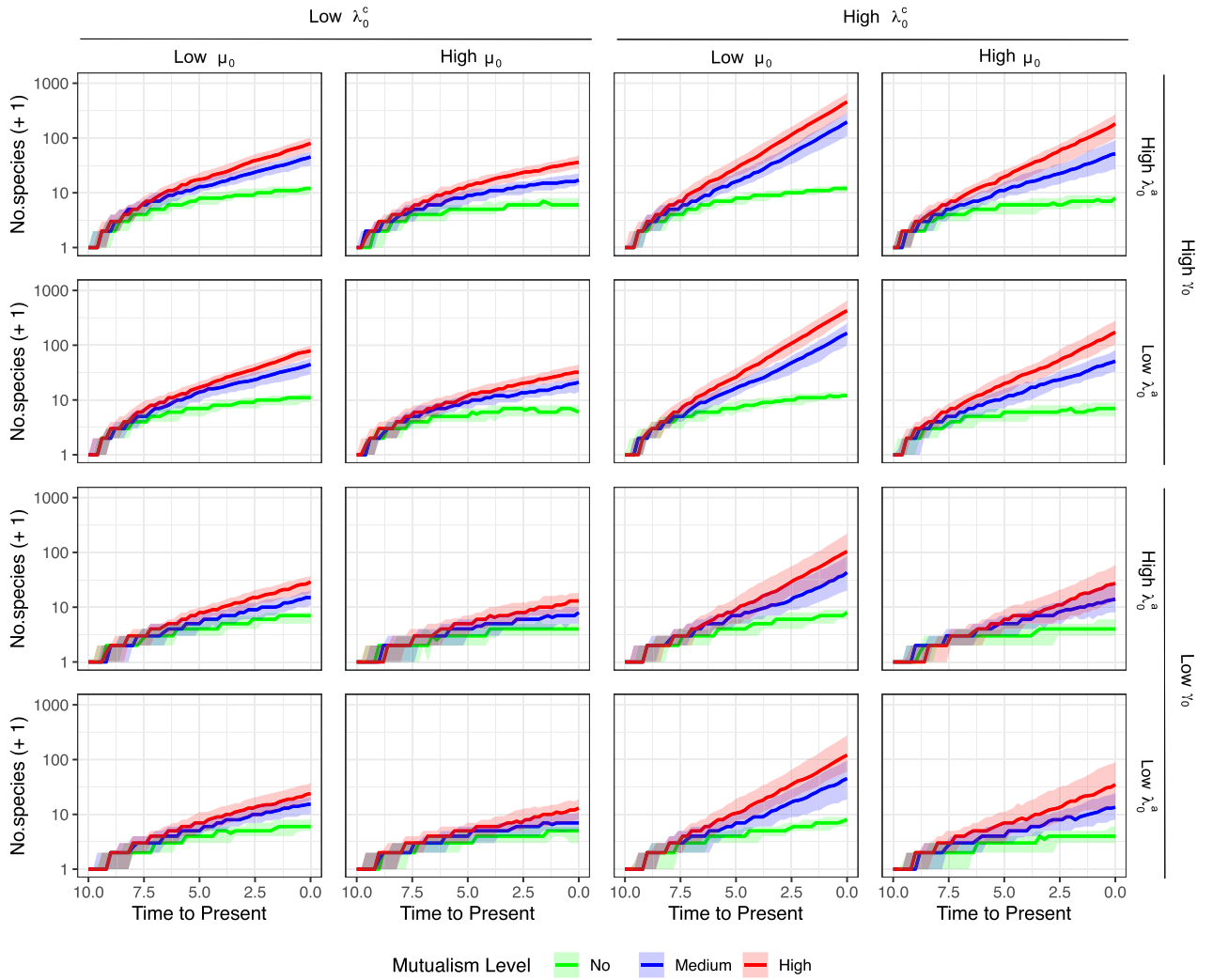


Fig. A.1. Plant species richness through time under different levels of mutualism and parameter combinations. The x-axis denotes evolutionary time from 10 million years ago to the present, and the y-axis shows the number of species (log scale), adjusted by adding one to prevent undefined $\log(0)$. Solid lines represent the median across 100 replicates, with shaded areas indicating the 25th (bottom) and 75th (top) quantiles. Each plot is a combination of different parameter values indicated in the outer axes. The exact values used as low and high parameter values are given in Table 2. Mutualism effect levels are represented by colors: green (No), blue (Medium), and red (High). λ_0^c , the intrinsic cladogenesis rate, μ_0 , the intrinsic extinction rate, γ_0 , the intrinsic immigration rate, λ_0^a , the intrinsic anagenesis rate. All intrinsic rates are symmetrically applied to both plant and animal species (e.g. $\gamma_{P0} = \gamma_{A0}$).

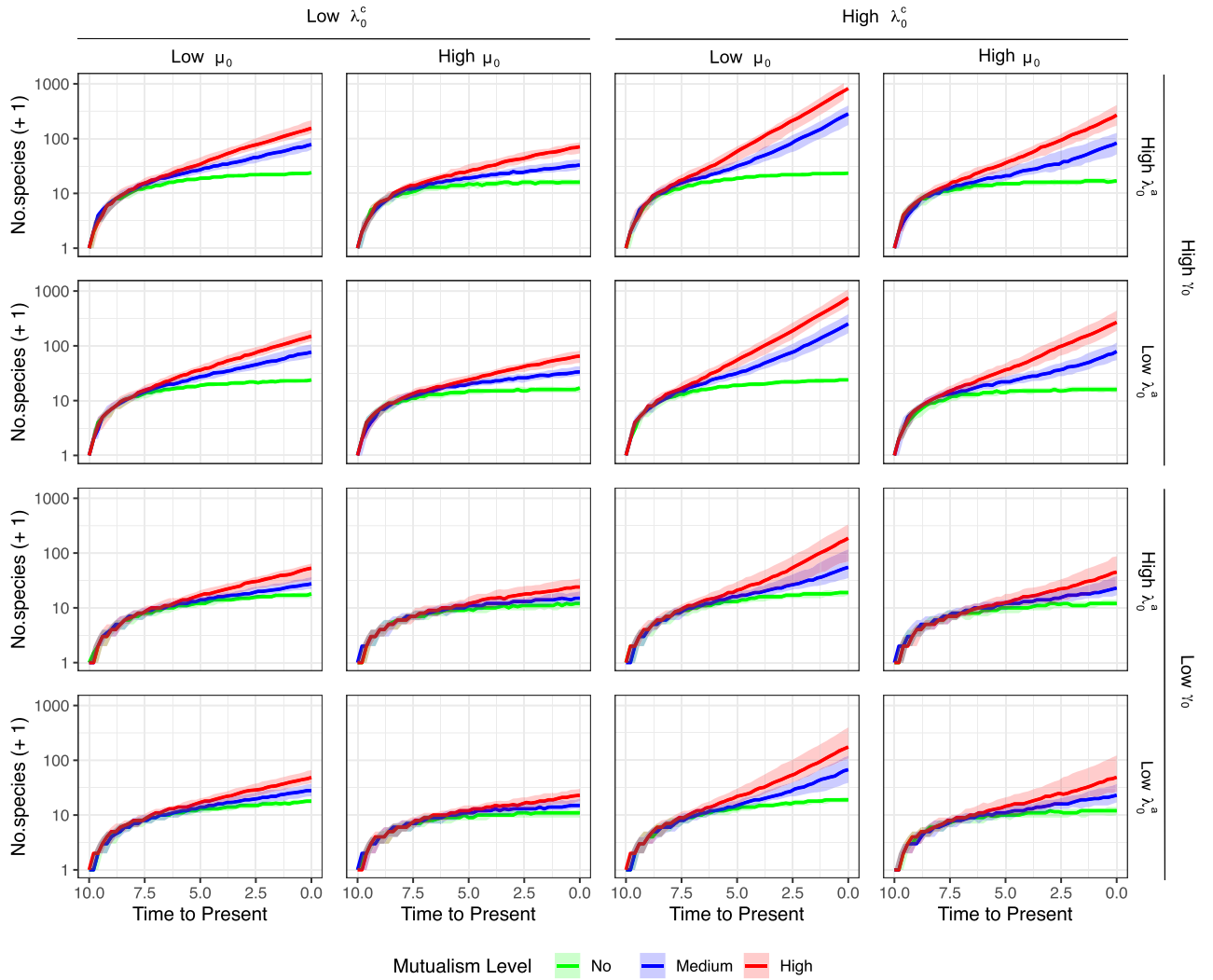


Fig. A.2. Animal species richness through time under different levels of mutualism and parameter combinations. The x-axis denotes evolutionary time from 10 million years ago to the present, and the y-axis shows the number of species (log scale), adjusted by adding one to prevent undefined $\log(0)$. Solid lines represent the median across 100 replicates, with shaded areas indicating the 25th (bottom) and 75th (top) quantiles. Each plot is a combination of different parameter values indicated in the outer axes. The exact values used as low and high parameter values are given in Table 2. Mutualism effect levels are represented by colors: green (No), blue (Medium), and red (High). λ_0^c , the intrinsic cladogenesis rate, μ_0 , the intrinsic extinction rate, γ_0 , the intrinsic immigration rate, λ_0^a , the intrinsic anagenesis rate. All intrinsic rates are symmetrically applied to both plant and animal species (e.g. $\gamma_{P0} = \gamma_{A0}$).

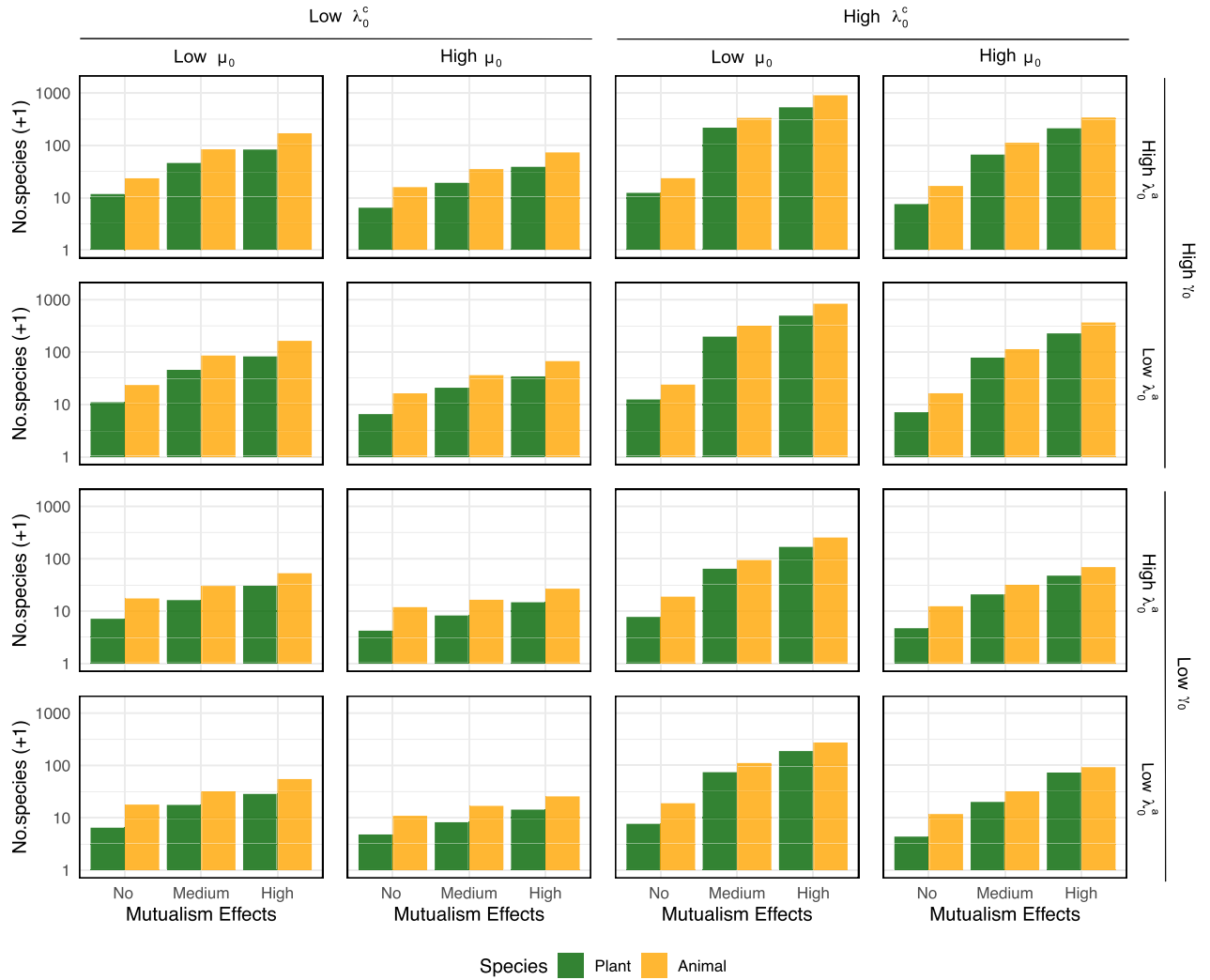


Fig. A.3. The number of plant and animal species across different levels of mutualism effects and parameter combinations. The x-axis denotes No, Medium and High mutualism effects, and the y-axis shows the number of species (log scale), adjusted by adding one to prevent undefined $\log(0)$. Green bars represent plant species while yellow bars as animal species. Each plot is a combination of different parameter values indicated in the outer axes. The exact values used as low and high parameter values are given in Table 2. λ_0^c , the intrinsic cladogenesis rate, μ_0 , the intrinsic extinction rate, γ_0 , the intrinsic immigration rate, λ_0^a , the intrinsic anagenesis rate. All intrinsic rates are symmetrically applied to both plant and animal species (e.g. $\lambda_{P0} = \lambda_{A0}$).

A.3. Effects of anagenesis on species richness

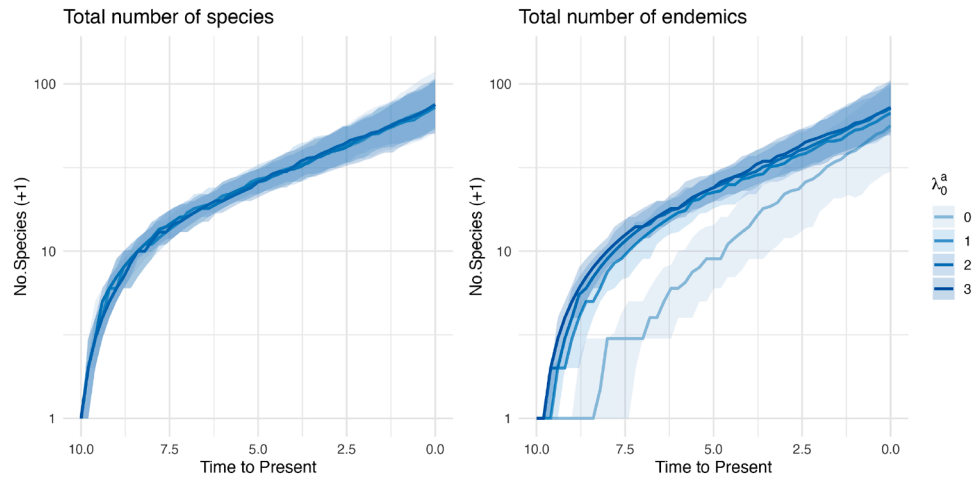


Fig. A.4. Number of species (plant and animal) over time under different intrinsic anagenesis rates. The x-axis denotes evolutionary time from 10 million years ago to the present, and the y-axis shows the number of species (log scale), adjusted by adding one to prevent undefined $\log(0)$. Solid lines represent the median across 100 replicates, with shaded areas indicating the 25th (bottom) and 75th (top) quartiles. Intrinsic anagenesis rates are 0, 1.0, 2.0, 3.0. Other parameters are the middle of high and low values in Table 2: $\lambda_0^c = 0.45$, $\mu_0 = 0.125$, $\mu_1 = 0.005$, $K_0 = K_1 = 50$, $\gamma_0 = 0.05$, $\lambda_0 = 0.25$. We keep $q_{\text{gain}} = q_{\text{loss}} = 0.001$, $\alpha = 100$ fixed. All intrinsic rates are symmetrically applied to both plant and animal species.

A.4. Degree of animal species

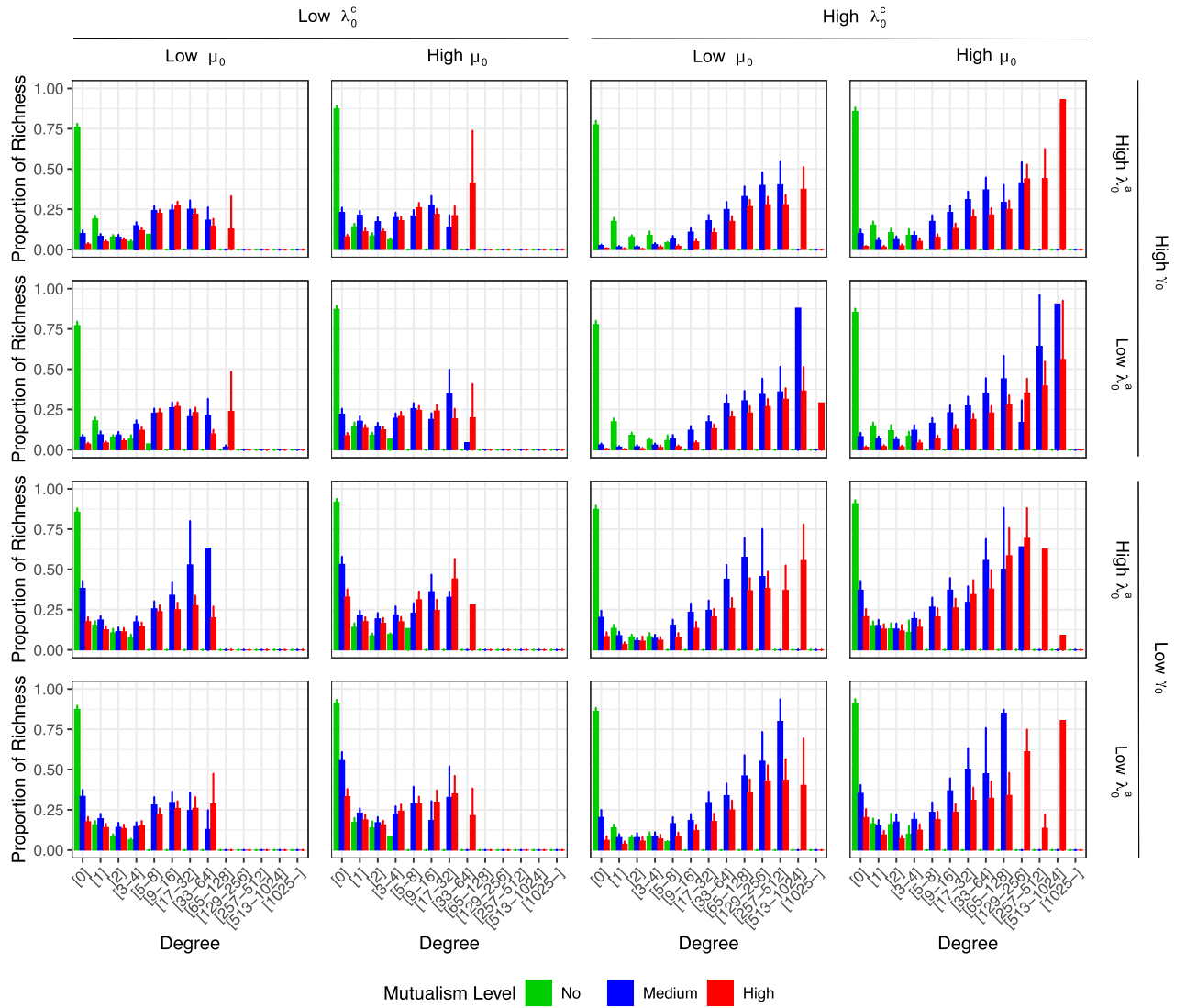


Fig. A.5. Proportion of animal species richness of several degree ranges under different intrinsic macroevolutionary rates across different levels of mutualism effect. The x-axis represents different degree ranges on a logarithmic scale, while the y-axis shows the average number of animal species with 95% confidence intervals over 100 simulation replicates. Different mutualism effect levels are indicated by color: green for no mutualism effect, blue for medium mutualism effect, and red for high mutualism effect. Each panel corresponds to a specific combination of parameter levels indicated by the outer axes. The exact values used as low and high parameter values are given in Table 2. λ_0^c , the intrinsic cladogenesis rate, μ_0 , the intrinsic extinction rate, γ_0 , the intrinsic immigration rate, λ_0^a , the intrinsic anagenesis rate. Specific values for each parameter combination are given in Table 2. All intrinsic rates are symmetrically applied to both plant and animal species (e.g., $\gamma_{P0} = \gamma_{A0}$).

A.5. Fragmentation vs connectance

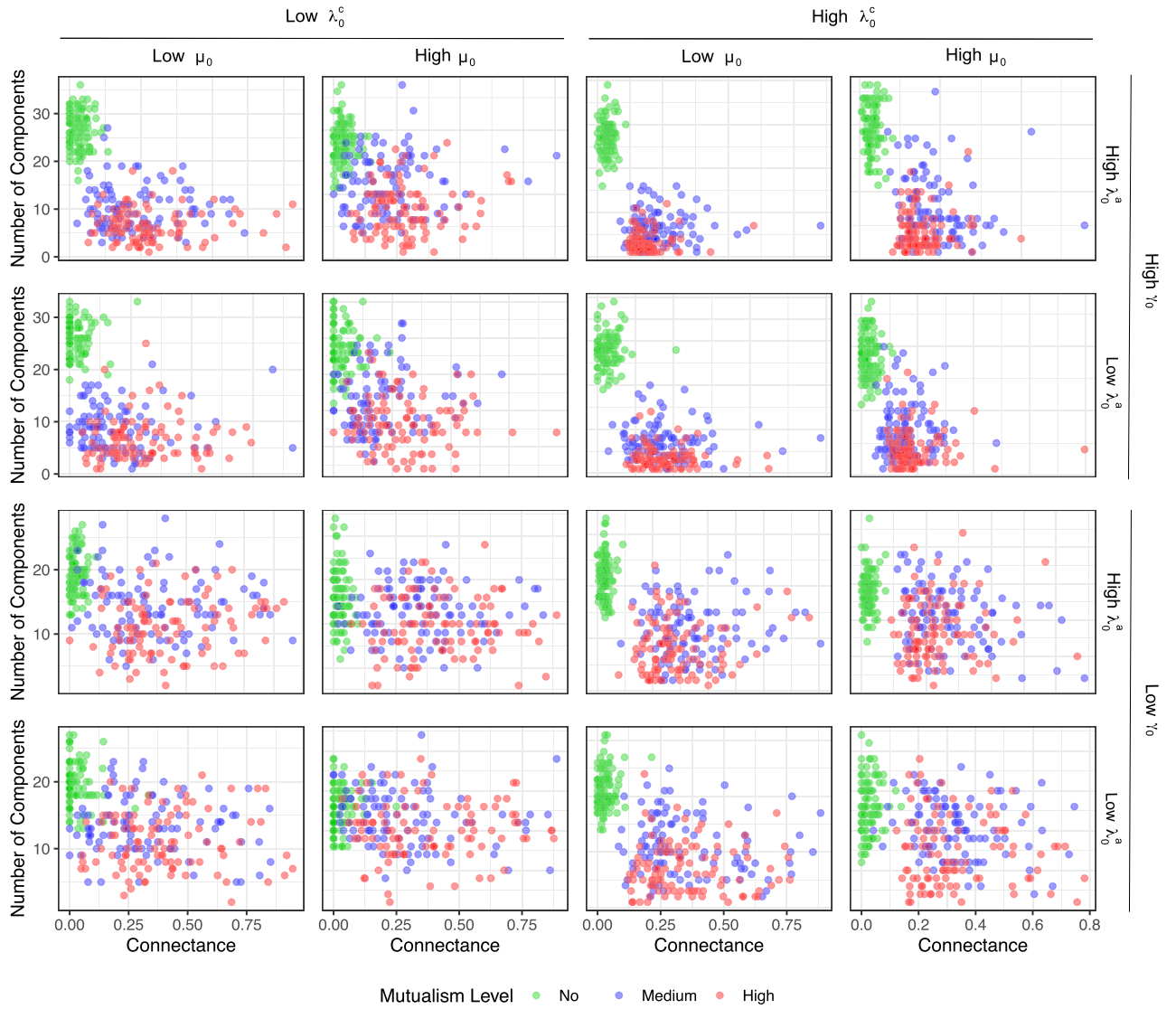


Fig. A.6. Relationship between the number of components and connectance under different levels of mutualism effect and different parameter combinations. A component is defined as a group of species that are connected to each other. The x-axis represents the connectance, and the y-axis shows the number of components in the networks. Each dot represents a single simulation. Colors indicate different mutualism effect levels: green (No), blue (Medium), and red (High). Outer axes denote parameter settings for λ_0^c , the intrinsic cladogenesis rate, μ_0 , the intrinsic extinction rate, γ_0 , the intrinsic immigration rate, λ_0^a , the intrinsic anagenesis rate. See the exact values of these in Table 2. All intrinsic rates are symmetrically applied to both plant and animal species (e.g., $\gamma_{P0} = \gamma_{A0}$).

A.6. Network component statistics

Table A.1

Network component statistics. Values are mean (Standard deviation) across mutualism effect levels.

Mutualism effect Level	Number of Components	Largest Component Size
No	19.8 (5.98)	3.03 (1.90)
Medium	10.4 (4.84)	132 (223)
High	7.35 (4.51)	363 (552)

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