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Eco-evolutionary processes and community patterns--- novel avenues for studying biodiversity across spatial and temporal scales

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Novel avenues for studying biodiversity across spatial and temporal scales

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DEPARTMENT OF BIOLOGY | FACULTY OF SCIENCE | LUND UNIVERSITY

Eco-evolutionary processes and community patterns – novel avenues
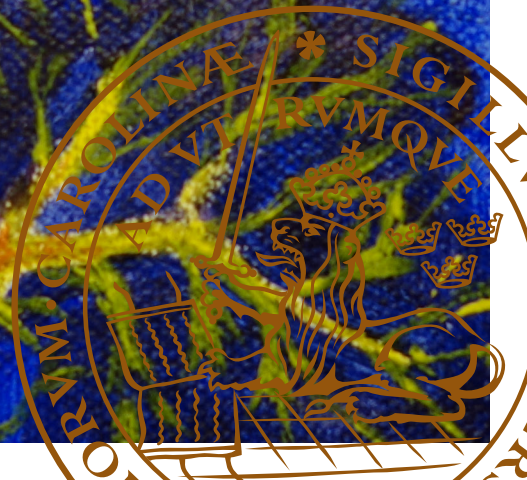for studying biodiversity across spatial and temporal scales

Eco-evolutionary processes and community patterns

novel avenues for studying biodiversity across spatial and temporal scales

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Abstract:

Understanding biodiversity patterns poses a persistent challenge due to the complex interconnections of ecological and evolutionary processes. The particular difficulty comes from the various processes influencing biodiversity patterns across different spatial scales. This thesis aims to enhance comprehension of community diversity patterns by employing theoretical models that are capable of generating community diversity patterns on local and regional spatial scales, including commonly used diversity metrics such as species, trait, and phylogenetic diversity. These models incorporate eco-evolutionary dynamics encompassing competition, predation, dispersal, environmental gradients, and adaptive radiation. Combining the results from each paper provides nuanced insights into the interconnected mechanisms governing community diversity patterns, summarized as five general conclusions: First, competition is the primary driver for community diversity patterns on the local scale. Second, environmental gradients play a crucial role in driving community diversity patterns on the regional scale. Third, predation interacts with competition, leading to changes in adaptive radiation on the local scale, thus changing diversity patterns. In general, predators hinder competition-induced disruptive selection by reducing prey abundance. Fourth, dispersal and environmental gradients influence adaptive radiation on the regional scale, changing the spatial diversity patterns. High dispersal can reduce the directional selection imposed by the environmental gradient, leading to species that can survive in multiple environments. Finally, there is a dynamic interplay between local and regional processes. Such temporal dynamics may be revealed by patterns that contain both temporal and spatial signals, such as phylogenetic diversity. In conclusion, this thesis not only advances our understanding of the mechanisms shaping community diversity patterns across spatial and temporal scales but also opens new avenues for biodiversity research. Theoretical models integrating local and regional processes in continuous space hold significant promise for advancing our comprehension of community patterns.

Key words:

Eco-evolutionary dynamics; Spatial phylogenetic patterns; Community diversity patterns; Scales; Predation; Competition; Environmental gradient; Dispersal; Adaptive dynamics; Elevational diversity gradients; Theoretical ecology, Simulation models
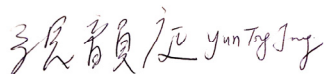
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Eco-evolutionary processes and community patterns

novel avenues for studying biodiversity
across spatial and temporal scales

Yun-Ting Jang

LUND
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"Having lost paradise, the unity with nature, he has become the eternal wanderer (Odysseus, Oedipus, Abraham, Faust); he is impelled to go forward and with everlasting effort to make the unknown known by filling in with answers the blank spaces of his knowledge. He must give account to himself of himself, and of the meaning of his existence."

-Man for Himself: An Inquiry Into the Psychology of Ethics, Erich Fromm

Table of Contents

Abstract

Understanding biodiversity patterns poses a persistent challenge due to the complex interconnections of ecological and evolutionary processes. The particular difficulty comes from the various processes influencing biodiversity patterns across different spatial scales. This thesis aims to enhance comprehension of community diversity patterns by employing theoretical models that are capable of generating community diversity patterns on local and regional spatial scales, including commonly used diversity metrics such as species, trait, and phylogenetic diversity. These models incorporate eco-evolutionary dynamics encompassing competition, predation, dispersal, environmental gradients, and adaptive radiation. Combining the results from each paper provides nuanced insights into the interconnected mechanisms governing community diversity patterns, summarized as five general conclusions: First, competition is the primary driver for community diversity patterns on the local scale. Second, environmental gradients play a crucial role in driving community diversity patterns on the regional scale. Third, predation interacts with competition, leading to changes in adaptive radiation on the local scale, thus changing diversity patterns. In general, predators hinder competition-induced disruptive selection by reducing prey abundance. Fourth, dispersal and environmental gradients influence adaptive radiation on the regional scale, changing the spatial diversity patterns. High dispersal can reduce the directional selection imposed by the environmental gradient, leading to species that can survive in multiple environments. Finally, there is a dynamic interplay between local and regional processes. Such temporal dynamics may be revealed by patterns that contain both temporal and spatial signals, such as phylogenetic diversity. In conclusion, this thesis not only advances our understanding of the mechanisms shaping community diversity patterns across spatial and temporal scales but also opens new avenues for biodiversity research. Theoretical models integrating local and regional processes in continuous space hold significant promise for advancing our comprehension of community patterns.

Populärvetenskaplig sammanfattning

Att utforska mångfalden av livet på jorden kan vara en utmanande gåta. Utmaningen beror särskilt på komplexa interaktioner mellan de ekologiska och evolutionära processer som styr hur arter interagerar och anpassar sig evolutionärt. Att studera dessa interaktioner lämnar oss ofta med fler frågor än svar. Vi försöker förstå hur olika arter lever tillsammans, anpassar sig och skapar nya arter men det är som att lösa ett gigantiskt ekologiskt och evolutionärt pussel. Ett av de stora mysterierna är att förstå hur exempelvis konkurrens mellan arter och predator-bytesförhållanden påverkar arters anpassning och hur dessa interaktioner i sin tur påverkar den mångfald av liv som vi ser omkring oss. Vad som gör det ännu mer komplicerat är att detta pussel också påverkas av var arter befinner sig och hur de anpassar sig till olika platser. Man kan se arter som resenärer, som färdas genom olika miljöer. Dessa resor påverkar mönstren av liv vi observerar. I min forskning har jag omfamnat denna komplexitet genom att använda matematiska modeller och datorsimuleringar för att studera hur samhällen av arter förändras och utvecklas i tid och rum. Här är några nyckelresultat från mitt arbete:

Konkurrens är en central aktör när det gäller att forma mångfalden av arter på en lokal platts.

Förändringar i miljöförhållandena, som klimat eller andra livsmiljöer, har också en stor påverkan på mångfaldsmönster på en större skala.

Rovdjur kan förändra artsammansättningen på en lokal plats, och ofta minskar antalet byten.

Förmågan hos arter att röra sig och anpassa sig till olika miljöer är avgörande för att förstå varför vi ser vissa arter på specifika platser.

Det finns ett fascinerande samspel mellan vad som händer lokalt och vad som händer över en större region. Genom att studera biologisk mångfald över tid och rum kan vi avslöja dessa komplexa relationer.

Sammanfattningsvis hjälper min forskning oss inte bara att bättre förstå hur livet på vår planet fungerar, utan den väcker också spännande nya frågor. Jag har löst en del av det ekologiska och evolutionära pusslet men jag har även öppnar upp nya dörrar för ytterligare forskning inom biodiversitetens fantastiska värld.

科普摘要

隨著時間和空間的推移，探索地球生命的多樣性是一項令人困惑的挑戰。這是因為對影響物種如何相互作用和演化的生態和演化過程的研究通常讓我們得到更多問題而非答案。最終，試圖弄清楚不同物種如何共存、適應和創造新物種，就像解決一個巨大的生態和演化拼圖一樣。其中一個重要的謎團是理解競爭和捕食者-獵物關係等事物如何影響物種演化，以及這些相互作用如何反過來影響我們周圍所看到的生命多樣性。使情況變得更加複雜的是，這個拼圖還受到物種所在地以及它們如何適應不同地方的影響。想像物種如同旅行者，在各種環境中遊歷。這些旅程影響我們觀察到的生命模式。在這篇論文中，我通過使用數學和電腦模擬來研究物種社群如何變化和發展，嘗試簡化這種複雜性。以下是這篇論文的一些主要結論：

- 競爭是形塑區域物種多樣性的重要因素。

- 環境條件的變化，如氣候或棲息地，也對較大範圍的多樣性產生重大影響。

- 捕食者可以改變區域物種的多樣性，通常是減少獵物物種的數量。

- 物種在不同環境中移動並適應的能力對於理解為什麼我們在特定地方看到某些物種至關重要。

- 區域性發生的事情與大面積地理範圍發生的事情之間存在著迷人的關聯。通過研究生物多樣性隨著時間已經空間的變化，我們可以揭示這些複雜的關係。

總之，我的研究不僅增進我們對地球上的生命運作方式的理解，還提出了一些有趣的新問題。這就像解決一個龐大的生態和演化拼圖的一部分，為生物多樣性領域的研究開啟了新的大門。

Popular science summary

Exploring the diversity of life on Earth over time and space can be a puzzling challenge. This is because studies of the ecological and evolutionary processes that affect how species interact and evolve often leave us with more questions than answers. Ultimately, trying to figure out how different species live together, adapt, and create new species is like solving a giant ecological and evolutionary puzzle. One of the big mysteries is understanding how things like competition and predator-prey relationships impact the way species evolve, and how, in turn, these interactions affect the variety of life we see around us. What makes it even more complicated is that this puzzle is also influenced by where species go and how they adapt to different places. Imagine species as travelers, journeying across diverse environments. These journeys influence the patterns of life we observe. In this thesis, I've embraced this complexity by using math and computer simulations to study how communities of species change and develop. Here are some key takeaways from my work:

Competition is a key player in shaping the diversity of species in a local area.

Changes in environmental conditions, like climate or habitats, also have a big say in shaping diversity patterns on a larger scale.

Predators can alter the mix of species in a local area, often reducing the number of prey species.

The ability of species to move around and adapt to different environments is essential for understanding why we see certain species in specific places.

There's a fascinating contrast between what's happening locally and what's happening over a larger region. By studying biodiversity over time, we can uncover these intricate relationships.

In summary, my research not only helps us better understand how life on our planet works but also raises exciting new questions. It's like solving one piece of a massive ecological and evolutionary jigsaw puzzle, and it opens up new doors for further exploration in the world of biodiversity.

List of papers

Paper I (published)

Jang, Y. T., Brännström, Å., & Pontarp, M. (2022). The interactive effects of environmental gradient and dispersal shape spatial phylogenetic patterns. *Frontiers in Ecology and Evolution*, 10, 1037980.

Paper II (manuscript)

Jang, Y. T., Pontarp, M., & Brännström, Å. Combined competition and predation effects on prey diversification: A mechanistic approach.

Paper III (manuscript)

Jang, Y. T., Brännström, Å., & Pontarp, M. Predator-prey dynamics in adaptive radiations: evolutionary consequences for community patterns and diversity metrics.

Paper IV (manuscript)

Jang, Y. T., Brännström, Å., Graham, C., Coelho, M.T.P., & Pontarp, M. Elevational Diversity Gradients: insights from eco-evolutionary models of habitat heterogeneity and primary productivity.

Author's contribution to the papers

Paper I

Jang, Y.T and Pontarp, M conceived the idea for the study. Jang, Y.T wrote the code for the simulation software under the guidance of Brännström, Å, analyzed the model with input from Pontarp, M and Brännström, Å, and wrote the first draft of the manuscript. All authors constructed the model and contributed to the analysis and interpretation of the material and the writing of the manuscript.

Paper II

All authors conceived the idea for the study. Jang, Y.T. developed the method under the guidance of Brännström, Å. Jang, Y.T wrote the code for the simulation software under the guidance of Brännström, Å, analyzed the model with input from Pontarp, M and Brännström, Å, and wrote the first draft of the manuscript. All authors constructed the model and contributed to the analysis and interpretation of the material and the writing of the manuscript.

Paper III

Jang, Y.T and Pontarp, M conceived the idea for the study. Jang, Y.T. developed the method under the guidance of Brännström, Å. Jang, Y.T wrote the code for the simulation software under the guidance of Brännström, Å, analyzed the model with input from Pontarp, M and Brännström, Å, and wrote the first draft of the manuscript. All authors constructed the model and contributed to the analysis and interpretation of the material and the writing of the manuscript.

Paper IV

Jang, Y.T and Pontarp, M conceived the idea for the study. Jang, Y.T. developed the conceptual framework with Graham, C and Coelho, M.T.P. Jang, Y.T. developed the method under the guidance of Brännström, Å. Jang, Y.T wrote the code for the simulation software under the guidance of Brännström, Å analyzed the model with input from Pontarp, M, Brännström, Å, Graham, C and Coelho, M.T.P. Jang, Y.T wrote the first draft of the manuscript. All authors contributed to the analysis and interpretation of the material and the writing of the manuscript.

Introduction

In contemporary understanding, it is widely recognized that the community patterns we observe in nature, such as species and functional trait diversity, phylogenetic relatedness, etc., arise from a broad set of ecological and evolutionary processes that interact across both spatial and temporal scales (Figure 1) (Urban et al., 2006; Urban et al., 2008; Vellend, 2010). Traditionally, competition has been viewed as the primary local process influencing species coexistence and determines the functional diversity of communities locally. However, the dynamics of competition is heavily influenced by other processes as well. For example, spatial processes such as dispersal can impact the community composition and affect competition. Furthermore, evolution in functional traits that are crucial for competition may occur in response to both environmental and ecological conditions, creating the so-called eco-evolutionary dynamics (Hendry, 2017). For example, competition between species may introduce selection which may prompt adaptive changes in traits, subsequently influencing community composition and competition. The intricacy of the interdependence between ecology and evolution becomes more pronounced when accounting for spatial and temporal interactions. Both local and regional diversity of metacommunities have been shown to be affected by dispersal, resource distribution, and environmental gradient through changes in scale-dependent competition (Matthiessen et al., 2010).
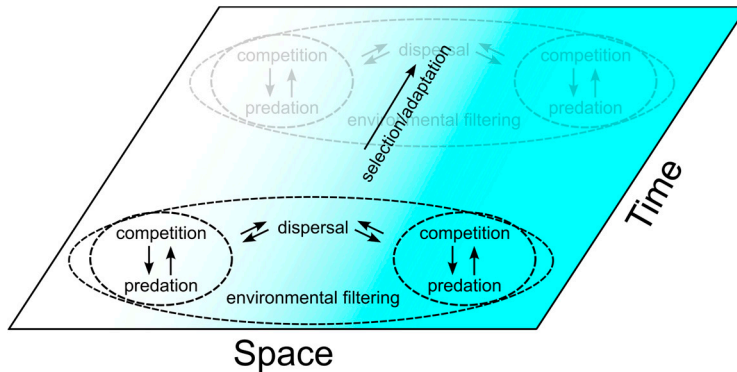
Figure1 Illustration of ecological and evolutionary processes that interact across both spatial and temporal scales
This figure illustrates processes that give rise to community diversity patterns, highlighting their interactions across various spatial and temporal scales. Local processes, such as competition and predation, operate on a local scale, while dispersal and environmental filtering act on larger spatial scales. Notably, dispersal can influence local processes like competition and predation. Moreover, the interplay of these processes creates selection pressures, contributing to evolutionary dynamics over extended temporal scales.

Moreover, the distribution of resources, whether homogeneous or heterogeneous across space, has distinct effects on competition and leads to different evolutionary outcomes (Wickman et al., 2019). Temporal dynamics such as variation in population abundance and trait distribution that arise across time (at a single location or across space), the emergence of new mutation or invasion into the population through time, and the fluctuations in the abiotic environment, have also been proven to have both ecological and evolutionary consequences (Hendry, 2017). Recognizing the interdependence between ecological and evolutionary processes across different spatial and temporal scales is thus a key step towards understanding community assembly and diversity patterns. In the following sections, I will introduce the current understanding of eco-evolutionary dynamics, highlight key processes, and discuss a new perspective on this topic.

What are eco-evolutionary dynamics?

In a recent book about Evo-evolutionary dynamics (Hendry, 2017), the author, Dr. Andrew P Hendry, humorously described the fields of ecology and evolutionary research *"have periodically dated but never married."* Ecology and evolution have often been studied separately, partly to avoid over-complexity and due to differing timescales —ecological processes are typically considered over short timescales, while evolution unfolds over longer timescales. An increasing number of studies have, however, shown that ecology and evolution can not be divorced (Yoshida et

al., 2003; Hart et al., 2019; Tan et al., 2021). Instead, recent studies reveal that ecology and evolution are intricately linked, and observations of a community at a specific time reflect a snapshot of parallel and interacting ecological and evolutionary processes (Harmon et al., 2019).

Hendry's (2017) description of eco-evolutionary dynamics offers a clear conceptual framework when exploring questions related to the interactions between ecological and evolutionary processes: Eco-evolutionary dynamics describe how ecological and evolutionary changes reciprocally influence each other within contemporary timescales. This reciprocity can originate from an ecological change (e.g., population density) that influences evolution (e.g., selection), which then leads back to an ecological response (e.g., population density). Conversely, it can also begin with an evolutionary change (e.g., mutation) that influences ecology (e.g., competition), which then results in an evolutionary response (e.g., selection).

While considerable evidence of eco-evolutionary dynamics exists in observed patterns (Bolnick et al., 2010; Yoder et al., 2010; Stroud et al., 2016; Harmon et al., 2019; Gillespie et al., 2020), much remains unknown about the underlying mechanisms of the reciprocal influence between ecology and evolution (Yoder et al., 2010; Stroud et al., 2016; Herrmann et al., 2020; Pontarp, 2021). This knowledge gap is partly attributed to the challenge of studying the joint effect of ecological and evolutionary processes under the nested nature of community patterns (Cavender-Bares et al., 2009; Segar et al., 2020). While achieving a "marriage" between ecology and evolution in field studies is challenging, the theoretical approach with community models provides an opportunity to explore the intricate relationship between between ecology and evolution.

Study eco-evolutionary dynamics with adaptive radiation

Adaptive radiation, defined as the "evolutionary divergence of a single phylogenetic lineage into a variety of different adaptive forms" (Futuyma, 1998), has been studied as an example of adaptive diversification influenced by eco-evolutionary dynamics (Figure 2) (Simpson, 1953; Losos, 2010; Yoder et al., 2010; Stroud et al., 2016; Pontarp, 2021). Adaptive radiation has been studied extensively in theoretical models (Dieckmann et al., 1999; Bolnick, 2006; Gavrilets, 2006; Dieckmann et al., 2007; Brännström et al., 2011) with links to empirical studies such as that of the West Indian Anolis lizards (Irschick et al., 1997; Stroud et al., 2020), Cichlid fish (Genner et al., 2005; Genner et al., 2007), the Hawaiian silversword alliance (Baldwin et al., 1998), and the Galápagos finches (Grant et al., 2008).
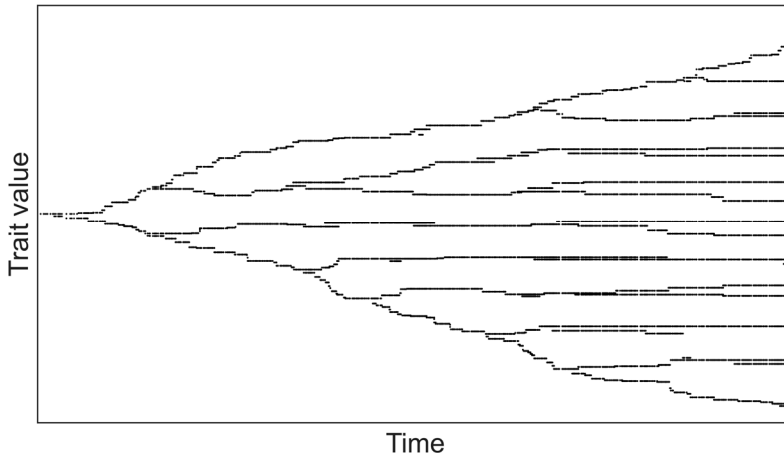
Figure 2 Illustration of an adaptive radiation based on diversification in trait
This figure depicts a simulation output of adaptive radiation. Each lineage is characterized by a functional trait value (vertical axis). Across time (horizontal axis), changes in trait values may occur due to evolution. Under specific conditions, diversification events lead to the emergence of coexisting lineages exhibiting distinct trait values.

Eco-evolutionary dynamics appears to be a primary driver of adaptive radiation, often tied to the prerequisite of ecological opportunity (Simpson, 1953; Schluter, 2000; Losos, 2010; Stroud et al., 2016). Ecological opportunity describes the availability of unexploited resources driven by the removal of biotic constraints or the emergence of a new resource which changes the composition of the niche space (Simpson 1953). For example, colonization of a previously isolated island without competitors provides opportunities to fill up an unoccupied niche (Seehausen, 2006; Grant et al., 2008; Losos, 2009). While ecological opportunity is pivotal in facilitating phenotypic diversification by providing available niche space, other driving forces, including ecological interactions, adaptation to the abiotic environment, and utilization of biotic resources, are essential for divergent natural selection. The interplay between these driving forces and the resulting emergence of adaptive radiation serves as an ideal context for studying eco-evolutionary dynamics and its correlation with community patterns. In the following sections, I will briefly introduce several processes explored in this thesis from the perspective of eco-evolutionary dynamics and its relevance to adaptive radiation.

(A)

(B)
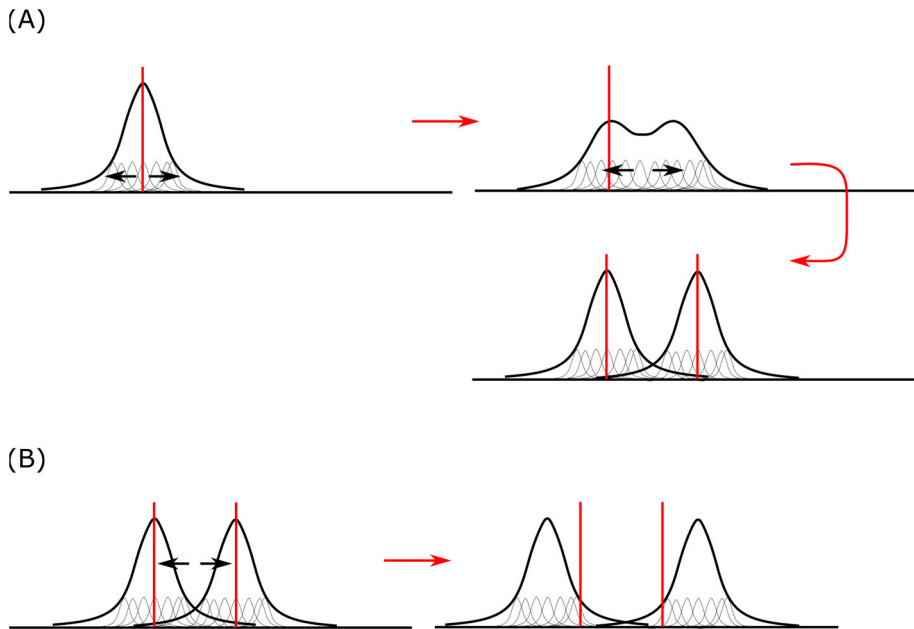
Figure 3 Illustration of intraspecific and interspecific competition
This figure illustrates (A).Intraspecific and (B) interspecific competition. The thick black line represents the niche/trait distribution of a species within a specific niche/trait space. The fine black lines indicate individual niche/trait distribution, with the red line marking the average niche/trait position of the species. In panel A, the presence of ecological opportunity (unoccupied niche space on the right) allows the species to expand in the niche distribution and diversify into two distinct species. Repeating this cycle may lead to adaptive radiation. In panel B, two species compete due to niche overlap, and the selection pressures may lead to evolutionary divergence between species in trait/niche, leading to an increase in the distance between the average niche/trait positions.

Ecological and evolutionary processes of interest

According to Vellend (2010), there are four high-level processes involved in patterns of community ecology: selection, drift, dispersal, and speciation. While selection and dispersal are ecological, drift and speciation are evolutionary. In this thesis, I focus on selection arising from competition, and predation as ecological processes, dispersal and environmental gradient as spatial processes, and diversification as a loose form of ecological speciation.

Competition

Competition is a major driver for diversification in adaptive radiation. From the theoretical perspective, competition is important in the ecological dynamics considering coexistence, and in the evolutionary time frame, competition serves as

a driver of selection through the negative frequency dependency. In our models, as an example, intraspecific competition appears when the population abundance increases and approaches carrying capacity. With the presence of ecological opportunity, competition would favor divergent selection for niche partitioning (Macarthur et al., 1972) (Figure 3A). Interspecific competition, on the other hand, describes the decrease of carrying capacity due to overlapping niches between two species (Figure 3B). Competition may then impose selection on the two species and lead to partitioning of niches. Details about how competition is modeled can be found in the method section. In summary, competition is indeed a dominant driver of adaptive radiation, but other processes such as predation also play an equally important role.

Predation

Predation is ubiquitous and acts as a major driver of selection (Langerhans et al., 2004; Losos et al., 2006; Lapiedra et al., 2018; Mitchell et al., 2020). Numerous studies have demonstrated that predation can induce both directional selection and disruptive selection on prey (Meyer et al., 2007; Marchinko, 2009; Walsh et al., 2011; Walsh et al., 2012). However, its role in the context of adaptive radiation and the resulting diversity pattern within a community remains largely unexplored, particularly in terms of its interplay with competition. Some studies show that adaptive radiation is affected by predation. Predation is suggested to have both direct and indirect effects on prey diversification through frequency-dependent competition between prey (Rainey et al., 1998; Vamosi, 2003; Vamosi, 2005; Meyer et al., 2007; Marchinko, 2009; Walsh et al., 2012). In this thesis, paper two and three focus on the influence of predation on adaptive radiations and its consequences on community diversity patterns. Such an understanding is a crucial step in advancing the interpretation of diversity patterns within the framework of adaptive radiation.

Dispersal

Existing theories suggest that dispersal plays a major role in spatial diversity patterns (Webb et al., 2002; Graham et al., 2008). Dispersal as a spatial process may influence adaptive radiation due to its effect on eco-evolutionary dynamics (Gillespie et al., 2020). For example, dispersal ability may affect the direction of selection. The fitness of organisms with low mobility or encountering geographic barriers may be strongly influenced by the local environment, promoting ecological specialization (Swenson, Enquist, et al., 2012; Weinstein et al., 2014; Mammola et al., 2020). However, how dispersal influences eco-evolutionary dynamics and thus the spatial phylogenetic structure remains largely unknown. In summary, understanding the mechanism of dispersal, its effect on adaptive radiations, and the subsequent community diversity patterns may advance our ability to infer processes from observed community diversity patterns.

Environmental gradients and environmental filtering

Environmental filtering describes when the abiotic environment provides selection pressure on a specific phenotypic trait of organisms. It is a process with a very intuitive effect when viewed alone, but it becomes interesting to study when space and time are taken into consideration. If a phenotypic trait of the organisms correlates with their phylogenetic relatedness, environmental filtering could lead to phenotypic and phylogenetic patterns that are easily recognized. (Webb et al., 2002; Cavender-Bares et al., 2004; Cavender-Bares et al., 2009). For example, Webb et al. (2002) hypothesized that if a trait is phylogenetically conserved (i.e., species are more similar when they are more related) and if the community is phylogenetically clustered (i.e., closely related species co-occur more than randomly distributed), one can suggest a strong environmental filtering that leads to the coexistence of species with similar traits. Despite the influence on ecological patterns, the environmental gradient can also lead to evolutionary changes such as diversification (Doebeli et al., 2003). I am interested in how environmental filtering may interact with other processes, such as dispersal and competition along environmental gradients, which has seldom been discussed. Understanding the mechanisms of environmental gradients and environmental filtering would help us understand spatial diversity patterns such as the elevational diversity gradients and latitudinal diversity gradients.

Selection: adaptation and diversification

Selection comes from the difference in fitness between individuals of different species (Vellend, 2010) and is the driver of evolution. In this thesis, I focus on trait-mediated fitness differences that arise through the interactions between organisms' traits and the (biotic and abiotic) environment around them. With the premise that traits are heritable, adaptation describes an evolutionary optimization process via which the goal is to maximize fitness. The direction and the endpoint of such an optimization process are dictated by the abiotic environment (e.g., an environmental gradient) and/or the biotic environment (e.g., competition and predation).

Diversification describes a specific case where the selection converges towards a point in the trait space but then diverges in two directions. Favorable conditions for diversification can appear due to the interactions of the optimization process and competition (Doebeli et al., 2000). For example, when adaptation favors evolution towards a specific resource, the competition for that specific resource increases. Such changes in environment consequently shift the location for realizing maximal fitness in the trait space. If maximal fitness can be acquired in two opposite directions on the trait space, diversification could happen (Figure 6). Under the scope of this thesis, we examine the interactions of selection and processes mentioned above within a single trait space.

Community models for studying eco-evolutionary dynamics

The intricate relationship between ecology and evolution in influencing community patterns makes it challenging to design experiments to explain patterns observed in field data. Community models that can integrate both ecology and evolution serve as useful tools in navigating this complexity. However, processes and patterns may be intertwined on various spatial and temporal scales and need to be modeled differently depending on the fundamental units of the model (e.g., individuals, population, and species level) (Brännström et al., 2012; Pontarp et al., 2017; Pontarp et al., 2019; Hagen et al., 2021). Identifying the specific spatial and temporal scale on which eco-evolutionary dynamics operate is essential for setting assumptions for the mode. Existing models exploring community patterns can be roughly categorized into three types depending on the scale and assumptions concerning the processes and patterns (Figure 4). In the following sections, I introduce the basic assumptions of each type of model and further discuss the most relevant processes and patterns to study considering the scale of each model.
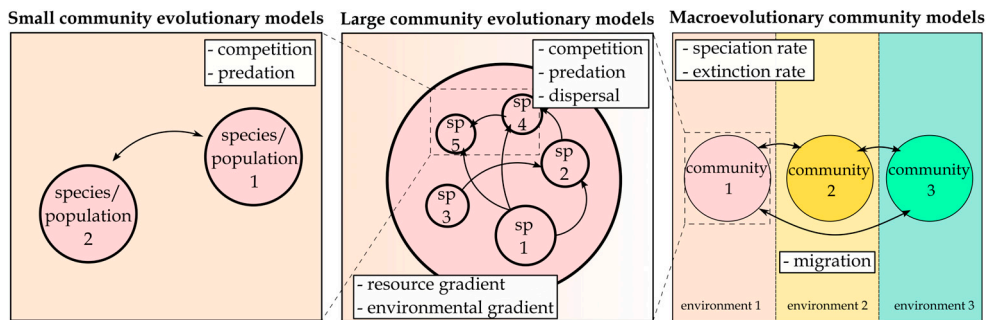
Figure 4 Illustration of existing community evolutionary models based on different spatial and temporal scales

Existing models examining community patterns can be broadly categorized into three types based on scale and assumptions regarding processes and patterns. **Macroevolutionary community models** concentrate on large spatial and temporal scales. **Small community evolutionary models** typically incorporate one or two well-known ecological and evolutionary processes, such as competition or predation, and model individuals, populations, or up to species levels. **Large community evolutionary models** emphasize eco-evolutionary dynamics across communities with multiple populations or species, spanning from local to regional spatial scales.

Macroevolutionary community models

Theories on macroevolution focus on evolution on a large spatial scale across deep time. Macroevolutionary community models (MCMs) thus focus on large and often diverse communities. MCMs usually ignore individual dissimilarity and focus on processes and patterns beyond the species level. Community composition is

simulated by several pre-defined, static rates of high-level processes such as speciation, extinction, and immigration rates (Figure 4). Nevertheless, the influence of eco-evolutionary dynamics can be modeled by functions of ecological or evolutionary factors. For example, diversity may come from a pre-defined speciation rate with trait evolution based on Brownian motion, whereas environmental conditions, dispersal, and competition for resources are introduced as functions that affect the final assembly of communities (Münkemüller et al., 2015). Diversity may also change through immigration and local stochastic speciation or extinction, while immigration success can be modeled as a function of niche in a pre-defined environmental niche structure (Munoz et al., 2018). Lower-level processes such as dispersal distance and maximal competition for coexistence can also be simply defined as basic parameters. When the parameters are chosen wisely and well connected, such a model can produce patterns with striking similarity to the empirical observations (Rangel et al., 2018). Furthermore, with advancing computational power, recently developed eco-evolutionary models (See 'gen3sis', Hagen, et al. (2021)) can implement multiple spatially explicit processes throughout local to global spatial scales, generating various empirical biodiversity patterns, including phylogenetic patterns. Such advancement improves the traditional macroevolutionary model in connecting local-scale mechanisms with macroevolutionary patterns on a large spatial scale.

In summary, although MCMs do not have the resolution for a detailed mechanism of specific processes, they can provide insight into the influence of high-level processes such as speciation, extinction, and immigration on patterns with large spatial and temporal scales. The flexibility in parameterization according to empirical data makes MCMs a good tool for cross-validating suitable assumptions and the most relevant processes under a specific pattern.

Small community evolutionary models

Small community evolutionary models (SCEMs) usually include one or two ecological and evolutionary processes that are empirically well-known, such as competition or predation. The ecological role of the evolving organisms is usually pre-defined and not subjected to evolution. For example, competitive interactions will not become predation or mutualism. Small community size and pre-defined interactions enable the focus on the general underpinnings of a target pattern, for example, the relationship between competition and adaptive diversification (Doebeli, 1996b; Goldberg et al., 2012). SCEMs are therefore suitable for studying how a process affects divergence in traits of a local population (Figure 4). SCEMs on co-evolutionary dynamics of competitors (Meszéna et al., 1997; Dieckmann et al., 1999; Doebeli et al., 2000), and mutualism (Doebeli et al., 2000) allow robust investigations on the evolutionary consequences of ecological interactions. SCEMs thus allow for an improved understanding of general principles in eco-evolutionary

dynamics. Although the emergent patterns may not be directly comparable to empirical data, the generality of such a model provides insights into the mechanistic connection between processes and patterns, which helps to verify hypotheses raised from empirical observations.

Large community evolutionary models

All the models designed in this thesis belong to the third type of model that falls between macroevolutionary community models and small community evolution models. Here, I refer to these models as large community evolutionary models (LCEMs). Unlike small community evolutionary models (SCEMs), LCEMs focus on the eco-evolutionary dynamics in communities with multiple populations or species, spanning from local to regional spatial scale (Figure 4). Similar to SCEMs, LCEMs focus on the temporal scale that includes both ecological and evolutionary dynamics, forming a natural bridge between small community evolution models and the macroevolutionary models mentioned earlier. LCEMs leverage the mechanistic insights into ecological and evolutionary processes gained from SCEMs. LCEMs are thus well-suited for identifying important processes and traits of eco-evolutionary dynamics and linking them to the emergence and maintenance of community patterns. The scope of community that LCEMs cover includes the formation of, for example, food webs (Brännström et al., 2011; Wickman et al., 2019; Wickman et al., 2020) or adaptive radiations (Pontarp et al., 2012; Pontarp et al., 2017; Pontarp et al., 2018; Jang et al., 2022). LCEMs may encompass multiple processes (e.g., dispersal, biotic resource utilization, abiotic tolerance). For instance, Paper IV of this thesis examines the impact of habitat heterogeneity and primary productivity on elevational diversity gradients, revealing how two ecological processes interact to produce diverse evolutionary outcomes. Simulated patterns in this paper resemble observed empirical patterns (Rahbek, 2005; McCain, 2007; McCain et al., 2010; Szewczyk et al., 2016; Dillon et al., 2021), suggesting that such generalized models unveil essential mechanisms behind real-world patterns, offering a novel understanding of natural systems. In summary, due to the integration of multiple processes or trophic interactions, it is no longer possible to develop analytical solutions for LCEMs. Nevertheless, the strength of LCEMs lies in simultaneously incorporating ecological interactions and evolutionary dynamics and offering valuable mechanistic insights into the link between eco-evolutionary dynamics and large-scale diversity patterns.

Studying eco-evolutionary dynamics with large community evolutionary models

A process-based and trait-based approach

In this thesis, I study eco-evolutionary dynamics with a focus on the interactions between processes of interest and their relationship with community patterns. Moreover, I formulate the eco-evolutionary dynamics in the context of biological traits. The process- and trait-based approach for studying eco-evolutionary dynamics uses ecological niches as the common ground. According to the fundamental ecological niche theory, the niche of a species is "the environmental conditions that allow a species to satisfy its minimum requirements so that the birth rate of a local population is equal to or greater than its death rate along with the set of per capita impacts of that species on these environmental conditions." (Chase et al., 2003) Studying eco-evolutionary dynamics with intermediate variables such as traits within a unifying niche framework allows us to draw links between processes and patterns. More details on incorporating eco-evolutionary dynamics, processes, and traits into the community model can be found in the method section.

Recognizing eco-evolutionary dynamics in patterns

We have been emphasizing the complexity of community patterns due to a limited understanding of the underpinning mechanisms and the intertwined relationship of ecological and evolutionary processes. Despite such complexity, progress has been made throughout the past years, and various syntheses on the interplay between processes and patterns offer valuable hypotheses and research directions (Webb et al., 2002; Graham et al., 2008; Vellend, 2010; Gillespie et al., 2020; Stroud et al., 2020). Large community evolutionary models integrated with processes as functions of traits present a significant opportunity to scrutinize existing hypotheses and explore similar patterns that may emerge through distinct mechanisms.

In this thesis, I study the relationship between processes mentioned above with several community diversity patterns, including species diversity (**Paper II**, **Paper IV**), phylogenetic beta-diversity (PBD) (**Paper I**), mean phylogenetic distance (MPD), mean nearest phylogenetic distance (MNPD), mean trait distance (MTD), and mean nearest trait distance (MNTD). Below we provide the independent aim for each Paper on the journey of unravelling the eco-evolutionary dynamics shaping community patterns, with the overarching goal to improve understanding of biodiversity in general.

Aim of the thesis

The overarching aim of this thesis is to improve the understanding of mechanisms behind observed community diversity patterns in the context of eco-evolutionary dynamics. I emphasize that mechanistic understanding requires consideration of both the spatial and temporal scale of a system. The papers of this thesis cover from local to regional spatial scales and incorporate both ecological and evolutionary timescales. Focusing on the important ecological and evolutionary processes mentioned above, the four papers of this thesis aim to answer four questions:

Q1. How do environmental gradients and dispersal affect phylogenetic diversity across space?

The emergence and sustenance of biodiversity are dependent on the intricate relationships between environmental conditions, adaptation to these conditions, and dispersal. Empiricists strive to quantitatively comprehend these interacting ecological, evolutionary, and spatial processes behind an observed pattern. We turn to the pattern of phylogenetic relatedness across space (i.e. phylogenetic beta diversity, PBD) which encapsulates signals from all these processes. **Paper I** aims to bridge the gap between environmental gradients, organismal dispersal, and phylogenetic beta diversity through a trait-based eco-evolutionary model. By unravelling the eco-evolutionary mechanisms linking environmental and dispersal effects to community phylogenetic patterns, we aim to enhance the interpretation of phylogenetic beta diversity.

Q2. How does predation affect prey adaptive radiation?

Adaptive radiations are commonly viewed as the outcome of natural selection due to recourse competition. An increasing number of studies show that trophic interaction may also affect adaptive radiations, but the mechanisms are unexplored. **Paper II** aims to investigate how predation impacts prey adaptive radiation. Specifically, I explore the influence of predator specialization and evolvability on predator-prey radiation dynamics. This paper highlights the need to consider trophic

interactions in our understanding of adaptive radiations and biodiversity dynamics in complex ecological communities, moving beyond a competition-focused perspective.

Q3. How does predation affect different community diversity patterns?

As a natural extension of question 2, which focuses on changes in adaptive radiations due to trophic interactions, we want to know how the changes in adaptive radiations from predation affect community diversity patterns. In **Paper III**, I examine the influence of predation on several community diversity patterns that are seldom linked with trophic interactions, including phylogenetic and trait diversity. This paper focuses on the importance of predation in shaping community diversity, offering a deepened understanding of trophic interactions and community diversity patterns.

Q4. How do resource distribution, resource heterogeneity, and competition affect the formation of an elevational diversity gradient?

Despite the long-standing interest, the drivers of biodiversity patterns across elevations remain elusive. Commonly known as Elevational Diversity Gradients (EDGs), four ubiquitous biodiversity patterns across elevations are observed across the globe, including the low-elevational plateau, the low-elevational plateau with a mid-elevational peak, mid-elevational peak, and monotonic decrease in diversity (Figure 5). The current paradigm attributes different EDGs to habitat heterogeneity and primary productivity. Habitat heterogeneity is suggested to foster species diversification, while productivity may support high population abundance and coexistence. These factors are often studied separately and not in the context of eco-evolutionary dynamics. Paper IV emphasizes the potential interplay between habitat heterogeneity and productivity across elevational gradients and aims to elucidate the mechanistic links between habitat heterogeneity, primary productivity, and EDGs in an eco-evolutionary context.
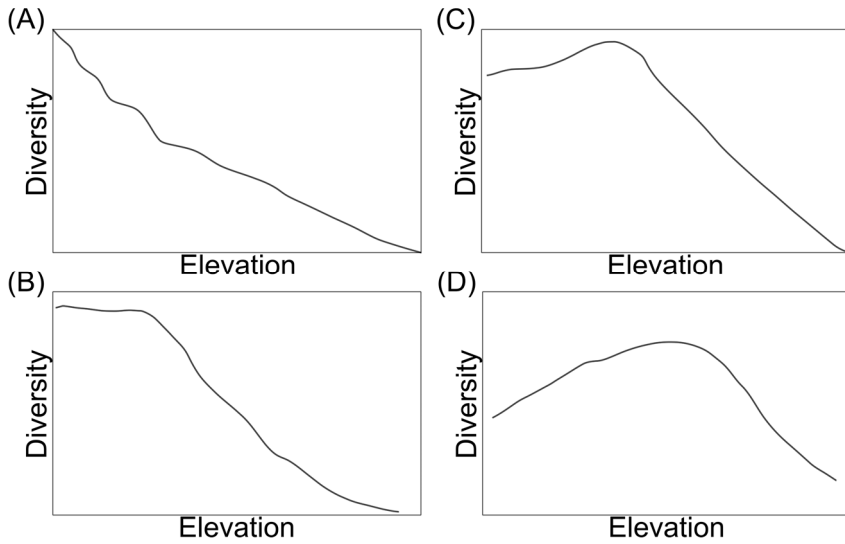
Figure 5 The four most ubiquitous elevational diversity patterns according to McCain (2019) and McCain (2010)

This figure illustrates the four most frequently observed elevational diversity gradients: (A) monotonic decrease in diversity (B) low-elevational plateau, (C) low-elevational plateau with a mid-elevational peak, (D) mid-elevational peak. Despite being ubiquitous, the mechanisms leading to these diverse patterns remain inconclusive, and there is currently no consensus on the underlying mechanisms shaping these distinct elevational diversity gradients.

Method

Modelling ecological interactions

In this thesis, I focus on several ecological processes, including environmental filtering through environmental gradient (**Paper I**), competition (**Paper II, III, IV**), and predation (**Paper II, III**). I model these processes on a one-dimensional niche space, mediated by a single functional trait. Such a functional trait could be interpreted as temperature tolerance, resource utilization, or body size. These processes are then incorporated into the population dynamics, and the responses in population dynamics in the ecological timescale further propagate into the evolutionary dynamics of the system under an evolutionary timescale. Throughout the thesis, I model population dynamics of the population as generalized Lotka–Volterra equations, i.e., a set of ordinary differential equations:

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i f_i(\boldsymbol{N}),\qquad\qquad\qquad(1)$$

Where i ranges from 1 to n, and $\boldsymbol{N}$ is a vector of n populations. The function $f_i(N)$ can represent any function that describes the interactions between these n populations through the processes of interest. In the following sections, I briefly introduce the general concept of integrating each process into the model. Specific implementation details can be found in each paper.

Environmental filtering

To model environmental filtering, which depends on abiotic factors such as temperature, I assume that the match between an organismal trait, s_i, and the abiotic environment of a habitat (u_{opt}) will dictate the carrying capacity, $K(s_i)$, of such an organism in the habitat. A complete match between s_i and u_{opt} maximizes the carrying capacity, while the carrying capacity decreases according to a Gaussian function:

$$K(s_i) = K_{\max}\, e^{-\frac{\left(u_{\mathrm{opt}} - s_i\right)^2}{2\sigma_u^2}}.\qquad\qquad\qquad(2)$$

The parameter σ_u can thus be described as the abiotic environmental niche width or the environmental tolerance range of the species (Doebeli et al., 2000; Pontarp et al., 2017). The incorporation of $K(s_i)$ into the population dynamics is specific to the model. Examples can be found in **Paper I** and **Paper IV**.

Competition

The strength of competition between populations i and j is modeled as follows:

$$\alpha_{ij} = \alpha(s_i, s_j) = \alpha_{\max} e^{-\frac{1}{2}\left(\frac{s_i - s_j}{\sigma_\alpha}\right)^2}. \tag{3}$$

In this context, s_i is interpreted as an organismal trait closely related to biotic resources. The competition coefficient, α_{ij}, reaches its maximum value, $\alpha_{\max}$, when u_i equals u_j (i.e., when populations i and j are identical). In contrast, the competition coefficient declines as u_i deviates from u_j at a rate dependent on σ_α, which is defined as the niche width representing the intensity of competition between similar species (Slatkin, 1980; Doebeli, 1996a). Without loss of generality, we assume that $\alpha_{\max}$ equals 1. The incorporation of trait-specific competition into the population dynamics can be found in **Paper II**, **Paper III**, and **Paper IV**.

Predation

To model predator-prey dynamics, I incorporate the predator population into the generalized Lotka–Volterra equations, which are represented as follows:

$$\frac{dN_i}{dt} = N_i f_i(\mathbf{N}) - g_i(\mathbf{P}) N_i P_k, \tag{4}$$

$$\frac{dP_k}{dt} = h_k(\mathbf{N}) N_i P_k - q_k(\mathbf{P}) P_k, \tag{5}$$

Here, $\mathbf{P}$ represents a vector of predator populations. The function $g_i(\mathbf{P})$ describes the influence of predation on prey growth rates, while $h_k(\mathbf{N})$ describes the influence of prey on the growth rates of predators, and $q_k(\mathbf{P})$ describes the per capita death rate of predators. The intensity of predation, also known as the attack rate, is modeled as a function of both predator and prey trait values:

$$a_{ik}(s_i, z_k) = b_{\max} e^{-\frac{1}{2}\left(\frac{s_i - z_k}{\sigma_a}\right)^2}. \tag{6}$$

In equation (6), the predator's functional trait, z_k, and the predator niche width, σ_a, dictate the predator's ability to attack prey with trait s_i. The maximal attack rate

from a predator ($b_{\max}$) occurs when predator k is perfectly adapted to acquire prey i (i.e., when $s_i = z_k$), and it decreases as z_k deviates from s_i following a Gaussian function with a variance of σ_a^2. Here, σ_a describes the niche width of the predator, with a large σ_a representing a generalist predator and a small σ_a representing a specialist predator. The incorporation of trait-specific predation into the population dynamics can be found in **Paper II** and **Paper III**.

Eco-evolutionary modelling

Adaptive dynamic framework

This thesis employs an evolutionary modeling framework based on evolutionary game theory. This theory centers around the success of a strategy, which is determined by the frequency with which the strategy is played in an 'evolutionary game.' In our case, the trait of interest is directly equivalent to the strategy in game theory, and success is measured by fitness i.e., the reproductive output of an individual with a particular trait. A notable innovation in evolutionary game theory, as compared to classical game theory, is the consideration of a strategy being played against a population of opponents employing different strategies. This approach allows us to understand how strategies change in frequency over time, akin to multiple games being played. These changes in strategy frequencies occur because success is influenced by environmental factors, which are simultaneously linked to the frequencies of all strategies in play. The framework of evolutionary game theory facilitates the connection between population dynamics in the ecological world and the process of evolution, offering insight into the evolutionary outcomes of complex ecological systems without delving into genetic mechanisms (McGill et al., 2007). In the following paragraphs, I adopt the conventional terminology of evolutionary game theory and briefly introduces the fundamental link between evolutionary games and ecology. A more in-depth and approachable introduction can be found in McGill (2007).

In an evolutionary game, the fitness of a strategy in a given environment is defined as the per capita growth rate (Crow et al., 2009):

$$W(u, U, N) = \frac{1}{N}\left(\frac{\mathrm{d}N}{\mathrm{d}t}\right). \tag{7}$$

W, in this context, is a function that depends on variables u, U, and N. The variable u represents the strategy employed by the player of interest, often referred to as the mutant. As mentioned earlier, a strategy is essentially an inheritable trait of interest. U represents the strategy used by the opponent, which typically called as the resident population. N denotes the population size of this population. Together, U and N are

considered as the resident environment. The outcomes of evolutionary games have a direct impact on the fate of the mutant, the strategy adopted by the resident population, and the population size of the resident population. Therefore, assessing the behaviour of $W(u, U, N)$ provides valuable insights into the evolution of the strategy (trait) of interest. Extending from Fisher's (1930) Fundamental Theorem of Natural Selection, the evolutionary game theory models the change in the strategy of the resident population U as proportional to the so-called 'adaptive landscape' (Roughgarden, 1983), represented as $\frac{dW}{du}$. This leads to the equation:

$$\frac{dU}{dt} = k \frac{d}{du} W(u, U, N), \tag{8}$$

where k is a constant parameter. This equation is later derived the structurally similar canonical equation of adaptive dynamics from the assumption of rare and small mutations in trait value (Dieckmann et al., 1996), which we will explain in the next section covering the incorporation of evolution.

The adaptive dynamics framework is founded on the stochastic birth and death process of individuals. It provides a deterministic approximation of the stochastic process and models trait evolution in response to changes in the adaptive landscape. This modeling relies on certain assumptions: first, the resident population is assumed to be at equilibrium ($\frac{1}{N} \frac{dN}{dt} \big|_{N=N*} = 0$) when a mutant emerges. Second, the fate of the mutant can be inferred from its initial growth rate when it is rare in comparison to the resident strategy. In this case, given the resident strategy U^* at equilibrium, $W(u, U^*, N^*)$ is known as the 'Invasion fitness' of the rare mutant. In summary, adaptive dynamics serves as a bridge between ecological and evolutionary dynamics, assuming a separation between the slower evolutionary timescale and the faster ecological timescale. In the next section, we will discuss the method I used to incorporate the adaptive dynamics framework into the modeling of evolution in different Papers.

Implementing evolution

Deterministic model
The invasion fitness of a mutant is defined as the initial per capita growth rate of a rare mutant in the resident environment. Following the notation from the previous section, a mutant with a trait u in a resident environment with trait U^* and population size N^* is denoted as:

$$W(u, U^*, N^*). \tag{9}$$

If we consider U^* and N^* as constants, W as a function of u represents the fitness landscape of the initially rare mutant with trait u. Importantly, with each successful invasion (i.e., when a mutant has a positive invasion fitness and can grow in abundance to become the resident environment), U^* and N^* change subsequently, thus leading to changes in $W(u)$. In the context of a monomorphic population, to understand the direction and rate of evolution, we need to determine the direction of selection. This is assessed as the slope of the fitness landscape at each resident environment:

$$\frac{\mathrm{d}W(u)}{\mathrm{d}u}\Big|_{u=U^*}. \tag{10}$$

If the slope of the function $W(u)$ at a resident trait U^* is positive, it implies that mutants with traits slightly higher than U^* may invade, and vice versa. This assumes that mutations are small, meaning u is approximately equal to U^*, and sign of Eq.10 determines the direction of selection. The actual rate of evolution is modeled through the canonical equation of adaptive dynamics (Dieckmann & Law 1996), which is derived as the mean evolutionary path of the stochastic evolutionary dynamics, taking into account intrinsic mutation probability (μ), resident population size (N), and variance of the size of mutations (σ_μ^2):

$$\frac{\mathrm{d}u}{\mathrm{d}t} = \frac{1}{2}\mu\sigma_\mu^2 N^* \frac{\mathrm{d}W(u)}{\mathrm{d}u}\Big|_{u=U^*}. \tag{11}$$

As evolution progresses, we may encounter different outcomes in the evolutionary games where $\frac{\mathrm{d}W(u)}{\mathrm{d}u}\Big|_{u=U^*} = 0$. At these points, the selection gradient of the rare mutant u ceases, potentially indicating the end of trait evolution. These different outcomes are sometimes referred to as 'evolutionarily singular strategies.' For a more detailed introduction, see Geritz et al. (1998). Here, I will primarily discuss the cases where evolution may either come to a halt or polymorphisms can arise, which are defined as Evolutionarily Stable Strategies (ESS) or branching points.

ESS is defined when the mutant trait has reached a fitness maximum, and no other nearby strategy can invade (Figure 6 A-C). Another prerequisite is that the strategy should be convergent and stable, meaning the direction of the selection gradient around the trait should always point toward the ESS trait. On the other hand, a branching point describes a scenario where the strategy is both convergent and stable and has a fitness minimum. In this case, mutants with slightly lower or higher trait values than the resident strategy can both invade and coexist (Figure 6 D-F).
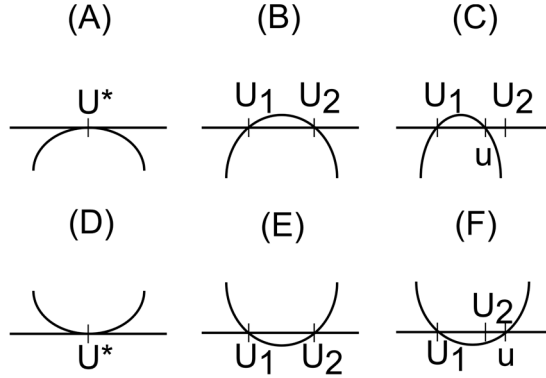
Figure 6 Illustration of the fitness landscape of mutant trait considering Evolutionary Stable Strategies (ESSs)

This figure is adapted from Geritz (1998). It illustrates scenarios related to evolutionarily stable strategies (ESS) where U* is an ESS (A, B, C), and when U* is not an ESS (D, E, F). Consider a scenario with a dimorphic resident population, represented by traits U1 and U2, If a mutant trait falls between U1 and U2, the mutant can invade and move closer to U*. However, in cases where U* is not an ESS (D, E, F), mutations between U1 and U2 can not survive and invade the community. Instead, the mutant can only successfully invade if its trait is either less than U1 or greater than U2.

There are various ways to define a deterministic evolutionary branching criterion for use alongside the canonical equation. In my work in **Paper I**, I assume that evolutionary branching occurs if there is a mutant trait value within a maximum distance, which (1) allows the mutant to invade and coexist with the resident and (2) results in divergent selection, with the nearby old and new resident strains evolving away from each other. Details of how this situation arises are provided in Figure from **Paper I**: a resident strain has a trait value and is evolving toward a lower trait value, but within a distance σ_μ, a mutant strain can invade, leading to the formation of protected dimorphs and evolution in the opposite direction toward higher trait values.

I begin by examining the potential for disruptive selection near the resident strain by assessing whether the curvature of the invasion fitness is positive. To do this, I consider the invasion fitness of a rare mutant trait u in the resident environment U^*, denoted as $W(u)$. Specifically, I check whether the second derivative of the invasion fitness at the resident trait U^* is positive, i.e., whether $\frac{d^2W(u)}{du}\big|_{u=U^*} > 0$. Next, I evaluate whether a mutation of maximal size σ_μ is sufficient to cross the 'fitness valley' and ensure positive invasion fitness on the other side, as depicted in the Figure. For mathematical simplicity, I approximate the invasion fitness to the second order as follows:

$$W(u) \approx W'(U^*)(u - U^*) + \frac{1}{2}W''(U^*)(u - U^*)^2. \qquad (12)$$

This approximation is valid as long as σ_μ is small, and it's worth noting that a similar assumption of a small mutational step size also forms the basis for the derivation of the canonical equation (Dieckmann and Law 1996). The resulting quadratic polynomial has two roots: $u = U^*$ and $u = U^* + \frac{2W'(U^*)}{W''(U^*)}$ (Figure 7).

$\left| \frac{2W'(U^*)}{W''(U^*)} \right|$ represents the minimum distance between the resident trait and a mutant trait that permits the establishment of a protected dimorphism followed by divergent selection.

Consequently, I assume that evolutionary branching occurs when two conditions are met: (1) the invasion fitness exhibits positive curvature at the resident trait value, i.e., $\frac{d^2 W(u)}{du} \Big|_{u=U^*} > 0$, and (2) the mutational step required for a divergently selected protected dimorphism to arise is sufficiently small, i.e., $\left| \frac{2W'(U^*)}{W''(U^*)} \right| \leq \sigma_\mu$.
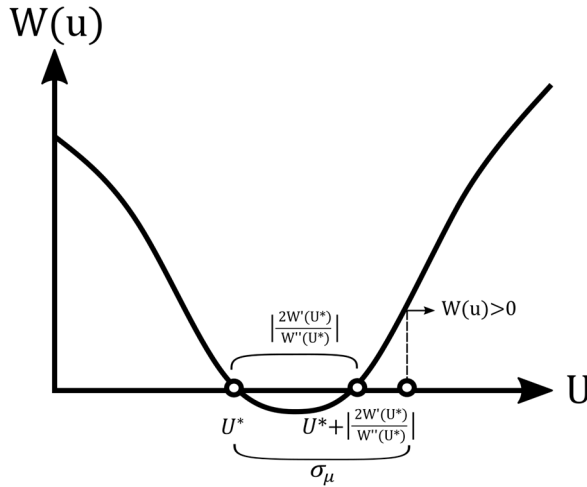
Figure 7 illustration of condition of evolutionary branching
Function $W(u)$ approximates the invasion fitness of u_m when $u_m \approx U^*$. Protected dimorphism may occur for mutant trait $u_m = U^* + \left| \frac{2W'(U^*)}{W''(U^*)} \right|$, but the mutational step should be smaller than σ_μ.

Therefore, $\left| \frac{2W'(U^*)}{W''(U^*)} \right| \leq \sigma_\mu$ for evolutionary branching to occur.

Oligomorphic stochastic model

In Papers II, III, and IV, I employ an evolutionary model based on the concept of the oligomorphic stochastic model presented by Ito and Dieckmann in 2007, which has been further developed by Brännström et al. (2011). I still maintain the assumption that mutations are rare, and the ecological and evolutionary timescales remain separated. Under these conditions, we can analyze the fitness of a mutant.

The key distinction between the stochastic approach and the deterministic approach discussed in the previous section is that the fate of a mutant, although influenced by its fitness, is now also subject to stochasticity.

Drawing on the theory of birth-death processes (Goel et al., 1974; Stirzaker et al., 1992; Bailey et al., 2004; Csernica, 2015), I assume that the probability of a mutant with trait s_i' arising from parents with a trait value s_i in a resident environment with n populations represented as $\boldsymbol{s} = (s_1, \ldots, s_n)$ is as follows:

$$p_m(s_i', \boldsymbol{s}) = \left(\frac{b_m(s_i', \boldsymbol{s}) - d_m(s_i', \boldsymbol{s})}{b_m(s_i', \boldsymbol{s})} \right)_+, \tag{13}$$

where $b_m(s_i', \boldsymbol{s})$ is the birth rate of the mutant and is defined as the intrinsic growth rate of population dynamics, and $d_m(s_i', \boldsymbol{s})$ is the death rate of the mutant, typically equivalent to the negative influence from competition or predation. In other words, $b_m(s_i', \boldsymbol{s}) - d_m(s_i', \boldsymbol{s})$ is, in our case, the invasion fitness of the mutant, denoted as $\lambda(s_i', \boldsymbol{s})$. Intuitively, if b_m is less than d_m, then p_m equals zero, indicating that it is impossible for the mutant to successfully invade the resident environment.

The probability of fixation depends not only on p_m but also on the likelihood of a mutant with trait value s_i' arising from parents with trait value s_i. This follows a probability density function of a standard normal distribution, denoted as $\phi(s_i - s_i')$. By combining the average rate of mutations from population i, the fitness of the mutant randomly drawn from the trait distribution, and the probability of mutant invasion, we can calculate the rate at which a specific mutant emerges and successfully fixates in the resident environment. Integrating the probability density function of mutant emergence and mutant invasion provides us with the probability of fixation, $p_i(s_i)$, which represents the likelihood that a mutation arises from population i and becomes fixated:

$$p_i(s_i) = \int \phi(s_i - s_i') \, p_f(s_i', \boldsymbol{s}) \, ds_i'. \tag{14}$$

Taking demographic into consideration, the rate at which a mutant successfully invades population i, denoted as S_i, is then calculated as:

$$S_i = \{ \text{rate of mutant birth} \} \times \{ \text{probability of fixation} \}. \tag{15}$$

The rate of mutant birth is calculated as τN_i^*, where τ represents the per capita probability of mutation upon reproduction, and N_i^* is the population size at equilibrium.

Upon reaching ecological equilibrium, we select the lineage that will undergo mutation with a probability S_i/S, where S is the sum of S_i for i ranging from 1 to n

$(S = \sum_{i=1}^{n} S_i)$. When determining which resident will undergo mutation, we draw a mutant trait from the probability density function:

$$p_m(s_i') = \frac{C}{\sigma_\mu} \phi\left(\frac{s_i'-s_i}{\sigma_\mu}\right) p_f(s_i', \boldsymbol{s}), \qquad (16)$$

where C is the normalizing constant to ensure the integral of $p_m(s_i')$ equals one.

To decide whether a mutant trait will invade, I use the rejection method similar to (Press et al., 2012) (See also Brännström (2011)). I draw two variables, x and y, from a uniformly distributed bivariate random deviate, with $|x - s_i| < 6\sigma_\mu$, where σ_μ denotes the variance in the trait mutation, and $y < P_m$ where $P_m > p_m(s_i')$ for all s_i'. If $y < p_m(x)$, I take x as the mutant trait value; otherwise, I repeat the bivariate random draw. Simultaneously, I update the time that has passed since the last mutation to be $\Delta t = 1/S$.

To determine whether such mutant invasion is a trait evolution or coexistence (diversification), I assess the mutual invasivibility of s_i' and s_i by calculating the invasive fitness $\lambda(s_i', \boldsymbol{s_1})$ and $\lambda(s_i', \boldsymbol{s_2})$, where $\boldsymbol{s_1} = (s_1, \dots, s_i, \dots s_n)$ and $\boldsymbol{s_2} = (s_1, \dots, s_i', \dots s_n)$. If both $\lambda(s_i', \boldsymbol{s_1})$ and $\lambda(s_i', \boldsymbol{s_2})$ are positive, the mutant with trait s_i' and the original strain with trait s_i can coexist, and the mutant is defined as a branching event. If $\lambda(s_i', \boldsymbol{s_1}) > 0$ and $\lambda(s_i', \boldsymbol{s_2}) < 0$, the original population trait s_i will replace by s_i', defined as a trait evolution.

One of the advantages of the oligomorphic method is that I do not need to arbitrarily define the criteria for the branching point since diversification becomes an emergent property when mutants can coexist with the original parent population. A second advantage is that I can introduce an actual unit of time instead of an arbitrary 'simulation time step,' which is valuable for analyzing temporal patterns, such as phylogenetic patterns.

Analyses of community patterns

The theoretical approach in this thesis assumes one-to-one mapping between phenotype and species, i.e., using evolutionary branching as a proxy for speciation. Following the processes of adaptive radiation, phylogenetic and trait relationship between species is recorded as they differentiate through evolutionary time. I record each speciation event and construct a pairwise distance matrix between all existing species in the community at the end of each simulation.

A phylogenetic tree is constructed from each simulated adaptive radiation for each model realization using the "seqlinkage" function in MATLAB, with the UPGMA (unweighted pair group method with arithmetic mean) algorithm and the pairwise distance matrix as the input. UPGMA is a straightforward approach to constructing

a phylogenetic tree from a distance matrix. It assumes a consistent evolution rate (Weiß et al., 2011), aligning with models included in this thesis that employ a constant mutation rate for evolution.

Phylogenetic beta diversity (PBD)

The phylogenetic diversity (Faith, 1992) of a specific habitat k (PD_k) is calculated according to:

$$PD_k = \sum B_k .$$

(17)

B_k is the set of branches in the phylogenetic tree that corresponds to species present in habitat k. Knowing the PD of several habitats allows us to compute the PBD, which is a pairwise index. PBD measures the phylogenetic dissimilarity between two habitats, j and k, following (Leprieur et al., 2012):

$$PBD_{j,k} = \frac{2PD_{j,k} - PD_k - PD_j}{PD_k + PD_j} .$$

(18)

PD_k and PD_j consider species present in habitats j or k, whereas $PD_{j,k}$ is the phylogenetic diversity corresponding to all species present in either habitat j or k ($PD_{j,k} = \sum B_j \cup B_k$). Eq.18 thus presents the proportion of phylogenetic diversity that is unique to one habitat. If two habitats have no species in common, they share no evolutionary history, leading to a high PBD (PBD = 1). An increasing number of common species that are closely related will reduce the numerator of Eq. 18, hence reducing PBD between two habitats (PBD < 1).

Mean phylogenetic distance (MPD) and mean nearest phylogenetic distance (MNPD):

MPD (Clarke et al., 1998; Webb et al., 2002; Kembel et al., 2006; Webb et al., 2008; Cadotte et al., 2010) are patterns that address questions related to whether branching occurs deep or recently within a tree. They are calculated as follows:

$$MPD = \frac{\sum_i \sum_j d_{ij}}{S(S-1)}.$$

(19)

$$MNPD = \frac{\sum_i \min (d_{ij})_{j=1,...,n}}{S}.$$

(20)

S represents the total number of species present in the final community, where d_{ij} represents the distance between species i and species j to their last common ancestor.

Mean trait distance (MTD) and the mean nearest trait distance (MNTD):

Following a concept similar to phylogenetic distance (Kraft et al., 2007), the community structure of traits is calculated as:

$$MTD = \frac{\sum_i \sum_j u_{ij}}{S(S-1)}. \tag{21}$$

$$MNTD = \frac{\sum_i \min{(u_{ij})}_{j=1,\dots,n}}{S}. \tag{22}$$

Here, u_{ij} represents the difference in trait values between species i and species j.

Main results

The primary objective of this thesis is to advance our understanding of the mechanisms influencing observed community diversity patterns within the context of eco-evolutionary dynamics. Specifically, the focus is on elucidating the roles of ecological and evolutionary processes operating across local and regional spatial scales. These processes include competition, predation, dispersal, environmental gradient (filtering), and adaptive radiation. The four main questions of this thesis revolve around how interactions between these processes may induce variations in adaptive radiation and how such variations manifest in community diversity patterns. These patterns encompass species diversity, phylogenetic diversity, phylogenetic beta diversity, trait diversity, and Elevational Diversity Gradient. Presented below are the outcomes within a broader context of the four central questions posed in the thesis. Detailed results and figures are described in each corresponding paper attached.

Paper I: The interactive effects of environmental gradient and dispersal shape spatial phylogenetic patterns

Paper I investigates the link between phylogenetic relatedness across space (i.e. phylogenetic beta diversity, also written as PBD), environmental gradient, and dispersal. The results indicate environmental gradient is the primary driver of diversification. These results align with the commonly held assumption that environmental gradients shape phylogenetic structure by exerting abiotic filtering on functional diversity (Kembel et al., 2006; Cavender-Bares et al., 2009). However, dispersal plays a crucial role in either facilitating or hindering disruptive selection in combination with the environmental gradient. When the gradient is steep and dispersal is low, species experience strong directional selection toward local environmental optima, leading to sequential diversification, high species diversity, and high PBD. In contrast, a shallow environmental gradient and high dispersal result in lower species diversity (Figure 3A in Paper I) and lower PBD (Figure 8).
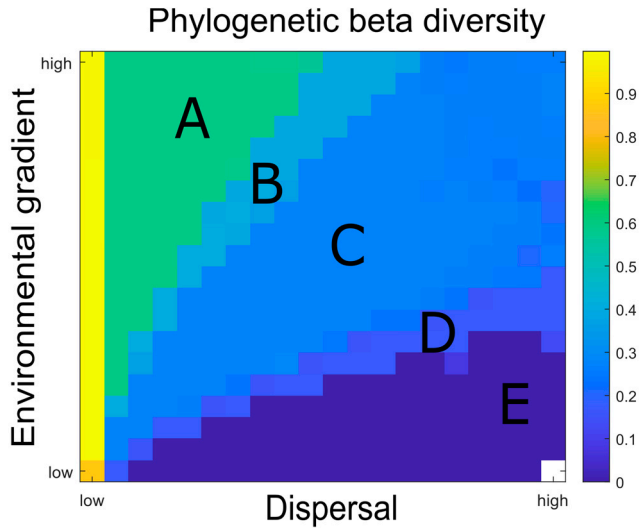
Figure 8 The phylogenetic beta diversity (PBD) reveals the interaction of the environmental gradient (y-axis) and dispersal (x-axis)
Each grid shows the average pairwise phylogenetic relatedness between habitats quantified as Phylogenetic Beta Diversity (PBD) from each simulation. A PBD of 1 shows no shared evolutionary history between species in the compared habitats, while a PBD of 0 indicates that species in both habitats share an identical evolutionary history.

Moreover, dispersal also affects the shape of adaptive radiation, with high dispersal leading to more symmetric adaptive radiation (Figure 4 in Paper I). The shape of adaptive radiation influences PBD as a function of increasing geographical distance. In general, PBD increases with distance, but the pace varies between different combinations of dispersal and environmental gradient. A steep gradient combined with low dispersal results in a linear increase of PBD with geographical distance, while an intermediate gradient combined with low to intermediate dispersal leads to a sigmoidal increase of PBD. Shallow gradients with high dispersal create a plateau of PBD around the center of the gradient, and very shallow gradients result in no change in PBD with distance (Figure 6 in Paper I).

Paper I emphasizes the significance of understanding the interplay between environmental gradients, dispersal, and phylogenetic diversity in the context of community assembly processes. Paper I also suggests that researchers can gain insights into the underlying assembly processes by studying PBD as a function of distance along environmental gradients. The results stress the importance of taking both environmental gradients and dispersal into account when interpreting phylogenetic diversity patterns, as environmental gradients and dispersal both play a crucial role in shaping phylogenetic diversity.

Paper II: Combined competition and predation effects on prey diversification: a mechanistic approach

Paper II examines the effects of predation on prey adaptive radiation. Specifically, a trait-based and eco-evolutionary model is developed to explore the influence of predator niche width and evolvability.
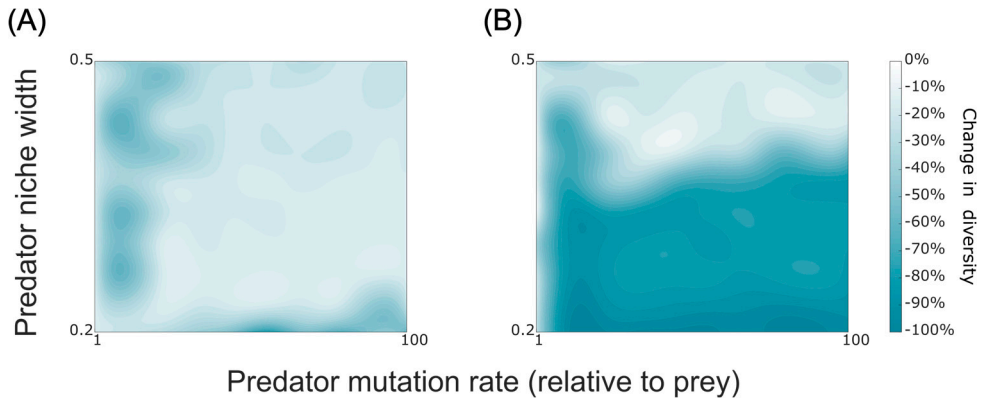
(A)

(B)

Figure 9 Predator induces a reduction in prey diversity that varies across predator and prey specialization
This figure illustrates the effect of predator presence on prey diversity, revealing varying levels of reduction in different predator and prey specialization and mutation rates. (A) Predator effects on prey with narrow niche width. (B) Predator effects on prey with wide niche width. The percentage changes are derived from a comparison between the diversity of the baseline prey-only community and communities influenced by predator presence.

The results extend previous knowledge on adaptive radiation (Yoder et al., 2010; Wellborn et al., 2015) by confirming the primary role of competition in driving adaptive adaptation, and the negative relationship between niche width and diversity under a fixed resource distribution (niche space). Such a relationship has been extensively studied (Brown et al., 1992; Doebeli, 1996b; Ackermann et al., 2004; Stroud et al., 2016; Pontarp et al., 2018; Pontarp, 2021). By tracking competition-induced disruptive selection over evolutionary time, the results show that the strength of competition-induced disruptive selection decreases with increasing niche width and diminishes over time as the niche space is filled.

The primary findings of Paper II include three key aspects. First, the results show a general negative effect of predation on prey diversity (Figure 9). Predators hinder competition-induced disruptive selection by reducing prey abundance. Such a negative effect has been suggested by experimental studies (Meyer et al., 2007). Second, the reduction in prey diversity depends on predator niche width. Predators with narrow niche widths lead to unstable predator-prey evolutionary dynamics resembling Red-Queen dynamics, drastically reducing prey diversity (Figure 10).

Generalist predators lead to stable evolutionary dynamics, sustaining competition-induced disruptive selection and resulting in a mild reduction in prey diversity (Figure 9). Third, predator evolvability, while not influencing apparent differences in prey diversity compared to predator niche width, plays a crucial role in whether predators exert directional or disruptive selection on prey. Predators with intermediate evolvability may lead to unstable evolutionary dynamics and a significant reduction in prey diversity (Figure 7 in Paper II).

Paper II demonstrates the intricate interplay between competition, predator niche width, and predator evolvability. While competition for resources is the primary driver of prey diversification (Meyer et al., 2007), active interactions across trophic levels play a substantial role in driving adaptive radiation and community diversity.
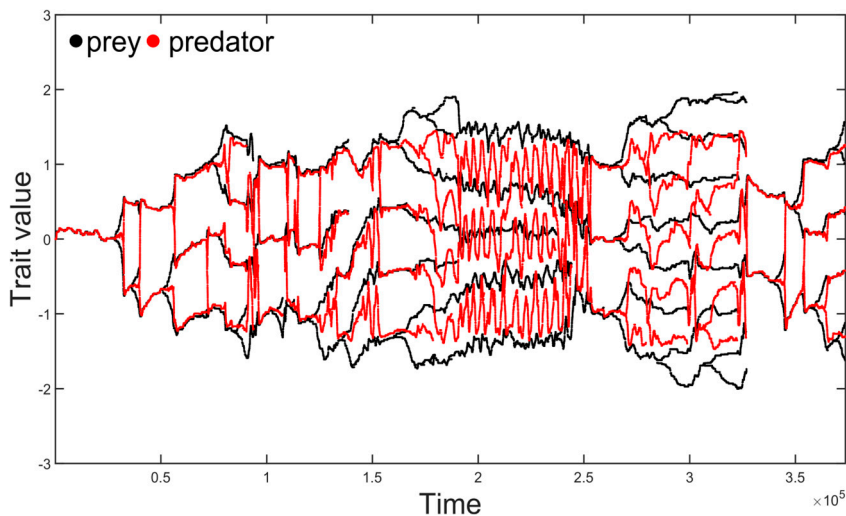
Figure 10 Specialist predator leads to Red-Queen dynamics that drastically reduce prey diversity
This figure shows the adaptive radiation of prey (black) and predator (red) when predators have narrow niche widths.

Paper III: Predator-prey dynamics in adaptive radiations: evolutionary consequences for community patterns and diversity metrics

Paper III examines how predation affects community diversity patterns in comparison to competition. Specifically, it explores the influence of predator niche width and evolvability on diversity metrics that are commonly used to infer competition, including mean phylogenetic distance (MPD), mean nearest phylogenetic distance (MNPD), mean trait distance (MTD) and mean nearest trait distance (MNTD).
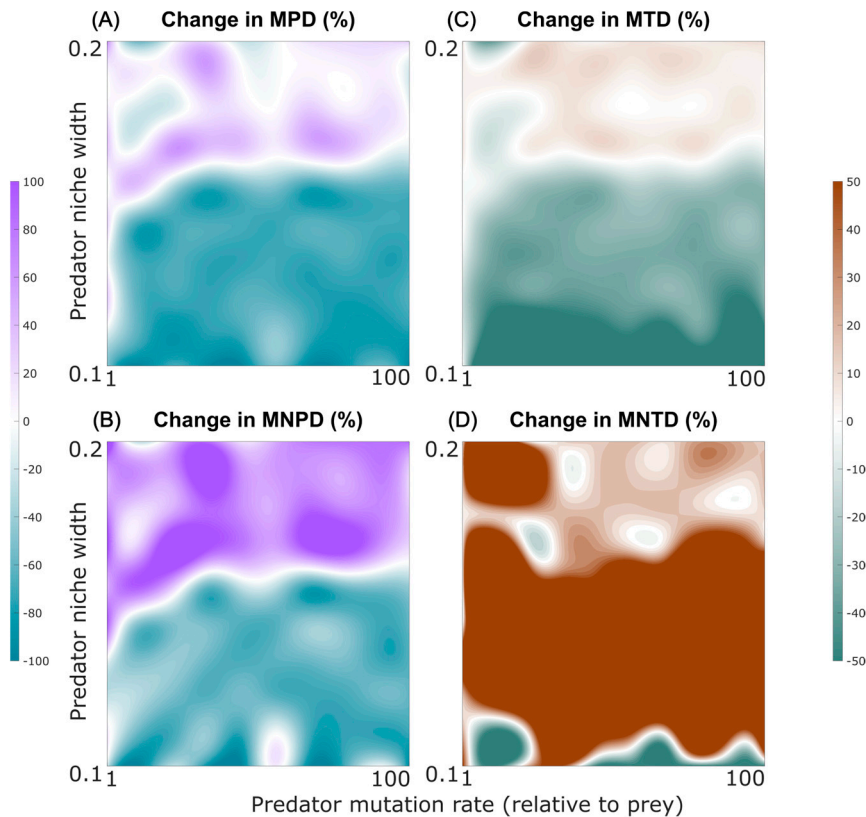
Figure 11 Predator niche width plays an important role in the distance metrics of prey: (A) mean phylogenetic distance (MPD), (B) mean nearest phylogenetic distance (MNPD), (C) mean trait distances (MTD), (D) mean nearest trait distance (MNTD)
Predators with wider niche widths tend to maintain or increase MPD, while predators with narrow niche widths decrease MPD. Additionally, predators with wider niche widths increase MTD, whereas predators with narrow niche widths reduce MTD. Generalist predators generally increase MNTD. Specialist predators, on the other hand, can either increase or decrease MNTD. Predators with extremely narrow niche widths impede prey radiation and drastically reduce MNTD.

The results show that predation always reduces and generally delays prey diversification. This leads to consequences in the phylogenetic patterns (Figure 11 A-B). First, the effect of predation on phylogenetic patterns depends on predator niche width. Predators with wide niche widths increase MPD and MNPD because prey diversifications still occur in the early stage of the radiation. Predators with narrow niche widths reduce MPD and MNPD because they drastically reduce and delay diversifications in prey radiation. Second, an increase in MTD is related to directional selection from predators in the early evolutionary stage (Figure 6 in Paper III). Predators with wider niche widths increase MTD while predators with narrow niche widths reduce MTD (Figure 11C). Third, an increase in MNTD is related to constant directional selection from predation across evolutionary time. While predation in general increase MNTD, generalist predator with low mutation rate drastically increases MNTD, and predators with extremely narrow niche width hinder prey radiation altogether and drastically decrease MNTD (Figure 11D).

Paper III underscores how predation impact patterns traditionally attributed to competition (Vamosi, 2005; Emerson et al., 2008; Cavender-Bares et al., 2009; Cadotte et al., 2010; Pausas et al., 2010; Mouquet et al., 2012; Adler et al., 2013). Specifically, predation can lead to patterns that are typically considered a sign of competition. This emphasizes the importance of recognizing the interactions in predation and competition on community diversity patterns for a better interpretation of community diversity patterns.

Paper IV: Elevational Diversity Gradients: insights from eco-evolutionary models of habitat heterogeneity and primary productivity

Paper IV explores the formation of Elevational Diversity Gradients (EDGs), emphasizing habitat heterogeneity and primary productivity as pivotal factors (Hawkins et al., 2003; Mittelbach et al., 2015; Dillon et al., 2021). Habitat heterogeneity is distinguished into local and regional types: local habitat heterogeneity (LHH) relates to resource variety and competition, while regional habitat heterogeneity (RHH) involves adaptation and environmental filtering. Primary productivity (PP) is integrated into the model as carrying capacity.

Results indicate that LHH shapes the EDG (Figure 12). The form of EDG depends on how LHH varies with elevation: constant LHH yields a shallow mid-elevational peak, unimodal LHH results in a steep peak, and decreasing LHH leads to a low-elevational plateau. This dependence confirms the link between diversity and resource variety.

RHH does not alter the overall shape of EDG or peak position but significantly influences diversification and temporal dynamics across evolutionary time (Figure 5 in Paper IV). High RHH accentuates the role of LHH, producing distinctive EDG patterns at different evolutionary stages.

PP subtly impacts the final shape of EDG but influences its temporal dynamics. High mid-elevation productivity fosters diversification, while high productivity in low elevations encourages stepwise colonization toward higher elevations (Figure 7 in Paper IV).

Paper IV underscores the intricate interplay of local and regional habitat heterogeneity, primary productivity, and their effects on EDGs. Results imply that the interpretation of observed EDGs may be challenging due to the temporal differences, emphasizing the need to combine patterns with temporal signals, such as spatial phylogenetic patterns.
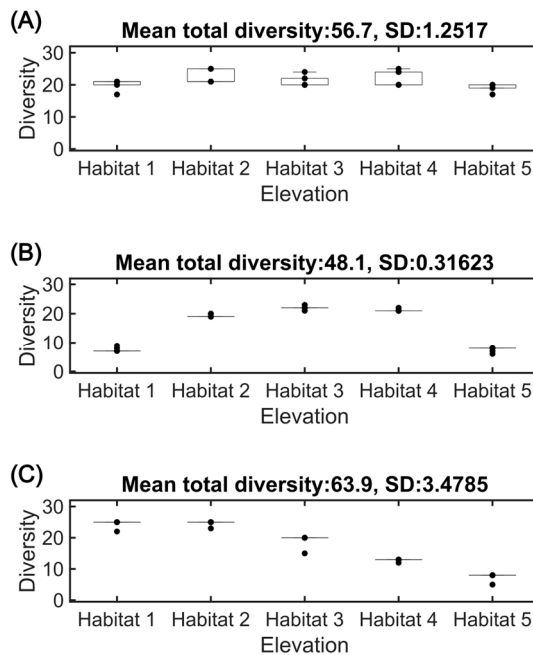
Figure 12 Local habitat heterogeneity (LHH) dominates in shaping diversity across elevations
In this figure, we illustrate how local habitat heterogeneity influence diversity patterns across elevations A) No change in LHH B) Mid-elevation peak in LHH C) Monotonic decrease in LHH

Discussion, conclusion, and outlook

This thesis serves to elucidate the intricate biodiversity through eco-evolutionary dynamics. By systematically addressing the specific questions outlined in this study, an advanced understanding of the interplay between community patterns and underlying mechanisms is achieved, leading to several points for discussion and comprehensive conclusions.

This thesis highlights competition as the primary driver for adaptive radiation on the local scale. Although predation influences the dynamics of competition, the relationship between niche width and a fixed resource distribution ultimately dictates local species diversity (Brown et al., 1992; Doebeli, 1996a; Ackermann et al., 2004; Stroud et al., 2016; Pontarp et al., 2018; Hagen et al., 2021). This thesis contributes to the existing body of knowledge by revealing a clear negative correlation between niche widths (Yoder et al., 2010; Wellborn et al., 2015) and the intensity of competition-induced disruptive selection, establishing a crucial mechanistic link between competition, eco-evolutionary dynamics, and adaptive radiation.

The results emphasize the significance of environmental gradients as the driving force behind adaptive radiation on the regional scale. Community structures are intricately shaped by habitat specialization in distinct environmental conditions (Weinstein et al., 2014; Saladin et al., 2019). The model introduced in this study provides valuable insights into the mechanistic link between these observed patterns and environmental gradients by showing the environmental-induced directional selection towards local conditions in different habitats across the gradient. A steep environmental gradient, therefore, fosters rapid adaptation and diversification across different habitats.

This thesis illustrates how predation interacts with competition, resulting in changes in adaptive radiation on the local scale. In general, predators hinder competition-induced disruptive selection which is the dominant driver for prey diversification. Such a negative effect between predation and competition-induced selection via prey abundance has been suggested (Chase et al., 2002; Meyer et al., 2007; Chesson et al., 2008). This thesis contributes novel insights by addressing predator-prey interactions within the broader context of eco-evolutionary dynamics and adaptive radiation. The results show that predation niche width alters competition-induced disruptive selection and leads to either stable or unstable evolutionary dynamics.

Moreover, predator evolvability plays a crucial role in whether predators exert directional or disruptive selection on prey. Such mechanistic information advances our understanding of stable and unstable evolutionary dynamics between predator and prey previously found in the microbial system (Decaestecker et al., 2007) and previous work on negative frequency-dependent selection (Marrow et al., 1992).

The results indicate that dispersal interacts with environmental gradients, exerting influence on adaptive radiation on the regional scale. Specifically, high dispersal can reduce the directional selection imposed by the environmental gradient, leading to species with intermediate trait values that can survive in multiple environments. Under steep environmental gradients, local adaptation and trait diversification still occur despite high dispersal, but in the later stage of the macro-evolutionary trajectory. These findings align with empirical patterns reported in various ecosystems, such as hummingbird assemblages, tropical tree communities, and mammal assemblages (Graham et al., 2012; Swenson, Enquist, et al., 2012; Si et al., 2022).

This thesis highlights the interconnectedness of these processes, demonstrating how their interactions lead to changes in adaptive radiations, subsequently influencing phylogenetic and trait patterns. This holistic understanding enhances our ability to interpret observed community patterns in the context of trophic interactions and spatial processes (Schmitz et al., 1997; Brown et al., 2001; Graham et al., 2008; Montoya et al., 2009; Kraft et al., 2010; Morlon et al., 2011; Graham et al., 2012; Swenson, Erickson, et al., 2012; Amundrud et al., 2015; Gross et al., 2022). On the local scale, the effects of predation may be identified by comparing phylogenetic patterns and trait diversity. For example, low MPD, MNPD, and MTD contrasting with high MNTD could be an indication of specialist predators, while high MPD, MNPD, and MTD contrasting with low MNTD could be an indication of generalist predators. On the regional scale, the results confirm the hypotheses that low dispersal can lead to high PBD between sites regardless of environmental gradients and that high dispersal leads to low or random PBD (Graham et al., 2008). Additionally, the results reveal a response of PBD to geographical distance under different levels of environmental gradients and dispersal. Despite the limitation that our simulated patterns may not be directly comparable to any natural system, a general mechanistic understanding between PBD and geographical distances due to the combined effects of the environmental gradient and dispersal provides insight into eco-evolutionary dynamics on the regional scale.

Finally, this thesis underscores the dynamic interplay between local and regional processes. Empirical studies have suggested that spatial community diversity patterns are influenced by its natural history or local processes such as competition and resource distribution (Rainey et al., 1998; Lomolino, 2001; McCain, 2005; McCain, 2007; McCain et al., 2010; Pigot et al., 2016; Szewczyk et al., 2016). The results reveal that the EDG can exhibit distinct patterns in different evolutionary stages. Despite the predominant influence of local processes in shaping EDG near

an evolutionary equilibrium, the results reveal that interplays between local and regional processes introduce temporal dynamics, resulting in distinct patterns across evolutionary time. Since natural systems rarely reach equilibrium (O'Meara et al., 2016; Wessinger et al., 2019; Wiens, 2023), the temporal dynamics caused by the interactions between local and regional processes become relevant and may be revealed by patterns that contain both temporal and spatial signals, such as phylogenetic diversity (Baraloto et al., 2012; Graham et al., 2012; Swenson, Erickson, et al., 2012; Weinstein et al., 2014).

From a forward-looking perspective, future work focusing on integrating local and regional processes linked with changes in phylogenetic and trait diversity patterns holds significant value in advancing our interpretation of community patterns. A promising avenue for further exploration lies in continuous space models, building on existing research exploring how heterogeneity in continuous resource distribution and competitive mechanisms affect food-web evolution (Wickman et al., 2019; Wickman et al., 2020). This thesis, therefore, not only contributes to the understanding of the mechanisms behind community diversity patterns in the context of both spatial and temporal scales but also paves the way for novel avenues in the study of biodiversity.

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現在是凌晨一點三十分，在二零二三年十二月二十日，我在寫論文最後的一部分，也就是感謝詞。

謝謝爸爸和媽媽，讓我從降生到走到這個時刻，我的人生是如此的豐富，圓滿及幸運，我之所以為我，都是因為你們。謝謝。同樣的，謝謝張乃云作為我的妹妹，自我在實體上遠離你們的時刻開始，才是我在心靈上開始靠近你們的時刻。這四年是一個階段，我們變得更加緊密，也開始互相認識彼此。謝謝阿公阿嬤，謝謝外婆，謝謝慧儀阿姨，雖然你們大概不會看到。這本論文不是什麼多重要的東西，他的價值大概在於，它承載了這過去的四年，我對於長大的想像跟實證。

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"All living beings, whether born from eggs, from the womb, from moisture, or spontaneously; whether they have form or do not have form; whether they are aware or unaware, whether they are not aware or not unaware, all living beings will eventually be led by me to the final Nirvana, the final ending of the cycle of birth and death. And when this unfathomable, infinite number of living beings have all been liberated, in truth not even a single being has actually been liberated."

佛告須菩提：諸菩薩摩訶薩應如是降伏其心！所有一切眾生之類：若卵生、若胎生、若濕生、若化生；若有色、若無色；若有想、若無想、若非有想非無想，我皆令入無餘涅槃而滅度之。如是滅度無量無數無邊眾生，實無眾生得滅度者。何以故？須菩提！若菩薩有我相、人相、眾生相、壽者相，即非菩薩。

-Diamond Sutra

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Eco-evolutionary processes and community patterns

Exploring the diversity of life on Earth over time and space can be a puzzling challenge. This is because studies of the ecological and evolutionary processes that affect how species interact and evolve often leave us with more questions than answers. Ultimately, trying to figure out how different species live together, adapt, and create new species is like solving a giant ecological and evolutionary puzzle. One of the big mysteries is understanding how things like competition and predator-prey relationships impact the way species evolve, and how, in turn, these interactions affect the variety of life we see around us. What makes it even more complicated is that this puzzle is also influenced by where species go and how they adapt to different places. Imagine species as travelers, journeying across diverse environments. These journeys influence the patterns of life we observe. In this thesis, I've embraced this complexity by using math and computer simulations to study how communities of species change and develop. In summary, my research not only helps us better understand how life on our planet works but also raises exciting new questions. It's like solving one piece of a massive ecological and evolutionary jigsaw puzzle, and it opens new doors for further exploration in the world of biodiversity.

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