Co-evolution of ecosystems and their environments: modeling the evolution of ecosystem-level responses to, and impacts on, environmental temperature

by

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B.A., Colorado College, 2015

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We acknowledge and respect the Lək̓ʷəŋən (Songhees and Xʷsepsəm / Esquimalt) Peoples on whose territory the university stands, and the Lək̓ʷəŋən and W̱SÁNEĆ Peoples whose historical relationships with the land continue to this day.

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ABSTRACT

Throughout the history of life on Earth, major changes in both the environment and the biota have occurred. Organisms have simultaneously adapted to and affected a tremendous variety of physical and biological conditions. Many species alive today engage in niche construction: their modifications to the environment feed back on their own evolution. Some extant species also affect the evolutionary pressures experienced by other species. However, while organisms are known to affect both the environment and the evolution of their own and other species, a general understanding of how organismal impacts on the environment evolve in ecosystems, and how these impacts feed back on ecosystem characteristics, is still lacking. This is necessary for understanding Earth system evolution and the pressures that drive the evolution of macroecological patterns.

In this dissertation, I modify a model of ecology and evolution called the Tangled Nature (TaNa) model to investigate ecosystem-level responses to and impacts on temperature. I first characterize how ecosystem properties depend on temperature, and find that ecosystem survival probability, species richness, and ecological interaction strengths are strongly temperature dependent in different ways.

Next, I couple this temperature-dependent version of the TaNa (the TaNa+T) with a climate model and enable organisms to increase or reduce atmospheric carbon, thus affecting the climate. In this version, called the Tangled Nature + Climate (TaNC) model, I demonstrate and characterize ecosystem-level niche construction, showing that ecosystems in the TaNC evolve toward cooler temperatures where death rates are reduced, and this can feed back on ecosystem properties, increasing ecosystem survival probability and reducing species richness and abundance.

I then test the sensitivity of the TaNC to assumptions about how species respond to and affect the environment. I find that species with similar thermal optima of reproduction do not modify the climate to maximize reproduction. Instead, minimizing death rates guides the evolution of ecological impacts on the environment.

Finally, I probe into ecosystem-level inheritance by making species' responses to and impacts on the environment heritable during speciation. Inheritance of species-environment interactions increases ecosystem extinction probability, but surviving ecosystems acquire larger species richness and abundance when thermal optima of reproduction are heritable.

Overall, this work illustrates general properties of ecosystem-environment coevolution, making an important contribution to Earth science and Eco-Evolutionary feedbacks and providing a powerful tool for further investigation of ecosystem evolution.

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I also want to thank my partner, Michael Jiang, for his constancy in my life, moral support, cooking and cleaning, and hugs and kisses that sustained me throughout this research. His endless reservoir of love, warmth, and calm rooted and restored me. His brilliant intuition for the way things naturally work helped me understand people, in addition to the physics of motion (which I applied to climbing and thus directly fed my joy).

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Dedication

I dedicate this dissertation to the animals that kept me company while I was writing this dissertation, especially the cats, dogs, chickens, and horse. In spite of all the theories about nature and the environment that I have strained to learn and contemplate over the last several years, these creatures will always be my most important teachers about how the world really is.

Chapter 1

Introduction

1.1 Evolution of ecological impacts on the environment

Darwin's foundational theory of evolution by natural selection proposes that heritable variation and differential fitness (survival and reproduction) of members of reproducing populations lead to gradual changes in the distribution of traits within populations (Darwin, 2017, first published in 1859)[1]. By this process, over time, "individual entities will come to possess traits that increase their likelihood of survival and reproduction – i.e, 'fitness'" in their specific environment (Maynard Smith, 1991).

Species do not just passively adapt to environments, however; they also modify their environments. In fact, after publishing his seminal work on evolution by natural selection, Darwin dedicated 40 years of his career to studying earthworms for this reason: he was interested in how they decompose and bury organic matter, bring minerals from the bedrock to the surface, and burrow into the soil and thereby promote moisture retention, among other impacts (Feller et al., 2003). In the century and a half since Darwin's books on natural selection (1859) and on worms (1881), the widespread impacts of species on their environments, and the ways that these impacts can feed back on species evolution, have come to be greatly appreciated (Bonduriansky & Day, 2009; Matthews et al., 2014; Corenblit et al., 2011). Every species on Earth affects its environment, at a bare minimum through chemical exchange due to metabolism (Odling-Smee et al., 1996; Brown et al., 2004). However, organismal impacts on the environment can even be global in scale: or-

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[1] In Darwin's Introduction to the *Origin of species*, he writes that "[...] any being, if it vary however slightly in any matter profitable to itself, under the complex and sometimes varying conditions of life, will have a better chance of surviving, and thus be NATURALLY SELECTED. From the strong principle of inheritance, any selected variety will tend to propagate its new and modified form."

ganisms cycle the chemicals that make up the atmosphere (R. A. Berner, 1998; Lenton, Daines, & Mills, 2018; Schlesinger & Jasechko, 2014; Fowler et al., 2009; Lenton & Watson, 2000) and pH of the ocean (Eichenseer et al., 2019), and affect chemical weathering rates (Schwartzman, 2017; Lenton & Watson, 2004) and albedo (Charlson et al., 1987; von Oppen et al., 2022), as just a few examples (for other examples of biotic impacts on the physical environment see Corenblit et al., 2011).

Organisms' impacts on the environments can feed back on their evolution (niche construction) or on the evolution of other species in their ecosystem (eco-evolutionary feedbacks; Matthews et al. (2014)). Species' direct interactions with one another can also affect the evolution of different species (also part of eco-evolutionary feedbacks; Matthews et al. (2014)), and these interactions can stabilize the composition of ecosystems (Vuorinen et al., 2021). In fact, the theory of Punctuated Equilibria, which posits that species generally remain evolutionarily stagnant for long periods of time (Eldredge & Gould, 1972), has also been explained by the stabilizing impacts of species on one another's evolution (Christensen et al., 2002).

Because species interact with one another, and each species interacts with the environment, and all these different biotic and abiotic components of ecosystems evolve over the course of millions of years, general properties of ecosystem-environment interactions are very difficult to characterize. Some models of the biotic impacts on atmospheric evolution have focused on key impacts of life on the environment such as the Great Oxidation Event (Lenton, Daines, & Mills, 2018; Luo et al., 2022), the colonization of land by plants (Algeo et al., 1995; R. A. Berner, 1998), biotic enhancement of weathering (Schwartzman, 2017; Lenton & Watson, 2004), and the role of the biosphere in mitigating contemporary climate change (Munang et al., 2013; Haverd et al., 2020; Li et al., 2023). In a more general sense, Lovelock and Margulis proposed in their "Gaia hypothesis" that evolution may cultivate a global biosphere that stabilizes the composition and temperature of the climate (Lovelock & Margulis, 1974; Margulis & Lovelock, 1974; Lovelock & Watson, 1982), and there has been renewed interest in this idea in recent years (Doolittle, 2017, 2019; Lenton, Daines, Dyke, et al., 2018; Pausas & Bond, 2022; Arthur & Nicholson, 2023).

Many have questioned the evolutionary mechanisms that could produce a biosphere that collectively stabilizes or improves the environment (Doolittle, 1981; Dawkins, 1982; Kirchner, 2002; Volk, 2004). Critics have argued that selective pressures guide adaptation to environmental changes, but not the impacts that species have on the environment, so species continually adapt to the "waste products" of previous generations (Volk, 2004). Some also suggested that biotic regulation of the global environment would require collaboration between very distantly related species, but no evolutionary mechanism would select against “cheaters” that do not participate — and in fact natural selection might favor cheaters (Dawkins, 1982). The concept of ecosystem-level selection was also questioned since there is no evidence of Earth’s biota competing with biospheres on other planets, or of Earth’s biota reproducing (Dawkins, 1982). Critics wrote that the concept of the global biota harmoniously in balance with the environment is “poetic”, but dangerous because it could give people the idea that ecosystems are more resistant and resilient to perturbations than they really are (Doolittle, 1981).

Although merging the Gaia hypothesis with evolutionary theory has been tenuous, biologists have increasingly come to recognize that evolution and the environment interact on multiple time scales, and that these interactions are critical for understanding evolution by natural selection (Woods et al., 2021). A whole field of eco-evolutionary dynamics, which focuses on the interactions between ecology and evolution, has sprung up in the last 15 years (Hendry, 2016). One important biologist who originally criticized the Gaia hypothesis, Ford Doolittle, later contributed important biological theory to how environmental stabilization could be selected for. He theorized that ecosystem-level selection could select for ecosystems with “persistence-enhancing” traits because ecosystems which do not degrade their environments may persist longer, and so selection by differential survival (rather than differential reproduction rates) could lead to evolution of ecological traits that stabilize the environment (Doolittle, 2017, 2019). Over the course of many ecological collapses and mass extinction events, ecosystems that stabilize their environments might become more common as ecosystems that degrade their environments drive themselves extinct (Lenton, Daines, Dyke, et al., 2018). Therefore, even if organisms do not experience selective pressures to improve their environments, ecosystems may evolve to minimize their impacts on the environment simply because mass extinction events eliminate species and ecosystems that do not. This process is called *selection by survival* (when driven by total extinctions of certain lineages) or *sequential selection* (when driven by differential durations of ecological steady states) (Betts & Lenton, 2008; Doolittle, 2017, 2019; Lenton, Daines, Dyke, et al., 2018). However, the extent to which selection by survival and sequential selection influence ecosystem-level evolution remains poorly quantified.

Understanding the ways that species’ impacts on the environment evolve continues to be a major challenge (Moorcroft, 2006), but is essential, especially as humanity simultaneously faces a biodiversity crisis (Butchart et al., 2010; Cowie et al., 2022) and unprecedented climate change (Calvin et al., 2023). Ecosystems perform many crucial functions that sustain the climate (Steiner, 2020; Munang et al., 2013), affecting the rate of carbon cycling in numerous ways (L. T. Berner & Schädel, 2023; R. A. Berner, 2001; Canadell et al., 2000; Casado, 2021; Field et al., 1998; Li et al., 2023), and the modern biosphere has taken up more than 30% of anthropogenic emissions (Haverd et al., 2020). However, climate change is also projected to affect biodiversity, biomass, and ecosystem functions (e.g. Rosenzweig et al., 2008; Tittensor et al., 2021; Qin et al., 2022; Jones et al., 2014), which could in turn affect the impacts that species have on the environment (IPCC, 2023).

There are many gaps in our understanding of how ecosystems and the environment are coupled. First, understanding how ecosystem and climate evolution are coupled requires an understanding of how ecosystem responses depend on the underlying physiological responses of their constituent species. We can then ask whether, and how, organisms evolve to affect their environments. Do feedbacks between environmental and organismal evolution produce certain ecological or environmental characteristics? Does ecosystem-level selection drive the environments experienced by organisms towards a physiological optimum, or do species randomly affect their environments and then adapt to new conditions?

In this thesis, I address these questions by modifying the Tangled Nature (TaNa) model of ecology and evolution (Christensen et al., 2002). The TaNa model is a stochastic, agent-based model of species interacting in a community, with new mutant species occasionally being produced during reproduction. I first modify the TaNa model to be temperature-dependent based on physiological thermal response curves, and investigate how ecosystem-level responses to temperature emerge from the underlying organismal thermal responses (Febvre et al., 2024). Then, I allow species in the TaNa model to affect a model climate, and investigate how ecosystems evolve to affect the climate, and how these modifications to the climate feed back on the evolution of ecosystem characteristics.

1.2 Aims

The research presented in this dissertation is an investigation of how ecosystems and their environments co-evolve, bridging the gap between ecological impacts on ecology and evolution and environmental change over time. I focus on organismal impacts on and responses to temperature. Temperature is a major driver of organismal fitness (Amarasekare & Savage, 2012), and affects most organisms similarly (Brown et al., 2004). Additionally, every organism on Earth interacts with the carbon cycle (a major greenhouse gas which therefore affects global temperature), and organisms are known to have caused major changes to the climate through interactions with greenhouse gases and albedo throughout Earth history (L. T. Berner & Schädel, 2023; R. A. Berner, 2001; Canadell et al., 2000; Casado, 2021; Field et al., 1998; Li et al., 2023). The thesis chapters outlined below contribute to characterizing general properties of ecosystem-level responses to and impacts on the climate on geologic timescales. The chapters are also illustrated in Fig. 1.1, and some key terms used throughout this dissertation are defined in Table 1.1.

1.3 Dissertation Structure

This dissertation is comprised of four scientific studies.

In **Chapter 2**, I begin by investigating ecosystem-level responses to temperature on geologic timescales. I introduce the model of ecology and evolution used throughout the rest of the thesis: the Tangled Nature (TaNa) model (Christensen et al., 2002), and then I explain our modifications to the TaNa model in the Tangled Nature + Temperature (TaNa+T) model; incorporating physiological thermal responses of species into the TaNa. I use the TaNa+T to investigate how species' physiological thermal responses shape ecosystem characteristics. This chapter, published in *Journal of Theoretical Biology* in 2024, lays the groundwork for the next chapters.

In **Chapter 3**, I modify the temperature-dependent TaNa model from Chapter 2 to enable species to affect their environment by increasing or reducing the amount of carbon in the atmosphere. I then use this new model, which I call the Tangled Nature + Climate (TaNC) model, to investigate how species' impacts on the environment evolve, and how this affects the evolution of both the climate and ecosystem characteristics. I test the sensitivity of the results to the strength of species' impacts on the climate, and to the different physiological thermal responses of species.

In **Chapter 4**, I examine the sensitivity of the TaNC to the assumptions we make about how species respond to and affect the environment. In particular, I investigate how species with more similar thermal optima affect their environments in comparison to our original assumption that species have an equal probability of adapting to any climate. Additionally, I investigate a scenario where species' impacts on the climate are drawn from a bimodal distribution, and test whether species' impacts on the environment are more likely to cancel out in this configuration.

In **Chapter 5**, I investigate ecosystem-level inheritance by making species' thermal optima and impacts on the environment heritable in the TaNC. I examine how accumulation by natural selection of traits associated with species-environment interactions affect ecosystem and climate properties.

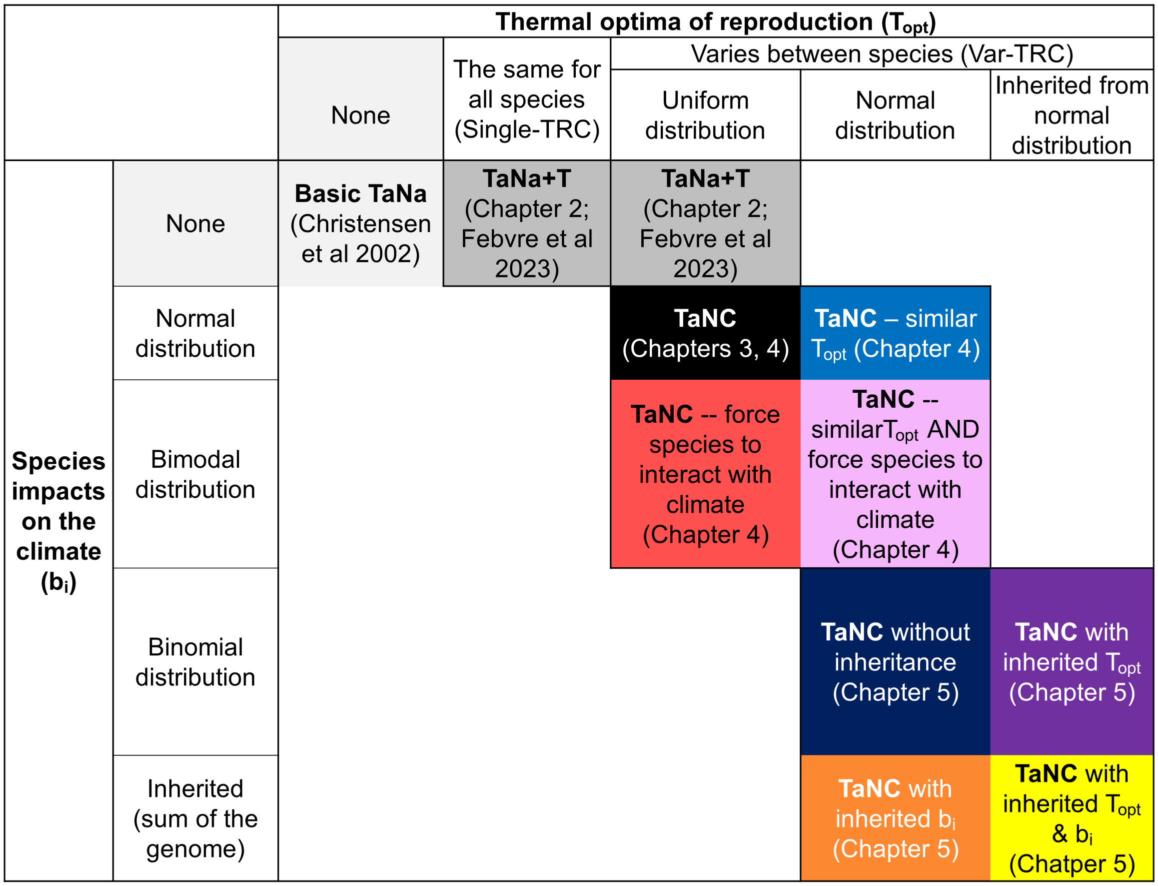
In **Chapter 6**, I conclude the dissertation by summarizing and discussing the main results of each of the thesis chapters, connecting this research to the greater picture, and suggesting areas for future research.

1.4 Model output availability

The model output generated and analyzed in this dissertation is archived in Federated Research Data Repositories. The model output for Chapter 2 is archived with the doi 10.20383/103.0924; for Chapter 3 with the doi 10.20383/103.01369; for Chapter 4 with the doi 10.20383/103.01373; and for Chapter 5 with the doi 10.20383/103.01374.

1.5 Authorship

The work presented in this thesis is my own work. In the science chapters I use first person plural to reflect collaboration with my supervisors, following the style of co-authored journal articles.



		Thermal optima of reproduction (T_{opt})				
		None	The same for all species (Single-TRC)	Varies between species (Var-TRC)		
				Uniform distribution	Normal distribution	Inherited from normal distribution
Species impacts on the climate (b_i)	None	**Basic TaNa** (Christensen et al 2002)	**TaNa+T** (Chapter 2; Febvre et al 2023)	**TaNa+T** (Chapter 2; Febvre et al 2023)		
	Normal distribution			**TaNC** (Chapters 3, 4)	**TaNC** – similar T_{opt} (Chapter 4)	
	Bimodal distribution			**TaNC** -- force species to interact with climate (Chapter 4)	**TaNC** -- similarT_{opt} AND force species to interact with climate (Chapter 4)	
	Binomial distribution				**TaNC** without inheritance (Chapter 5)	**TaNC** with inherited T_{opt} (Chapter 5)
	Inherited (sum of the genome)				**TaNC** with inherited b_i (Chapter 5)	**TaNC** with inherited T_{opt} & b_i (Chatper 5)

Figure 1.1: Overview of the model designs used in this dissertation. In Chapter 2 (dark grey boxes), I make species' reproduction rates temperature-dependent in the Tangled Nature + Temperature (TaNa+T) model, and compare the cases where all species have the same versus different thermal optima (T_{opt}) of reproduction. In Chapter 3 (black box), in the Tangled Nature + Climate (TaNC) model, I allow species to also impact the climate, with biotic impacts on the climate drawn from a normal distribution with different standard deviations (σ_{bio}). In Chapter 4 (black, blue, red, and light purple boxes), I choose a standard deviation of biotic impacts that causes noticeable climate change but still has relatively high ecosystem survival probability, $\sigma_{\text{bio}} = 10^{-8}$ per year, and test different distributions of thermal optima and biotic impacts. Finally, in Chapter 5 (dark blue, purple, orange, and yellow boxes), I make biotic impacts and thermal optima heritable in the TaNC, both together and separately.

Species roles in ecosystems	
Core species	The most abundant species in an ecosystem and all other species with populations at least 5% as large.
Cloud species	All species that are not **core species** — i.e. species with small populations.
Ecology	
Ecological effect	A change in ecosystem characteristics, such as abundance or species richness.
Environmental effect	A change in abiotic properties, such as temperature or carbon concentration in the atmosphere.
Ecological steady state	Period of time during which the **core species** of an ecosystem remain the same. The populations of core species may fluctuate, and the ecosystem configuration is not robust to all perturbations, so this is elsewhere referred to as a "quasi-stable state".
Mass extinction	Many species, including the **core species**, simultaneously go extinct (i.e. in an "ecological collapse"); however, some species survive and form a new ecosystem.
Total extinction	All species go extinct, terminating all life in the lineage and simulation.
Evolution	
Evolution	Change over time in a (biotic or abiotic) property.
Speciation	Emergence of a new species (i.e. due to mutation).
Natural selection	Differential survival or reproduction rate between variable entities.
Unit of selection	Entity experiencing **natural selection** (e.g. individual, population, or community). Selection on this entity only leads to evolution if the entity has heritable characteristics.
Level of selection	Biological level (i.e. involving one **unit of selection**) at which **natural selection** is occurring.
Selection by survival	**Evolution** of the statistics of ecosystem characteristics due to **total extinctions** of certain ecosystems.
Sequential selection	**Evolution** of the statistics of ecosystem characteristics, often over the course of many **mass extinction events**, due to differential durations of **ecological steady states**.
Niche construction	Organismal impacts on the environment which feed back on the pressures of **natural selection** experienced by members of the same species.
Ecological inheritance	(Nongenetic) inheritance of the environment which may have been previously modified by other species.

Table 1.1: Key terms used throughout this dissertation, and their definitions. References between terms in the table are indicated in **bold**.

Chapter 2

Thermal performance of ecosystems: modeling how physiological responses to temperature scale up in communities

C. Febvre[1], C. Goldblatt[1], and R. El-Sabaawi[2]

This chapter was published in the Journal of Theoretical Ecology (https://doi.org/10.1016/j.jtbi.2024.111792). Here I have reformatted the journal article to align with the format of the dissertation.

Abstract

Understanding how ecosystems respond to their environmental temperature is a major challenge. Thermodynamic constraints on species' metabolic rates are expected to affect ecosystem characteristics, but species interactions and interspecific variation in physiological thermal response curves (TRC) may obscure ecosystem-level responses to temperature. As a result, macroecological patterns related to temperature are still poorly understood.

We investigate how physiological TRC scale up to ecosystem-level thermal responses by modifying the Tangled Nature (TaNa) model, a stochastic network model of ecology and evolution. We include new parameterizations that make reproduction, death, and

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mutation temperature-dependent. We find that ecosystem survival probability depends on the minimum fitness threshold for species survival, which depends on temperature. The thermal response of ecosystem survival probability is the only ecosystem property that is sensitive to interspecific variation in TRC. Species richness scales up directly from the TRC of mutation rate, and average species population sizes are inversely related to mutation rate, with Species Abundance Distributions (SADs) exhibiting more rare species in warmer temperatures. Interactions between species are also inversely related to mutation, with positive interactions occurring more frequently in colder temperatures. The abundance of surviving ecosystems is not sensitive to temperature. This work helps clarify the specific relationships between physiological responses to temperature and ecosystem-level repercussions when species are interacting and adapting to their thermal environments.

2.1 Introduction

Understanding how temperature affects ecosystems is crucial to facing major challenges of the 21st century such as combating the biodiversity crisis (Butchart et al., 2010; Cowie et al., 2022); understanding the impact of climate change on biodiversity, biomass, and ecosystem functions (e.g. Rosenzweig et al., 2008; Tittensor et al., 2021; Qin et al., 2022); and projecting the ways that ecosystem responses to climate change may feed back on the climate and other aspects of the environment (e.g. Moorcroft, 2006; Peters et al., 2013; Odling-Smee et al., 1996; Lewontin & Levins, 1997; Day et al., 2003; K. N. Laland, 2004; Lenton & Watson, 2000; Eichenseer et al., 2019; Braghiere et al., 2019). Furthermore, building an understanding of ecological responses to the environment improves our ability to interpret the history and dynamics of life on Earth recorded in the fossil record, with implications for the past, present, and future (McGill et al., 2006). However, measuring and predicting the responses of ecosystems to their environments is a major challenge (Walther, 2010; Ezard et al., 2011; Moorcroft, 2006) because different species in a shared ecosystem may respond differently to temperature (e.g. H. Chen et al., 2022), and the fitness of coexisting species are often directly or indirectly intertwined, making it difficult to predict the response of even a single species in the context of an ecosystem (Odling-Smee et al., 1996; Kordas et al., 2011; Guimarães et al., 2017; Bailey, 2012; Strona & Bradshaw, 2022; Remolina-Figueroa et al., 2022; Remke et al., 2022; Allsup et al., 2023).

Similar thermal responses can be observed from the scale of molecules to organisms. Metabolic rates of almost every species on Earth increase approximately exponentially with temperature, peak, and then decline more steeply than they increased (Farrell, 2016; Rezende & Bozinovic, 2019; Arroyo et al., 2022). Thermal Response Curves (TRC) of various measures of performance, such as running or swimming speed, also commonly follow this typical shape (Rezende & Bozinovic, 2019; Dell et al., 2011). Many physiological rates are temperature-dependent as well; birth rates show the typical hump-shaped response to temperature (Amarasekare & Savage, 2012), while death (Amarasekare & Savage, 2012) and mutation rates (Gillooly et al., 2005) increase exponentially with temperature.

Temperature also affects ecological properties and processes. Species richness generally decreases from the equator to the poles in a pattern called the Latitudinal Diversity Gradient (LDG), and the strength of the LDG is correlated with equator-to-pole temperature gradients (Brodie & Mannion, 2022). Analysis of the fossil record suggests that temperature is correlated with speciation and diversification rates (Ezard et al., 2011), and that dispersal of species has been limited by the strength of global-scale temperature gradients (Griffin et al., 2022). Some studies also suggest that interaction strengths (Dell et al., 2011) and connectance between species in ecological networks (Yuan et al., 2021) may increase with increasing temperature. Contemporary global warming has caused numerous detectable changes to ecosystems (Walther, 2010), and is predicted to decrease ocean biomass in the next decades and centuries (Jones et al., 2014). However, the ways temperature impacts ecology are much less certain than the impacts of temperature on individual organisms (Dell et al., 2011; Walther, 2010), and the extent and mechanisms by which individual-level thermal responses are responsible for producing ecosystem-level thermal responses also remains unclear.

The Metabolic Theory of Ecology (MTE) posits that biological rates from the scale of molecules to ecosystems are mechanistically linked via metabolism (Gillooly et al., 2001; Allen et al., 2002; Brown et al., 2004). The TRC of metabolism are explained by the Arrhenius-Boltzmann equation:

$$r = e^{-E_a/kT} \tag{2.1}$$

(where r is the rate of metabolic reactions, E_a is activation energy, k is the Boltzmann constant, and T is temperature). At organismal- and population-levels, many biological rates have the same average activation energy as that of either metabolism (for rates that increase with temperature) or protein denaturation (for rates associated with death or the declining portion of hump-shaped TRC; Dell et al., 2011; Amarasekare & Savage, 2012), suggesting that metabolism and protein denaturation drive many processes from physiological to ecological scales (Brown et al., 2004). For example, MTE predicts that birth and death rates depend on metabolism (Brown et al., 2004; Price et al., 2010), leading to temperature-dependence of intrinsic growth rates of species (Price et al., 2010; Amarasekare & Savage, 2012). Species population sizes are predicted to decrease exponentially with increasing temperature as a result of the increasing metabolic requirements of each individual at warmer temperatures (Brown et al., 2004; Price et al., 2010). Furthermore, MTE suggests that patterns in species richness such as the LDG may be described by the Arrhenius equation (Allen et al., 2002). The thermal response of ecosystem abundance (the total number of individuals in an ecosystem) has received less attention than some other ecosystem metrics (e.g. Wilkinson, 2007), partially because it requires a lot of data (He et al., 2019) and is difficult (and abstract) to measure. Some studies assume abundance follows the same trend as the population sizes of constituent species (Price et al., 2010), while others have assumed it to be temperature-invariant (e.g. supported by data on trees; Allen et al., 2002). Controlling for bodymass, biomass is treated similarly to population or abundance (Price et al., 2010), but the thermal response of biomass is also uncertain due to a paucity of data and reliable models, and because measuring and controlling for resource availability is often challenging (Price et al., 2010).

Empirical studies have provided mixed support for general relations between ecological characteristics and temperature. Measurements of species richness have produced a wide range of activation energies — not always the metabolic value predicted by MTE (Stegen et al., 2009). A study comparing the heating tolerances of fish to their population sizes in the wild suggests links between physiology and demography via species distribution patterns (Payne et al., 2021), but does not explain how phsyiological TRC scale up to the thermal response of population sizes. In a review of the rates of activities associated with ecological interactions (such as attack or escape velocity), it was found that the average activation energies were near that of metabolism, supporting MTE predictions about interactions (Dell et al., 2011). However, variability of activation energies for a variety of biological rates was found to increase from organismal to ecological levels (Dell et al., 2011). Additionally, data on mean activation energies of metabolism, physiological rates, performance rates, and interaction-related activities are only near the mean activation energy of metabolism when comparing species from very different environments or species of very different mass; variability increases considerably when comparing species from similar temperatures or of similar sizes (Tilman et al., 2004).

Some ambiguity in empirical tests of MTE arises because the effects of temperature are difficult to separate from many other internal and external variables in empirical observations (e.g. Huete-Stauffer et al., 2015; Irlich et al., 2009), posing challenges to reconciling theory with data. Additionally, interactions between species may play an important role in determining speciation, extinction, and diversification rates, and thereby obscure the effects of temperature (Ezard et al., 2011). Interspecific variation in TRC within ecosystems may also obscure patterns in ecosystem-level thermal response (Tilman et al., 2004; Stegen et al., 2009; Isaac et al., 2012). Indeed, modelling suggests that interspecific variation may impact ecosystem biomass structure (Bideault et al., 2021) and growth rates (B. Chen, 2022), and may decrease the thermal dependence of species richness (Stegen et al., 2009). Consequently, it remains unclear how biological responses propagate from organismal to ecosystem scales, and what layers of complexity obscure ecosystem-level thermal responses.

In this study, we incorporate MTE and TRC into the Tangled Nature (TaNa) model (Christensen et al., 2002), a model of ecology and evolution, to examine the propagation of physiological TRC to ecological properties that arise on geological timescales. We additionally investigate the effects of interspecific variation in species' optimal temperature of reproduction; a commonly used proxy for species fitness (Amarasekare & Savage, 2012). The TaNa model has been modified for temperature dependence before: Arthur and Nicholson (2023) scaled species fitness with temperature in the TaNa model by giving species an arbitrary, symmetrical hump-shaped TRC for interactions. Arthur and Nicholson (2023) focused on emergent feedbacks between species and climate, so ecosystem thermal responses were not expounded upon, and the paper did not incorporate any elements of MTE. Here, we integrate ecological theory into the TaNa model to investigate the mechanisms of scaling up thermal responses and the effects of diverse thermal optima. Our study additionally complements the work done by Stegen et al. (2009), in which a model developed by Loeuille and Loreau (2005) was modified to incorporate MTE principles, with the aim of explaining the variety of activation energies that have been measured for species richness. The model used by Stegen et al. (2009) is similar to the TaNa model: both define abstract species by a few traits (rather than representing specific species living on Earth), allow random mutations to produce new random species, and represent evolutionary timescales. The simplicity and long timescales of both models make them well-suited to testing MTE since MTE finds patterns shared by distinct species and ecosystems and assumes that species have had time to adapt to their environments (Price et al., 2010). The major difference between the TaNa model and the model used by Stegen et al. (2009) is that the TaNa model does not consider bodymass or trophic levels, which enables us to isolate the temperature component of MTE and minimize constraints on species interactions in our investigation. We also broaden the focus to investigate how physiological responses to temperature scale up to a variety of ecosystem thermal responses: ecosystem survival probability, abundance, species richness, species populations sizes and distributions, and interspecific interactions. This allows us to analyse how the physiological assumptions of MTE scale up to ecosystem-level properties if all species responded to temperature in the same way, and to investigate the extent to which interspecific variation in thermal optima obscures these responses.

2.2 Description of the Tangled Nature Model

2.2.1 General properties

The TaNa model is a mathematical model of ecology and evolution (Christensen et al., 2002). Ecology is represented by interactions between species which affect specific reproduction rates, and evolution is enabled by allowing mutations to produce new species. The model was originally developed to capture the dynamics of Punctuated Equilibria (Christensen et al., 2002), a widely observed pattern in the fossil record in which species morphology remains relatively constant over long periods of time (tens of thousands to tens of millions of years), and then changes in rapid bursts associated with changes in the biotic or abiotic environment experienced by species (Gould & Eldredge, 1977).

Stochasticity in the TaNa model causes every realization to follow a different trajectory, but Punctuated Equilibria emerge in all model simulations: the abundance of model communities fluctuates around the same mean for long periods called quasi-stable states, until a state is interrupted by an abrupt transitional period, called a quake, and a subsequent change in mean abundance, which is then maintained in the next quasi-stable state (Fig A.1). During quasi-stable states, ecological communities are dominated by just a few "core" species, defined as the most populous species and all other species with populations at least 10% as large[3]. The rest of the species are called "cloud" species, and these rarer species make up the majority of species richness during quasi-stable states.

Punctuated Equilibria arise in the TaNa model purely as a result of the interactions between species: positive interactions between core species stabilize the community in quasi-stable states, and these are only occasionally disrupted by mutant species with parasitic effects on core species (Arthur et al., 2017). Parameters are chosen in the model to reproduce realistic distributions of species populations (called Species Abundance Distri-

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[3] This terminology was first introduced by Becker and Sibani (2014).

butions, SADs; e.g. McGill et al., 2007), such that during quasi-stable states, the majority of the population is in the core and the majority of the species richness is made up of “cloud” species with relatively small populations (Anderson & Jensen, 2005).

2.2.2 Properties and operation of the TaNa model

Each TaNa model simulation is initialized with $D_0 = 60$ random species. The initial abundance ($N_0 = 500$) of individuals in the ecosystem is equally distributed between the species (some randomly selected species have one more initial individual than others to avoid fractional populations). Species are defined by binary numbers of $L = 20$ bits (allowing the potential for $2^L = 1,048,576$ distinct model species in each simulation).

In each timestep (t), $N(t)$ individuals are sequentially selected randomly with replacement. For each selected individual, a random number is drawn between 0 and 1, and if the number is smaller than the death probability ($p_{\text{death}} = 0.2$), the individual dies. If the selected individual survives, another random number is drawn, and the individual reproduces if the number is smaller than its reproduction probability (which depends on its fitness, explained below). If the individual reproduces, L more random numbers are drawn, and for each random number below the mutation probability ($p_{\text{mut}} = 0.01$), a bit in the species-specific binary number flips, giving the offspring a new binary number and thus a new species identity. As the evolutionary dynamics of the TaNa model represent geological timescales, it is assumed that each mutant species has already sufficiently diverged from the ancestral species to fill a new ecological niche (such that new interactions with the other species in the ecosystem have evolved).

The reproduction probability ($p_{\text{off,f}}$) of each species depends on ecological interactions of species i in a sigmoidal function of its fitness (f_i):

$$p_{\text{off,f}}(f_i, t) = \frac{1}{1 + e^{-f_i(t)}}. \tag{2.2}$$

Eq. 2.2 is centered at zero, such that a species with $f_i(t) = 0$ has a 50% chance of reproducing, $\lim_{f_i \to \infty} p_{\text{off}} = 1$, and $\lim_{f_i \to -\infty} p_{\text{off}} = 0$. The fitness of species i at time t is determined by its interactions with each other species j:

$$f_i(t) = -\mu N(t) + \sum_{j=1}^{D} J_{ij} \frac{N_j(t)}{N(t)}, \tag{2.3}$$

where μ is a damping factor (representing ecological resource constraints) that limits

TaNa model parameters (and their value in the original TaNa model)	
$p_{\text{off,T}}$	Temperature-dependent scaler of reproduction probability (1).
p_{death}	Probability of an individual dying in a timestep (0.2).
p_{mut}	Probability of a mutant species arising during reproduction (0.01).
μ	Damping coefficient on population growth (0.2).
L	Number of bits in species' identifying binary numbers (20).
C	Scale of interactions between species (100).
θ	Fraction of species pairs that have interactions (0.25).
Randomly assigned constants	
J_{ij}	Impact of species j on species i
State variables	
$N(t)$	Abundance (number of individuals in ecosystem) at time t.
$N_i(t)$	Population of species i at time t.
$D(t)$	Species richness (number of species in ecosystem) at time t.
Functions	
$f_i(t)$	Fitness of species i at time t (eq. 2.3)
$p_{\text{off,f}}(f_i, t)$	Interaction-dependent component of reproduction probability of species i at time t (Eq. 2.2)

Table 2.1: Parameters in the TaNa model remain constant for the duration of a simulation. The functions, fitness and reproduction probability, depend on the fitness of each species at each timestep.

growth of each species in proportion to the abundance ($N(t)$) of the ecosystem, $D(t)$ is the species richness (number of extant species) at time t, J_{ij} is the effect of species j on species i, and $N_j(t)$ the population of species j at time t.

The interactions between species are prescribed from the interaction matrix (**J**), made up of random numbers J_{ij} drawn from a product normal distribution centered at zero and for which each normal distribution has a standard deviation of $C = 100$. The leading diagonal of the matrix is set to zero ($J_{\text{ii}} = 0$), such that organisms cannot have ecological interactions with members of their own species (other than through density-dependence, which is included at the ecosystem-level through the negative μ term in Eq. 2.3). A fraction $1-\theta$ of the elements in matrix **J** are set to zero, representing species pairs that do not interact at all. Connectance (θ) is set to 0.25 to produce realistic SADs in the model (Anderson & Jensen, 2005). TaNa model variables are summarized in Table 2.1.

2.3 Methods: TaNa+T

2.3.1 Temperature-dependence of physiological parameters

We modify the three physiological parameters of the TaNa model to create a temperature-dependent version called the TaNa+T. To include the impact of temperature on reproduction rates ($b(T)$), we use a unimodal, left-skew curve from the Python scipy toolkit (called "skewnormal" in the Scipy package; Fig. 2.1, red dashed line). This curve can be shifted to any temperature without changing shape. It is parameterized to match the general TRC for reproduction derived in Amarasekare and Savage (2012) (the second term in Eq. 11 of that paper), and the parameters we used in that equation are listed in A.2.

The TaNa model uses probabilities to determine which individuals die, reproduce, and mutate (rather than prescribing population-level rates), so we scale $b(T)$ to have a maximum of 1 (using a scaling factor of 3.0), giving a temperature-dependent reproduction probability with a peak at T_{opt}:

$$p_{\mathrm{off,T}} \propto b(T) \tag{2.4}$$

(Fig. 2.1, black dot-dash line). The combined effect of both temperature and fitness on reproduction probability is then modeled as

$$p_{\mathrm{off,total}}(f_i, t, T) = p_{\mathrm{off,T}} p_{\mathrm{off,f}}(f_i, t), \tag{2.5}$$

where $p_{\mathrm{off,total}}$ is the temperature- and fitness-dependent reproduction probability (Fig. 2.2).

The temperature dependence of death probability is modeled in the form of the Arrhenius-Boltzmann equation:

$$p_{\mathrm{death}}(T) = d_0 \exp\left(-E_{\mathrm{a}}/(kT)\right), \tag{2.6}$$

where d_0 is a scaling factor and E_{a} is the activation energy of death (set to $E_{\mathrm{a}} = 0.49\mathrm{eV}$) (Amarasekare & Savage, 2012). We set $d_0 = 8.17 \times 10^7$ such that at a control temperature ($T_{\mathrm{ctrl}} = 303K$), $p_{\mathrm{death}}(T_{\mathrm{ctrl}}) = 0.2$; the value of death probability in the orignial TaNa model (Fig. 2.1, 2.3)).

The temperature dependence of mutation probability (p_{mut}) also takes the form of the Arrhenius-Boltzmann equation:

$$p_{\mathrm{mut}}(T) = m_0 \exp\left(-E_{\mathrm{a}}/(kT)\right), \tag{2.7}$$

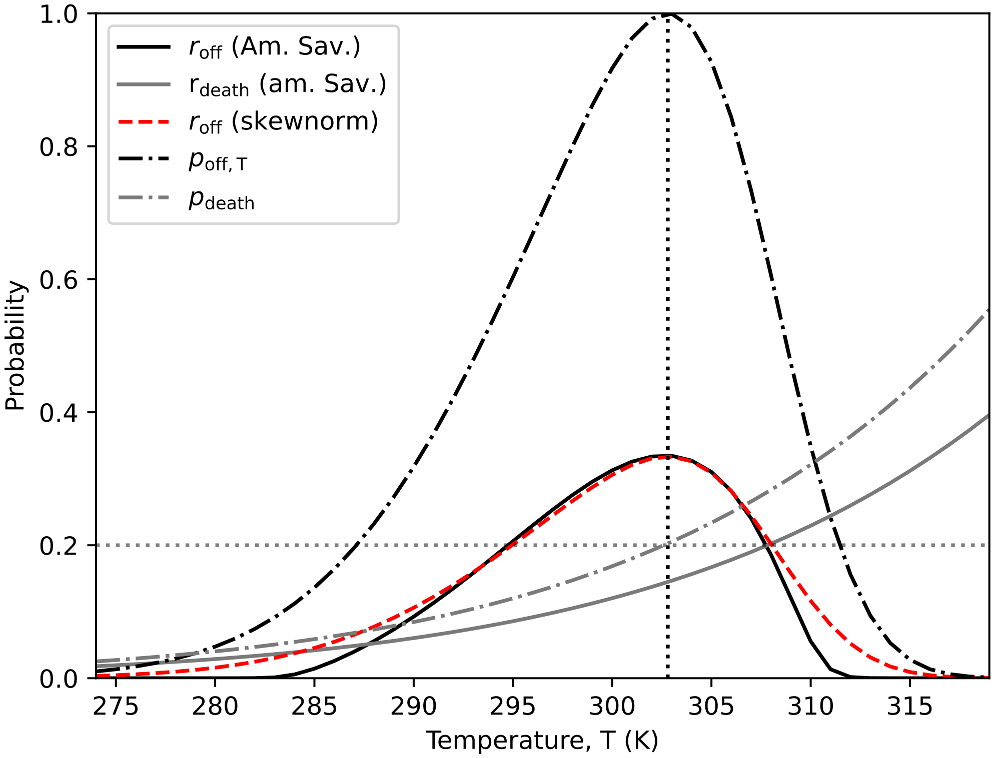

Figure 2.1: Birth and death rates from Amarasekare and Savage, 2012 Eqs. A.1 and 2.6 (solid black and grey lines, respectively), the skewnormal curve used to approximate Eq. A.1 in various-TRC experiments (red dashed line), and reproduction and death probabilities used in the TaNa+T (black and grey dot-dashed lines, respectively). The vertical dotted line shows the temperature at which $p_{\mathrm{off,T}}$ peaks ($T_{\mathrm{ctrl}} = 303\mathrm{K} \approx 30^{o}\mathrm{C}$), and the horizontal line at 0.2 shows that p_{death} is at its control value at T_{ctrl}. Temperature is reported in Kelvin, ranging from about 1^{o}C at 274K to 47 ^{o}C at 320K.

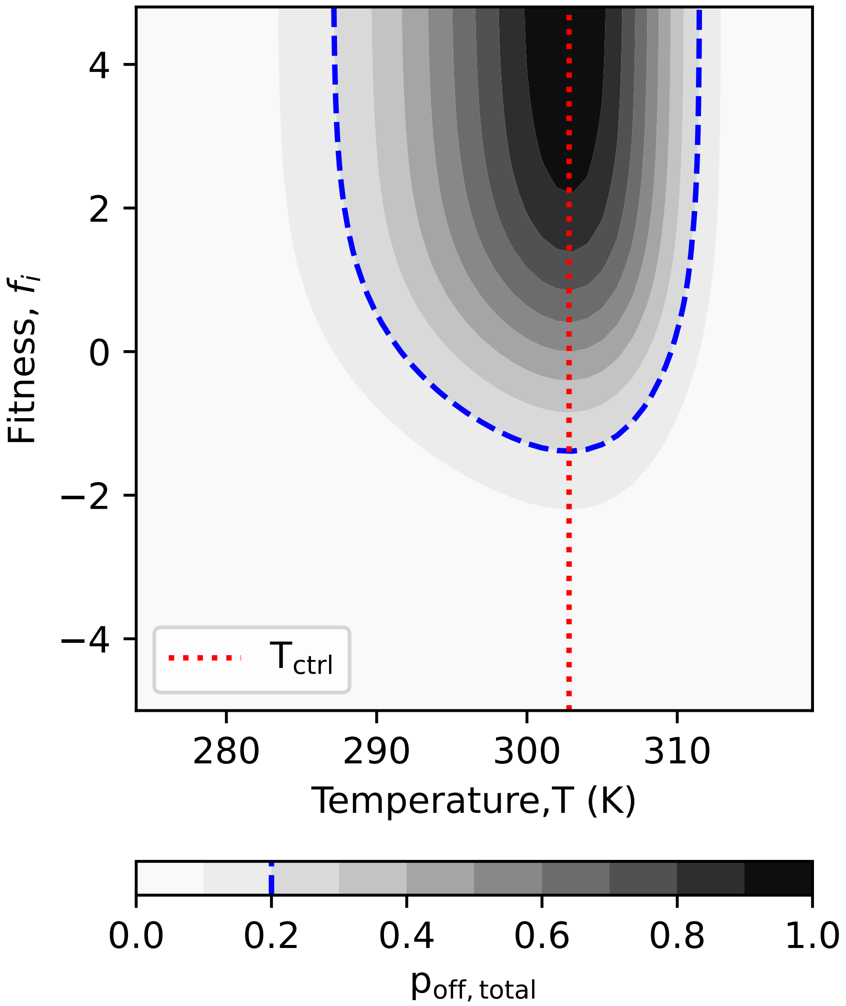

Figure 2.2: Reproduction probability ($p_{\text{off,total}}$; Eq. 2.5) as a function of temperature (T; horizontal axis) and fitness (f_i; vertical axis). The dotted red line shows the control temperature ($T_{\text{ctrl}} = 303$K), at which $p_{\text{death}}(T_{\text{ctrl}}) = 0.2$ and $p_{\text{off,T}}(T_{\text{ctrl}}) = 1$. The dashed blue contour shows $p_{\text{off,total}} = 0.2$, the minimum $p_{\text{off,total}}$ required for a species to survive at the reference death probability ($p_{\text{death}}(T_{\text{ctrl}}) = 0.2$) from the original TaNa model. Note that at a fixed T, the fitness of a species can change over time due to changes in ecosystem abundance (N) or changes to the relative abundances of other species (n_j; see Eq. 2.2), so $p_{\text{off,total}}(i, t, T)$ may vary between species and over time for each species.

where m_0 is a scaling factor (set to 3.58×10^6 so $p_{\mathrm{mut}}(T_{\mathrm{ctrl}}) = 0.01$; the control value) (Gillooly et al., 2005; Stegen et al., 2009, shown in Fig. 2.3). Although the form of p_{death} and p_{mut} is exponential, the values of p_{death} and p_{mut} realized in the TaNa+T (for T between 274K and 320K) do not approach 1, so we do not modify the equation to saturate at 1.

2.3.2 Experimental set-up

We perform in silico experiments with three model configurations to: 1) explore the effects of each of the three physiological parameters on the model generally (parameter exploration; 50 simulations at each parameterization); 2) investigate ecological response to temperature without the complication of thermal diversity ("single-TRC" experiment; 250 simulations at each temperature); and 3) examine the effects of interspecific variation in TRC on ecological response to temperature ("various-TRC" experiment; 250 simulations at each temperature). All simulations are run for 10,000 generations.

In the parameter exploration, we examine the effects of reproduction, death, and mutation probabilities on the model without linking their values to temperature. Although the term we use to scale the interaction-dependent component of reproduction is not associated with temperature in the parameter exploration, we still refer to it as $p_{\mathrm{off,T}}$ for consistency with Eq. 2.5 and with the temperature-dependent sections. We vary both $p_{\mathrm{off,T}}$ and p_{death} from 0.1 to 1 along intervals of 0.1, (while allowing $p_{\mathrm{off,f}}$ to emerge in the model as usual). This parameter range includes the control values or reproduction ($p_{\mathrm{off,T}} = 1$) and death ($p_{\mathrm{death}} = 0.2$) and also ranges across all possible probabilities. We linearly vary mutation probability from 0.004 to 0.019 along intervals of 0.003. One-dimensional explorations of the other parameters in the model are reported in A.3. Fifty simulations were run at each parameterization.

In "single-TRC" experiments, $T_{\mathrm{opt}} = T_{\mathrm{ctrl}}$, so all species have identical TRCs for reproduction, death, and mutation probabilities (Fig. 2.3a). We run 250 single-TRC experiments at each constant temperature between 274K and 320K (1-47^{o}C; the range of temperatures in which most species live; Gillooly et al., 2001) in intervals of 3K. Single-TRC experiments simplify the scaling up of thermal response from a single species to a community, and isolate the effects of ecological interactions on affecting community-level thermal response, enabling us to investigate how thermal response propagates from the individual to the ecosystem in a scenario without interspecific variation in thermal preferences. These experiments also set a baseline to which results from more complicated evolutionary set-ups can be compared, and the similaries and differences between the idealized and

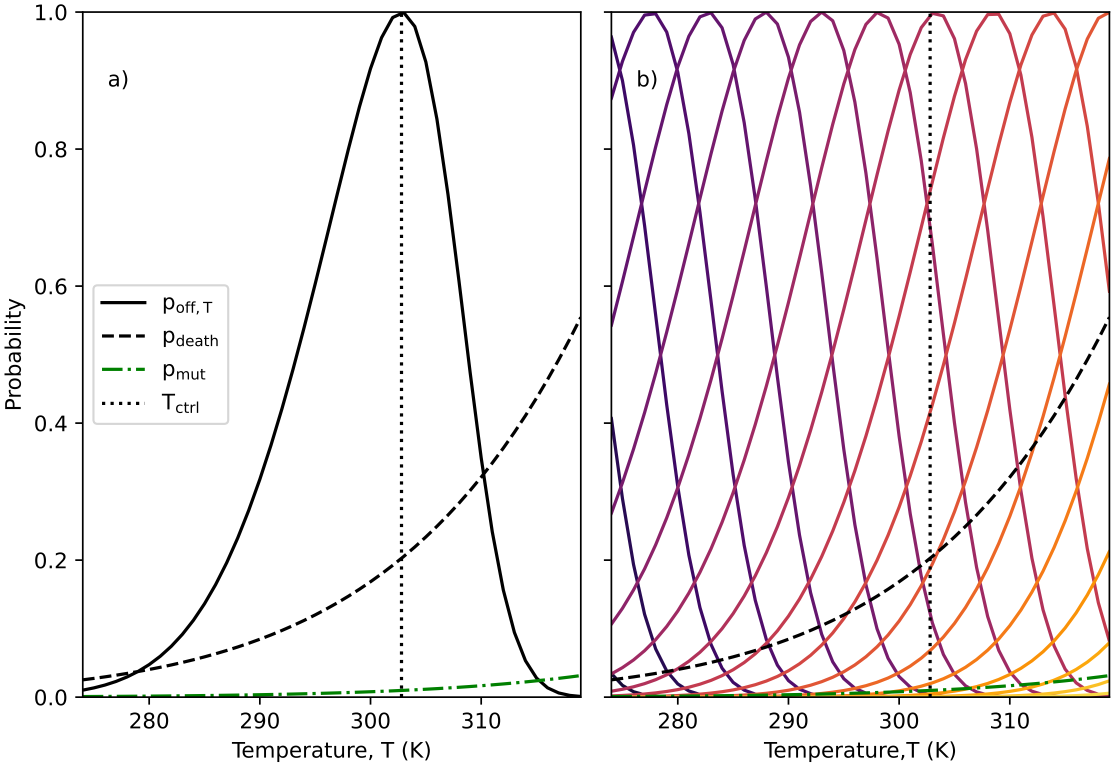

Figure 2.3: The experimental set-ups of a) single-TRC and b) various-TRC experiments. Solid lines show reproduction probabilities; several example TRC are shown for various-TRC experiments (colors in panel b). Black dashed lines show death probability (p_{death}); the same exponential curve in both setups. Green dot-dashed lines show mutation probability (p_{mut}) in both experimental set-ups. The vertical black dotted line shows the control temperature, at which all TaNa+T parameters correspond to those used in the original TaNa model.

more realistic cases provide insight into the effects of evolution on community response to temperature.

In "various-TRC" experiments, we allow the TRC of reproduction to vary between species (Fig. 2.3b). These simulations enable species to adapt to their environment, and species experience selective pressures both due to temperature-adaptation and to species interactions. In various-TRC simulations, species-specific T_{opt} values ($T_{\mathrm{opt,i}}$) are drawn from a uniform distribution between 263 and 330K (-10 and 53^{o}C) — extending above and below the temperature range at which experiments are run in order to minimize edge-effects. 250 various-TRC simulations are run at each constant temperature between 274K and 320K in intervals of 3K.

2.4 Results

We first present the results of the parameter exploration (Sec. 2.4.1), in which we vary the temperature-dependent component of reproduction probability ($p_{\mathrm{off,T}}$), death probability (p_{death}), and mutation probability (p_{mut}) in the same way for all species. We then present the results of the temperature-dependent TaNa model (TaNa+T), in which each temperature corresponds to a specific value of p_{death} and p_{mut} (Sec. 2.4.2). This section includes both the results for single-TRC experiments (in which $T_{\mathrm{opt}} = T_{\mathrm{ctrl}}$ for all species) and various-TRC experiments (in which species have different thermal optima of reproduction ($T_{\mathrm{opt,i}}$)).

We analyse ecosystem-level responses to temperature based on five different ecosystem characteristics all measured at the end of the 10,000 generation simulations. The section on temperature-dependence of the TaNa model (Sec 2.4.2) is broken down into subsections corresponding to each of these five model outputs. First, ecosystem survival probability is the fraction of experiments in which any organisms exist at the end of the simulation. Second, abundance is the total number of individuals in the ecosystem. Third, species richness is the number of species in the ecosystem. Fourth, SADs are distributions of species populations. Finally, interactions are the J_{ij} values of surviving organisms in ecosystems.

2.4.1 Parameter exploration

In the simulations presented in this section, parameters are varied independently from each other, and reproduction, death, and mutation probabilities are not associated with

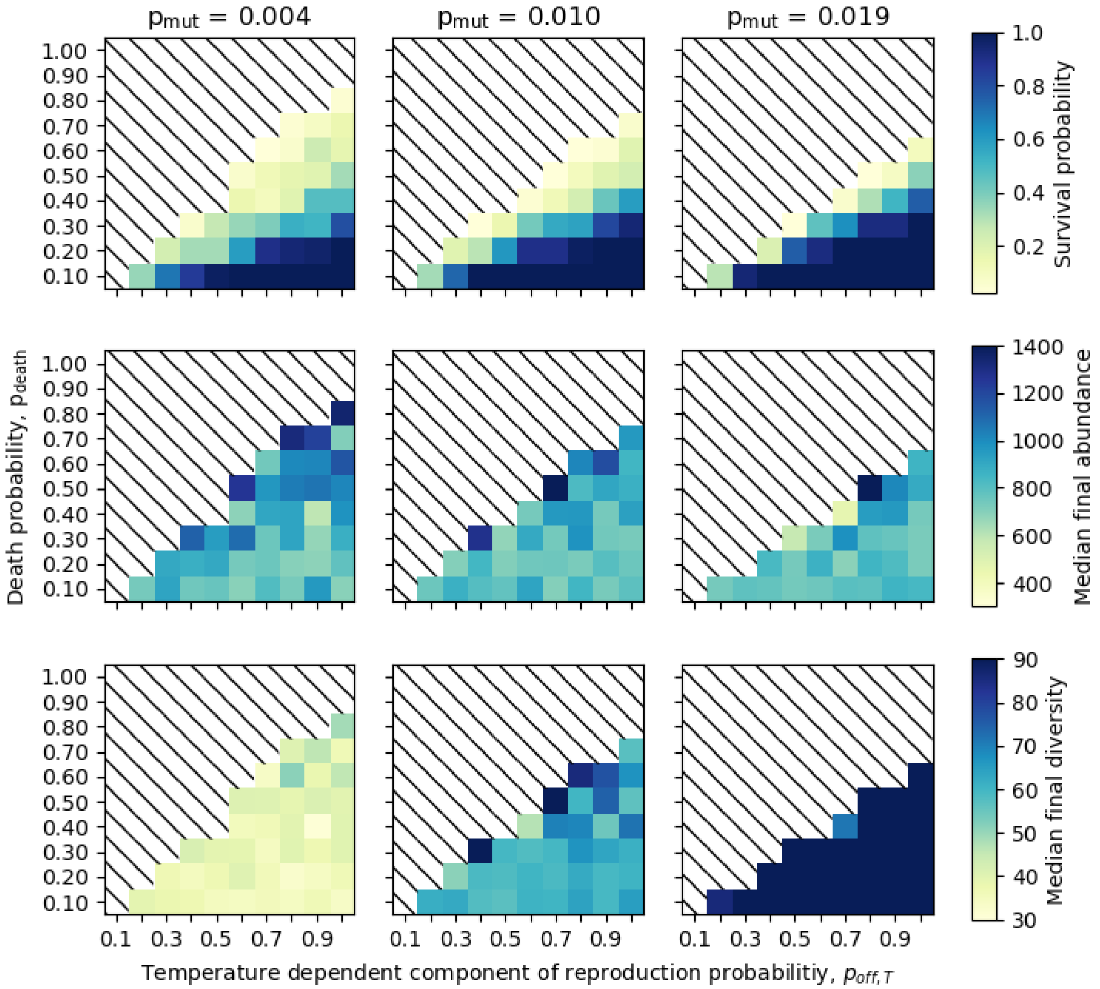

Figure 2.4: Parameter exploration of the temperature-dependent component of reproduction probability ($p_{\mathrm{off,T}}$; here not associated with temperature; horizontal axes), death probability (p_{death}; vertical axes), and mutation probability (p_{mut}; columns). Fifty TaNa model simulations were run for 10,000 generations at each parameterization. Colors of the boxes indicate the fraction of surviving experiments (top row), median abundance (middle row), and median species richness (bottom row) at the end of simulations. The hashed regions indicate parameterizations at which no simulations survived to 10,000 generations.

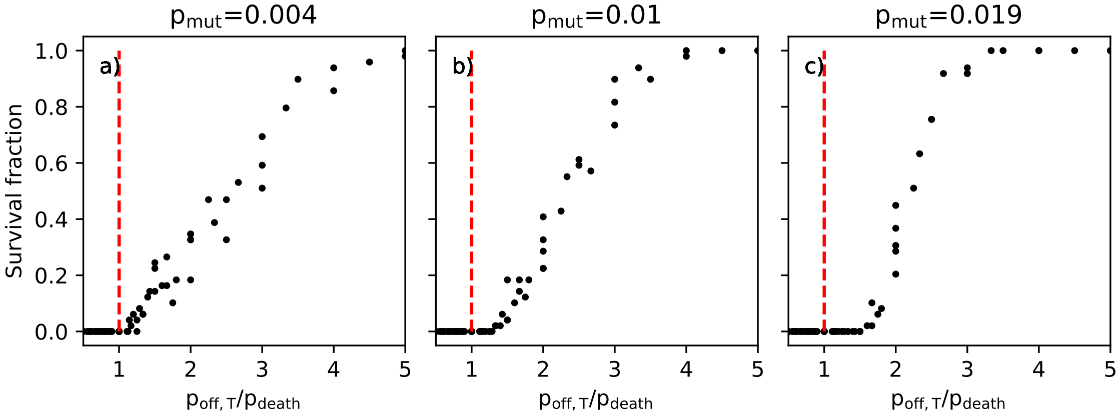

Figure 2.5: The relationship between survival fraction and $\frac{p_{\mathrm{off,T}}}{p_{\mathrm{death}}}$ is shown for $p_{\mathrm{mut}} = 0.004$, 0.01, and 0.019 (panels a,b,c, respectively). The dashed red lines show $p_{\mathrm{off,T}}/p_{\mathrm{death}} = 1$. Values of $p_{\mathrm{off,T}}/p_{\mathrm{death}}$ less than 0.5 (not shown) are all zero; values greater than 5 are all near 1.

temperature.

In the parameter exploration, we find that ecosystem survival probability is positively correlated with $p_{\mathrm{off,T}}$ and inversely correlated with p_{death} (Fig. 2.4, top row). No ecosystems survive if $p_{\mathrm{death}} > p_{\mathrm{off,T}}$ because no species could survive with $p_{\mathrm{off,total}} < p_{\mathrm{death}}$. For $\frac{p_{\mathrm{off,T}}}{p_{\mathrm{death}}} > 1$, ecosystem survival probability increases monotonically with $\frac{p_{\mathrm{off,T}}}{p_{\mathrm{death}}}$ (Fig. 2.5).

The slope of increase in ecosystem survival probability relative to $\frac{p_{\mathrm{off,T}}}{p_{\mathrm{death}}}$ depends on mutation probability (Fig. 2.5). Smaller values of p_{mut} increase ecosystem survival probability in harsher conditions (when $p_{\mathrm{off,T}}$ is near p_{death}), but also decrease the rate at which ecosystem survival probability increases relative to $\frac{p_{\mathrm{off,T}}}{p_{\mathrm{death}}}$; consequently, larger values of $\frac{p_{\mathrm{off,T}}}{p_{\mathrm{death}}}$ are required before ecosystem survival probability finally reaches 1 when p_{mut} is small. At larger mutation probabilities, a larger ratio of $\frac{p_{\mathrm{off,T}}}{p_{\mathrm{death}}}$ is required for ecosystem survival when $p_{\mathrm{off,T}}$ is close to p_{death}, but ecosystem survival probability then increases more steeply and reaches 1 at smaller $\frac{p_{\mathrm{off,T}}}{p_{\mathrm{death}}}$.

Ecosystem survival probability is indicative of the values of $p_{\mathrm{off,f}}$ occurring in ecosystems. Recall that species specific values of $p_{\mathrm{off,f}}$ depend on the random interactions between species, leading to selection on species depending on their interactions, so the distribution of $p_{\mathrm{off,f}}$ is an emergent property in the TaNa+T. Survival of any species requires $p_{\mathrm{off,total}} > p_{\mathrm{death}}$ for that species, and using $p_{\mathrm{off,total}} = p_{\mathrm{off,T}} p_{\mathrm{off,f}}$ (Eq. 2.5), species survival requires $\frac{p_{\mathrm{off,T}}}{p_{\mathrm{death}}} > \frac{1}{p_{\mathrm{off,f}}}$. In the control case ($p_{\mathrm{mut}} = 0.01$), ecosystem survival probability is first positive when $\frac{p_{\mathrm{off,T}}}{p_{\mathrm{death}}} \approx 1.2$, suggesting that $p_{\mathrm{off,f}} > 0.83$ is very unlikely. The value of $\frac{p_{\mathrm{off,T}}}{p_{\mathrm{death}}}$ at which ecosystem survival probability first reaches ≈ 1 occurs when $\frac{p_{\mathrm{off,T}}}{p_{\mathrm{death}}} \approx 4$. As almost all ecosystems survive in these conditions, it suggests that values of $p_{\mathrm{off,f}}$ of at least 0.25 are a common occurrence amongst mutant species outside of quasi-steady states at this mutation probability. The threshold value of $p_{\mathrm{off,f}}$ required for ecosystem survival depends on p_{mut}.

Abundance of all surviving ecosystems is not affected by $p_{\mathrm{off,T}}$, death probability, or mutation probability (Fig. 2.4, second row). Consequently, we do not expect abundance to vary with temperature, unless interspecific variation in TRC produces its own effect on abundance in various-TRC simulations.

Species richness increases with increasing mutation probability (Fig. 2.4, bottom row). It is unaffected by $p_{\mathrm{off,T}}$ and death probability.

The impacts of all 7 model parameters are summarized in A.3.

2.4.2 Effects of temperature on the TaNa model

We now present our investigation of the behaviour of the TaNa+T model, in which each temperature is associated with a particular value of p_{death} and p_{mut}, and $p_{\mathrm{off,T}}$ depends on temperature and species specific values of $T_{\mathrm{opt,i}}$.

Ecosystem survival probability

In TaNa+T simulations, ecosystem survival probability is temperature-dependent, with a response shape that is sensitive to interspecific variation in TRC. When all species have the same TRC (single-TRC simulations), ecosystem survival probability has a top-hat-shaped response to temperature: it is zero at temperatures below approximately $280\mathrm{K}$ ($\approx 7^{o}$C; temperatures at which $p_{\mathrm{death}} > p_{\mathrm{off,T}}$) and above $T \approx 310\mathrm{K}$ ($\approx 37^{o}$C; the upper temperature at which $p_{\mathrm{death}} > p_{\mathrm{off,T}}$; Fig. 2.6a, black line), and ecosystem survival probability is near 1 between those temperatures. The shape of this thermal response is wider and more symmetrical than the TRC of reproduction.

The thermal response of single-TRC ecosystem survival probability is controlled by the constraints on species fitness. For a species to survive, its total reproduction probability ($p_{\mathrm{off,total}}$) must be larger than its death probability (p_{death}). Substituting Eq. 2.5 for $p_{\mathrm{off,totoal}}$ and rearranging the equation, we can see that species survival requires $p_{\mathrm{off,f}} > \frac{p_{\mathrm{death}}}{p_{\mathrm{off,T}}}$. Solving for fitness ($f_i$) using Eq. 2.2, an individual must have a fitness

$$f_i > -\log\left(\frac{p_{\mathrm{off,T}}}{p_{\mathrm{death}}} - 1\right) \tag{2.8}$$

in order to survive. Indeed, ecosystem survival probability increases as the threshold fitness required for species survival decreases (Fig. 2.6a). The thermal response of ecosystem survival probability is very similar when mutation probability (p_{mut}) is held constant (Fig. 2.6a, red line), suggesting that mutation probability does not have a strong impact on ecosystem survival probability, and the minor effect of mutation probability can be explained by Fig. 2.5a from the parameter exploration.

In various-TRC experiments ($T_{\mathrm{opt,i}}$ varies between species), the thermal response of ecosystem survival probability decreases quasi-linearly from around 0.95 at the coldest temperature to zero at the warmest temperature (Fig. 2.6b). The shape of the thermal response of various-TRC experiments is again determined by the threshold fitness required for species survival, $-\log(\frac{p_{\mathrm{off,T}}}{p_{\mathrm{death}}} - 1)$ (shown for several example $T_{\mathrm{opt,i}}$ in the blue lines in Fig. 2.6b). In temperatures below $297\mathrm{K}$, ecosystem survival probability is slightly smaller

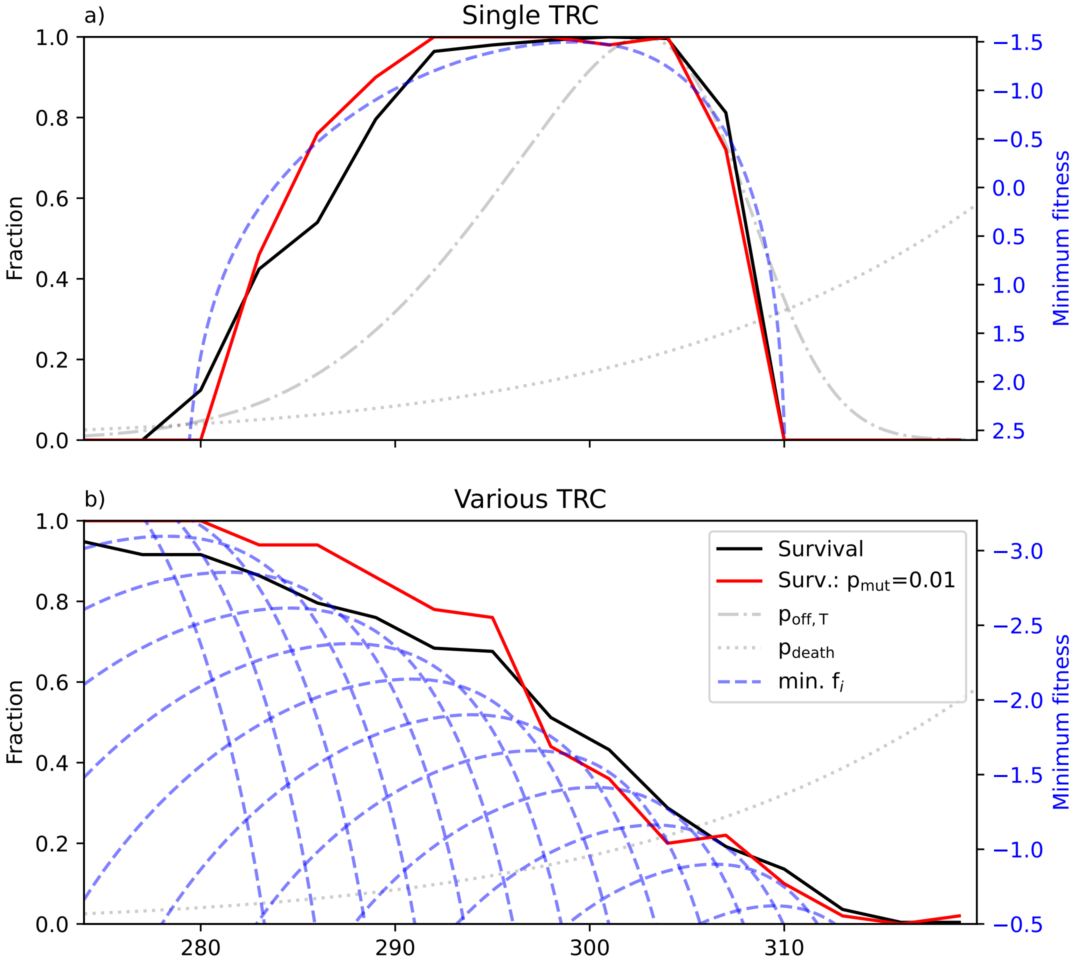

Figure 2.6: a) The fraction of surviving experiments out of 250 single-TRC TaNa+T simulations at each temperature (black), compared to the fraction of surviving ecosystems out of 50 single-TRC simulations run at each temperature with $p_{\mathrm{mut}} = 0.01$ (red). The light grey dash-dotted and dotted lines shows the input $p_{\mathrm{off,T}}$ and $p_{\mathrm{death}}(T)$, respectively. The blue dashed line shows the minimum fitness required for a species to survive (- $\log(\frac{p_{\mathrm{off,T}}}{p_{\mathrm{death}}} - 1)$) at each temperature (corresponding to the vertical axis on the right, axis inverted for comparison to ecosystem survival fraction). b) Same as for a), but for various-TRC simulations, and the blue dashed lines in b) show the minimum fitness threshold for several example values of $T_{\mathrm{opt,i}}$ that various-TRC organisms could have.

when p_{mut} varies with temperature than when it is held at $p_{\mathrm{mut}} = 0.01$ (Fig. 2.6b, red dashed line) showing that smaller values of p_{mut} still decrease large values of ecosystem survival probability when TRC vary between species (the same as when all species have the same TRC; Fig. 2.5). The survival fraction decreases with temperature because the maximum probability of reproduction in various-TRC experiments does not vary with temperature, whereas the probability of death does.

Ecosystem abundance

The abundance of individuals in surviving ecosystems, as well as their partitioning of individuals into cores and clouds, is relatively constant across temperatures, regardless of whether TRC vary between species or not (Fig. 2.7 a,b,g,h). This aligns with findings from Sec. 2.4.1. Additionally, as $p_{\mathrm{off,T}}$ does not affect abundance (Fig. 2.4), interspecific variation in $p_{\mathrm{off,T}}$ has no effect on abundance and the thermal response of abundance is the same in single-TRC and various-TRC simulations. Consequently, the only possibly response of abundance to temperature would be through the thermal response of ecosystem survival probability: if mean abundance was measured across both surviving and extinct ecosystems, with zeros in harsher climates driving the mean down, the thermal response of abundance would have the same shape as that of ecosystem survival probability (not shown), and abundance would therefore appear to depend on both temperature and interspecific variation in TRC.

Species richness

Species richness of ecosystems (the number of species) increases in warmer temperatures, whether TRC vary between species or not (Fig. 2.7 c,d). In Arrhenius plots, the logarithm of the response metric is plotted against $\frac{1}{kT}$, such that exponentials appear as straight lines with a slope equal to the actiavtion energy (E_a) in the Arrhenius equation (Eq. 2.1). In Fig. 2.7 c,d, species richness indeed appears as a straight line, with a slope close to that of metabolism (blue dashed line), suggesting that the TRC of richness scales up from metabolic processes. As shown above (Sec. 2.4.1), mutation drives the thermal response of species richness in single-TRC simulations. The thermal response of species richness in various-TRC is the same because reproduction does not affect species richness (Sec. 2.4.1), so interspecific variation in the TRC of reproduction has no effect.

The number of core species also increases with warmer temperatures in single-TRC and various-TRC experiments; from about 2 to 4 core species in both (Fig. 2.7 i,j). How-

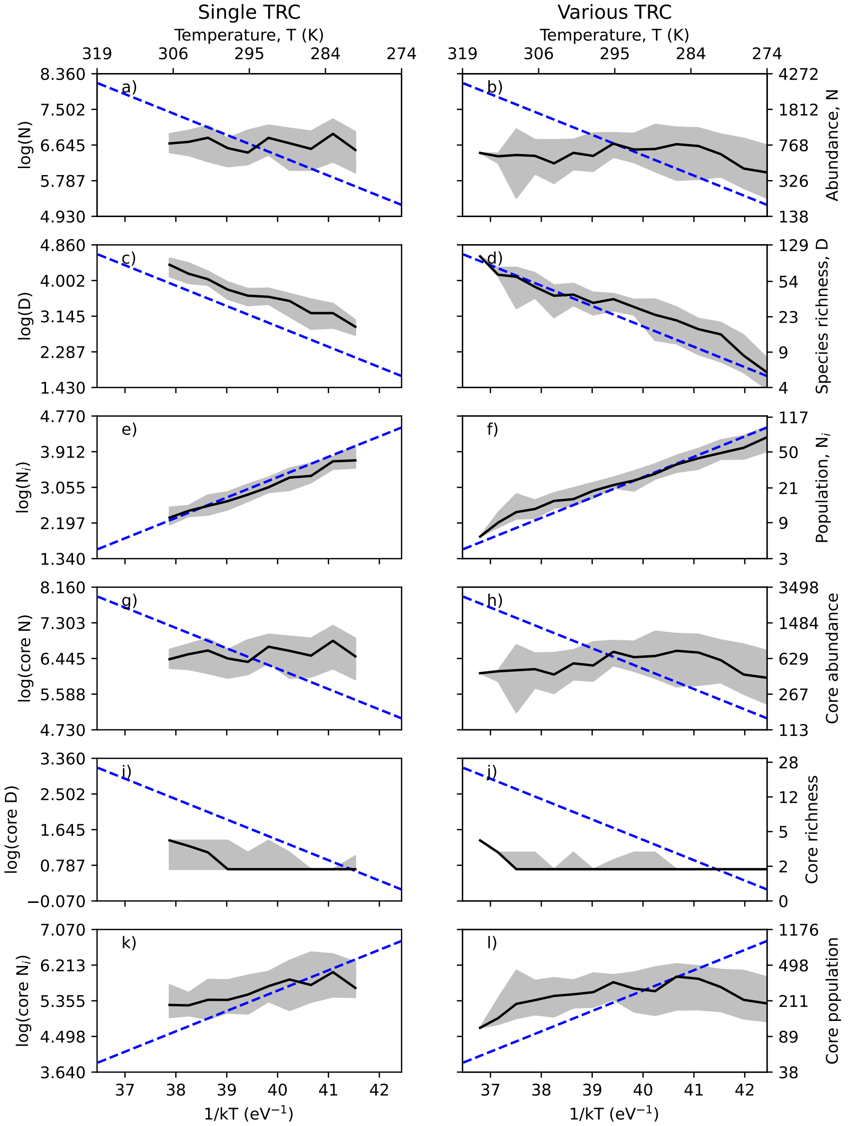

Figure 2.7: Rows from top to bottom: Arrhenius plots of 1. median abundance, 2. species richness, 3. population size, 4. core abundance, 5. core species richness, and 6. core population size for single-TRC (left) and various-TRC (right) experiments (interquartile ranges in the shaded grey regions). Blue dashed lines have slopes of -0.49eV (a-d, g-j) and 0.49eV (e,f,k,l), showing the activation energy (E_a) of metabolism. Horizontal axes are labeled in units of Kelvin along the top, and units of $\frac{1}{kT}$ on the bottom. Vertical axes are logarithmic, with corresponding real values on the right.

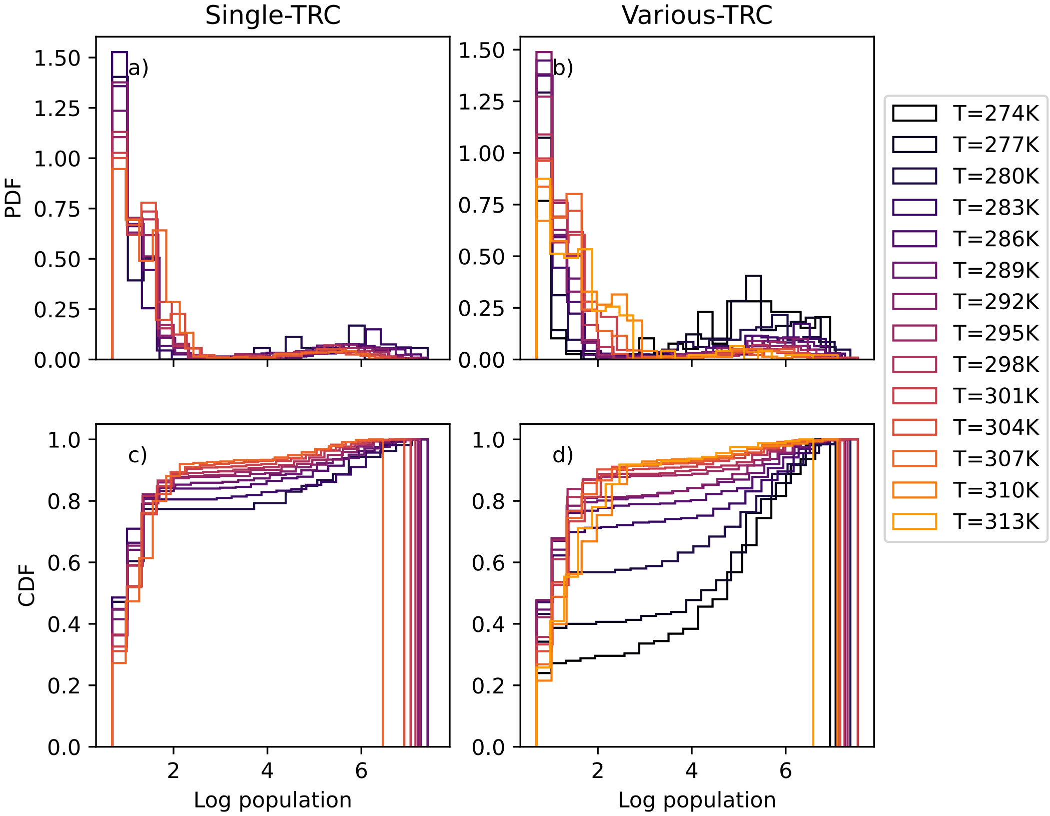

Figure 2.8: Histograms plotted as Probability Density Functions (PDFs; top row) and Cumulative probability Density Functions (CDFs; bottom row) of Species Abundance Distributions (SADs) for single-TRC (left) and various-TRC (right) experiments. The bimodality of the PDFs shows the cloud (left) and core (right) species. The CDFs exhibit the temperature dependence more clearly.

ever, the activation energy of core species richness is smaller than the metabolic value (i.e. the slope of core species richness in the Arrhenius plots is shallower than the blue dashed lines). Thus, metabolic processes have a weaker impact on core species richness than on cloud species richness.

Population sizes and SADs

Average population sizes of species in ecosystems decrease exponentially as temperature increases in both single-TRC and various-TRC experiments (Fig. 2.7 e,f), while they remain relatively constant across temperatures in cores (Fig. 2.7 k,l). The thermal response

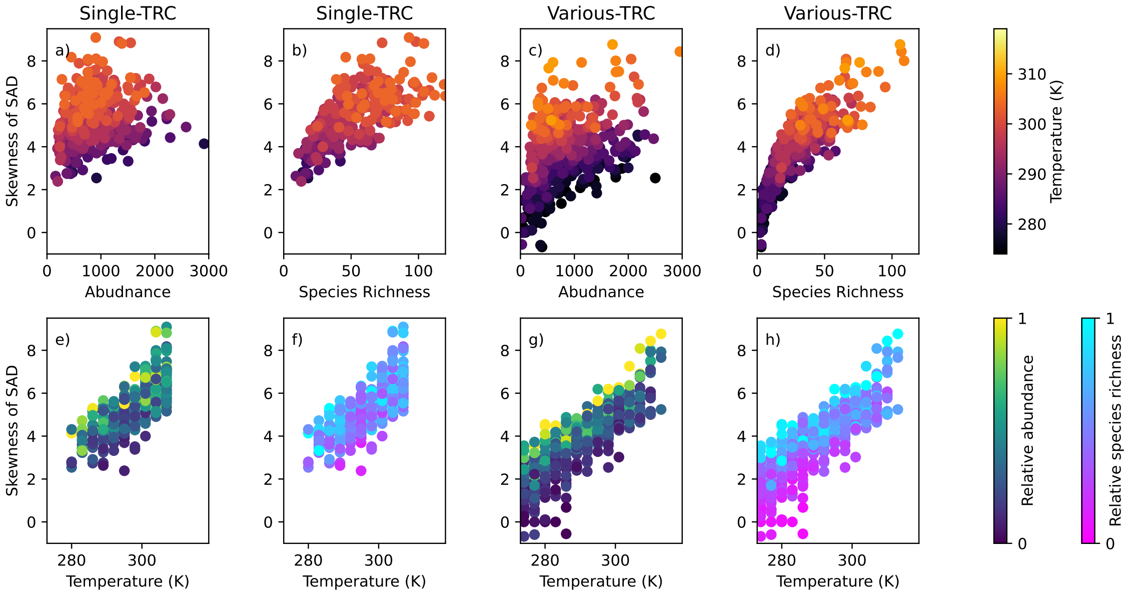

Figure 2.9: Scatter plots of skewness of Species Abundance Distributions (SADs) of the logarithm of species populations relative to: a,c) ecosystem abundance, b,d) species richness, and e-h) temperature. Colors in panels a-d) correspond to the temperature of the single model runs. The first two columns correspond to single-TRC exeperiments and the last two to various-TRC. In panels e) and g), the colors at each temperature correspond to the relative abundance at that temperature, and in panels f) and h), the colors correspond to the relative species richness at that temperature. The information in each column is the same, with the x-axis and colorscheme switched between rows.

of average population size in ecosystems is driven by the thermal response of species richness (since abundance is temperature-independent), and species richness is in turn driven by the thermal response of mutation rate (Sec. 2.4.2). Interspecific variation in TRC does not affect the thermal response of average population sizes because it does not affect abundance or species richness.

All ecosystems exhibit a typical SAD shape, with the majority of the abundance made up by a few core species, and with many more cloud species than core species (Fig. 2.8). The shape of SADs is temperature-dependent, with increasing diversity of cloud species emerging in warmer temperatures (Fig. 2.8). As a result, SADs become more positively skewed as temperature increases (Fig. 2.9 e,f,g,h). SAD skewness is additionally correlated with both species richness and abundance (Fig. 2.9 a,b,c,d). In single-TRC experiments, there is no relationship between SAD skewness and abundance or species richness for ecosystems at the same temperature (no color gradient in Fig. 2.9 e,f), so abundance and species richness do not drive SAD skewness. However, in various-TRC experiments, abundance and species richness do appear to affect skewness within each temperature (trend in colors in Fig. 2.9 g,h), with more abundant and more diverse ecosystems exhibiting more positive SAD skewness (more cloud species).

Interactions between species

In both single-TRC and various-TRC experiments, mean interactions (J_{ij}) are more positive in colder temperatures, and decrease to almost zero in the warmest temperatures (Fig. 2.10, black). In particular, core species show a clear decreasing trend in mean interaction strength relative to temperature (Fig. 2.10, top row, black dots). However, Arrhenius plots show that the rate of decrease in mean interaction strengths is steeper in the ecosystem than for core species (Fig. 2.10, bottom row, black lines). The thermal response of mean ecosystem interactions has an activation energy near the metabolic value ($E_a = 0.49$eV; Fig. 2.10, bottom row, black dashed lines), whereas core interactions have a slightly smaller activation energy. No thermal response is detectable in experiments in which p_{mut} was held constant (red dots and lines in Fig. 2.10), so as for species richness and average population size, the thermal response of ecosystem and core interactions is caused by the TRC of mutation ($p_{\text{mut}}(T)$).

Pairwise interactions can be categorized into five types: mutualistic (both species benefit one another), competitive (both species harm one another), predatory (one species benefits while the other is harmed), one-way positive (one species benefits without im-

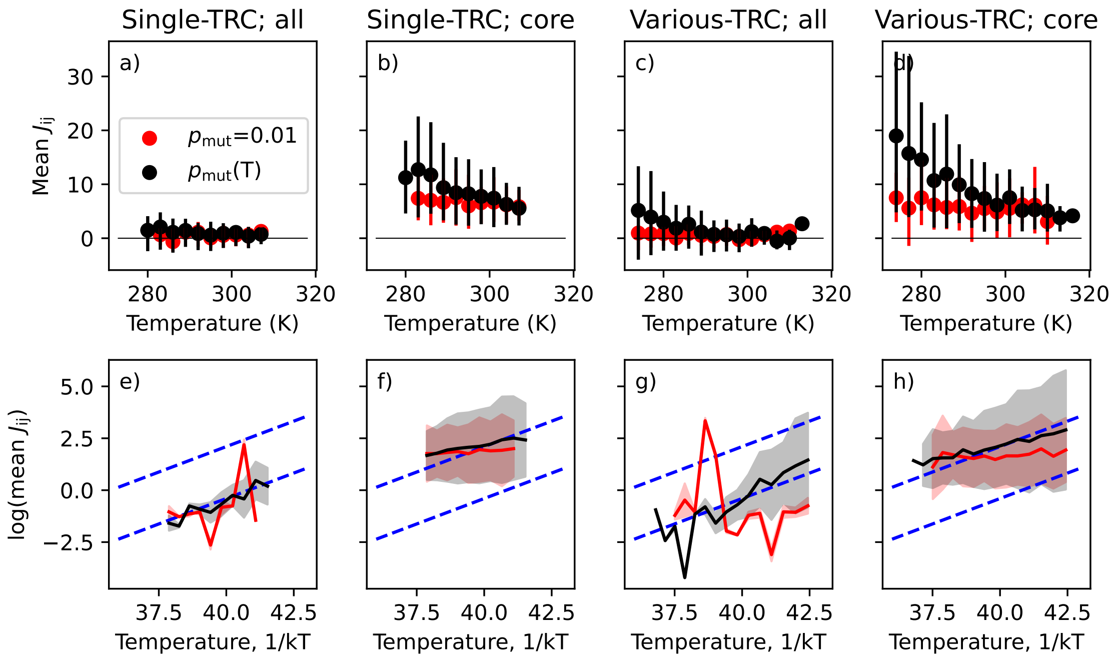

Figure 2.10: Top row: Mean of within-ecosystem mean interactions (J_{ij}) for single-TRC (first two panels) and various-TRC (last two panels) between all species in the ecosystem and between core species only. Vertical lines show the 10th to 90th percentiles. Results from 250 TaNa+T simulations at each temperature are shown in black ($p_{\mathrm{off,T}}$, p_{death}, and p_{mut} all vary with with temperature). Results from 50 simulations in which p_{mut} was held constant are shown in red. Bottom row: The same information is shown on Arrhenius plots, except the shaded regions show mean ± one standard deviation. The blue dashed lines have a slope corresponding to the activation energy of metabolism ($E_a = 0.49$eV).

pacting the other), one-way negative (one species is harmed without impacting the other), or no interaction. The fraction of species pairs with any interactions relative to all possible interactions is the emergent connectance. In TaNa+T simulations, interaction types do not vary with temperature for ecosystems or cores in any of the simulations run (not shown). Ecosystem connectance does not evolve away from θ (the preset fraction of species that interact) for core or cloud species in any temperature, and the fractions of each interaction type are relatively constant across temperatures. This suggests that interaction types are not important traits that undergo selection in the TaNa+T.

2.5 Discussion

The primary aim of this study is to investigate how physiological TRC scale up to ecological characteristics. We find that species richness, average population size, and interaction strength all scale up in proportion to mutation rate, with stronger responses from cloud than core species. Ecosystem survival probability is also sensitive to temperature, but does not scale up directly from any physiological TRC. Ecosystem abundance and interaction types are not sensitive to temperature at all. Additionally, only the thermal response of ecosystem survival probability is sensitive to interspecific varaiation in the optimal temperature of reproduction. These results arise from the ecological and thermal assumptions we built into the TaNa+T, and warrant further discussion.

Ecosystem survival probability is mainly controlled by the ratio between reproduction and death probabilities in single-TRC TaNa+T simulations (Fig. 2.5). Since that ratio is affected by interspecific variation in the TRC of reproduction, ecosystem survival probability depends on interspecific variation in TRC in TaNa+T simulations (Fig. 2.6). Traditionally, species fitness is often considered in terms of intrinsic growth rate; the difference between birth and death rates, rather than their ratio. The ratio is important in this model because the temperature-dependent response of reproduction is only one component of reproduction probability, and species survival requires that total reproduction probability (the product of two probabilities) be larger than death probability. Therefore, we suggest that more attention be paid to the ratio between reproduction and death probabilities, especially when a partial measure of reproduction rate is being studied. The specific thermal responses found for ecosystem survival probability in this study are difficult to validate, however, because ecosystem survival probability is not readily measured in the real world — the geological record is incomplete, and environments in which ecosystems failed to establish do not necessarily leave a record. Additionally, while there are clear boundaries between ecosystems in different TaNa+T simulations, ecosystems on Earth are often overlapping and lack clearly defined boundaries.

While the number of ecosystems that survive depends on temperature, the average abundance of those ecosystems that do survive shows no temperature response and no sensitivity to interspecific variation in TRC (Fig. 2.7). Evidence from trees supports our finding that abundance is temperature-independent (Allen et al., 2002). However, data on the thermal response of abundance is lacking (He et al., 2019), partially due to the challenges of defining ecosystem boundaries. Our finding that abundance is temperature-independent differs from the result of Arthur and Nicholson (2023), who also modified the TaNa model to include temperature. Arthur and Nicholson (2023) focus on feedbacks arising when TaNa ecosystems affect temperature in addition to responding to it, but their paper also includes simulations in which species do not modify temperature, and abundance scales with the organism-level TRC in those simulations. The difference between our results arises because Arthur and Nicholson (2023) vary interaction strength scaler (C) with temperature, rather than $p_{\mathrm{off,T}}$, p_{death} and p_{mut}. Abundance is affected by C in the TaNa model because in a steady state, $p_{\mathrm{off,total}} \approx p_{\mathrm{death}}$, leading to $N \approx \frac{1}{\mu}\left[\log(\frac{p_{\mathrm{off,T}}}{p_{\mathrm{death}}} - 1) + \sum_j \left(J_{\mathrm{ij}}\frac{N_j}{N}\right)\right]$[4]. The first term in the parentheses is small, whereas the second term can be on the order of C, here set to 100[5], making C (in addition to μ) the dominant parameters controlling abundance. In our study, holding C and μ constant enabled us to test how ecosystem characteristics evolve in response to physiological TRC alone. Our result that reproduction, death, and mutation rates do not affect ecosystem abundance provides a helpful addition to MTE predictions, and clearly distinguishes the thermal response of abundance from that of species populations.

We find that species richness increases exponentially with increasing temperature, as predicted by MTE (Allen et al., 2002; Price et al., 2010), with or without interspecific variation in TRC (Fig. 2.7 c,d). The temperature-dependence of species richness is driven by temperature-dependence of mutation rate (Fig. 2.4). In a similar model, Stegen et al. (2009) found that species richness loses its temperature-dependence over time; a result we do not reproduce. The discrepancy in results from the two models probably arises because Stegen et al. (2009) allow mutation rates to vary between species at the same temperature (depending on species' bodymass), whereas we keep mutation probability the same for all species at the same temperature. An intriguing direction of future study would be to test

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[4] The $\frac{p_{\mathrm{off,T}}}{p_{\mathrm{death}}}$ term was wrongly inverted in the 2024 manuscript.

[5] Realized interaction strengths are generally on the scale of 10 (Fig. 2.10), so a smaller choice of C could possibly make abundance sensitive to temperature in the TaNa+T. This footnote not included in the original publication.

the effect of interspecific variation in mutation rates in the TaNa+T to confirm whether a time-decaying temperature-dependence of species richness would arise. The relationship between interspecific variation in mutation rates and species richness could also help explain the persistence of a latitudinal biodiversity gradient, since it is usually measured for related species, which may have quite similar sizes and thus less interspecific variation in mutation rate.

Average species richness of core species increases with temperature in the TaNa+T as well, but more gradually than the overall species richness and with a smaller activation energy than that of metabolism (Fig. 2.7 i,j). In other words, the richness of the most abundant species is less sensitive to temperature than the richness of rare species. These results should also be considered in the context of the latitudinal diversity gradient.

The different thermal-dependencies of species richness for core and cloud species drives a temperature-dependent effect on Species Abundance Distributions (SADs) in the TaNa+T, with a larger proportion of rare species in warmer populations (Fig. 2.8). SADs are one of the few ecological properties to have a "universal" shape, but the mechanisms generating this shape, and the factors controlling differences like SAD skewness, remain poorly understood (McGill et al., 2007). Previously, SAD skewness has been associated with species richness (e.g McGill et al., 2007), but we find that temperature is the primary driver of SAD skewness (Fig. 2.9). Additionally, while species richness affects SAD skewness for ecosystems of the same temperature in various-TRC experiments, it has no effect on SAD skewness in single-TRC experiments (Fig. 2.9). These findings can advance our understanding of "universal laws" in ecology.

Interaction strengths are more positive in cold temperatures and become increasingly neutral in warmer temperatures in the TaNa+T (Fig. 2.10). Because some empirical studies indicated that the rates of activities related to interactions increase according to the Arrhenius equation (Dell et al., 2011), we tested whether an exponential increase in TaNa interaction strengths could arise secondarily to the more basic physiological TRC. Our results, however, show that interactions are inversely related with the Arrhenius curve, which implies that an exponential increase in interaction strengths is not a higher-level response to physiological TRC. Future work could consider the effect of simultaneously varying mutation and interaction strength scaler (C) with temperature, and determine which TRC would have a stronger effect on the evolution of interactions between species. Additionally, the relationship between interaction strength and species richness could be further investigated.

The TaNa+T model isolates a few components of ecological complexity, but many more layers of complexity remain to be disentangled. For example, interspecific variation in other TRC probably affects other ecosystem thermal responses (Stegen et al., 2009; Bideault et al., 2021). The width of TRC may also vary between species (TRC width may be correlated with latitude; Amarasekare and Savage (2012), predator-prey relationships; Dell et al. (2011), or climate variability; H. Chen et al. (2022)). Additionally, there may be constraints on the ways that TRC can vary between species; for example, MTE predicts that TRC peak height is controlled by metabolic rate (Gillooly et al., 2001; Brown et al., 2004; B. Chen, 2022). Another particularly interesting direction of future research is the feedback that could arise through biotic effects on the climate (Wilkinson, 2006; Arthur & Nicholson, 2023), and the ways in which ecological complexity affects it.

2.6 Conclusions

Here we have pieced together three fundamental ways species respond to temperature and extrapolated them to ecosystem-level outcomes in the TaNa+T model. In the TaNa+T, we make reproduction, death, and mutation probabilities temperature-dependent in a model of ecology and evolution in order to investigate how these physiological Thermal Response Curves (TRC) can create ecosystem-level thermal responses. We find that ecosystem survival probability, species richness, Species Abundance Distributions (SADs), and interactions all respond to temperature via physiological TRC, while mean abundance of surviving ecosystems and interaction types do not. Even when all species have the same TRC, ecosystem properties do not always have the same thermal responses as species-level TRC, and ecosystem metrics respond differently to the underlying TRC. Addionally, while it has been suspected that thermal diversity may diminish ecosystem-level thermal responses, we find that interspecific variation in the optimal temperature of reproduction only affects the thermal response of ecosystem survival probability.

This work helps clarify how thermal responses propagate from molecular to ecological scales according to the Metabolic Theory of Ecology (MTE). We show that mutation alone can drive the thermal responses of species richness and population sizes. On the other hand, an exponential increase in interactions does not arise from the TRC of reproduction, death or mutation rates (and mutation actually drives the opposite response in interactions). This study additionally highlights the importance of a relatively uncommon thermal response, ecosystem survival probability, which dominates the thermal response of abundance. When ecosystem survival probability is controlled for, abundance shows no thermal response. We also emphasize the distinction between the thermal responses of abundance and population size, which have sometimes been considered interchangeably in the past, but which respond very differently to temperature in the TaNa+T.

Understanding how ecosystems respond to the environment at a coarse level can provide a baseline from which to investigate the variety and complexity of ecology. We hope this work contributes to clarifying how TRC scale up in the theory of MTE and in ecology in general.

2.7 Data and code availability

The TaNa+T model, model output, and the scripts used for plotting are publicly available in a Federated Research Data Repository (Thermal response of the Tangled Nature Model + Temperature (Febvre, C., 2024), https://doi.org/10.20383/103.0924).

Chapter 3

Ecosystem-level niche construction in the climate: modelling co-evolution of ecosystems and temperature

Abstract

Every organism on Earth modifies its environment in some way. Some species' impacts on the environment also affect their own evolution or the evolution of other species in their community. However, the evolutionary pressures experienced by ecosystems composed of many species that modify the environment, and the environmental repercussions of these ecosystems, remain poorly characterized.

Here, we couple a temperature-dependent ecosystem evolution model, called the Tangled Nature + Temperature (TaNa+T) model, with a climate model, producing the Tangled Nature + Climate (TaNC) model. To do this, we enable species in the TaNC to increase or decrease the amount of carbon in the atmosphere, thus affecting the strength of the greenhouse effect. We then investigate the co-evolution of ecosystems with the climate. We probe into how ecosystem-climate co-evolution depends on the strength of biotic impacts on the climate, in addition to how different species-level thermal responses (birth, death, and mutation) contribute to co-evolutionary outcomes. We find that, when organismal impacts are large enough to affect the climate, ecosystems are more likely to cool the climate than warm it, both due to reduced death rates in colder climates and because the asymmetry of species' thermal response of reproduction makes it easier for species to withstand cooling than warming. The strength of environmental feedback on ecosystem

evolution also increases as the strength of species' impacts increase, resulting in smaller, less diverse ecosystems when species' impacts are the largest. This demonstrates the emergence of ecosystem-level niche construction, and suggests that ecosystems modify their environments to reduce species' death rates, rather than to maximize species' reproduction rates. More generally, the TaNC also provides a tool for future work to continue investigating the evolution of ecosystem-level niche construction.

3.1 Introduction

Every organism on Earth affects its environment at some scale, through chemical exchange, chemical reaction, or physical alterations (Odling-Smee et al., 1996; Brown et al., 2004; Matthews et al., 2014). This modifies biotic and abiotic pressures on natural selection, feeding back on species evolution in a process called niche construction (Odling-Smee et al., 1996). Through this process, some species (such as beavers, earthworms, rain forests or phytoplankton) cause such important impacts on their environments that these impacts can feed back on their own evolutionary pressures or the evolutionary pressures experienced by other organisms (Odling-Smee et al., 1996; Pausas & Bond, 2022; Lenton & Watson, 2000). Furthermore, the Gaia hypothesis proposes that the global climate could even be actively stabilized by biotic activities (Lovelock & Margulis, 1974; Margulis & Lovelock, 1974), and although this claim is contentious (Doolittle, 1981; Dawkins, 1982; Kirchner, 2002; Volk, 2004; Quinn & Bates, 2011), there is ongoing interest in understanding the global-scale feedbacks between Earth's species and the climate (Lenton, Daines, Dyke, et al., 2018; Doolittle, 2019; Pausas & Bond, 2022; Arthur & Nicholson, 2023; Bagdassarian et al., 2007; Woods et al., 2021).

Species not only co-evolve with their environments, but also with other species that share their environments. Species co-evolution can produce ecosystems of many different species living together in relatively stable configurations that can last for long durations of time (Stenseth & Maynard Smith, 1984; Coulson, 2021; Ebenhoh, 1994). Diverse ecosystems can be stable in terms of resistance and resilience to perturbation (e.g. Tilman & Downing, 1994; Coyte et al., 2015). The theory behind how this arises is debated (May, 1971), but the Red Queen hypothesis suggests that, even though species constantly evolve better strategies to exploit their environments and out-compete other species, ecological stability can still arise because different species evolve at similar rates, and so each species prevents any other from getting ahead, leading to long-lasting eco-evolutionary stale-mates which look like stable ecosystems (Vuorinen et al., 2021; van Valen, 1973; Solé, 2022).

However, species do not always stabilize their biotic and abiotic environments. The fossil record is punctuated by mass extinction events and geologically rapid transitions to new ecosystems, creating a pattern called Punctuated Equilibria (Eldredge & Gould, 1972). Data (Ezard et al., 2011) and models (Christensen et al., 2002) suggest that these mass extinctions can sometimes be biotically driven. Indeed, some of the largest mass extinction events in Earth history were biotically caused: the Great Oxidation (Falkowski, 2012) and the Neoproterozoic Snowball Earth event (Lenton & Watson, 2011; Cartapanis et al., 2018) are two important examples. Today, humans are also causing global extinctions at a rate on par with a mass extinction event (Butchart et al., 2010; Cowie et al., 2022). Furthermore, some biotic responses to global warming enhance warming, such as increased respiration rates in warmer climates (T. Wang et al., 2025) or pine beetle outbreaks converting forests from carbon sinks to sources (Kurz et al., 2008).

How different interactions between ecosystems and their environments evolve remains poorly understood. One possibility is that ecosystem interactions with the environment may be driven by higher levels of selection than individuals. In other words, species may not directly experience selective pressures that push them towards certain environmental impacts, but ecosystems that stabilize their environments last longer than those that disrupt their environments, so over time, ecosystems containing disruptive species become less common (Betts & Lenton, 2008; Doolittle, 2019; Lenton, Daines, Dyke, et al., 2018). When disruptive ecosystems are driven to total extinction (no descendants of the lineage survive), this ecosystem-level selection is called *selection by survival* (since the surviving lineages that did not degrade their environments become more common over time) (Doolittle, 2019). However, even if ecosystems do not experience total extinctions, mass extinction events (in which most, but not all species go extinct) can still lead to ecosystem-level selection. Ecosystems that disrupt their environments may more quickly produce mass extinction events, so ecosystems that do not disrupt their environments may last longer than those that do (Betts & Lenton, 2008; Lenton, Daines, Dyke, et al., 2018). This process, called *sequential selection*, may also make ecosystems that do not disrupt their environments become more common over the course of many mass extinction events.

Ecosystem-level evolution is difficult to study because it involves long timescales, large spatial scales, and numerous species (Dorneles et al., 2004; Senthilnathan & D'Andrea, 2024). Therefore, models can be very useful to investigate ecosystem evolution and its relationship with environmental evolution (Bytnerowicz et al., 2022; Schimel, 2023). One conceptual model, called *rein control*, suggests that different species with opposite impacts on the environment can stabilize the environment. In this conception, an environmental change in either direction results in an increase in the impact of the species that pushes the environment the other direction, thereby preventing it from changing either way. The most famous formalization of the rein control theory in a computational model is called Daisyworld (Watson & Lovelock, 1983); a model with populations of black and white daisies that respectively warm and cool the climate. Because the two daisy species have small differences in environmental preferences and population sizes that depend on the suitability of their environment, the Daisyworld model successfully produces rein control, stabilizing the model climate against external forcing (Watson & Lovelock, 1983). Biologists have doubted whether this mechanism can or does evolve in real ecosystems (e.g. Kirchner, 2002; Dawkins, 1982), and this criticism along with the intrigue of the concept have spurred many variations of the Daisyworld model (Wood et al., 2008). Variations allowing species to adapt to different climates, for example, show that environmental stabilization breaks down when species can adapt to any environment (Wood et al., 2008). The timescale of environmental changes was also found to be an essential control of the emergence of regulation (Weaver & Dyke, 2012). More recently, the Daisyworld model was connected to a foodweb model to show how ecosystem-environment feedbacks can promote biodiversity maintenance in foodwebs (Bagdassarian et al., 2007). However, the extent to which Daisyworld-like interactions between species and the environment actually emerge in evolution still remains unknown. The constraints on species in the Daisyworld model do not allow evolution as a creative process, and so the findings of versions of the Daisyworld model remain difficult to extrapolate to processes on Earth (Wood et al., 2008).

Another model that has been used to study the emergence of environmental regulation is the stochastic, evolving ecosystem model called the Tangled Nature (TaNa) model (Christensen et al., 2002). This model is advantageous because it produces quasi-stable, long-lasting ecosystems similar to those observed in the fossil record, and includes minimal assumptions about ecology and it allows species to freely evolve (Christensen et al., 2002; Arthur & Nicholson, 2017). The TaNa was originally developed to demonstrate that Punctuated Equilibria can emerge without any abiotic impacts. More recently, it has been modified by Arthur and Nicholson (2023) and Febvre et al. (2024) to include an environmental temperature. In our temperature-dependent version of the TaNa model, called the Tangled Nature + Temperature (TaNa+T; Chapter 2), we show how temperature-dependence of ecosystem properties, such as species richness and ecosystem survival probability, can arise from the thermal responses of reproduction, death and mutation rates, but we do not consider species' impacts on the climate. On the other hand, Arthur and Nicholson (2023) allow species in their modified TaNa model to both respond to and affect temperature, giving species random impacts on the model climate. This configuration of the TaNa model demonstrates emergent evolution toward a universally optimum climate and ecosystems with increasing abundance, supporting the Gaian paradigm that ecosystems evolve to stabilize their environment and promote conditions that are well-suited for life. However, while species interactions and impacts on the climate are both able to evolve in this model, species environmental preferences are fixed and the same for all species, and do not encapsulate biological theory on species' responses to temperature. Therefore, the applicability of this model to ecosystem-climate co-evolution is still limited.

To progress the investigation of how ecosystems and their environments co-evolve, in this chapter we modify the temperature-dependent version of the TaNa model developed by Febvre et al. (2024, Chapter 2) to include a climate, producing the Tangled Nature + Climate (TaNC) model, and we use the TaNC to investigate ecosystem-climate interactions in a more freely evolving system than what has been studied before. As in Chapter 2, we maintain our focus on environmental temperature; a major driver of species fitness that affects most species similarly (Brown et al., 2004; Amarasekare & Savage, 2012), and an environmental variable which species affect through interactions with greenhouse gases (Trudinger & Swaine, 1979; Falkowski, 2012; Moorcroft, 2006) and albedo (Charlson et al., 1987; von Oppen et al., 2022). In the TaNa+T (Febvre et al., 2024, Chapter 2), species reproduction, death, and mutation rates have temperature-dependencies based on Metabolic Theory (Brown et al., 2004; Amarasekare & Savage, 2012), and species' optimal temperatures of reproduction can evolve. We build upon the TaNa+T in the TaNC model by enabling species to have random impacts on an atmospheric carbon reservoir which then determines the model temperature.

In this chapter, we present the TaNC model and use it to investigate how ecosystem-environment interactions evolve on geologic timescales. Our simulations enable us to observe how niche construction could emerge at the level of ecosystems: how the net impacts of ecosystems could feed back on ecosystem properties, and what that might look like. We hypothesize that the strength of species' impacts on the climate determines how strongly climate feeds back on species and ecosystem characteristics, and thus that the emergence of ecosystem-level niche construction depends on the strength of species' impacts on their environment. To test this, we characterize the TaNC model at a range of different interaction strengths between species and the climate and examine how ecosystems and climates co-evolve at these different strengths of interaction. We furthermore inspect the roles that different thermal responses play in producing these co-evolutionary outcomes by comparing a version of the TaNC in which only birth rates are temperature-dependent to a version in which birth, death, and mutation are all temperature dependent. Our investigation is broken into three main sections: climate responses to ecosystems, ecosystem responses to biotically-driven changes in the climate, and evolutionary responses of ecosystems to the coupled system.

3.2 Methods

3.2.1 Climate model

The TaNC model is comprised of the TaNa+T (described in Chapter 2) coupled with a zero-dimensional climate model. In the climate model, changes to global mean temperature (T) are determined by the imbalance between incoming and outgoing radiation. Radiative imbalances are compensated by changes of T in the direction that would restore radiative balance, at timescales determined mainly by the ocean's heat capacity (C). This is modeled as

$$\frac{dT}{dt} = \frac{A}{Cm}\left[\frac{S}{4}(1-\alpha) - \zeta\sigma T^4\right]. \tag{3.1}$$

where A is the surface area of Earth ($A = 5 \times 10^{14}\mathrm{m}^2$), C is the heat capacity of seawater (C = 4200 $\frac{J}{kgK}$), m is the mass of the top 100 meters of the ocean ($m = 5 \times 10^{19}$ kg), S is solar luminosity ($S = 1361$ $\frac{W}{m^2}$), α is planetary albedo ($\alpha = 0.3$), ζ is a parameter representing radiative forcing, and σ is the Stefan-Boltzman constant (Sagan & Mullen, 1972). Radiative forcing by CO_2 (ζ) is parameterized as

$$\zeta = 1 - r_{\mathrm{CO}_{2,0}} \log_e\left(\frac{m_{\mathrm{CO}_2} + m_{\mathrm{CO}_{2,0}}}{m_{\mathrm{CO}_{2,0}}}\right), \tag{3.2}$$

where $r_{\mathrm{CO}_{2,0}}$ is a coefficient for radiative forcing ($r_{\mathrm{CO}_{2,0}} = 0.031$), and $m_{\mathrm{CO}_{2,0}}$ is the amount of CO_2 in the atmosphere that would produce no radiative forcing ($m_{\mathrm{CO}_{2,0}} = 4.25 \times 10^{11}$ mols C = 0.00239 ppm). Note that a greater mass of carbon is required in our model than the real world to achieve a certain temperature because CO_2 is our only greenhouse gas. As such, we require 675ppm of CO_2 to reach the modern temperature of 288K (Fig. 3.1). The climate sensitivity of the model is 2.6K for a doubling from this CO_2 concentration.

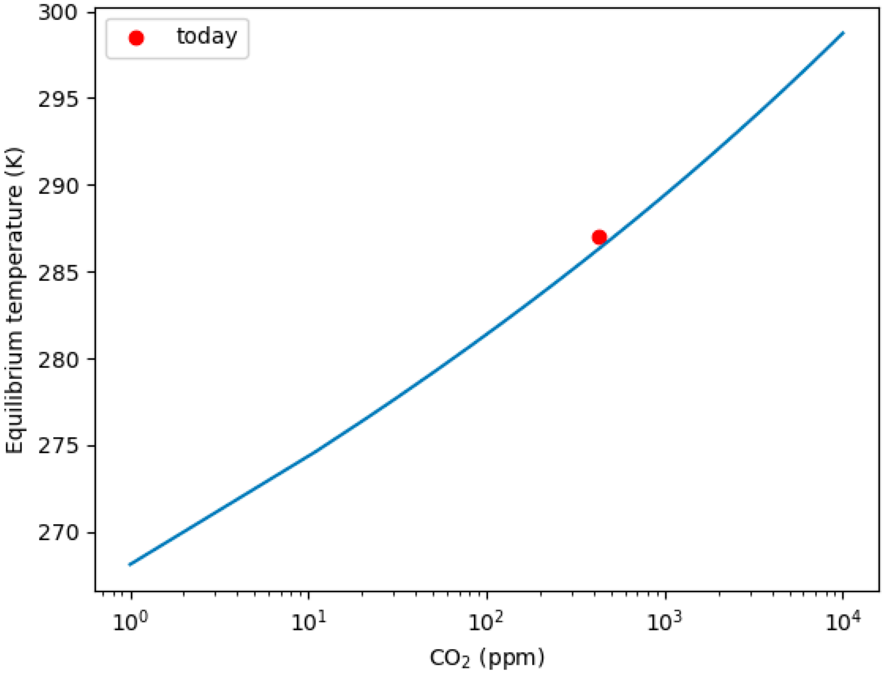


Figure 3.1: Equilibrium temperature in the climate model depends on CO_2. The red dot shows modern global mean temperature (288K) and CO_2 levels (420ppm at the Mauna Loa observatory). (The model slightly under-predicts modern temperature given modern CO_2 levels because it does not include all the greenhouse gases.)

3.2.2 Model coupling

Temperature in the climate model depends on the CO_2 concentration of the atmosphere, which is affected by species in the TaNa+T model. Each species produces a carbon flux, F_i, representing, for example, organic carbon burial, biomass production, respiration, enhancement of weathering, or any other biotically-driven carbon fluxes. To determine F_i, we first assign each species an intrinsic carbon impact (b_i), defined as the maximum fraction of atmospheric carbon with which an individual of species i can interact. Unitless values of b_i are randomly drawn from a normal distribution centered at zero with a standard deviation σ_{bio}, such that a species is equally likely to add or remove carbon from the atmosphere, and most species have $-\sigma_{\mathrm{bio}} < b_i < \sigma_{\mathrm{bio}}$. Examples of b_i values drawn from distributions with different σ_{bio} are shown in Fig. 3.2.

We assume that species' realized carbon fluxes (F_i) are proportional to b_i, but are also limited by the mass of CO_2 available in the atmosphere (i.e. a species cannot remove carbon from the atmosphere when there is none, and species absorb and emit more carbon when more is available). Additionally, we assume species' carbon fluxes are proportional to their annual metabolic rate ($r_i(T, T_{\mathrm{opt,i}})$) at the current temperature. As metabolic rates are the drivers of the thermal response of reproduction rates (Brown et al., 2004), we use the same curve for $r_i(T, T_{\mathrm{opt,i}})$ as for the temperature-dependent component of species' reproduction rates ($p_{\mathrm{off,T}}(T, T_{\mathrm{opt,i}})$); a unimodal, left-skew curve that peaks at 1 when $T = T_{\mathrm{opt,i}}$ (a skew-normal curve produced with the Python Scipy.stats package; Fig. 2.1). All together, species-specific, per-capita carbon fluxes (in moles of carbon per year) are thus modeled as

$$F_i(t) = b_i r_i(T, T_{\mathrm{opt,i}}) m_{\mathrm{CO_2}}(t). \tag{3.3}$$

Because temperature is logarithmically related to the amount of CO_2 in the atmosphere (Eq. 3.2), a species with a carbon flux F_i will have a larger impact on the climate at colder temperatures than at warm temperatures. Therefore, the rate at which a species actually affects the climate is $F_i/m_{\mathrm{CO_2}}$.

We assume the carbon flux emitted by species i is proportional to its population (N_i), and so the net flux of carbon into or out of the biosphere (F_{bio}) at a certain time t, is

$$F_{\mathrm{bio}}(t) = \sum_i F_i(t) N_i(t). \tag{3.4}$$

(As explained above, the rate at which ecosystems affect the climate is proportional to $F_{\mathrm{bio}}/m_{\mathrm{CO_2}}$).

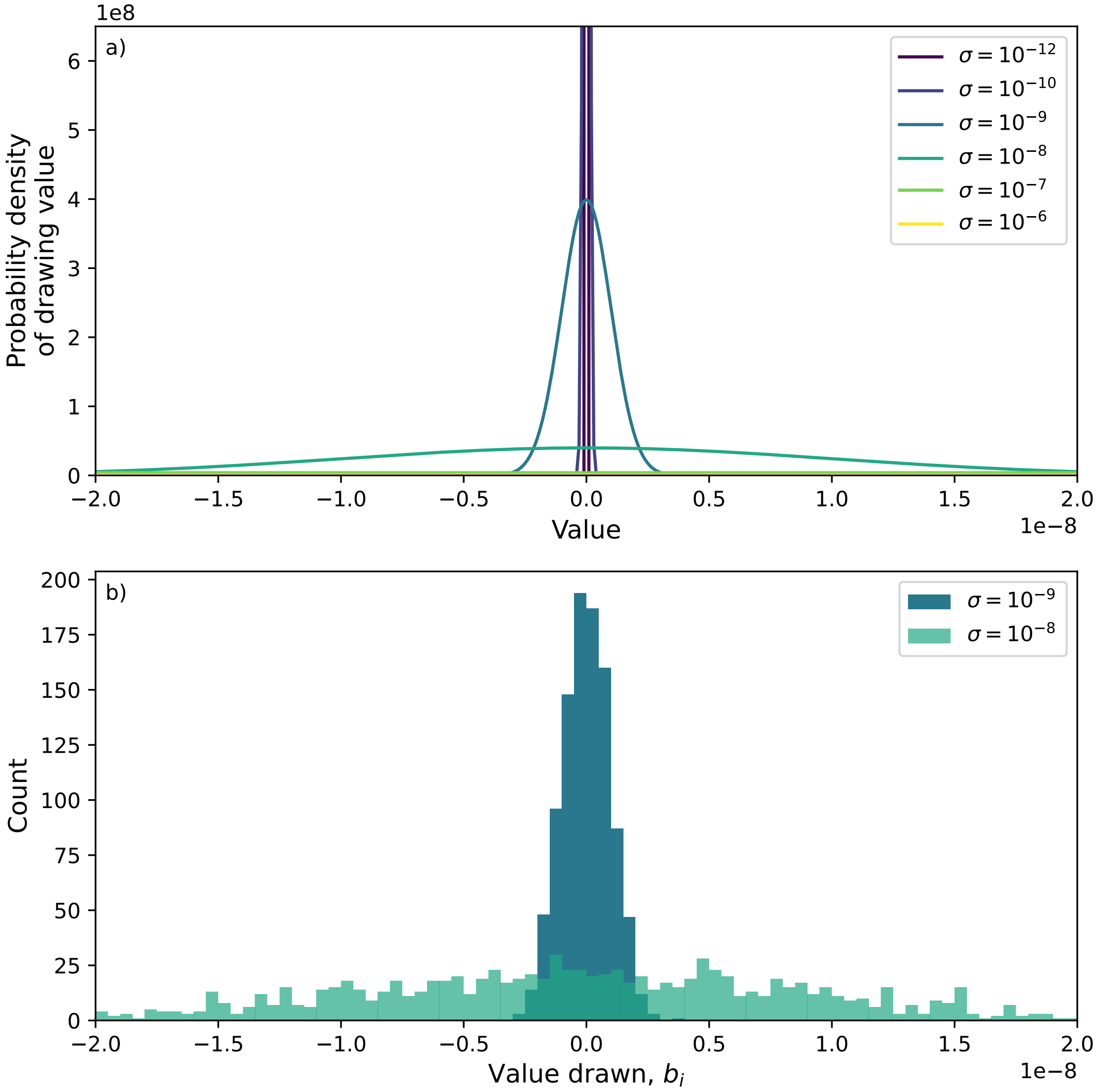


Figure 3.2: a) Normal distributions, with different standard deviations (σ_{bio}), from which b_i values are drawn. The values of σ_{bio} span across 6 orders of magnitude, so only the distributions with $\sigma_{\text{bio}} = 10^{-8}$ and 10^{-9} are well-contained at the scale shown here. b) One thousand random b_i values drawn from two example distributions which are similar enough to be able to visually compare: $\sigma_{\text{bio}} = 10^{-9}$ (blue) and 10^{-8} (green).

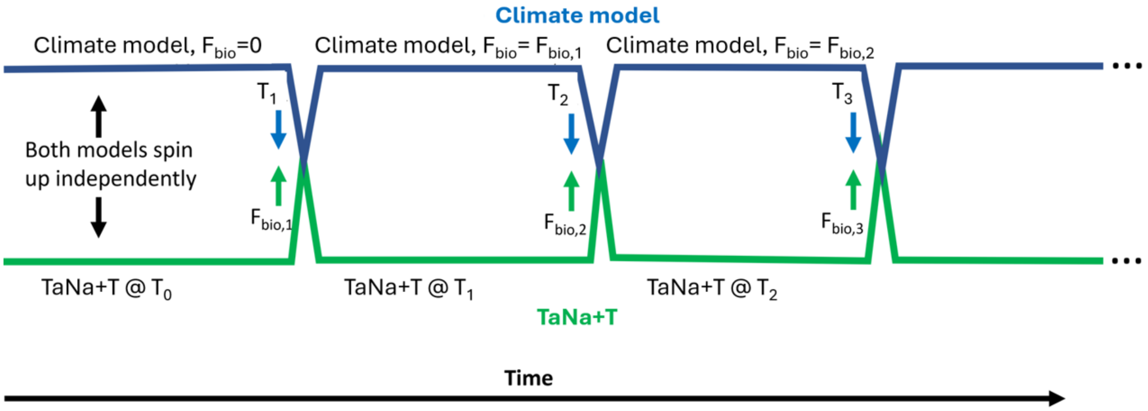


Figure 3.3: Simulation coupling routine of the climate model (blue) with the Tangeld Nature + Temperature (TaNa+T; green). Each model runs independently for 1 TaNa generation (1000 climate model years), and then the two models exchange information about the temperature (T) and the biotic flux of carbon (F_{bio}). The two models then run another 1 generation (1000 years) with the new information, and so on.

We isolate the interactions between species and their environment by setting all abiotic carbon fluxes to zero, so changes in atmospheric CO$_2$ are just

$$\frac{dm_{\text{CO}_2}}{dt} = F_{\text{bio}}(t). \tag{3.5}$$

Solar luminosity and albedo are also held constant in model simulations to isolate the impacts of species on the climate.

The TaNa+T is coupled with the climate model asynchronously: the carbon model and TaNa+T model each run independently for fixed intervals and then exchange information about CO_2 and T (from the climate model), and F_{bio} (from the TaNa+T; Fig. 3.3). As the TaNa represents macroevolutionary processes (each mutation event in the model produces an entirely new species), we set 1 TaNa generation equal to 1000 climate model years. The differential equations for carbon and temperature (Eqs. 3.1 and 3.5) are solved in the climate model with an ODE solver in the Python Scipy package.

3.2.3 Experimental set-up

To determine how large species' intrinsic impacts (b_i) on the carbon cycle should be, we ran preliminary tests to determine a range of different σ_{bio} values that produce ecosystems with negligible impacts up to ecosystems that rapdily change the climate (and often cause their own extinctions). We then selected this range of standard deviations of biotic impacts: $\sigma_{\text{bio}} = 0, 10^{-12}, 10^{-10}, 10^{-9}, 10^{-8}$, $10^{-7}, 10^{-6}$ (Fig. 3.2a). Simulations in which $\sigma_{\text{bio}} = 0$ do not impact the climate and are thus configured identically as in Chapter 2.

In order to understand which thermal responses (reproduction or death and mutation) drive climate-ecosystem interactions, we also compare two versions of the TaNC: one with temperature-dependent death and mutation probabilities (as in Chapter 2), and one with death and mutation probabilities held constant ($p_{\text{death}} = 0.14$; slightly lower than the default value to increase ecosystem survival probability, and $p_{\text{mut}} = 0.01$; the default value). This provides insight into how ecosystems receive feedback from their environments. Furthermore, this allows us to examine the differences between a unimodal response to the environment (reproduction), and two monotonically increasing responses (death and mutation).

Each model configuration (each standard deviation of biotic impacts, with and without temperature dependence of death and mutation) is run 250 times (i.e. with different sets of $D_0 = 60$ initial species and their interaction matrices). All simulations are initialized at present global mean temperature (T_0 = 288K $\approx$ 15°C), with an initial carbon mass of C_0 = 1.2$\times$$10^{17}$ moles = 675ppm. Each simulation is run for 10,000 TaNa generations (10 million years in the climate model).

3.2.4 Statistical analysis

We consider the results of each model configuration for several different metrics. For metrics such as final temperature or ecosystem abundance, each model configuration produces a distribution of results for each metric. To compare these output distributions across model configurations, we often present the results in the form of boxplots. In these cases, we compare the median of each configuration using the Mann-Whitney U-test (since most of the model output is either non-parametric or does not share variance with other configurations) and compare the variance using Levene's test (again because not all the model output is parametric).

3.3 Results

Results are organized into three general categories: climate responses to ecosystems (changes in temperature; Sec. 3.3.1), ecological responses to climate (ecosystem survival probability, duration of ecological steady states, and abundance and species richness of ecosystems; Sec. 3.3.2), and evolution of species' thermal optima and carbon impacts (Sec. 3.3.3). The statistical significance of differences between medians are presented in Tables 3.1 (constant death and mutation) and 3.2 (temperature-dependent death and mutation), and the statistical significance of differences between standard deviations of results are presented in 3.3 (constant death and mutation) and 3.4 (temperature-dependent death and mutation).

Metric	**Median and significance at σ_{bio}**						
	0	10^{-12}	10^{-10}	10^{-9}	10^{-8}	10^{-7}	10^{-6}
Temperature	288	288	288	288	283	274 **	255 *
Abundance	684	742	719	750	744	845	735
Core abundance	560	609	594	606	614	690	595
Species richness	49	56	53	54	58	53	49
Core spc. richness	2	2	2	2	2	2	2
Thermal mismatches	-1.81	-1.81	-2.27 ***	-0.96 ***	-5.85 ***	2.09 ***	-11.67 ***
Species' intrinsic carbon impact (b_i) divided by σ_{bio}	0	-0.146	-0.092 **	-0.039 ***	-0.039 ***	0.002 ***	-0.686 ***
Rate of spc. climate impacts (F_i) divided by σ_{bio}	0	-0.075	-0.028	-0.027	-0.017 **	0.002	-0.275 ***

Table 3.1: Statistical analysis of differences in medians for Chapter 3 results for experiments with constant temperature and mutation in. Results of each row are compared to the results for $\sigma_{\text{bio}} = 0$ (the second column) except for b_i and F_i, which are compared to $\sigma_{\text{bio}} = 10^{-12}$ (third row), since b_i is irrelevant when $\sigma_{\text{bio}} = 0$). Statistical significance of differences in medians is reported as: * (p < 0.05), ** (p < 0.01), or *** (p < 0.001).

Metric	**Median and significance at σ_{bio}**						
	0	10^{-12}	10^{-10}	10^{-9}	10^{-8}	10^{-7}	10^{-6}
Temperature	288	288	288	288	278 ***	261 ***	255 ***
Abundance	725	785	726	655	588	397 ***	376 ***
Core abundance	683	736 *	685	618	560	395 **	376 *
Species richness	28	29	28	25	14 ***	4 ***	3 ***

Core spc. richness	2	2	2	2	2	2	2
Thermal mismatches	-4.24	-4.22	-4.58 ***	-3.42 ***	-10.16 ***	-16.32 ***	-15.67 ***
Species' intrinsic carbon impact (b_i) divided by σ_{bio}	0	-0.101	-0.101	-0.079 ***	-0.224 ***	-0.404 ***	-0.431 ***
Rate of spc. climate impacts (F_i) divided by σ_{bio}	0	-0.016	-0.018	-0.017 ***	-0.019	-0.026 ***	-0.057 ***

Table 3.2: Statistical analysis of differences in medians for Chapter 3 results for experiments with temperature-dependent temperature and mutation in. Results of each row are compared to the results for $\sigma_{\text{bio}} = 0$ (the second column) except for b_i and F_i, which are compared to $\sigma_{\text{bio}} = 10^{-12}$ (third row), since b_i is irrelevant when $\sigma_{\text{bio}} = 0$). Statistical significance of differences in medians is reported as: * ($p < 0.05$), ** ($p < 0.01$), or *** ($p < 0.001$).

Metric	**Standard deviation and significance at σ_{bio}**						
	0	10^{-12}	10^{-10}	10^{-9}	10^{-8}	10^{-7}	10^{-6}
Temperature	0	0.0210	0.359***	2.895***	10.5***	0.200***	0.0
Species richness	16	17	16	14	18	4	0
Core spc. richness	0.6	0.7	0.8	0.6	0.6	0.0	0.0
Species' intrinsic carbon impacts (b_i) divided by σ_{bio}	0	1.096	1.038 ***	0.951 **	0.867 **	0.727 **	0.699 ***
Rate of spc. climate impacts (F_i) divided by σ_{bio}	0	0.808	0.790 ***	0.698 ***	0.643 ***	0.554 ***	0.321 ***
Rate of ecosystem climate impacts (F_{bio}) divided by σ_{bio}	0	298	263	247	328	130	27.4

Table 3.3: Statistical analysis of differences in variance for Chapter 3 results with constant death and mutation rates. Results of each row are compared to the results for $\sigma_{\text{bio}} = 0$ (the second column) except for b_i, F_i and F_{bio}, which are compared to $\sigma_{\text{bio}} = 10^{-12}$ (third row), to compare how the variance of those metrics evolves when $b_i \neq 0$). Statistical significance of differences in medians is reported as: * (p < 0.05), ** (p < 0.01), or *** (p < 0.001).

Metric	**Standard deviation and significance at σ_{bio}**						
	0	10^{-12}	10^{-10}	10^{-9}	10^{-8}	10^{-7}	10^{-6}
Temperature	0	0.0378	0.488^{*}	3.18^{***}	12.3^{***}	12.5^{***}	2.58^{**}
Species richness	10	10	11	12	18	10	2^{***}
Core spc. richness	0.5	0.5	0.5	0.6	0.6	0.6	0.3
Species' intrinsic carbon impacts (b_i) divided by σ_{bio}	0	1.037	1.020 ***	0.963 ***	0.793 ***	0.816 ***	0.907 ***
Rate of spc. climate impacts (F_i) divided by σ_{bio}	0	0.665	0.644 ***	0.651 ***	0.421 ***	0.302 ***	0.294 ***
Rate of ecosystem climate impacts (F_{bio}) divided by σ_{bio}	0	339	223	205^{*}	103^{***}	52.1^{***}	34.2^{***}

Table 3.4: Statistical analysis of differences in variance for Chapter 3 results with temperature-dependent death and mutation rates. Results of each row are compared to the results for $\sigma_{\text{bio}} = 0$ (the second column) except for b_i, F_i and F_{bio}, which are compared to $\sigma_{\text{bio}} = 10^{-12}$ (third row), to compare how the variance of those metrics evolves when $b_i \neq 0$). Statistical significance of differences in medians is reported as: * (p < 0.05), ** (p < 0.01), or *** (p < 0.001).

3.3.1 Climate responses to ecosystems

Ecosystems generally cool the climate

Temperature does not change much over the course of simulations in which species' intrinsic impacts (b_i) on carbon are drawn from a normal distribution with a small standard deviation ($\sigma_{\text{bio}} \leq 10^{-10}$) (Fig. 3.4a). However, as species' intrinsic impacts on carbon increase (with larger σ_{bio}), the impacts of ecosystems on the climate become more apparent

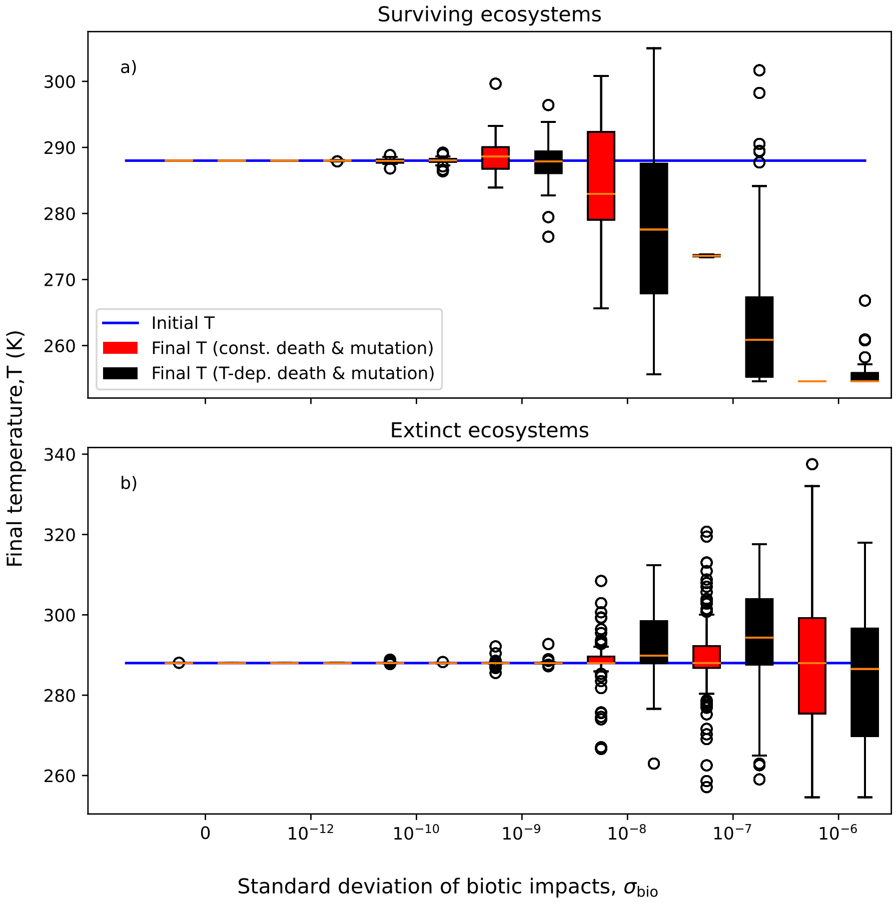


Figure 3.4: Boxplots of the final temperature of ecosystems that a) are surviving after 10,000 generations (10 million years) and that b) have gone extinct before then, at each of the six standard deviations (σ_{bio}) of biotic impacts. Red boxes show results from simulations in which death and mutation rates were held constant (p_{death}=0.14, p_{mut}=0.01), and black boxes show results from simulations in which death and mutation were temperature-dependent (Eqs. 2.6 and 2.7). The top and bottom of each box shows the first and third quartiles, with the orange line in the middle showing the median final temperature. The whiskers extend from the box to the farthest final temperature reached within 1.5 times the interquartile range, and final temperatures outside that are shown in black circles. The horizontal blue line indicates the temperature at which all simulations were initialized, 288K. Note that the small ranges in T at large σ_{bio} are a result of the small number of surviving ecosystems at that temperature.

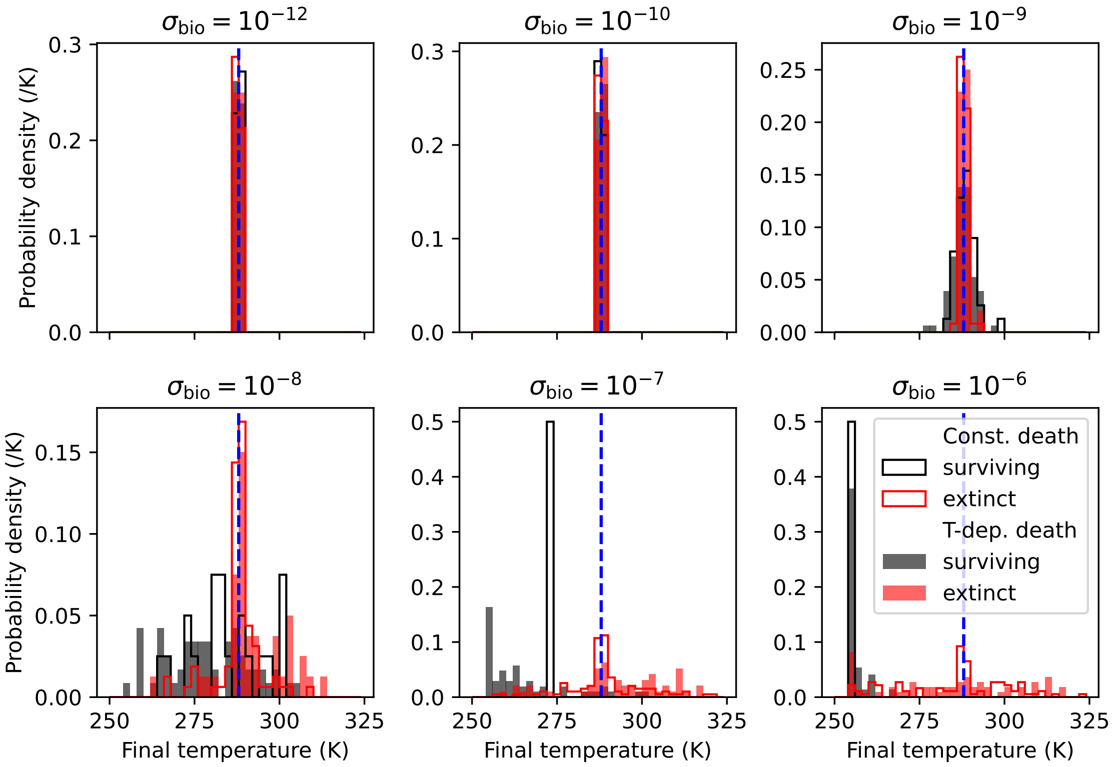


Figure 3.5: Histograms showing the distribution of final temperatures reached in ecosystems that are surviving after 10,000 generations (red) compared to those that have gone extinct before then (black). The unfilled, outlined histograms show results from simulations in which death and mutation were held constant ($p_{\rm death}$=0.14, $p_{\rm mut}$=0.01), and filled bars show results from simulations in which death and mutation probabilities were temperature-dependent (Eqs. 2.6 and 2.7). The dashed blue line shows the initial temperature, 288K.

(and statistically significant). With $\sigma_{\text{bio}} = 10^{-9}$, the standard deviation in final temperatures is 3K (3°C), indicating climate change of a few degrees from the starting point of $288K$ over the course of 10 million years. With larger standard deviations of biotic impacts (σ_{bio}), the change in climate can be up to 30K (30°C) over 10 thousand generations (10 million years), with surviving ecosystems more likely to cool the climate than warm it (Fig. 3.4a).

With $\sigma_{\text{bio}} = 10^{-9}$, the temperatures of surviving ecosystems are clustered around the initial temperature, but with larger standard deviations of biotic impacts, the distributions of final temperatures spread out and become more uniformly distributed (Fig. 3.5), and median temperatures cool by a 10-30K (10-30°C; $p < 0.001$). At the largest two standard deviations of biotic impacts ($\sigma_{\text{bio}} \geq 10^{-7}$), there are sharp peaks in the temperature of surviving ecosystems at very cold temperatures ($<$ 260K).

Cooling of surviving ecosystems arises both when birth, death, and mutation rates are all temperature-dependent, and also when death and mutation are held constant (Fig. 3.4a, 3.5, $p < 0.05$). As this cooling trend in surviving ecosystems is apparent even when death and mutation rates are held constant, the asymmetry of reproduction thermal response curves (described in Chapter 2) is probably partially responsible for the asymmetrical response of climate to the biosphere: species have a wider thermal tolerance below their thermal optimum than above it, making it possible for them to survive greater cooling than warming. However, temperature-dependence of death and mutation causes even greater cooling than when death and mutation are held constant. In Chapter 2, we saw that smaller death probabilities in colder climates leads to larger ecosystem survival rates, and here we see that this can drive selection for colder ecosystems.

The temperature at which ecosystems go extinct is usually very near the starting temperature when biotic impacts are small ($\sigma_{\text{bio}} \leq 10^{-9}$; Fig. 3.4b). With larger biotic impacts ($\sigma_{\text{bio}} \geq 10^{-8}$), extinctions are more likely to occur at warmer temperatures than the temperatures of surviving ecosystems (Fig. 3.4b), but interestingly, the most common temperature of extinction is still the initial temperature (Fig. 3.5). The temperatures of extinctions generally remain more tightly clustered than the temperatures of surviving experiments, indicating that many ecosystems go extinct even in rather equable climates. This could partially be because ecosystems have more time to change the climate when they survive than when they go extinct. However, this additionally implies that selective extinctions of warm climates are not the only driver of climate evolution toward cooler climates.

When death and mutation are temperature-dependent, the median temperature of extinction is warmer than the initial temperature for $\sigma_{\text{bio}} = 10^{-8}, 10^{-7}$ (Fig. 3.4b). With $\sigma_{\text{bio}} = 10^{-6}$, the median temperature of extinction is cooler than the initial temperature, but it is still warmer than the median temperature of surviving ecosystems. When death and mutation are held constant, on the other hand, the median temperature of extinction is very near the initial temperature at all standard deviations of biotic impacts. The range of temperatures of extinctions is also more symmetrically distributed above and below the initial temperature when death and mutation are held constant, whereas the whole range shifts warmer for $\sigma_{\text{bio}} = 10^{-8}, 10^{-7}$ and cooler for $\sigma_{\text{bio}} = 10^{-6}$. This suggests that the thermal responses of death and mutation enhance selective total extinctions of warm ecosystems, which is not surprising as warmer temperature are associated with larger death rates in those cases.

Importantly, even though the temperature of extinctions remains symmetrically distributed around the initial temperature at every σ_{bio} when death and mutation are constant, the temperature of surviving ecosystems still evolves colder, so selective total extinctions cannot be solely responsible for climate evolution. Additionally, as the temperatures of both surviving and extinct ecosystems are cooler than the initial temperature with $\sigma_{\text{bio}} = 10^{-6}$ and temperature-dependent death and mutation, selective extinctions of warm temperatures is not solely responsible for climate evolution in this case either.

Stable ecosystems do not always stabilize the climate

Ecosystems in the TaNC always produce Punctuated Equilibria, with the populations of a few core species fluctuating without trend for periods of hundreds to thousands of generations that are interrupted by abrupt mass or total extinctions (e.g. Fig. 3.6, left column). However, with sufficiently large biotic impacts ($\sigma_{\text{bio}} \geq 10^{-9}$), temperature generally varies within ecological steady states with less noise and with a stronger trend than abundance, and therefore is not generally in steady state (e.g. Fig. 3.6, right column). At very low temperatures, however, temperature can remain more constant, sometimes associated with larger fluctuations in species populations (Fig. 3.6, second to last row). Additionally, some (rare) ecological steady states are associated with larger temperature fluctuations with less overall trend (Fig. 3.6, last row).

When death and mutation are held constant, both the total amount of change in temperature (ΔT) within steady states and the rate of change of temperature (dT/dt) increase with the standard deviation (σ_{bio}) of biotic impacts (Fig. 3.7a,c). This unsurprisingly indicates that the climate changes more within ecological steady states when species have

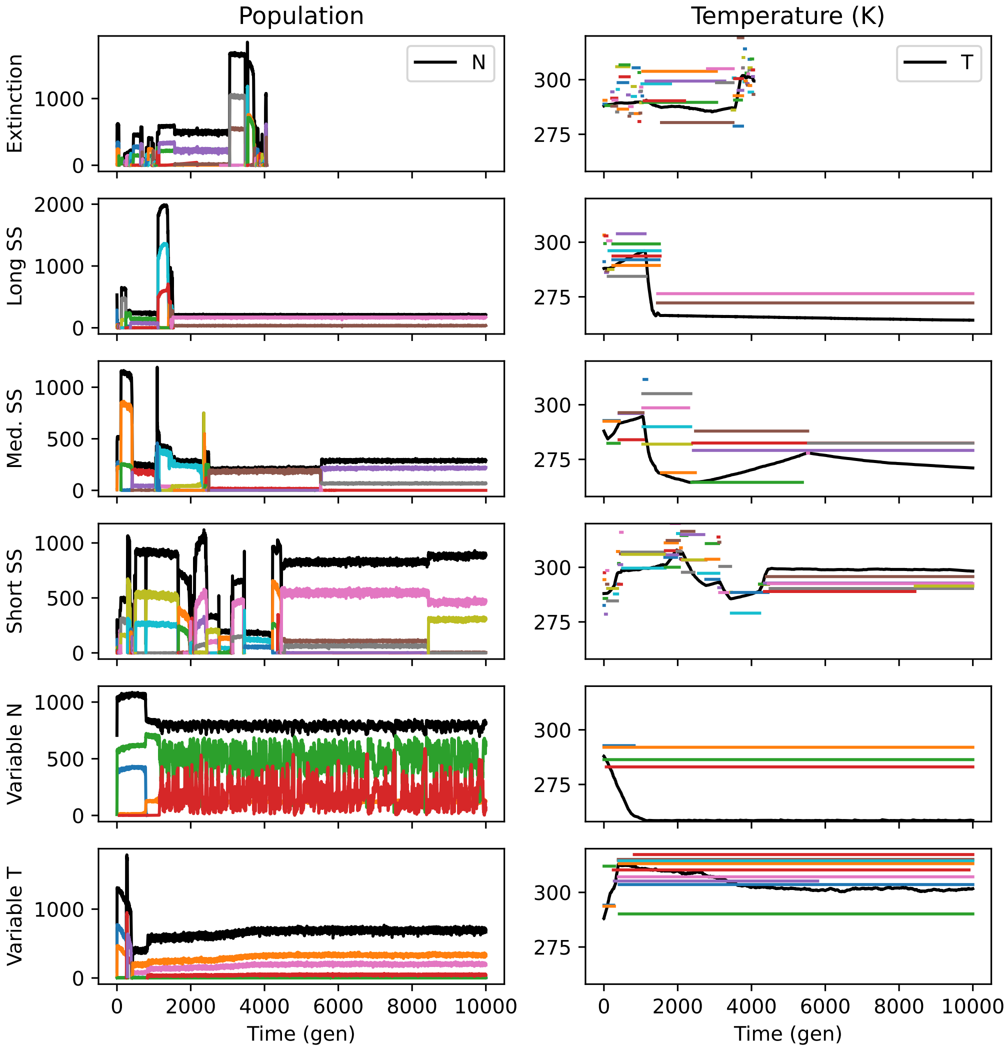


Figure 3.6: Example model outputs from six individual TaNC simulations run with the standard deviation (σ_{bio}) of biotic impacts of $\sigma_{\text{bio}} = 10^{-8}$. Timeseries in the left column show ecosystem abundance (black) and species populations (colors) in one simulation over time, and in the right column, environmental temperature (black) and species' optimal temperatures (colors associated with species to the left) of the same six example simulations. From top to bottom: one example run each of an extinction, a long steady state (lasting more than half the simulation period), medium steady states (simulations with at least two steady states lasting greater than a quarter of the simulation period), short steady states, variable ecosystem abundance and more constant temperature, and more variable temperature during a long ecological steady state.

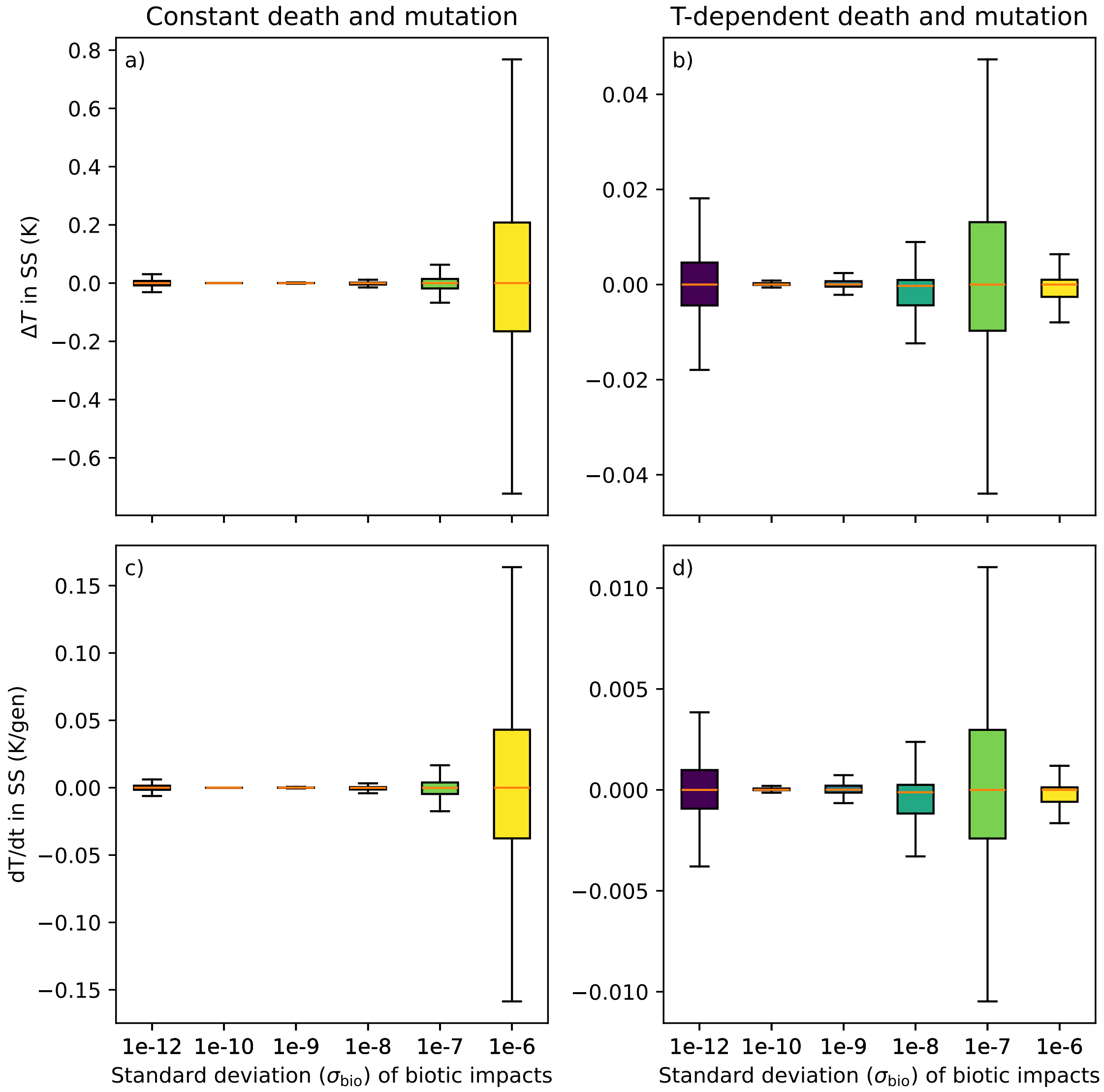


Figure 3.7: The first row shows total change in temperature during ecological steady states lasting at least 100 generations when a) death and mutation are held constant, and b) death and mutation are temperature-dependent. The second row shows the average rate of change of temperature within steady states, c) when death and mutation are held constant, and d) when death and mutation are temperature-dependent. Colors correspond to the initial standard deviation (σ_{bio}) of biotic impacts. As our focus here is on different ecological steady states, simulations that survived 10,000 generations and those that went extinct beforehand are considered together. The red line in the middle of each box shows the median value, the edges of the boxes show the quartiles, and the whiskers extend to the farthest point within 1.5 times the interquartile range. Outliers are not shown here so that the quartiles are visible; however, they extend in panels a,b) to 30K and -40K, and in panels c,d) to 5K/gen and -15K/gen (Fig. B.1).

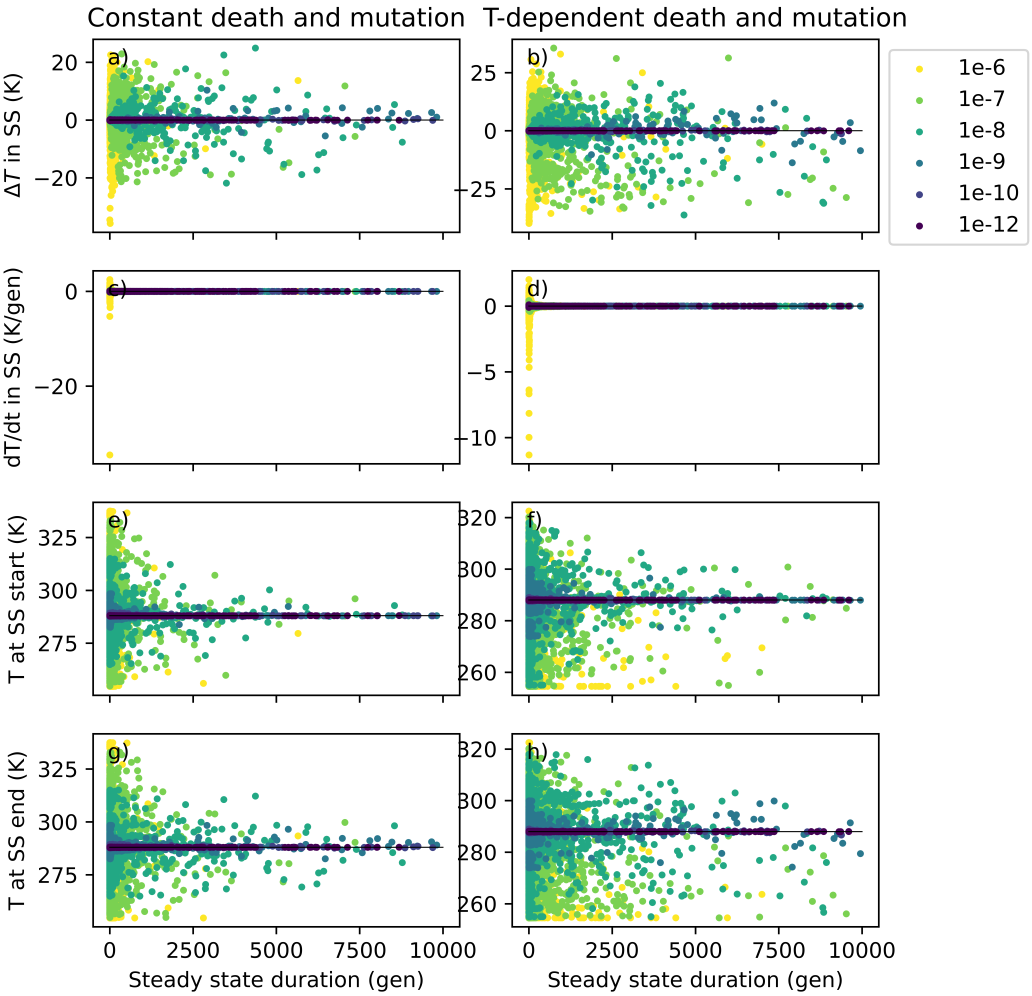


Figure 3.8: Steady state (SS) durations (in generations) relative to a,b) the change in temperature (T) from the beginning to the end of the steady state, c,d) the average rate of change in temperature (dT/dt) throughout the steady state, e,f) the temperature at which the steady state began, and g,h) the temperature at which the steady state ended. The left column shows results for simulations in which death and mutation are held constant, and the right column for when death and mutation are temperature-dependent. The black lines in a-d) are at zero and in e-h) at the temperature at which simulations were initialized (288K). Colors correspond to the standard deviation (σ_{bio}) of biotic impacts. Values of dT/dt in c) and d) extend from 5 to -15K/gen for very short steady states, but here we zoom in to show the majority of the values.

larger climate impacts. However, ΔT and dT/dt during steady states increase more gradually than σ_{bio} (Fig. B.1), suggesting that when species' impacts on the climate are larger, ecosystems have reduced climate change relative to a typical mutant species. This also indicates that the amount of climate change that an ecosystem can sustain affects ecosystem evolution more strongly when σ_{bio} is larger. Interestingly, though, median ΔT and dT/dt are all centered near 0K (0°C) and the quartiles are not strongly skewed, showing that positive and negative changes in temperature are about equally as likely in steady states, even though climate evolves cooler (Fig. 3.4a).

When death and mutation are temperature-dependent, on the other hand, the amount and rate of change in temperature within steady states remains more similar at all σ_{bio} (Fig. 3.7b,d). This is generally because temperature changes much less at large values of σ_{bio} when death and mutation are temperature-dependent than when they are constant. This could imply that ecosystems have a smaller limit of climate change which they can sustain when death and mutation are temperature-dependent, and that limit is being reached at all σ_{bio} and causing mass extinctions. This could also be because more ecosystems end up in cooler climates when σ_{bio} is large and death and mutation are temperature-dependent than when they are constant (Fig. 3.4a). If cooler steady states change temperature more slowly, this could also partially explain this result.

The commonality of small amounts ($\leq$ 1K) and rates ($\leq$ 0.1K/1000yr) of change in all cases suggests that climate change is not always the driving force of the mass extinctions that terminate ecological steady states. Indeed, the maximum amount of climate change that stable ecosystems can sustain before collapse is around 20-30K (20-30°C) when death and mutation are constant, and around 30-40K (30-40°C) when death and mutation are temperature dependent (Fig. 3.8a,b, respectively). Long steady states require slow climate change, but slow climate change does not guarantee that steady states will have long durations (Fig. 3.8c,d). The temperature at the beginning of steady states does not have a strong impact on the duration of steady states (Fig. 3.8e,f), but the longest lasting steady states generally end at cooler temperatures, especially when death and mutation are temperature-dependent (Fig. 3.8g,h). This implies that the temperature at which a steady state begins does not predict its chances of lasting a long time, but when ecosystems become or remain cool, mass extinctions become less frequent. As ecological steady states are terminated by mutants with large fitness (Becker & Sibani, 2014), the persistence of cooler ecosystems could also arise because there are fewer mutants in cooler temperatures and mutant species are less likely to have large reproduction rates at extreme than moderate temperatures. Therefore, ecosystems can evolve toward colder climates without total extinctions because ecosystems in colder states are more likely to remain at the same temperature (i.e. in a longer ecological steady state) than ecosystems in warmer states.

3.3.2 Ecological characteristics

We turn now to ecological responses to the climate in the TaNC: ecosystem survival probability, steady state duration, abundance, and species richness.

Total extinctions are more common when species have strong environmental impacts

The fraction of ecosystems that survive to the end of TaNC simulations decreases approximately exponentially as σ_{bio} increases, both in the case where death and mutation are temperature dependent and when they are held constant (Fig. 3.9). The approximately exponential relationship between ecosystem survival probability and σ_{bio} parallels the logarithmic relationship between temperature and CO_2 (Eq. 3.2), suggesting that species impacts on the climate are inversely related to ecosystem survival probability.

There are generally more ecosystems that survive to the end of simulations when death and mutation are temperature-dependent than when they are held constant (Fig. 3.9). In cases where biotic impacts on carbon are negligible (small σ_{bio}), this is because death and mutation rates are both lower at the initial temperature (288K) than when death and mutation are held constant. The lower death probabilities therefore increase ecosystem survival probability (as seen in Chapter 2). With larger values of σ_{bio}, extinction probabilities are even further reduced when death and mutation are temperature-dependent because there is more cooling, and death and mutation probabilities are lower in colder climates.

The duration of ecological steady states does not depend on the strength of biotic impacts on the climate

Unlike the probability of total extinctions, there is very little response of ecological steady state durations to the standard deviation of biotic impacts. When death and mutation probabilities do not depend on temperature, very short steady states are more common at the largest standard deviations of biotic impacts ($\sigma_{\text{bio}} = 10^{-6}$; Fig. 3.10a). However, at all other σ_{bio}, and at every σ_{bio} with temperature-dependent death and mutation probabilities, the distributions of steady state durations are very similar (Fig. 3.10a,b).

The lack of responsiveness of ecological steady state duration to σ_{bio} is counterintuitive as it indicates that ecosystems that have the ability to cause rapid climate change

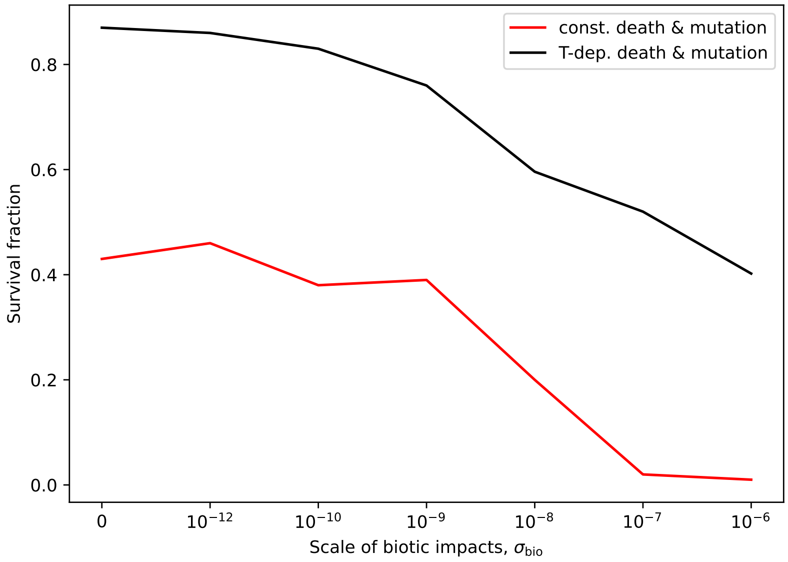


Figure 3.9: Fraction of surviving experiments after 10,000 TaNa generations (10 million years) out of 250 simulations run at each standard deviation (σ_{bio}) of biotic impacts for temperature-dependent (black) and constant (red) death and mutation rates.

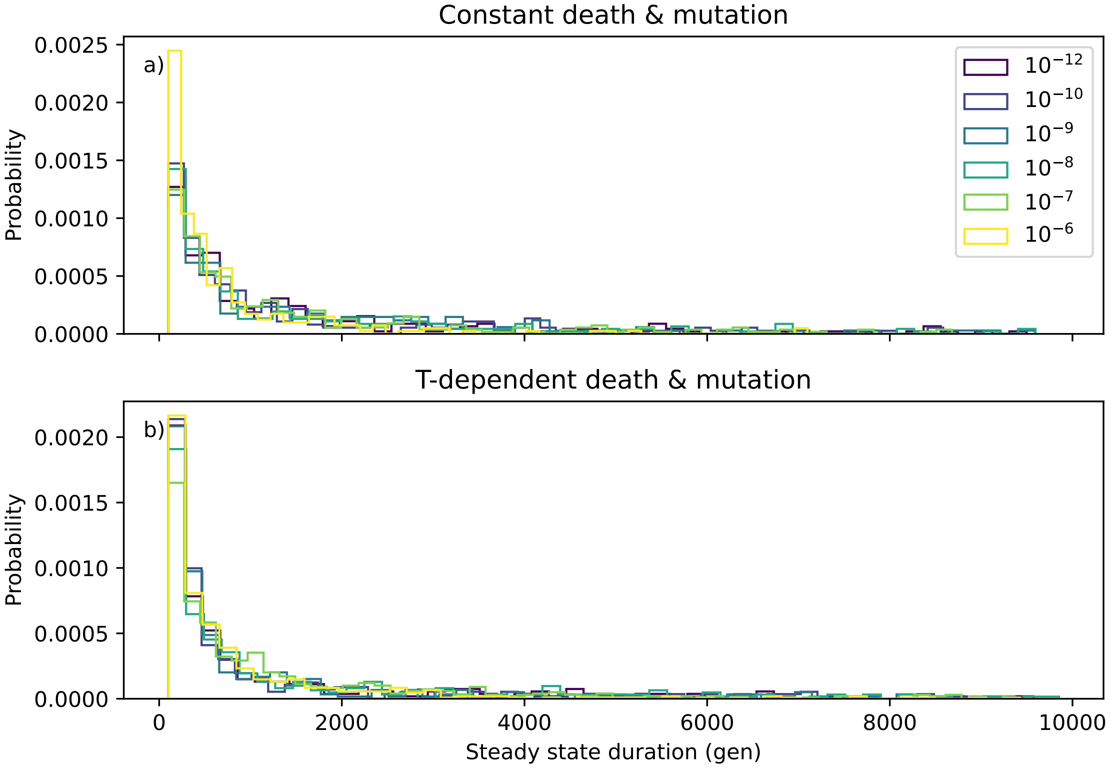


Figure 3.10: Histograms of steady state durations of simulations a) run with constant death and mutation probabilities ($p_{\mathrm{death}} = 0.14, p_{\mathrm{mut}} = 0.01$), and b) run with temperature-dependent death and mutation probabilities. Colors correspond to the standard deviation (σ_{bio}) of biotic impacts, with darker shades corresponding to smaller σ_{bio}.

(with large standard deviations of biotic impacts) do not necessarily hasten the termination of their ecological steady state (or if they do, the ecosystem is more likely to go totally extinct). However, ecological steady states are terminated by mutant species with large fitness (Becker & Sibani, 2014), and so ecosystems in cooler climates (which are more common with larger σ_{bio}) that also have reduced mutation rates may reduce the probability of mutant species invading and destabilizing the core.

Abundance and species richness reduced when climate impacts are large

Final ecosystem abundance (Fig. 3.11a) and abundance of core species (Fig. 3.11b) are both similar at most σ_{bio}, but decline at very large standard deviations of biotic impacts when death and mutation are temperature-dependent ($p < 0.05$). There is no reduction in abundance when death and mutation are temperature-independent (Fig. 3.11). Therefore the temperature-dependence of death and mutation either directly, or indirectly through cooler climates, reduce abundance when species have large impacts on the climate. In Chapter 2 we saw that abundance does not respond to death or mutation rates (Fig. 2.4) and is not temperature-dependent in the TaNa+T (Fig. 2.7). However, temperature in the TaNa+T is always constant, so the decline in abundance in the TaNC here could be a response to the rate of change of temperature in surviving ecosystems. On the other hand, it could indicate selection for small ecosystems at large σ_{bio}, which could arise as a form of selection for ecosystems with smaller climate impacts (as fewer individuals may produce smaller carbon fluxes; Eq. 3.4).

Species richness also declines at the largest scales of biotic impacts with temperature-dependence of death and mutation, leading to distinctly lower species richness at large scales of biotic impacts (Fig. 3.12a; $p < 0.001$). This decrease in species richness disappears when death and mutation are held constant. In Chapter 2, we saw that the temperature-dependence of species richness is driven by mutation rate, so species richness probably decreases with larger σ_{bio} because ecosystems are pushed to colder temperatures (Fig. 3.4), where mutation rates are lower. This is also why species richness does not respond to σ_{bio} when death and mutation are held constant, even though temperature is cooler with larger standard deviations of biotic impacts in those simulations too (Fig. 3.4). Additionally, this is why species richness is lower when death and mutation are temperature-dependent than when those rates are held constant even with small values of σ_{bio}: death and mutation rates are lower than the default values at the initial temperature in these simulations.

Although core species richness is less sensitive to σ_{bio} than the richness of entire ecosystems, the occurrence of cores with more than 2 species almost disappears at the largest standard deviation of biotic impacts when death and mutation are temperature-dependent (Fig. 3.12b). As for species richness of all species, the temperature-dependence of death and mutation affects core species richness because mutation is reduced in the cooler climates achieved by ecosystems with large σ_{bio}, giving new ecosystems fewer options for forming cores with mutualistic interactions. However, as in Chapter 2, core species richness is less sensitive to temperature than overall species richness, and differences in the median and variance of core species abundance are not statistically significant.

3.3.3 Adaptations of species' responses to and impacts on climate

Finally, we turn to the evolutionary responses of species' thermal optima ($T_{\mathrm{opt,t}}$) and carbon impacts (b_i) to the co-evolution of ecosystems and climate.

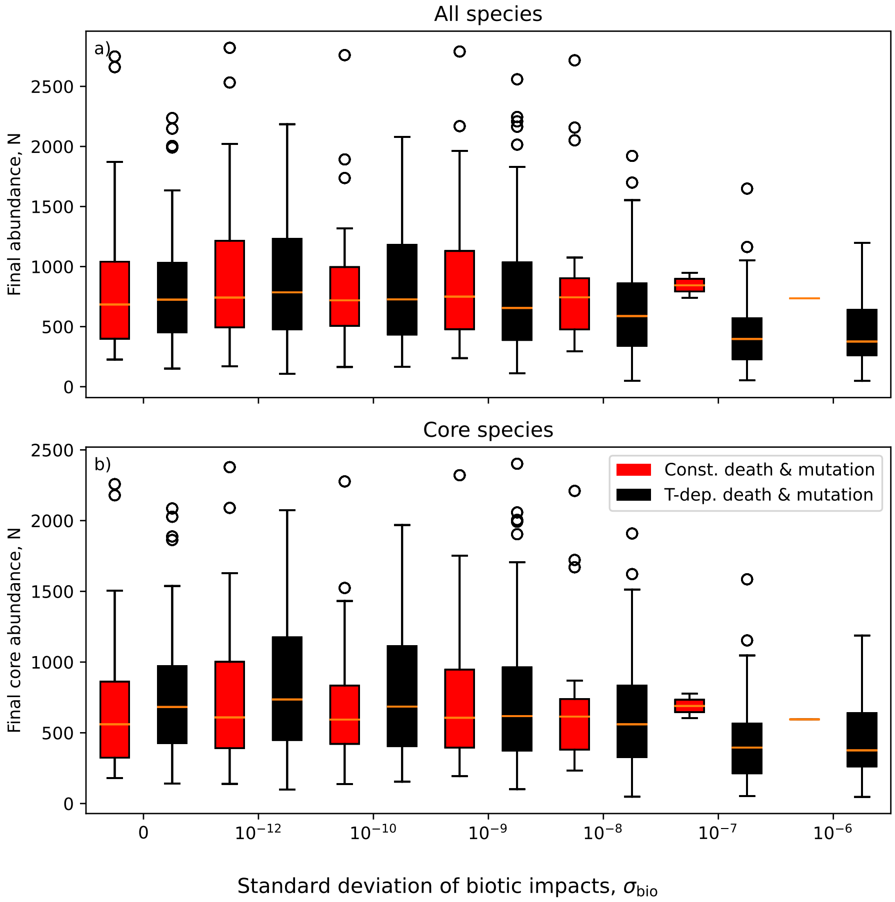


Figure 3.11: Final abundance of a) ecosystems and b) core species when death and mutation probabilities are held constant (red) and when they are temperature-dependent (black) at each standard deviation (σ_{bio}) of biotic impacts. The orange line in each box shows the median value, the edges of the boxes show the first and third quartiles, whiskers extend to the farthest point within 1.5 times the interquartile range, and points beyond the whiskers are circled.

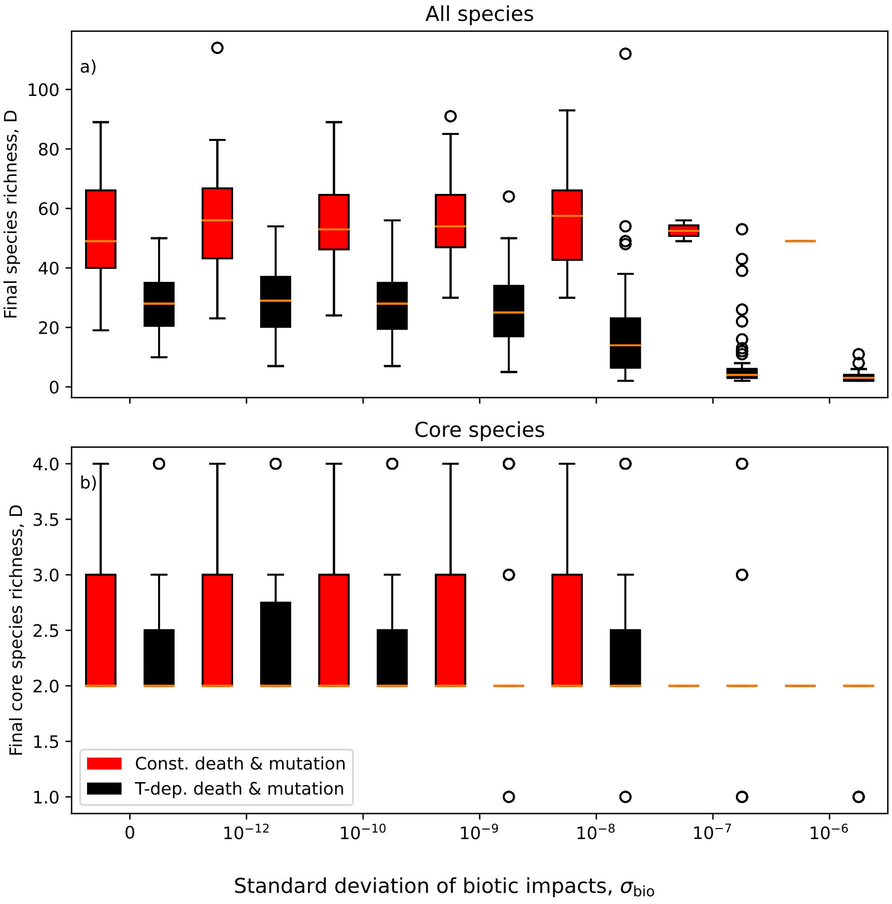


Figure 3.12: Final species richness of a) ecosystems and b) core species when death and mutation probabilities are held constant (red) and when they are temperature-dependent (black) at each standard deviation of biotic impacts (σ_{bio}). The orange line in each box shows the median value, the edges of the boxes show the first and third quartiles, whiskers extend to the farthest point within 1.5 times the interquartile range, and points beyond the whiskers are circled.

Selection for negative thermal mismatches

Species' thermal adaptation, the difference between their optimal temperature and the environmental temperature ($T - T_{\mathrm{opt,i}}$), scales their reproduction rate (Eq. 2.5), and thus their fitness. After 10,000 generations (10 million years) of evolution, the distribution of surviving species' thermal mismatches ($T - T_{\mathrm{opt,i}}$) becomes approximately normally distributed around 0 (representing perfect adaptation; Fig. 3.13a,b). However, with larger biotic impacts ($\sigma_{\mathrm{bio}} \geq 10^{-8}$), the distribution shifts toward more negative thermal mismatches, with more negative means ($p < 0.001$), indicating that more species exist at temperatures below their thermal optimum. The distribution of thermal mismatches in surviving ecosystems is especially negative when death and mutation are temperature-dependent, with species living up to 40K (40°C) below their optimum temperature, as compared to a maximum of 20K (20°C) when death and mutation are constant (Fig. 3.13a,b).

In ecosystems that go extinct, the distribution of thermal mismatches is wider, suggesting unsurprisingly that ecosystems are more likely to go extinct when species have larger thermal mismatches (and are thus more poorly-adapted to the climate; Fig. 3.13c,d). However, ecosystems also commonly go extinct containing some species with small thermal mismatches, suggesting that the presence of well-adapted species does not guarantee ecosystem survival — after all, model ecosystems require mutualistic interactions between at least two species, so species must find the right interactions with other species in addition to themselves being well-adapted to the climate. At the largest standard deviation of biotic impacts ($\sigma_{\mathrm{bio}} = 10^{-6}$) when death and mutation are temperature-dependent, there is also a peak of very negative thermal mismatches in extinct ecosystems, suggesting that many ecosystems went extinct with species that were too far below their thermal optima in that configuration (Fig. 3.13d). In other words, there is clear selection for species to be adapted to cooler climates, but this can also lead to total extinctions if the climate later warms.

Natural selection for ecosystems with smaller climate impacts

The evolution of temperature in the TaNC is driven by the evolution of core species' carbon fluxes (F_i). Species' carbon fluxes are the product of species' intrinsic impacts (b_i) on carbon, reproduction rates ($r_i(T, T_{\mathrm{opt,i}})$), and the mass of carbon in the atmosphere ($m_{\mathrm{CO_2}}$; Eq. 3.3). However, since temperature depends logarithmically on temperature (Eq. 3.2), a species with a certain carbon impact and metabolic rate will cause the same amount of warming or cooling regardless of the mass of carbon in the atmosphere, as explained in the

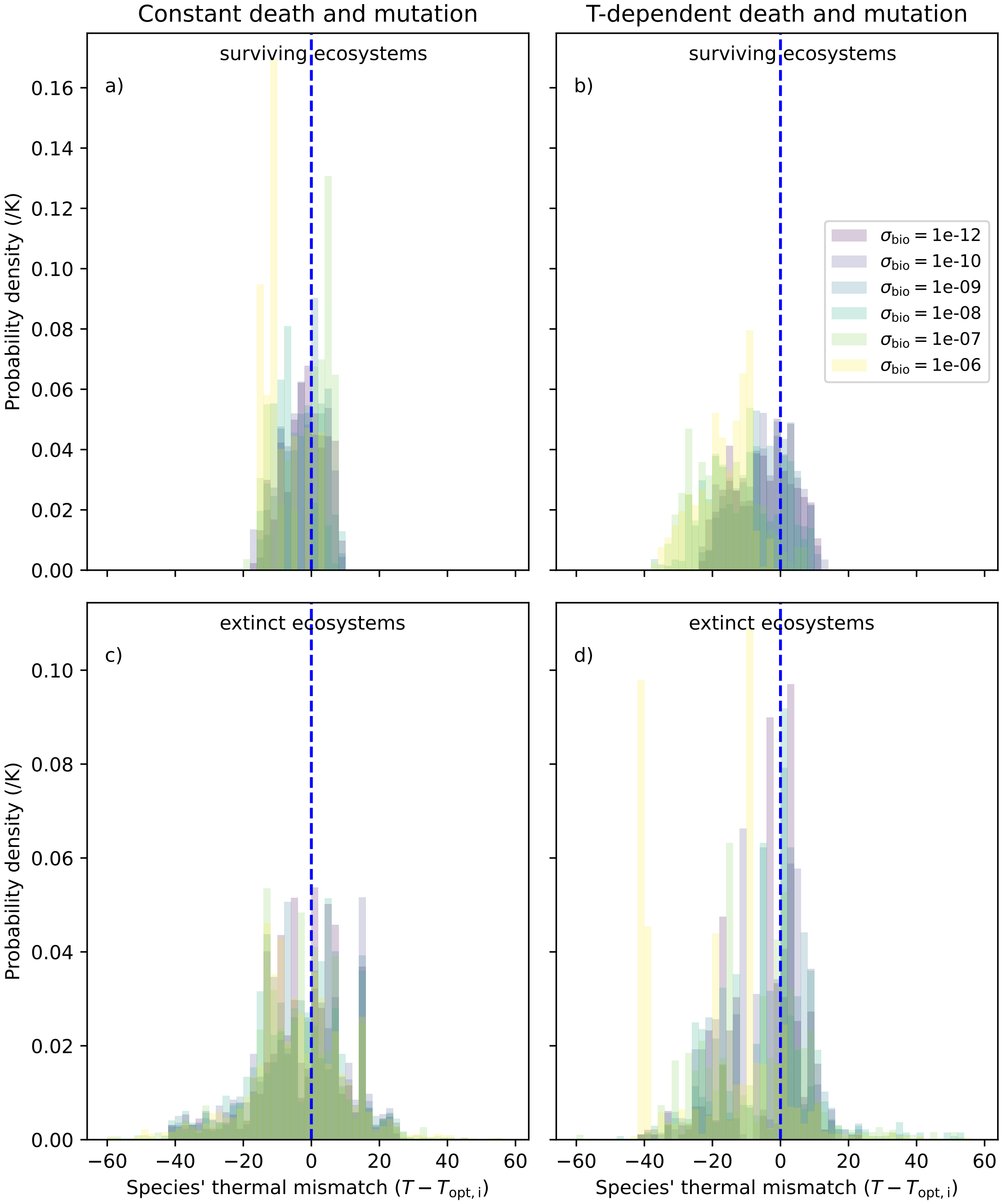


Figure 3.13: Species' thermal mismatches ($T - T_{\mathrm{opt,i}}$) after a,b) surviving 10,000 generations (10 million years), or after c,d) going extinct before then. The left column shows results when death and mutation are held constant, and the right column when death and mutation are temperature-dependent. The blue dashed line is at 0, representing perfect thermal adaptation. Colors correspond to the standard deviation (σ_{bio}) of biotic impacts.

Methods section above. Therefore, species' ability to warm or cool the climate depends only on b_i and $r_i(T, T_{\text{opt,i}})$, and not on m_{CO_2}. A species' metabolic rate depends on its thermal mismatch ($T - T_{\text{opt,i}}$), discussed in the previous section; so species' thermal mismatch affects not only species' adaptation to the environment (in terms of reproduction rate) but also species' impacts on the environment.

After 10,000 generations (10 million years) of evolution, the shape of the distribution of core species' intrinsic impacts (b_i) on carbon remains similar to the input curve (a normal distribution with standard deviation σ_{bio}), but some departures away from the input distribution are noticeable with larger values of σ_{bio} (Fig. 3.14a,b). In particular, with larger σ_{bio}, the evolved b_i distribution contracts relative to the initial distribution ($p < 0.01$), indicating selection for species with small intrinsic impacts on carbon (Fig. 3.14a,b, 3.15a,b). Interestingly, with constant death and mutation, the distribution of b_i becomes bimodal at the strongest standard deviation of biotic impacts ($\sigma_{\text{bio}} = 10^{-6}$), suggesting that more species survive with cooling or warming impacts than negligible impacts (Fig. 3.14a). When death and mutation are temperature-dependent on the other hand, the distribution remains unimodal at all σ_{bio}, and the distribution shifts to a slightly cooler median ($p < 0.001$), exhibiting selection for species with smaller and more cooling impacts (Fig. 3.14b). Additionally, whether death and mutation are constant or temperature-dependent, the median and quartile values of b_i/σ_{bio} are shifted toward negative values at the largest standard deviation of biotic impacts ($\sigma_{\text{bio}} = 10^{-6}$), indicating selection for cooling species when species' impacts are larger.

When death and mutation are constant, the quartile values of b_i in extinct ecosystems are slightly larger than the initial values, indicating that ecosystems are more likely to go extinct when species' intrinsic carbon impacts are larger (Fig. 3.15a,c). In conjunction with the slight contraction of quartile values of b_i in surviving ecosystems ($p < 0.01$), this also suggests that there is evolution of b_i driven by total ecosystem extinctions.

Compared to the distributions of species' intrinsic carbon impacts (b_i), the distributions of the rates at which species affect the climate (F_i/m_{CO_2}) are more sharply peaked at every σ_{bio} (with smaller variance in $F_i/m_{\text{CO}_2}/\sigma_{\text{bio}}$ than in b_i/σ_{bio}), showing strong selection for weak climate impacts (Fig. 3.14c,d). As mentioned above, differences between F_i/m_{CO_2} and b_i must be achieved by species living away from their thermal optima, and thereby reducing their metabolic rates ($r_i(T, T_{\text{opt,i}})$), which is associated with larger thermal mismatches of species at larger σ_{bio} (previous section). The distributions of F_i/m_{CO_2} are narrowest relative to σ_{bio} at the larger values of σ_{bio} (Fig. 3.14c,d; 3.16a,b; $p < 0.001$), showing that there is stronger selection for species with smaller carbon fluxes when the

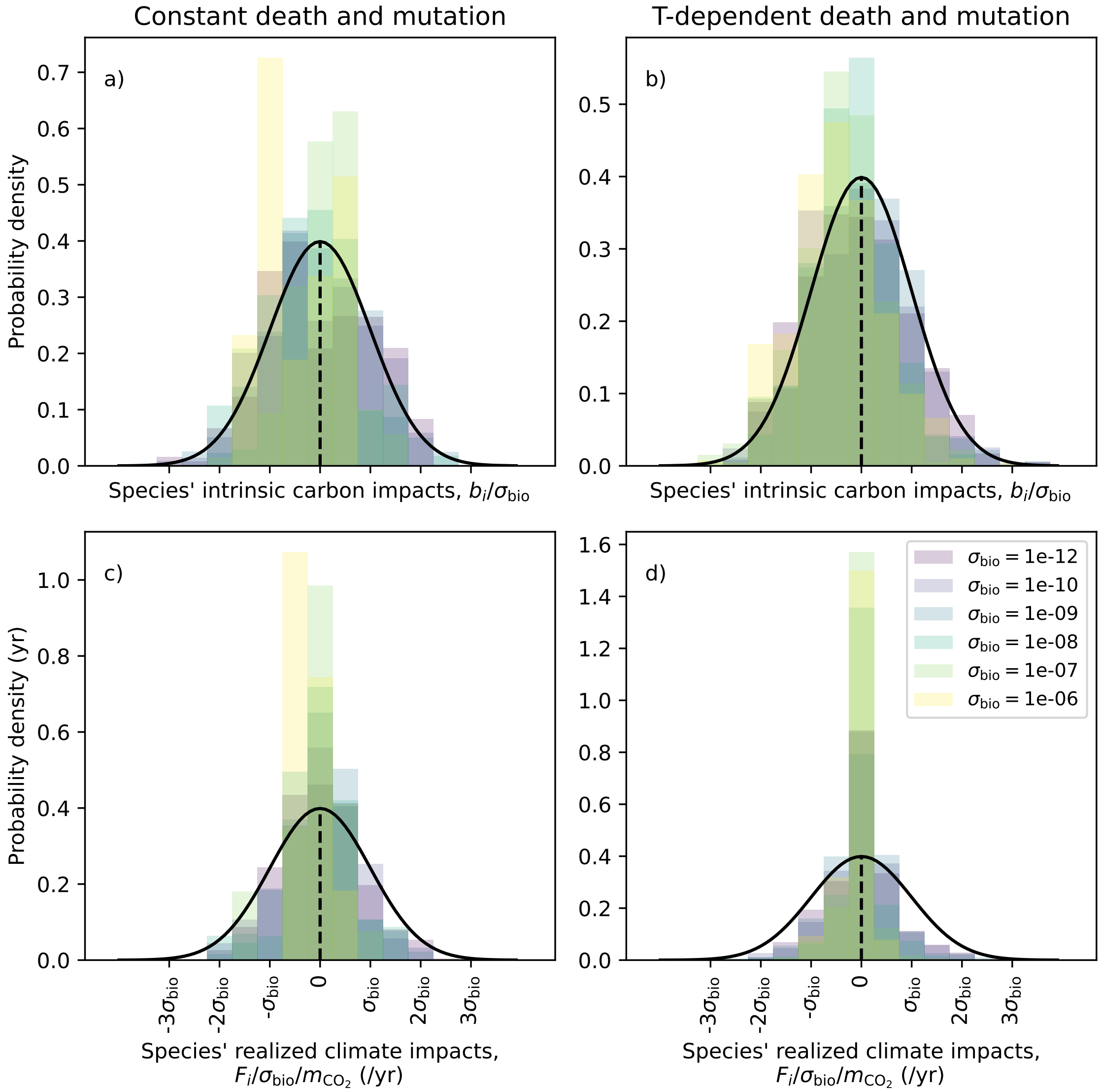


Figure 3.14: a,b) Histograms of core species' intrinsic impacts (b_i) on carbon, divided by the standard deviation (σ_{bio}) of biotic impacts, for simulations with a) constant and b) temperature-dependent death and mutation probabilities at the end of 10,000 generations (10 million years). The distributions are compared to the normal distribution with standard deviation σ_{bio} from which b_i were drawn to show how the distribution has evolved from its original shape. c,d) Histograms of species' per-capita carbon fluxes (F_i) divided by σ_{bio} and the mass of carbon in the atmosphere (m_{CO_2}), representing species' realized rate of climate impacts for c) constant and d) temperature-dependent death and mutation rates, at the end of 10,000 generations (10 million years) for different σ_{bio}.

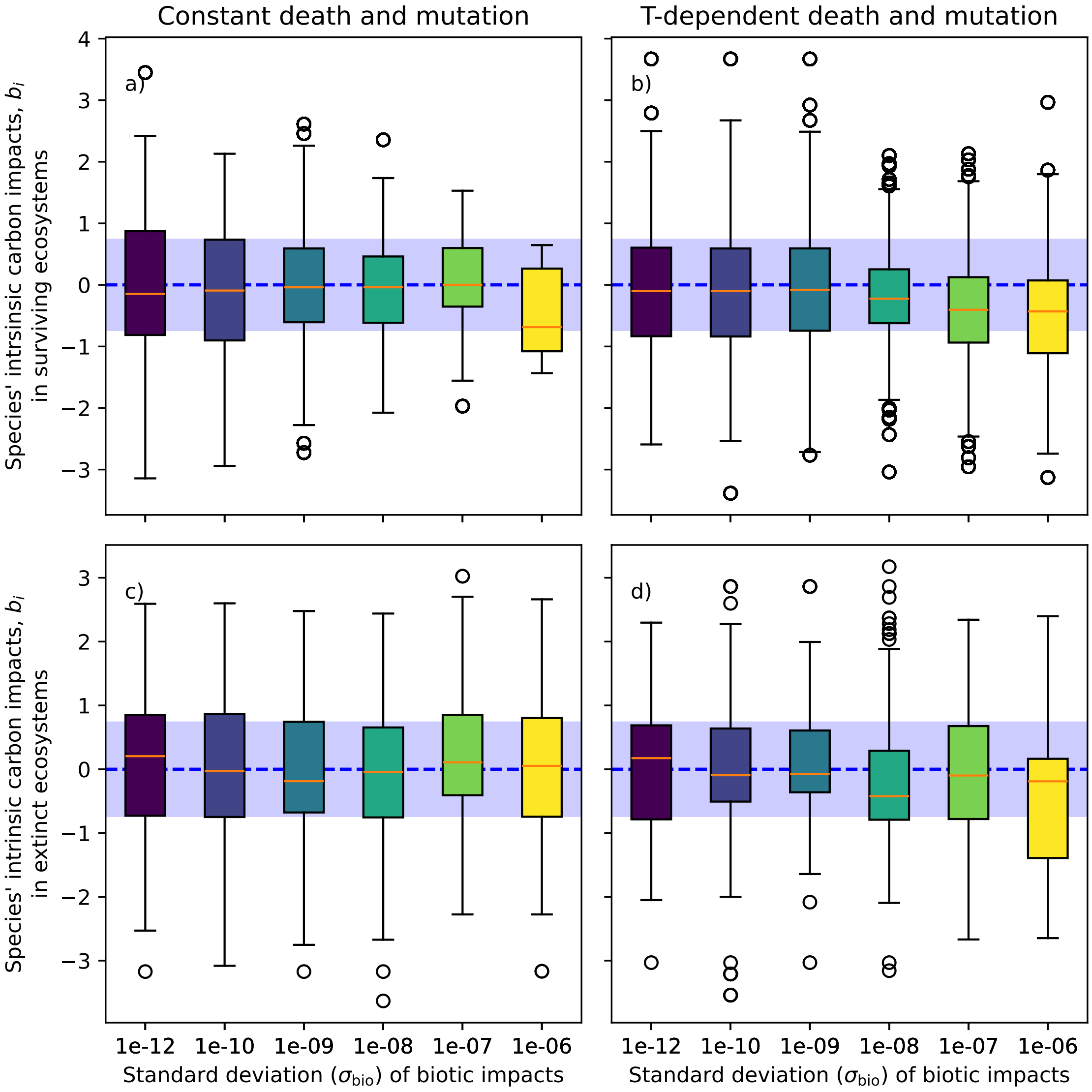


Figure 3.15: Boxplots of species' intrinsic impacts (b_i) on carbon divided by the standard deviation (σ_{bio}) from which b_i were originally drawn, in a,b) surviving ecosystems and c,d) extinct ecosystems, and when death and mutation are a,c) held constant and b,d) temperature-dependent. The blue dashed line is at 0 and the light blue shaded region shows the quartiles of the initial distribution of b_i. The red line in the middle of each box shows the median value, the edges of the boxes show the quartiles, and the whiskers extend to the farthest point within 1.5 times the interquartile range. Points beyond the whiskers are circled.

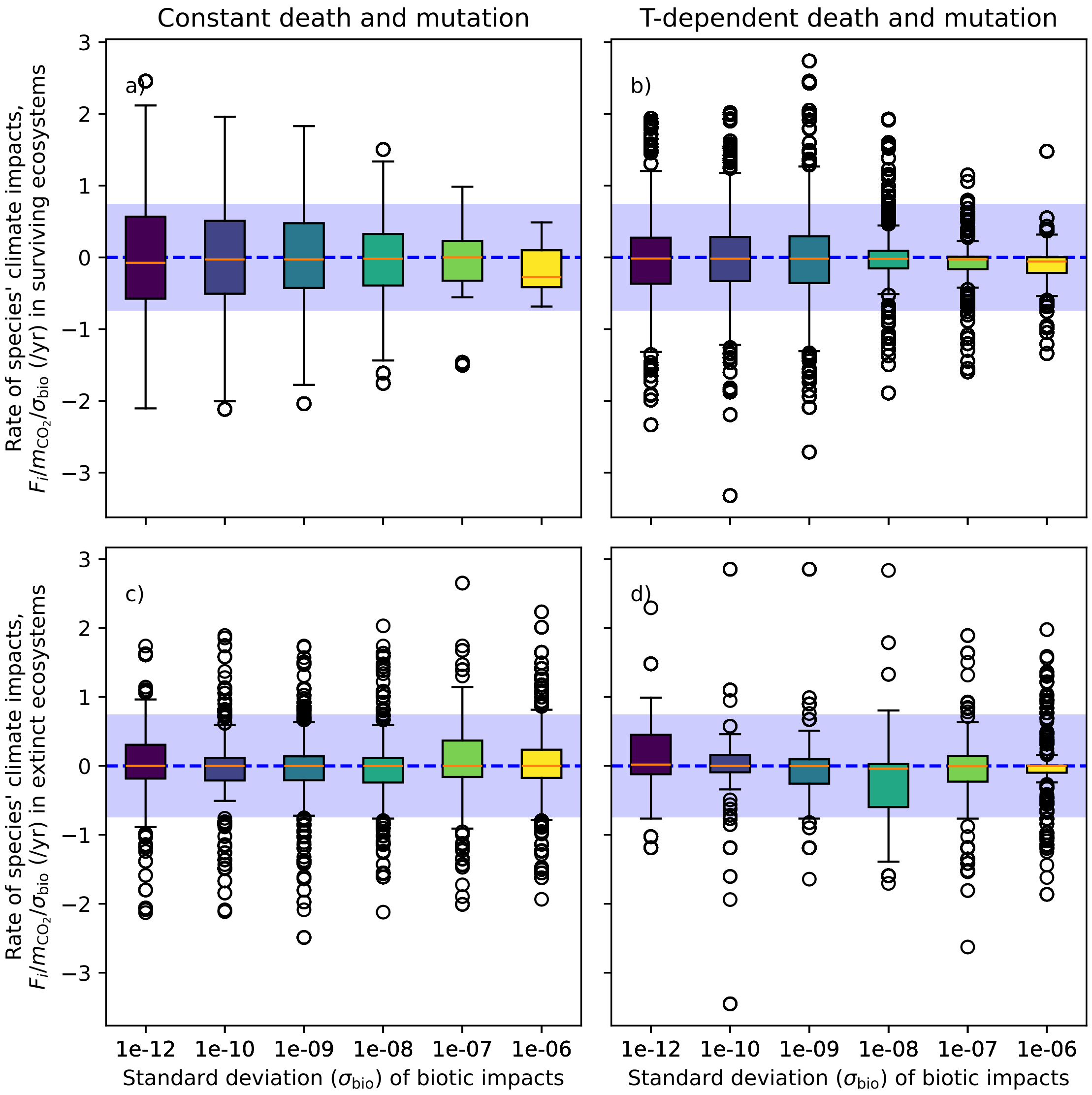


Figure 3.16: Boxplots of the rates at which species impact the climate (F_i/m_{CO_2}) divided by the standard deviation (σ_{bio}) from which intrinsic carbon impacts (b_i) were drawn, in a,b) surviving ecosystems and c,d) extinct ecosystems, and when death and mutation are a,c) held constant and b,d) temperature-dependent. The blue dashed line is at 0 and the light blue shaded region shows the quartiles of the initial distribution of b_i. The red line in the middle of each box shows the median value, the edges of the boxes show the quartiles, and the whiskers extend to the farthest point within 1.5 times the interquartile range. Points beyond the whiskers are circled.

standard deviation of biotic impacts is larger. There is also selection for negative F_i at the largest σ_{bio} when death and mutation are constant (Fig. 3.14 c; p < 0.001), but the distributions of F_i/m_{CO_2} at all other σ_{bio} remain more symmetrical and centered at zero, both when death and mutation are constant and temperature dependent (Fig. 3.14c,d).

Most species in extinct ecosystems also have smaller F_i/m_{CO_2} than the original distribution of b_i. As the distribution of b_i, on the other hand, evolves wider in extinct ecosystems than its original distribution, the narrower distribution of F_i/m_{CO_2} suggests that species in extinct ecosystems have large thermal mismatches, as seen earlier in Fig. 3.13.

The distribution of rates of ecosystem impacts on the climate (ecosystem carbon fluxes, F_{bio}, divided by the mass of carbon in the atmosphere, m_{CO_2}) is much wider than the initial distribution of species' intrinsic impacts (b_i) on carbon in surviving ecosystems (Fig. 3.17a,b; variance 4 orders of magnitude larger than F_i). This is not surprising since the carbon flux of an ecosystem includes all the fluxes of every individual of each species (Eq. 3.4). However, $F_{\mathrm{bio}}/(\sigma_{\mathrm{bio}} m_{\mathrm{CO}_2})$ is smaller at larger values of σ_{bio} in surviving ecosystems when death and mutation are temperature-dependent (Fig. 3.17a,b; p < 0.001]). This suggests that there is stronger selection for ecosystems with smaller carbon fluxes when the standard deviation of biotic impacts is larger.

Unlike in surviving ecosystems, ecosystems' rates of climate impacts just before they go extinct are generally smaller than the initial distribution of intrinsic carbon impacts (Fig. 3.17c,d). This is because ecosystems that are about to go extinct contain fewer species with smaller populations, and the species are often farther from their thermal optima.

In surviving ecosystems, species' total carbon fluxes ($F_i N_i$) are sometimes larger than ecosystem carbon fluxes (F_{bio}; Fig 3.18). This indicates that species' carbon fluxes sometimes cancel out with other species with the opposite impacts. When death and mutation are held constant, the amount of canceling is not strongly dependent on σ_{bio} (Fig. 3.18a,c). However, when death and mutation are temperature dependent, species are much more likely to cancel their carbon fluxes with other species at larger σ_{bio} (Fig. 3.18d). This indicates strong ecosystem-level selection for ecosystems with small carbon fluxes through a mechanism that depends on multiple species together.

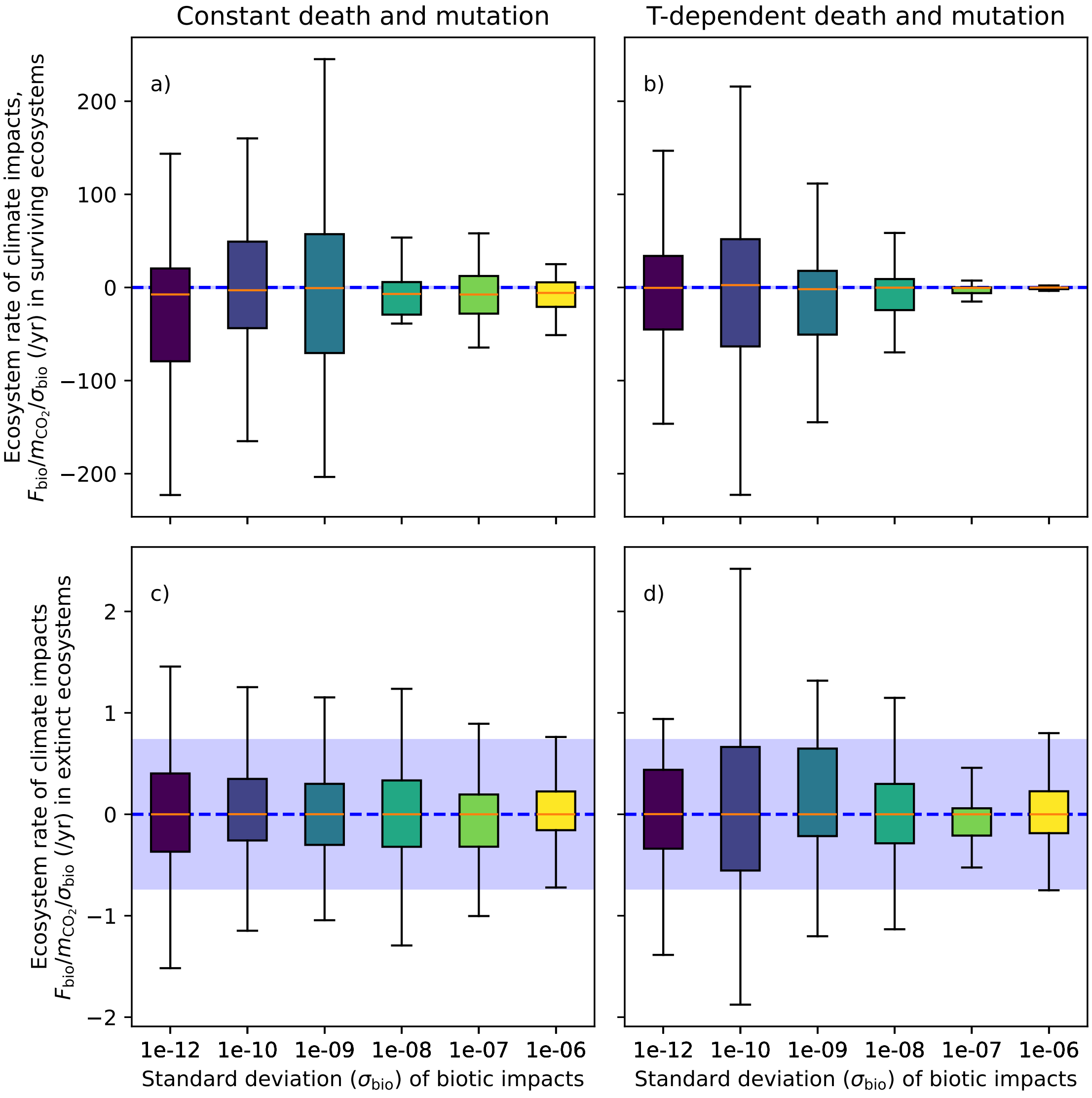


Figure 3.17: Boxplots of ecosystem rates of climate impact ($F_{\mathrm{bio}}/m_{\mathrm{CO_2}}$) divided by the standard deviation (σ_{bio}) from which species' intrinsic carbon impacts (b_i) were originally drawn, in a,b) surviving ecosystems and c,d) extinct ecosystems, and when death and mutation are a,c) held constant and b,d) temperature-dependent. The blue dashed line is at 0 and the light blue shaded region shows the quartiles of the initial distribution of b_i. The red line in the middle of each box shows the median value, the edges of the boxes show the quartiles, and the whiskers extend to the farthest point within 1.5 times the interquartile range. Outliers are omitted here but shown in Appendix Fig. B.2.

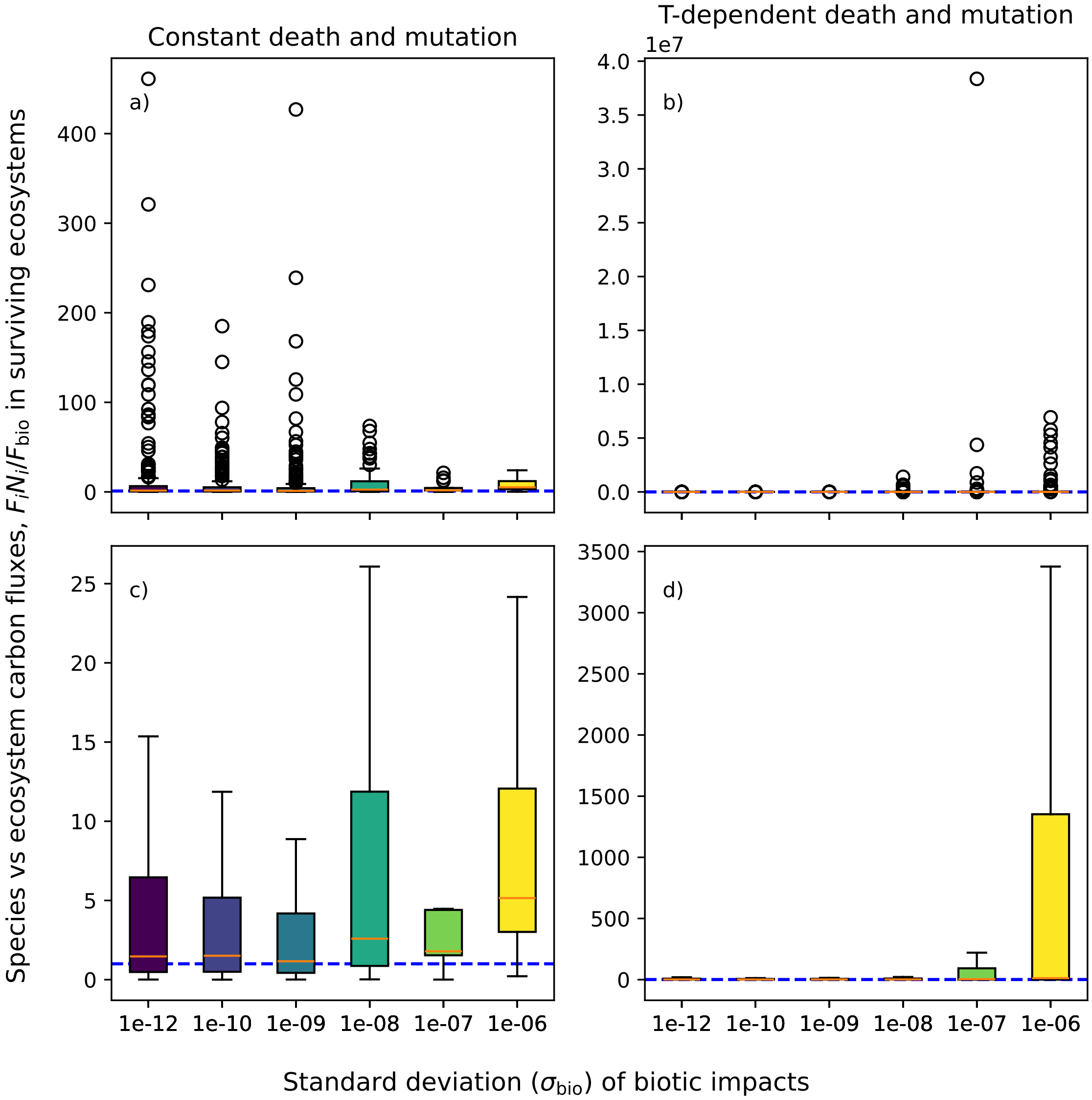


Figure 3.18: The ratio of species' carbon fluxes (F_iN_i) to the overall ecosystem carbon flux (F_{bio}) for a,c) simulations in which death and mutation are held constant, and b,d) simulations in which death and mutation are temperature-dependent. Ratios larger than 1 (horizontal, dashed blue line) indicate that species' carbon fluxes are larger than the ecosystem carbon fluxes, and therefore cancel out with other species in the ecosystem. In all boxes, the orange horizontal line shows the median values, the edges of the boxes show the 25th and 75th percentiles, and the whiskers extend to the farthest point within 1.5 times the interquartile range. Panels a) and b) show all data points (outliers circled) and panels c) and d) exclude outliers.

3.4 Discussion and Conclusions

3.4.1 Summary

In this study, we have coupled an agent-based, generalized Lotka-Volterra model of ecology and evolution (fleshed out in Arthur and Nicholson (2017, 2022)), in which species respond to temperature (the Tangled Nature +Temperature model from Chapter 2), with a simple climate model, producing the Tangled Nature + Climate (TaNC) model. We use the TaNC to examine how ecosystems and their environments co-evolve when each impacts the other. This allows us to investigate whether and in what form niche construction emerges at the level of ecosystems, and how its emergence and characteristics depend on species' thermal responses (birth, death, and mutation) and the strength (σ_{bio}) of biotic impacts on the environment.

We find that ecosystem impacts on the climate are logarithmically related to the standard deviation (σ_{bio}) of biotic impacts since temperature is logarithmically related to atmospheric CO_2. With large enough σ_{bio} (10^{-8} or larger), ecosystems become more likely to cool the climate than warm it, largely because of reduced death rates at colder temperatures, but also because of the asymmetrical thermal response curves of species reproduction rates (Fig. 3.4a). Total extinctions are more likely to arise in warmer climates than cooler ones, indicating that selective extinctions of warm ecosystems are at least partially responsible for shifting the median temperature of surviving ecosystems toward cooler climates (Fig. 3.4b). This demonstrates an ecosystem-level process of evolution called *selection by survival*, as conceptualized by Doolittle (2017, 2019) and Lenton, Daines, Dyke, et al. (2018). Ecological steady states also last longer in colder climates (Fig. 3.8), so in addition to selective total extinctions, mass extinctions occurring more frequently at warmer temperatures also push ecosystem evolution toward colder climates (Fig. 3.7). This demonstrates a second mechanism of selection called *sequential selection*, as proposed by Betts and Lenton (2008), further explored by Lenton, Daines, Dyke, et al. (2018), and more thoroughly investigated by Arthur and Nicholson (2017, 2022).

When species' impacts are negligible, the climate remains relatively constant, and so most ecosystems survive (Fig. 3.9), as in the basic form of the Tangled Nature model. With larger biotic impacts, however, climate change becomes more common (Fig. 3.8), and ecosystem survival probability declines (Fig. 3.9). Importantly, stable ecosystems do not always produce stable climates (Fig. 3.6, 3.7). However, the amount of climate change within steady states increases more slowly than the standard deviation of biotic impacts

(Fig. 3.7, B.1), suggesting selection for smaller biotic impacts on the climate. Interestingly, the duration of steady states in surviving ecosystems does not decrease with larger standard deviations of biotic impacts (Fig. 3.10). Ecological steady states can sustain many degrees of climate change, but generally terminate in mass extinction events with less than 1K (1°C) of climate change, suggesting that ecological interactions between species terminate ecological steady states more commonly than climate change does. These interspecific interactions could slow the rate of sequential selection as it results in multiple directions of selection.

Ecosystem impacts on the climate begin to feed back on species richness when the standard deviation of biotic impacts is at least 10^{-8} times the carbon reservoir, reducing species richness (Fig. 3.12). When the standard deviation of biotic impacts is 10^{-7} or larger and death and mutation are temperature dependent, ecosystems also become smaller (Fig. 3.11). These feedbacks decrease the strength of ecosystem impacts on the climate (Fig. 3.17), which is a key mechanism of sequential selection as theorized by Betts and Lenton (2008). Specifically, reduced abundance and species richness can act as limiting factors for biotic impacts on the environment, preventing ecosystems from changing the environment too drastically. We more generally propose that this could be a form of ecosystem-level niche construction, in which biotic impacts on the environment feed back on ecosystem characteristics.

The evolution of species' thermal optima and carbon impacts are key driving forces of the evolution of the climate and ecosystem characteristics. In the TaNC, species' thermal optima evolve toward a normal distribution centered just below the environmental temperature, and with larger standard deviations of biotic impacts, the difference between species' thermal optima and the environment increases (Fig. 3.13), which reduces species reproduction rates (Eq. 2.4) but also their climate impacts (Eq. 3.3, Fig. 3.16). Selection for species with small intrinsic impacts (b_i) on carbon also contributes to reducing species' climate impacts (F_i; Fig. 3.14, 3.15). At the ecosystem level, selection for smaller climate impacts ($F_{\text{bio}}/m_{\text{CO}_2}$) when standard deviations of biotic impacts are larger (Fig. 3.17) is partially driven by selection at the species-level for species with small carbon fluxes, but there is also selection at the ecosystem-level for species canceling out their carbon fluxes with other species in ecosystems when the standard deviation of biotic impacts is large and death and mutation are temperature-dependent (Fig. 3.18).

3.4.2 Implications

An important motivation for this study is trying to understand how species that both adapt to and modify the environment affect both the environment and the physiological fitness of the species. We find that species tend to cool the climate, often below the optimum temperatures of core species — so rather than driving the climate toward species' optimum temperatures (and thus optimizing reproduction rates), species tend to drive the climate toward a state with lower death probability. This suggests that there is stronger selection for species to modify their environments in a way that minimizes death than maximizes reproduction.

Cooling could arise in our model for two main reasons. The first reason is related to how species experience the environment. Because of the asymmetry of species' thermal response curves, there is a wider range of temperatures at which species can reproduce in temperatures below than above their thermal optima. Additionally, death rates decline in cold temperatures for all species, making it easier for all individuals to survive in colder temperatures. Mutation rates also decrease in colder temperatures, and so mutants that might destabilize the ecosystem and cause a quake are less common in cooler climates. All these aspects of species' thermal responses make it easier for species to persist if their ecosystem cools the climate than warms it. Indeed, studies on species' thermal responses show that species often live at temperatures below that at which their fitness peaks (Martin & Huey, 2008; Amarasekare & Savage, 2012). This can be because organisms experience a variety of temperatures, and as fitness declines more steeply at temperatures above species' optimal temperature of fitness than below, it is to their advantage to inhabit slightly cooler temperatures (Martin & Huey, 2008; Amarasekare & Savage, 2012). Studies on the evolution of thermal response curves also suggest that species more easily adapt to cooler than warmer temperatures (Araújo et al., 2013). These studies are supported by empirical evidence, and align with our findings from Chapter 2 that show that ecosystem survival probability increases in cooler climates. This helps validate our findings that TaNC ecosystems survive more easily in cooler environments.

The second reason that cooling arises in the TaNC is related to species' impacts on the climate. As temperature evolves away from species' thermal optima, their impacts on the climate decrease (again due to the asymmetry of the thermal response of metabolic rates). As species are also more likely to survive in cooling ecosystems for the reasons above, ecosystems in cooler climates therefore have a better chance of maintaining more stable climates.

Additionally, many of the most important biotic carbon fluxes in the real world are negative, consistent with our finding that ecosystems tend to cool the climate. Carbon burial (Falkowski, 2012; Cartapanis et al., 2018; Isson et al., 2020; Golubic et al., 1979) and enhancement of weathering (Schwartzman, 2017; Schwartzman & Volk, 1991; Lenton & Watson, 2004) are two of the most important biotic impacts on the climate, and both remove atmospheric carbon. Dimethyl-sulfide production has also been proposed as a biotically driven climate-cooling mechanism (Charlson et al., 1987). Additionally, most of the ways in which species can produce positive carbon fluxes draw from biogenic carbon reservoirs, so they are largely limited by biotic processes that originally removed carbon from the ocean-atmosphere system (Archer, 2010).

Our results can be compared to a similar coupling of the TaNa model with an environmental temperature performed by Arthur and Nicholson (2023). Model ecosystems in that work on average bring the temperature toward the universal optimum, but realized temperatures are bimodally distributed, with almost no ecosystems ending at the optimal temperature. Cooling ecosystems in climates that were initially warm, and warming ecosystems in climates that were originally cool, achieve larger abundances in the model, but small ecosystems with the opposite impacts also persist. In that work, model species respond to temperature in their interaction strengths, which then makes abundance temperature-dependent. Additionally, all species in their model have the same thermal optimum. This allows ecosystems in their model to become larger if they bring the climate toward the universal optimum. Larger ecosystems create a larger barrier for mutant species to destabilize the core, and thus enable ecosystems to last longer if they are larger. However, this process is weak, and so ecosystems that do not have these effect are still almost as common. Therefore, the model results of Arthur and Nicholson (2023) suggest that even if ecosystem abundance is maximized at a universally optimum temperature, ecosystem evolution is only weakly guided toward that temperature.

In our model, by contrast, species birth, death, and mutation rates are temperature dependent, and species thermal optima are uniformly distributed across 73K (73°C). This means that abundance does not peak at universal optimum, and explains why almost all surviving ecosystems evolve toward cooler climates in the TaNC. However, a smaller choice of the parameter controlling the scale of interspecific interactions (C in Chapter 2) could possibly introduce temperature-dependence of abundance into the model. Importantly, the comparison of these two studies highlights the fact that different types of thermal responses cause different effects on environmental evolution. This should motivate future research to continue building an understanding of how different thermal responses scale up to ecosystem-level impacts and contribute to shaping the environment.

The two mechanisms of ecosystem-level selection we investigate here are selection by survival (driven by selective total extinctions of ecosystems) and sequential selection (driven by selective mass extinctions of ecosystems). We find that both mechanisms of ecosystem-selection may be operating in the TaNC. Ecosystems in warm climates, and ecosystems containing species with large intrinsic impacts (b_i) on carbon, are both more likely to go extinct. As those ecosystems die off, ecosystems in cooler climates and those with species that have smaller intrinsic carbon impacts become more common. Additionally, ecological steady states do not last as long in warmer climates, so mass extinctions occur more frequently in warmer than cooler climates. Before reaching the point of mass or total extinction, however, species and ecosystems may not experience selective pressures that prevent them from having the types of impacts that will ultimately lead to their demise. This suggests that, rather than manicuring the environment it needs, species are constantly forced to adapt to the "waste-products" (in this case the temperature) produced by previous generations, as suggested by Volk (2004). In other words, the process of ecosystem adaptation works in tandem with selection by survival and sequential selection. This aligns with the view that both environmental modifications and adaptations to those modifications are part of evolution by natural selection, which has been suggested both in the Earth System Science community (Betts & Lenton, 2008; Arthur & Nicholson, 2023) and the ecological community (K. Laland et al., 2014).

3.4.3 Future directions

The TaNC model presented in this chapter illustrates some emergent properties of ecosystem-climate co-evolution. However, we make several simplifications which could influence our results and warrant further consideration.

The most important controls on the interplay between ecosystems and the climate in the TaNC are species' thermal responses and environmental impacts. While the three thermal responses we chose are well-characterized in ecology (e.g. Brown et al., 2004; Gillooly et al., 2005), the ways that species' thermal optima are distributed are not. Here we use a uniform distribution of species' optimal temperatures of reproduction to minimize bias in the model, but this may not accurately represent how species' thermal optima are really distributed (Costello et al., 2023; Lenton & Lovelock, 2000). Similarly, we make species' intrinsic impacts on carbon normally distributed in the TaNC. The normal distribution is a widely-occurring, symmetrical distribution, but again, species' impacts may not follow this distribution. Therefore, the next chapter is dedicated to examining the sensitivity of our results to these two distributions.

In order to extrapolate our results to other aspects of the environment, it is important to consider the types of impacts that species can have on different environmental components, and how different environmental components affect ecosystems differently. Here, we investigate a unimodal response to the environment (the thermal dependence of reproduction) and two monotonically increasing responses (the thermal responses of death and reproduction), and each of these responses affects a different aspect of ecosystems (Chapter 2). Different environmental responses, and interspecific variation in these responses, might lead to different environmental impacts (B. Chen, 2022). Furthermore, other aspects of the environment affect different characteristics of ecosystems. For example, both resource availability and interaction strength feed back on ecosystem abundance (Chapter 2), which could produce different types of feedbacks between ecosystems and their environments (as seen in the model produced by Arthur & Nicholson, 2023). Continuing to unravel the interplay between all these different types of environment-ecosystem interactions will help generalize our understanding of the evolutionary mechanisms of niche construction.

Another important simplification in our model is that the climate is unchanging when species do not affect it. This makes it easier for ecosystems to persist in the case where species do not affect the climate ($\sigma_{\text{bio}} = 0$) than in any of the climates influenced by species. This may not accurately reflect conditions on Earth, in which there are many abiotic factors that can perturb the climate: orbital changes, volcanic eruptions, movement of the continents, asteroid collisions, and the brightening of our Sun. In the real world, some biotic impacts such as biotic enhancement of weathering have evolved to minimize these perturbations (Schwartzman & Volk, 1991). Modeling a constant background climate in the TaNC removes the opportunity for species in the TaNC to dampen abiotic perturbations, though, so species with larger biotic impacts have an unrealistic disadvantage against species without biotic impacts in the TaNC. The constant background climate of the TaNC furthermore drives selection for species with minimal effects on the climate ($F_i \approx 0$). Therefore, future work should consider whether selection for perturbation-dampening ecosystems arises in variable environments.

The initial conditions and boundary conditions could also be important controls on our results. The main result of this model suggests that ecosystems evolve to cool the climate. However, if simulations were initialized in very cold conditions, there could be selection for warming ecosystems, which would be worth exploring in further investigations. Earth also has important boundaries on how life can evolve. For example, water freezes in temperatures around 273K (0°C), imposing challenges on all life forms through the crystallization of water in cells. Freezing of water also alters the physical landscape and species' habitats. Including some of these constraints might prevent the model from continuously cooling to temperatures below freezing in the model. Additionally, Metabolic Theory of Ecology suggests that species should be able to achieve larger maximum metabolic rates if their thermal optima are warmer (Gillooly et al., 2001; Brown et al., 2004; Amarasekare & Savage, 2012). This "hotter is better" phenomenon has been investigated in certain ecosystems with limited support (e.g. B. Chen, 2022; Araújo et al., 2013; Molinet & Stelkens, 2025), and as the extent of this macroecological pattern remains uncertain, it could be interesting to explore in the TaNC. Making hotter "better" in the model could add contrasting pressures on ecosystems as reproduction rates increase in warmer temperatures and death rates decrease in cooler temperatures, and it would be interesting to see whether this changes the tendency of the TaNC to cool.

3.4.4 Conclusion

Overall, this work helps foster an understanding of how whole ecosystems simultaneously modify and adapt to their environments. In our model, ecosystems feed back on their own properties through interactions with the climate. Importantly, the TaNC demonstrates that species' physiological responses to their environment can drive asymmetrical changes in the climate and feed back on ecological characteristics. Ecosystem survival probability increases in colder temperatures at which death rates are reduced (Chapter 2 and Fig. 3.9), and this drives ecosystems colder (Fig. 3.4). As a result, species richness (Fig. 3.12) and abundance (Fig. 3.11) are reduced at the largest standard deviations of biotic impacts. These impacts of species on heritable ecosystem properties exemplify what we call ecosystem-level niche construction: the net impacts of ecosystems feeding back on heritable ecosystem characteristics.

The TaNC also suggests that stable ecosystems do not inherently evolve to stabilize their environments; temperature within ecological steady states often trends away from its initial state (Fig. 3.6, 3.7). However, the rate of climate change is not proportional to the standard deviation of biotic impacts, suggesting some evolution toward environmental stabilization. Selection for species that cancel one another's impacts (Fig. 5.11) also suggests evolution toward environmental stabilization. Ecosystem-level selection is a weak process, though, and so ecosystems are often forced to adapt to the consequences of the environmental changes caused by their ancestors.

This model gives body to some theories about ecosystem-level selection, and is an important step toward investigating ecosystem-climate co-evolution. The TaNC also provides a tool that can be built off of in future work. Other feedback mechanisms between ecosystems and their environments which are at play in the real world could be incorporated into the TaNC to continue constructing a more general understanding of how niche construction evolves, and the spatial, temporal, and biological scales at which it can operate.

Chapter 4

Shared preferences and opposite effects: how similarity in thermal optima, and opposition of impacts, affect the co-evolution of climate and ecology

Abstract

The ways that ecosystems and their environments co-evolve depends on the nature of their interactions. In the previous chapter, we assumed that species' thermal optima of reproduction are uniformly distributed, and species' impacts on the environment are normally distributed. However, the true shapes of these distributions are not well-characterized, and the assumptions we made in Chapter 3 could have important impacts on the results. For example, agreement between species about an optimal temperature could make ecosystems more likely to maintain the temperature near that shared optimum. Additionally, if species impacts are bimodally distributed, they may be more likely to cancel out within an ecosystem, allowing species with larger carbon fluxes to co-exist in more stable climates.

In this chapter, we investigate the sensitivity of the results of the previous chapter to different distributions of species' thermal optima and carbon impacts. We compare a uniform to a normal distribution of thermal optima of reproduction, and a normal to a bimodal distribution of carbon impacts. We find that a normal distribution of thermal optima increases ecosystem survival probability, increases cooling, and surprisingly, de-

creases species' thermal adaptation. A bimodal distribution of carbon impacts decreases ecosystem survival probability and increases cooling, but does not increase the probability of species' carbon fluxes canceling within an ecosystem. The result from Chapter 3 that ecosystems tend to cool the climate is robust to these different assumptions about species responses and impacts on the climate.

4.1 Introduction

Investigation into the nature of interactions between ecosystems and climate, and how these interactions have evolved throughout Earth history, relies heavily on models due to the broad and multidisciplinary nature of the topic. Models simplify the complexity of the world to their fundamental components, aiming to capture "a maximum of empirical contents through logical deduction with a minimum of hypotheses or axioms" (Einstein, 1954). The Tangled Nature + Carbon (TaNC) model presented in Chapter 3 assembles fundamental aspects of ecology, evolution, and climate to simulate how ecosystems and climate may co-evolve over long timescales. As every physical model, including the TaNC, is built on physical concepts and assumptions, it is crucial to carefully investigate those assumptions and evaluate how they affect model results (Kooijman, 2004). In particular, for the biological and ecological assumptions made in the TaNC, robust tests of the assumptions are necessary because the massive amounts of data (across space, time, and taxa) required to verify macroecological patterns are still not available (Dorneles et al., 2004). Therefore, in this chapter we investigate two important design choices for the TaNC: the way species are enabled to adapt to temperature, and species' intrinsic impacts on the carbon cycle.

In the original configurations of the Tangled Nature + Temperature (TaNa+T) and TaNC, we enabled species to adapt to any temperature between 263 and 330 K (-10 to 63°C) with equal probability. In the TaNa+T (Chapter 2), we found that ecosystems are more likely to survive in cold climates than warm climates since death probabilities increase exponentially with temperature. In the TaNC (Chapter 3), we then found that surviving ecosystems are more likely to cool the climate than warm it. Both total extinctions and mass extinctions drive selection for cooler ecosystems in the TaNC: total extinctions are more likely to occur in warmer climates, while ecosystems that reach colder climates tend to last longer than than ecological steady states in warmer climates.

However, in reality there may be some constraints on the ability of organisms to adapt to extreme temperatures. It is thermodynamically favorable for species to adapt to climates at which water is liquid and at which chemicals and proteins are more stable (Gillooly et al., 2001; Brown et al., 2004). Additionally, global surveys of thermal performance of extant species show greater fitness, and fossil evidence shows lower extinction rates, both in moderate temperatures around 20°C (Costello et al., 2023).

In other models in which species all share the same thermal optimum (e.g. in the modification of the TaNa model of Arthur & Nicholson, 2023) or have a tight range of thermal optima (e.g. in the Daisyworld model of Watson & Lovelock, 1983), ecosystems bring the temperature toward the universal optimum. Arthur and Nicholson (2023) also find that this increases ecosystem abundance. The tendency for ecosystems to cultivate an "optimal" climate breaks down in the Daisyworld model when species can freely adapt to any temperature — species just adapt to new climates rather than maintaining a climate near a shared optimum (Roberston & Robinson, 1998). Climatic homeostasis is restored in Daisyworld, on the other hand, when bounds on species' ability to adapt are included (Lenton & Lovelock, 2000). Therefore, the uniform distribution of species' thermal optima could explain why climate varies rather continuously in the TaNC: species thermal optima can vary by up to 60K (60°C) with minimal biological constraints. In the version of the Tangled Nature model modified by Arthur and Nicholson (2023), on the other hand, species all have the same thermal optimum and tend to bring the climate toward that shared optimum. Therefore, the distribution of species' thermal optima may change selective pressures experienced by species, and which could affect the evolution of the model climate.

To probe into the impacts of the distribution of species' thermal optima on climate evolution in this chapter, we contrast the uniform distribution of thermal optima from the previous chapters with a normal distribution of thermal optima centered around a moderate temperature. This makes it so that species can adapt to any temperature but with decreasing probability as the difference from the universal optimum increases. This may better align with the thermodynamic constraints on evolution mentioned above (Costello et al., 2023). A normal distribution also increases the probability that species will share similar thermal optima near a moderate temperature, and thus enables to us to examine how increased similarity in species' thermal optima affects climate evolution. In particular, we test whether a normal distribution of thermal optima leads to a smaller range of final temperatures achieved by the TaNC, and whether this keeps the mean temperature closer to the universal optimum.

The second model assumption we test in this chapter is the distribution of species' intrinsic impacts on carbon. In Chapter 3, we saw that the process of selection for cool environments in the TaNC is paired with selection for ecosystems with small environmental impacts. This occurs primarily through selection for species with small carbon fluxes, but at larger values of σ_{bio}, species are also more likely to cancel out their impacts with others and reduce ecosystem-level fluxes that way. In Chapter 3 we initialize the model in a state where species already have a high probability of having negligible impacts on the climate, which may predispose the model to favoring species with minimal impacts on the climate. A normal distribution of species' intrinsic carbon impacts was a good starting point since the Central Limit Theorem states that the distribution of means of any distribution converges to a normal distribution. However, in reality most species must interact with the climate. Almost every species affects the climate through photosynthesis or respiration at a rate determined by their metabolism, and species (of similar mass) should have similar metabolic rates at the same temperature (Brown et al., 2004). No species should have a zero-impact on the climate, as every species interacts with the environment through their metabolism. Therefore, a bimodal distribution of species' intrinsic impacts on the climate could be more realistic.

A bimodal distribution of species' intrinsic impacts on the climate could affect ecosystem evolution in a couple ways. First, it could make it more likely for species to have stronger impacts on the climate. This could increase species-driven climate change in the model, and this could make total extinctions or mass extinctions more common, as seen in Chapter 3. However, a bimodal distribution of intrinsic carbon impacts could also make it more likely for species to have opposing impacts on the climate. This could result in ecosystems with relatively small carbon fluxes in spite of containing species with larger carbon fluxes. If opposing environmental impacts arise in ecosystems, it could also be possible for rein control to emerge in the model — the process by which opposite biotic processes each prevent environmental change in one direction, and thereby produce stability (Clynes, 1969; Harvey, 2004; Watson & Lovelock, 1983). Rein control could make the climate even more stable than when species do not affect the climate since it creates a mechanism to dampen perturbations (Wood et al., 2008). Therefore, in this chapter we investigate how a bimodal distribution of species' intrinsic impacts on carbon affects ecosystem-climate co-evolution. The bimodal distribution of carbon impacts forces species to affect the climate, and we test whether this results in more rapid climate change or whether selection for species with opposite impacts enables ecosystems to minimize carbon fluxes and persist in stable climates.

In the following sections, we investigate the sensitivity of the TaNC to these different distributions of species' responses (uniform versus normal) and intrinsic carbon impacts (normal versus bimodal). To better understand selection *on* the distributions of responses and impacts, we begin by determining how their evolution depends on their initial shapes. Then, to understand selection *by* responses and impacts, we consider how changes in these distributions affect the evolution of the climate and ecosystems.

4.2 Methods

All experiments are performed with the Tangled Nature + Carbon (TaNC) model, introduced in Chapter 3, configured with temperature-dependent death and mutation. Here, we introduce two new distributions for species' thermal optima ($T_{\rm opt,i}$) of reproduction and intrinsic impacts (b_i) on carbon.

In Chapters 2 and 3, we used a uniform distribution of thermal optima, giving new mutant species an equal probability of having a thermal optimum anywhere between 263K and 330k (-10°C to 67°C). Here, we compare this basic assumption to the assumption that species thermal optima are normally distributed. The normal distribution of $T_{\rm opt,i}$ we use is centered at 290K (≈17°C) with a standard deviation of 10K (10°C; Fig. 4.1a).

In Chapter 3, we then gave species a normal distribution of intrinsic carbon impacts (b_i) centered at zero. This made it most probable for species to have zero or almost zero impact on the environment. Here, we introduce a configuration where species are forced to interact with the environment by implementing a bimodal distribution of b_i centered at zero. We assume most species affect the climate at a similar rate determined by their metabolic rate in their optimal conditions, but some rare species have larger or smaller impacts. To model this, we produce a bimodal distribution by multiplying a random choice of 1 or -1 (which determines whether species increase or decrease atmospheric carbon) by a lognormal distribution: the log transform of a normal distribution with standard deviation $\sigma_{\rm bio} = 10^{-8}$ (Fig. 4.1b). This bimodal distribution therefore has a positive and a negative peak near the standard deviation of the normal distribution, and prevents any species from having no impact on the climate. The values of b_i drawn from these distributions determine the maximum fraction of atmospheric carbon with which an individual of species i can interact in a year. As in Chapter 3, a species' actual carbon flux is then determined by the product of b_i with its metabolic rate ($r_i(T, T_{\rm opt,i})$) and the amount of carbon in the atmosphere ($m_{\rm CO_2}$; Eq. 3.3). Since temperature is logarithmically related to temperature (explained in Chapter 3; Eq. 3.2), the rate at which a species affects the climate is $F_i/m_{\rm CO_2}$.

There are four different combinations of b_i and $T_{\rm opt,i}$ distributions: normal b_i and uni-

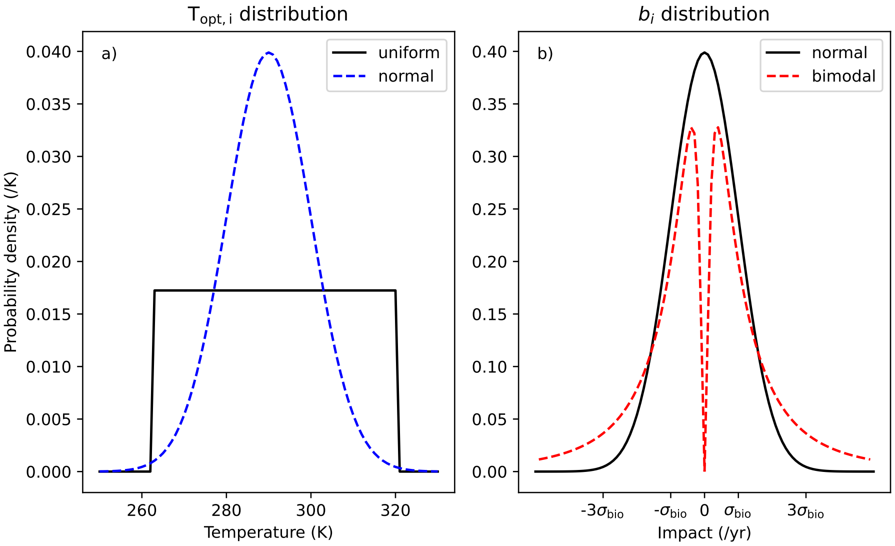
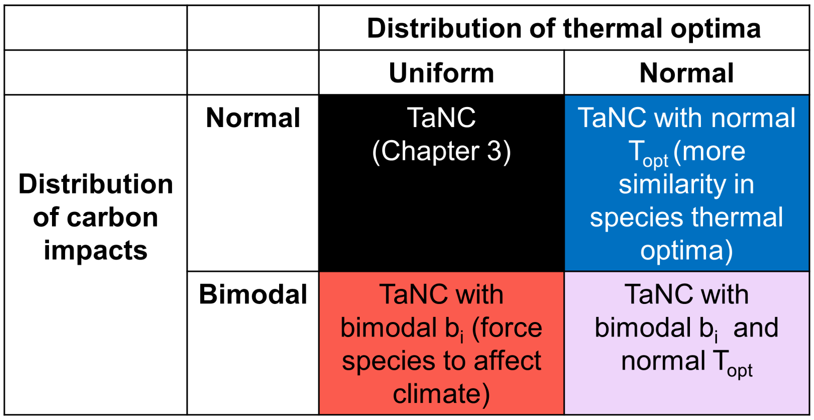


Figure 4.1: a) The two distributions considered for species' optimal temperature of reproduction ($T_{\mathrm{opt,i}}$): uniform (solid black) and normal (dashed blue). b) The two distributions of species' intrinsic carbon impacts (b_i): normal (solid black) and bimodal (dashed red), with the parameter σ_{bio} illustrated for both.



		Distribution of thermal optima	
		Uniform	Normal
Distribution of carbon impacts	Normal	TaNC (Chapter 3)	TaNC with normal T_{opt} (more similarity in species thermal optima)
	Bimodal	TaNC with bimodal b_i (force species to affect climate)	TaNC with bimodal b_i and normal T_{opt}

Figure 4.2: This chapter investigates four combinations of distributions of species' thermal optima ($T_{\mathrm{opt,i}}$) of reproduction and intrinsic impacts (b_i) on carbon. The configuration with a uniform distribution of thermal optima and a normal distribution of intrinsic carbon impacts (black) is the same as Chapter 3. We additionally investigate a normal distribution of thermal optima (red) and a bimodal distribution of intrinsic carbon impacts (blue) separately in the model, and then the combination of both a normal distribution of thermal optima and bimodal distribution of intrinsic carbon impacts together (purple). The colors of each of these four configurations are the same as for the rest of the plots in the Results.

form $T_{\mathrm{opt,i}}$ (the same as in Chapter 3), normal b_i and normal $T_{\mathrm{opt,i}}$, bimodal b_i and uniform $T_{\mathrm{opt,i}}$, and bimodal b_i and normal $T_{\mathrm{opt,i}}$ (Fig. 4.2). For each of these four configurations, we run 250 simulations, each with its own initial set of 60 random species, for 10,000 generations (equivalant to 10 million years in the climate model). As in Chapter 3, all simulations are initiated at 288K ($\approx$15°C).

The median and variance of results of the three new configurations (normal distribution of thermal optima, bimodal distribution of intrinsic carbon impacts, or both) are each compared to the control case (uniform distribution of thermal optima and normal distribution of intrinsic carbon impacts) using the Mann-Whitney U-test to compare medians and Levene's test to compare variance. We use these two tests as they are both applicable to data that is not normally distributed, and many of our model outputs are nonparametric according to the Shapiro test.

4.3 Results

In this section, we first consider how the distributions of species' thermal optima ($T_{\mathrm{opt,i}}$) and intrinsic carbon impacts (b_i) evolve depending on their initial shapes. Then we consider how these different distributions affect the evolution of the climate (in terms of temperature) and ecosystems (in terms of ecosystem survival probability, steady state duration, abundance, and species richness). The statistical significance of differences between distributions relative to the control case (uniformly distributed thermal optima and normally distributed carbon impacts) are presented in Table 4.1.

Distribution	**Median**	**Significance**	**Standard deviation**	**Significance**
Thermal mismatch ($T - T_{\mathrm{opt,i}}$)				
Control (uniform $T_{\mathrm{opt,i}}$, normal b_i)	-1.02	—	1.07	—
Normal $T_{\mathrm{opt,i}}$, normal b_i	-1.60	***	1.08	**
Uniform $T_{\mathrm{opt,i}}$, bimodal b_i	-1.33	***	1.19	***
Normal $T_{\mathrm{opt,i}}$, bimodal b_i	-1.75	***	1.13	***
Range of core species' thermal optima				
Control (uniform $T_{\mathrm{opt,i}}$, normal b_i)	8.37	—	1.32	—
Normal $T_{\mathrm{opt,i}}$, normal b_i	6.79		6.90	***
Uniform $T_{\mathrm{opt,i}}$, bimodal b_i	7.85		1.37	
Normal $T_{\mathrm{opt,i}}$, bimodal b_i	6.77	*	7.66	***
Species' intrinsic carbon impacts (b_i)				
Control (uniform $T_{\mathrm{opt,i}}$, normal b_i)	-2.24×10^{-9}	—	7.93×10^{-9}	—
Normal $T_{\mathrm{opt,i}}$, normal b_i	-2.86×10^{-9}	***	8.08×10^{-9}	***
Uniform $T_{\mathrm{opt,i}}$, bimodal b_i	-3.84×10^{-9}	***	1.90×10^{-8}	***
Normal $T_{\mathrm{opt,i}}$, bimodal b_i	-4.75×10^{-9}	***	2.64	***
Rate of species' realized climate impacts ($F_i/m_{\mathrm{CO_2}}$)				
Control (uniform $T_{\mathrm{opt,i}}$, normal b_i)	-1.89×10^{-10}	—	4.21×10^{-9}	—
Normal $T_{\mathrm{opt,i}}$, normal b_i	-1.61×10^{-10}	*	3.29×10^{-9}	***
Uniform $T_{\mathrm{opt,i}}$, bimodal b_i	-2.19×10^{-10}	***	7.77×10^{-9}	***
Normal $T_{\mathrm{opt,i}}$, bimodal b_i	-2.06×10^{-10}	***	7.14×10^{-9}	***
Rate of ecosystem climate impacts ($F_{\mathrm{bio}}/m_{\mathrm{CO_2}}$)				
Control (uniform $T_{\mathrm{opt,i}}$, normal b_i)	-1.93×10^{-9}	—	1.03×10^{-6}	—
Normal $T_{\mathrm{opt,i}}$, normal b_i	-9.50×10^{-8}	**	1.02×10^{-6}	
Uniform $T_{\mathrm{opt,i}}$, bimodal b_i	-2.81×10^{-8}		1.96×10^{-6}	*
Normal $T_{\mathrm{opt,i}}$, bimodal b_i	-6.12×10^{-8}		3.82×10^{-6}	
Final temperature (T)				

Control (uniform $T_{\text{opt,i}}$, normal b_i)	277.6	—	1.23	—
Normal $T_{\text{opt,i}}$, normal b_i	272.3		1.22	
Uniform $T_{\text{opt,i}}$, bimodal b_i	275.9		1.29	
Normal $T_{\text{opt,i}}$, bimodal b_i	270.7	*	1.32	
Steady state durations				
Control (uniform $T_{\text{opt,i}}$, normal b_i)	312.0	—	1357	—
Normal $T_{\text{opt,i}}$, normal b_i	381.0	*	1454	
Uniform $T_{\text{opt,i}}$, bimodal b_i	299.0		1285	
Normal $T_{\text{opt,i}}$, bimodal b_i	338.5		1300	
Abundance				
Control (uniform $T_{\text{opt,i}}$, normal b_i)	588	—	418	—
Normal $T_{\text{opt,i}}$, normal b_i	660		414	
Uniform $T_{\text{opt,i}}$, bimodal b_i	525		371	
Normal $T_{\text{opt,i}}$, bimodal b_i	568		353	
Species richness				
Control (uniform $T_{\text{opt,i}}$, normal b_i)	1.4	—	1.8	—
Normal $T_{\text{opt,i}}$, normal b_i	0.90		1.4	
Uniform $T_{\text{opt,i}}$, bimodal b_i	1.0		1.7	
Normal $T_{\text{opt,i}}$, bimodal b_i	0.90		1.5	

Table 4.1: Each of the three new distributions are compared to the control (used in Ch. 3). Statistical significance are computed using the Wilcox-Mann U-test to compare medians and Levene's test to compare variances. Stars indicate the level of significance: * ($p < 0.05$), ** ($p < 0.01$), or *** ($p < 0.001$), (and no star indicates that $p > 0.05$),).

4.3.1 Evolution of the distributions of species' responses to and impacts on temperature

Larger thermal mismatches when thermal optima are normally distributed

Species in surviving ecosystems generally have thermal optima ($T_{\text{opt,i}}$) at warmer temperatures than the environment, leading to negative thermal mismatches (the difference between species' optimal temperature and the actual temperature, $T - T_{\text{opt,i}}$) in all cases (Fig. 4.3a,b). However, a normal distribution of thermal optima increases the magnitude of thermal mismatch (Fig. 4.3a blue & purple; $p < 0.001$), making it more common for

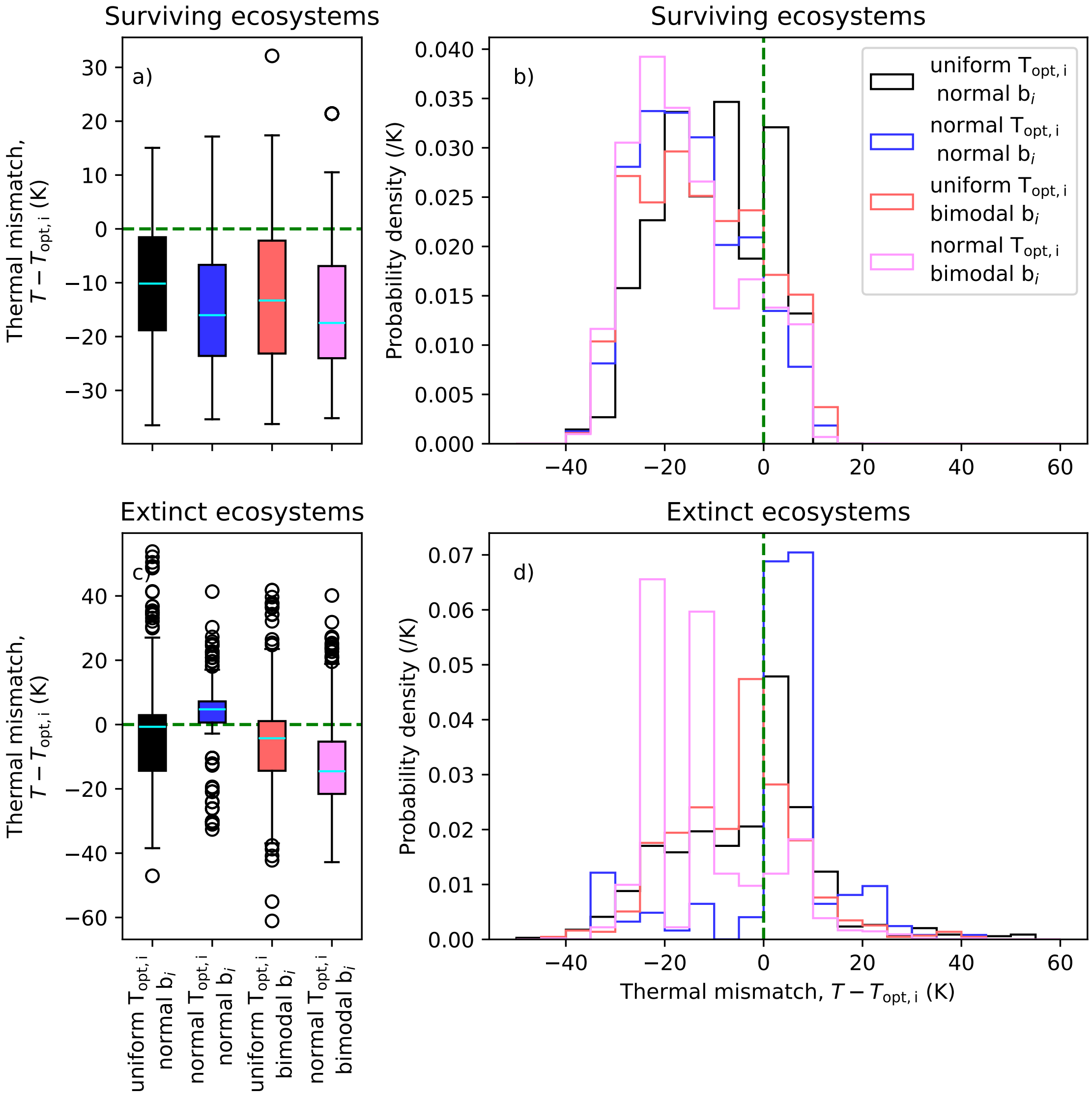


Figure 4.3: a,c) Boxplots and b,d) histograms showing species' thermal mismatches, defined as the difference between species' thermal optimum and the environmental temperature ($T_{\text{opt,i}} - T$), for each configuration for a,b) simulations that survived 10,000 generations (10 million years), and c,d) for those that did not. (For extinct ecosystems, the optimal temperatures are taken for species just before extinction and compared to the final temperature reached.) In the boxplots, the median is shown in cyan, the boxes extend to the first and third quartiles, and the whiskers extend to the farthest point within 1.5 standard deviations of the median. Points outside the whiskers are shown as empty circles.

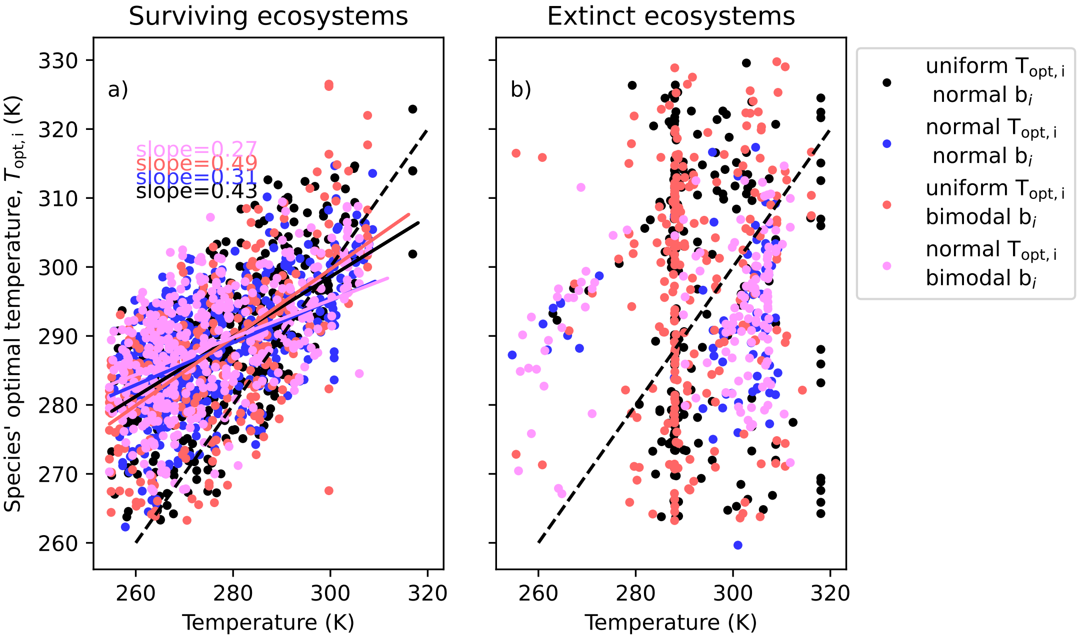


Figure 4.4: Core species' thermal optima ($T_{\mathrm{opt,i}}$) and the temperature (T) at the end of simulations in a) surviving and b) extinct ecosystems. The colored lines in a) show the line of best fit, with the corresponding slope printed above.

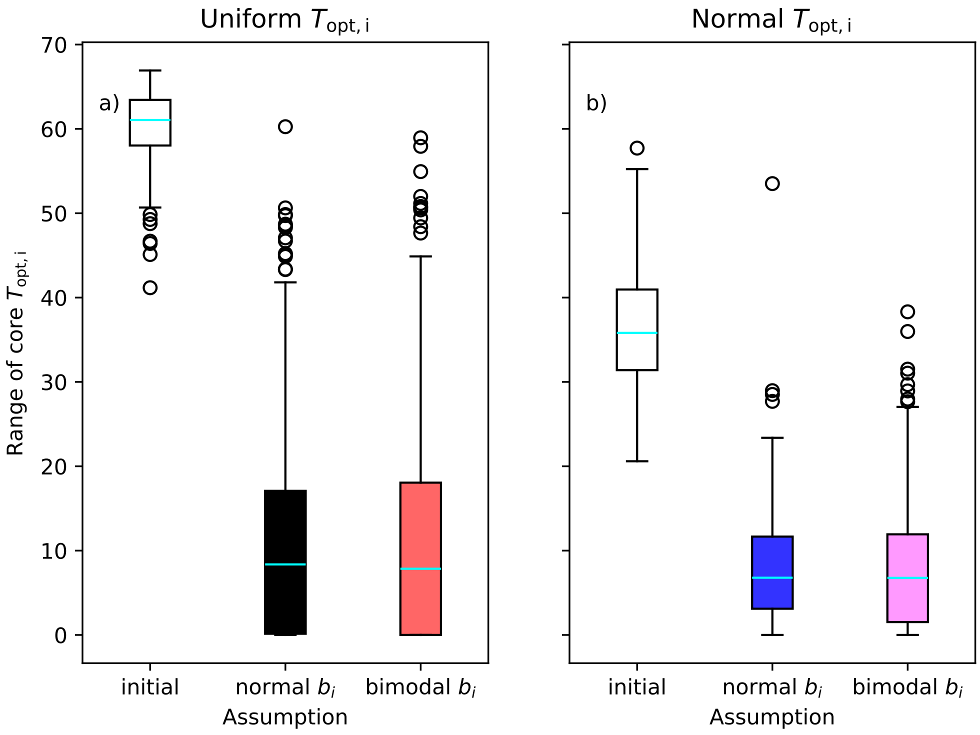


Figure 4.5: Range of thermal optima ($T_{\text{opt,i}}$) amongst core species in surviving ecosystems when a) $T_{\text{opt,i}}$ are initially uniformly distributed, and b) $T_{\text{opt,i}}$ are normally distributed. In each subplot, the white box shows the initial ranges of $T_{\text{opt,i}}$, and the two colored boxes show the final ranges of $T_{\text{opt,i}}$. In all boxes, the cyan line shows the median value, the edges of the boxes show the first and third quartiles, the whiskers extend to the farthest point within 1.5 times the interquartile range from the distribution, and points beyond the whiskers are shown in empty circles.

species to live in environments colder than their optimum temperature. Additionally, species' thermal mismatches depend on environmental temperature: species are more likely to be adapted to a colder temperature than the environment when the environment is warmer (Fig. 4.4a, points below the dotted line). This indicates that species cannot perfectly adapt to any environment, as the slope of thermal optima relative to temperature is less than 1. However, species are better adapted to the thermal environment (with the ratio of thermal optima to temperature closer to 1:1) with a uniform distribution of thermal optima (black & red), and worse adapted to the environment (with more similar thermal optima regardless of temperature) with a normal distribution of thermal optima (blue & purple; Fig. 4.4a), suggesting that a normal distribution limits species' ability to adapt to the environment.

The distribution of species' intrinsic carbon impacts (b_i) also affects thermal adaptation. When b_i are uniformly distributed, thermal mismatches of ecosystems that went extinct during simulations are generally negative, but more widely distributed than those in surviving ecosystems (Fig. 4.3c,d red). When b_i are normally distributed, on the other hand, species in ecosystems that go extinct are more likely to have small positive thermal mismatches, with a temperature about 0 - 10K (0 - 10°C) warmer than species' thermal optima (Fig. 4.3c,d black, blue). Additionally, a uniform distribution of species' thermal optima makes it more likely for ecosystems to go extinct at the initial temperature (black & red), and when species' intrinsic carbon impacts are also normally distributed, many ecosystems go extinct at about 320K (47°C) (black; Fig. 4.4b). On the other hand, when thermal optima are normally distributed, ecosystems are more likely to extinct around 300K (27°C) (Fig. 4.4 blue & purple). In all cases, the thermal optima of species in extinct ecosystems are more widely distributed than thermal optima in surviving ecosystems, showing that species with large thermal mismatches make ecosystems more susceptible to total extinctions (Fig. 4.4b).

The core species in all surviving ecosystems evolve to have smaller ranges of thermal optima than the randomly selected initial species, showing that species evolve to share more similar thermal optima in all surviving ecosystems (Fig. 4.5, colored boxes all have smaller medians than white boxes). When thermal optima are normally distributed, ecosystems start with cores with smaller ranges of thermal optima (since species are more likely to have moderate thermal optima), and evolve to have even smaller ranges of thermal optima than when thermal optima are uniformly distributed (the variance is smaller when thermal optima are normally distributed; Fig. 4.5; blue and purple; $p < 0.001$). This shows that the initial distribution of thermal optima does affect how it subsequently evolves. Particularly, when species' thermal optima are normally distributed, it enhances evolution of core species toward a shared thermal optimum.

Selection for small intrinsic carbon impacts and carbon fluxes in all cases

With all distributions of species' thermal optima ($T_{\mathrm{opt,i}}$) and intrinsic carbon impacts (b_i), species' median intrinsic carbon impacts evolve to be slightly negative, showing selection for cooling species (Fig. 4.6a). The distribution of species' intrinsic carbon impacts also evolves to become slightly narrower than the input distribution, with a greater frequency of near-zero values of b_i and a lower frequency of large b_i values (Fig. 4.6b). This indicates that regardless of the distributions of thermal optima and intrinsic carbon impacts, there is always selection for species with small negative intrinsic carbon impacts. However, when b_i are drawn from a bimodal distribution (red, purple), species evolve wider ranges of intrinsic carbon impacts ($p < 0.001$) with a more negative median ($p < 0.001$) than the control case.

Selection on species' realized rates of climate impacts ($F_i/m_{\mathrm{CO_2}}$)[1] is more pronounced than selection on b_i. In all cases, the distribution of rates at which species affect the climate ($F_i/m_{\mathrm{CO_2}}$) is much more sharply peaked than the distribution of b_i, showing strong selection for species with small climate impacts (Fig. 4.6d). For species to have smaller $F_i/m_{\mathrm{CO_2}}$ than b_i values, their metabolic rate must be reduced (as $F_i = b_i r_i m_{\mathrm{CO_2}}$; Eq. 3.3). Species' metabolic rates are 1 at $T = T_{\mathrm{opt,i}}$, and are reduced with larger thermal mismatches ($|T - T_{\mathrm{opt,i}}|$), so species' F_i are reduced by species existing away from their thermal optimum. The $F_i/m_{\mathrm{CO_2}}$ distribution with the most near-zero rates of species impact is that with a normal distributions of thermal optima and normal distribution of b_i (Fig. 4.6c,d blue; smaller variance than black with $p < 0.001$), and indeed, this is also a configuration in which more species have larger thermal mismatches (Fig. 4.3a blue; more negative median with $p < 0.001$). On the other hand, a bimodal distribution of carbon impacts increases the range of $F_i/m_{\mathrm{CO_2}}$ relative to the other distributions (Fig. 4.6c red; larger variance with $p < 0.001$), and this distribution has relatively smaller median thermal mismatches (Fig. 4.3a, red; median more similar to control case).

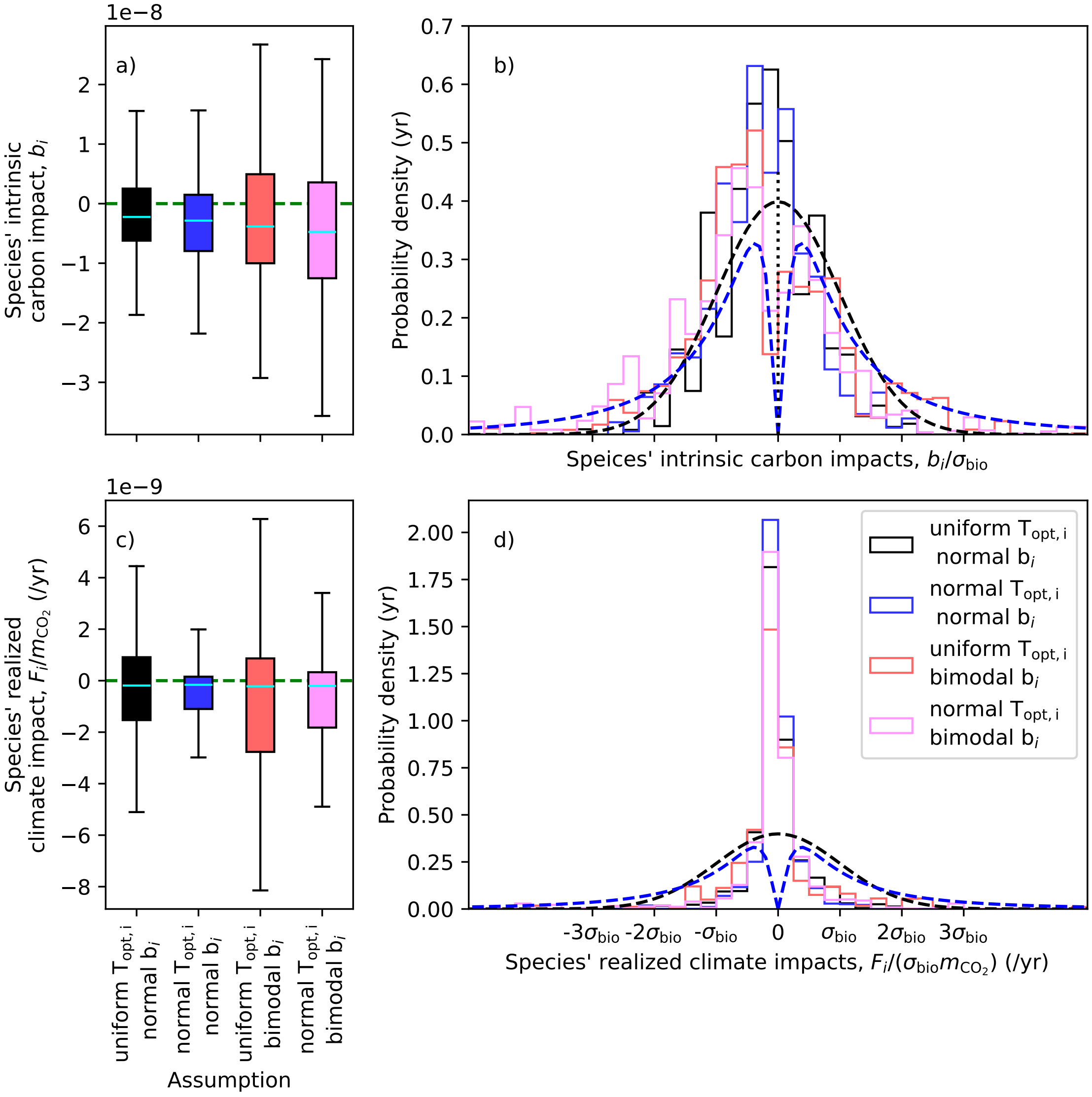


Figure 4.6: Species' intrinsic carbon impacts (b_i; top row) and realized rates of climate impacts (their carbon fluxes (F_i) divided by the mass of CO$_2$ ($m_{\mathrm{CO_2}}$); bottom row). a) Boxplots of species' intrinsic impacts on carbon. b) Histograms of species' intrinsic impacts divided by the standard deviation σ_{bio} of the normal distribution from which b_i were originally drawn ($\sigma_{\mathrm{bio}} = 10^{-8}$). The black dashed line shows the input distribution from which b_i are drawn when b_i are normally distributed, and the blue dashed line shows the input distribution from which b_i are drawn when b_i are bimodally distributed. c) Boxplots of species' realized rate of climate impacts. d) Distributions of species' realized rate of climate impact divided by σ_{bio}. In the boxplots, the cyan line shows the median, the edges of the boxes are at the first and third quartiles, and whiskers extend to the farthest point within 1.5 times the interquartile range from the median. Outliers not shown here but are shown in Appendix C.1.

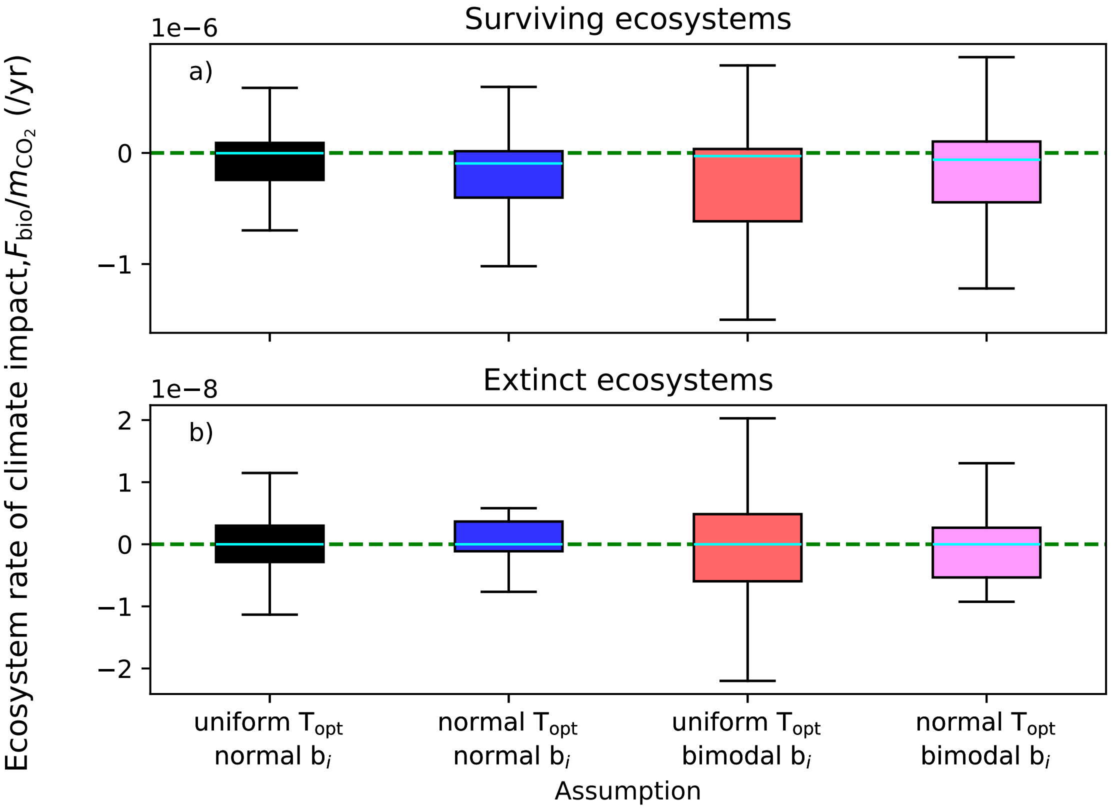


Figure 4.7: Rates of ecosystem climate impacts ($F_{\mathrm{bio}}/m_{\mathrm{CO_2}}$) in a) surviving ecosystems after 10,000 generations (10 million years) and b) extinct ecosystems at the time of extinction. In all boxes, the cyan line shows the median, the edges of the boxes are at the first and third quartiles, and whiskers extend to the farthest point within 1.5 times the interquartile range from the median. Outliers are not shown here but are shown in Appendix C.1.

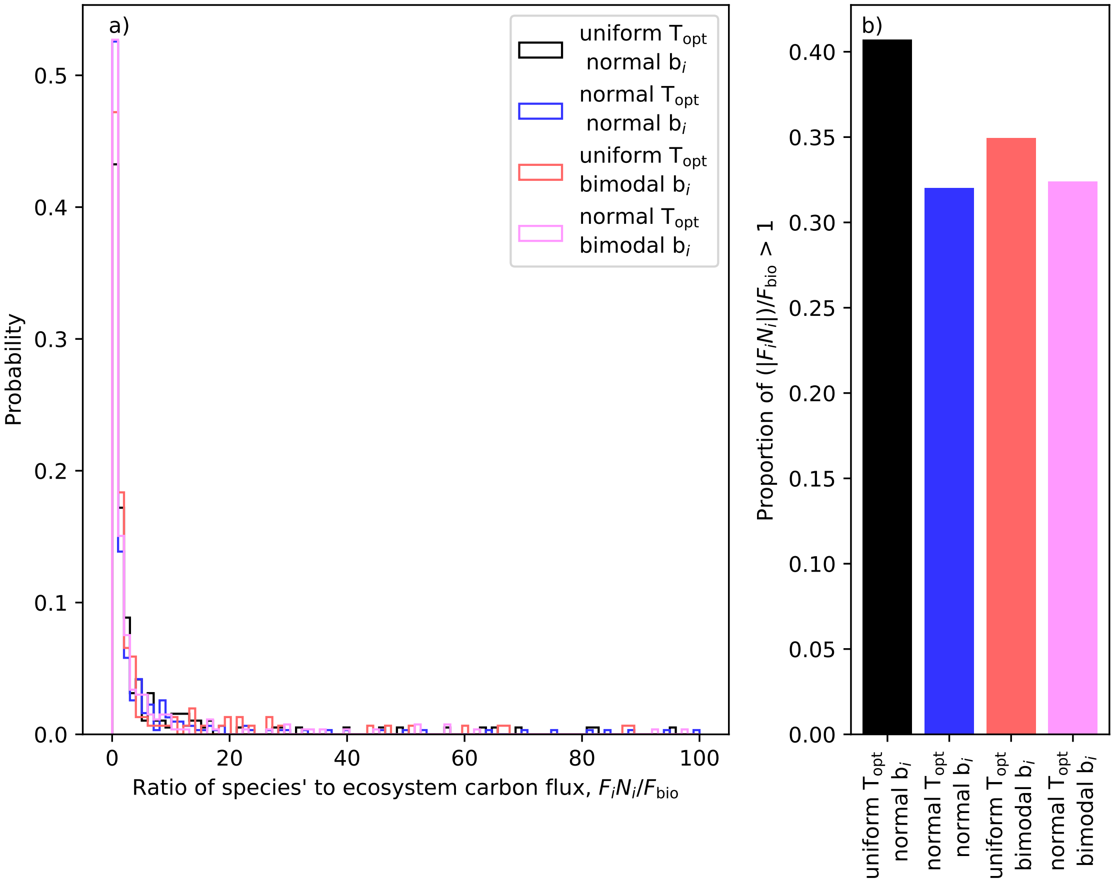


Figure 4.8: a) Histograms of the magnitude of core species' total carbon fluxes ($|F_i N_i|$) relative to the magnitude of ecosystem carbon fluxes ($|F_{\text{bio}}|$). b) Fraction of core species whose carbon fluxes are larger than the carbon fluxes produced by the whole ecosystem ($|F_i N_i / F_{\text{bio}}| > 1$). These are the species whose carbon fluxes are partially canceled out by the fluxes of other species in the ecosystem.

Larger climate impacts of ecosystems with normal distribution of thermal optima or bimodal distribution of carbon impacts

Although a normal distribution of thermal optima reduces the range of species' realized climate impacts (F_i/m_{CO_2}), it increases ecosystem-level cooling impacts (the median of distributions with a normal distribution of thermal optima is more negative than the control case; $F_{\mathrm{bio}}/m_{\mathrm{CO}_2}$; Fig. 4.7a;blue and purple; $p < 0.01$ and $p < 0.05$, respectively). This suggests that, even though each species has a smaller climate impact, species with cooling impacts evolve larger populations or co-exist with other cooling species when thermal optima are normally distributed.

In all configurations, a little less than half of the core species produce carbon fluxes with larger magnitudes than the fluxes produced by the whole ecosystem (Fig. 4.8). This occurs when a species' carbon flux is canceled out by the other species in the ecosystem, producing a smaller net carbon flux. Species are most likely to cancel out their carbon fluxes with other species (leading to $|F_i N_i| > |F_{\mathrm{bio}}|$) in the configuration from Chapter 3 than with any of the other distributions considered here. The configuration with the second most canceling is the configuration with a bimodal distribution of b_i and uniform distribution of $T_{\mathrm{opt,i}}$ – another case with a uniform distribution of $T_{\mathrm{opt,i}}$. This suggests that a uniform distribution of $T_{\mathrm{opt,i}}$ produces more canceling of carbon fluxes in ecosystems than does a bimodal distribution of b_i.

4.3.2 Repercussions of response and impact trait evolution on climate and ecology

The selection on species' thermal optima ($T_{\mathrm{opt,i}}$) of reproduction and intrinsic carbon impacts (b_i) discussed above produces different effects on the climate and on ecosystems, discussed below.

Cooling in all configurations

Ecosystems in all configurations cause cooling in the climate. When thermal optima are normally distributed, the distribution of final temperatures becomes more positively skewed (0.6 relative 0.09), such that more surviving ecosystems end up in cooler climates than when thermal optima are uniformly distributed (Fig. 4.9a blue). The median final

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[1] The ratio of F_i to the mass carbon (m_{CO_2}) in the atmosphere is proportional to the rate of species' realized impacts on climate because temperature is logarithmically related to CO_2 (Eq. 3.2), so the results on F_i presented here are divided by m_{CO_2}.

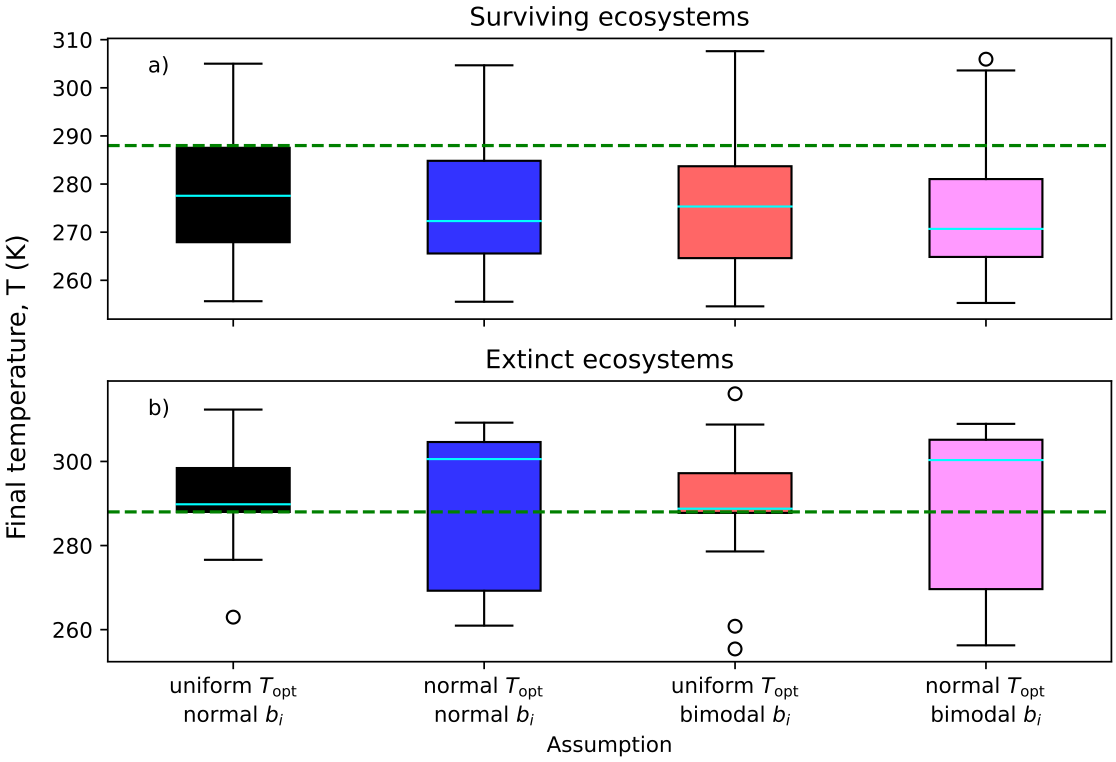


Figure 4.9: Final temperature for ecosystems that a) survived 10,000 generations (10 million years) and b) went extinct before then. The cyan lines in the boxes show the median value, boxes show the quartiles, whiskers extend to the farthest point within 1.5 times the interquartile range, and points outside that are shown in empty circles. The green dashed line shows the initial temperature, $T_0 = 288\text{K}$ (15°C).

temperature is cooler with a normal distribution of thermal optima (272K≈-1°C compared to 278K≈5°C), although the difference in medians is not statistically significant. Extinctions occur at a wider range of temperatures when thermal optima are normally distributed, with more extinctions occurring at both warmer and colder temperatures, compared to when thermal optima are uniformly distributed (Fig. 4.9b blue). This suggests that when more species are adapted to moderate temperatures, ecosystems in extreme temperatures are more likely to go extinct. The median temperature of extinctions is warmer that the median temperature of surviving ecosystems, which is likely caused both by the asymmetry of the thermal response curve of reproduction and to the monotonically increasing thermal response of death, as in Chapter 3. Both curves contribute to making species viable at a wider range of temperatures below their thermal optimum of reproduction than above it.

A bimodal distribution of species' intrinsic carbon impacts also increases the skewness of final temperatures (0.5 relatve to 0.09), and decreases the median final temperature by a few degrees relative to a normal distribution of intrinsic carbon impacts, although the differences in median final temperatures again are statistically insignificant (Fig. 4.9a red). As in the other cases (black, blue), the median temperature of extinctions is warmer than surviving ecosystems (Fig. 4.9a,b red). The distribution of temperatures of extinction is similar whether b_i are normally or bimodally distributed, with a median temperature of extinction just above the initial temperature, and both quartiles at or above the initial temperature (Fig. 4.9b; black and red boxes are similar). This indicates that a bimodal distribution of intrinsic carbon impacts may slightly increase cooling in simulations (Fig. 4.9a red), but does not affect the temperature of extinction (Fig. 4.9b red). Therefore, any increased cooling in surviving ecosystems with a bimodal distribution of intrinsic carbon impacts does not arise from selective extinctions of more warm and moderate temperatures but from a selective pressure driving evolution of surviving ecosystems toward cooler climates.

The combination of a normal distirbution of thermal optima and a bimodal distribution of carbon impacts produces the coolest median and quartile final temperatures of the four configurations (Fig. 4.9a purple). Again, this is produced by an increase in skewness (0.8 relative ot 0.09), and the difference in medians is not statistically significant. The temperatures of extinction are driven by the distribution of thermal optima, showing a wide range with a warmer median than the initial temperature when $T_{\mathrm{opt,i}}$ are normally distributed (Fig. 4.9b purple).

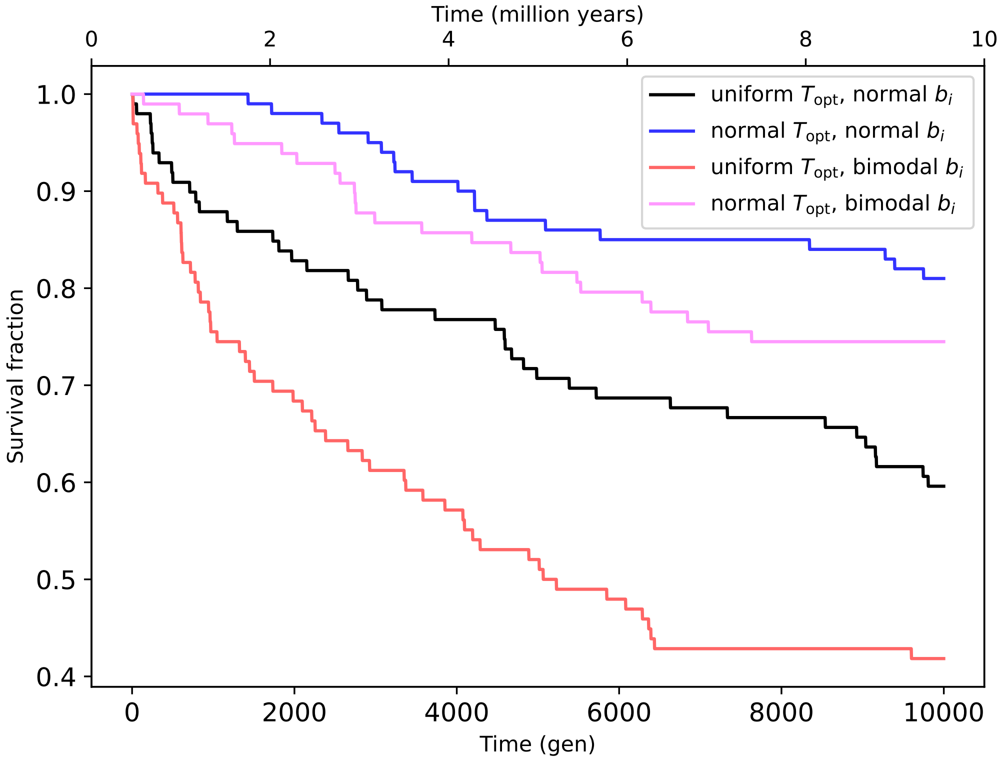


Figure 4.10: The fraction of surviving simulations (out of 250) over time for each of the four distributions considered.

More ecosystems survive with normal distribution of thermal optima; fewer survive with bimodal distribution of intrinsic carbon impacts

The fraction of surviving ecosystems declines over time in all cases, but it declines more slowly when $T_{\text{opt,i}}$ is drawn from a normal distribution that a uniform distribution (Fig. 4.10 blue). This is related to the fact that mutant species are more likely to be adapted to the initial temperature when $T_{\text{opt,i}}$ is normally distributed. A later decline in ecosystem survival probability is observed when $T_{\text{opt,i}}$ is normally distributed, around 2,000 to 6,000 generations, that probably aligns with the timing at which the temperature has sufficiently diverged from the center of the normal distribution of thermal optima. However, ecosystem survival probability remains larger at all times when $T_{\text{opt,i}}$ is normally than uniformly distributed.

Drawing species' intrinsic carbon impacts from a bimodal distribution decreases the number of ecosystems that survive 10,000 generations relative to a normal distribution of intrinsic carbon impacts (Fig. 4.10 red), which can be explained because ecosystems in which species have stronger intrinsic carbon impacts suffer more extinctions (Fig. 3.9). However, the rate of change of ecosystem survival fraction increases to near zero when intrinsic carbon impacts are drawn from a bimodal distribution, whereas the rate of change remains more negative when intrinsic carbon impacts are normally distributed. This suggests that there is harsher selection on ecosystems early on when intrinsic carbon impacts are bimodally distributed, but the ecosystems that survive the initial selection process are then more likely to persist than ecosystems evolved from the case where intrinsic carbon impacts are normally distributed.

Ecosystem survival probability is larger than the basic configuration from Chapter 3 when both distributions are changed together (normally distributed thermal optima and bimodally distributed intrinsic carbon impacts; Fig. 4.10 purple), but the case with the largest survival fraction overall is when both b_i and $T_{\mathrm{opt,i}}$ are normally distributed 4.10 blue). The rate of change of ecosystem survival fraction increases toward zero over time when both b_i and $T_{\mathrm{opt,i}}$ are normally distributed as well, with almost no total extinctions occurring in the last 3,000 generations (3 million years) of the simulation.

Slightly longer steady states with normal distribution of thermal optima

Steady state durations are logarithmically distributed in all cases, with exponentially more short steady states than long ones (Fig. 4.11a). However, a normal distribution of thermal optima slightly increases the number of longer steady states relative to the other configurations (Fig. 4.11b, blue and purple; $p < 0.05$). The other configurations do not significantly affect the duration of ecological steady states.

Ecosystem abundance and species richness un-affected by distributions of thermal responses and intrinsic carbon impacts

Neither the distribution of thermal optima nor the distribution of intrinsic carbon impacts has a strong effect on ecosystem or core abundance ($p > 0.05$), although the largest abundances are obtained with normal distributions of both thermal optima and carbon impacts (Fig. 4.12a,b). Species richness also shows negligible response to the distributions of thermal optima and carbon impacts (Fig. 4.12c,d; $p > 0.05$). However, the upper quartile of ecosystem species richness is slightly larger in the two configurations with a normal distribution of thermal optima (Fig. 4.12c, blue & purple), and the upper quartile of ecosystem species richness is decreased by a few species when species' thermal optima are uniformly distributed and intrinsic carbon impacts are bimodally distributed

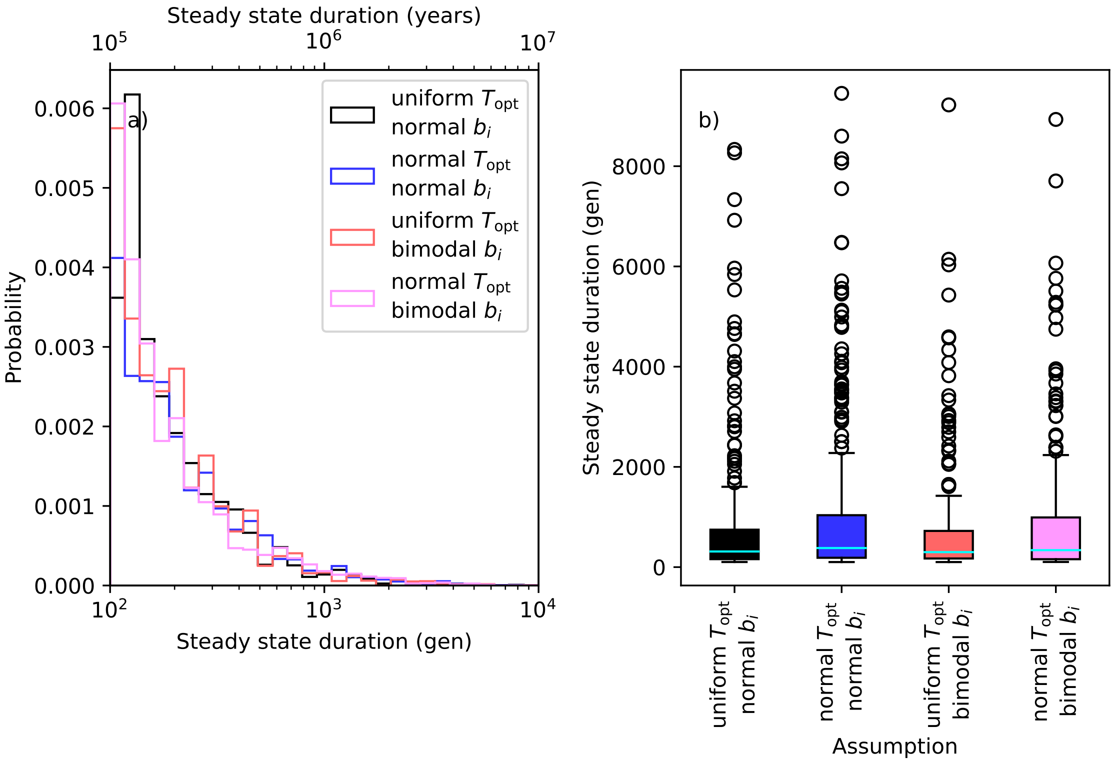


Figure 4.11: a) Histograms of ecological steady state durations for each of the four combinations of distributions considered. The bin sizes of steady state durations are logarithmic — so each bin is exponentially wider than the bin to its right. The histograms are normalized such that the sum of the bin heights times the bin widths gives a probability of 1. b) Boxplots of the same information. Cyan lines show the median value, boxes extend to the first and third quartiles, and whiskers extend to the farthest point within 1.5 times the interquartile range from the median. Points beyond the whiskers are shown as empty circles.

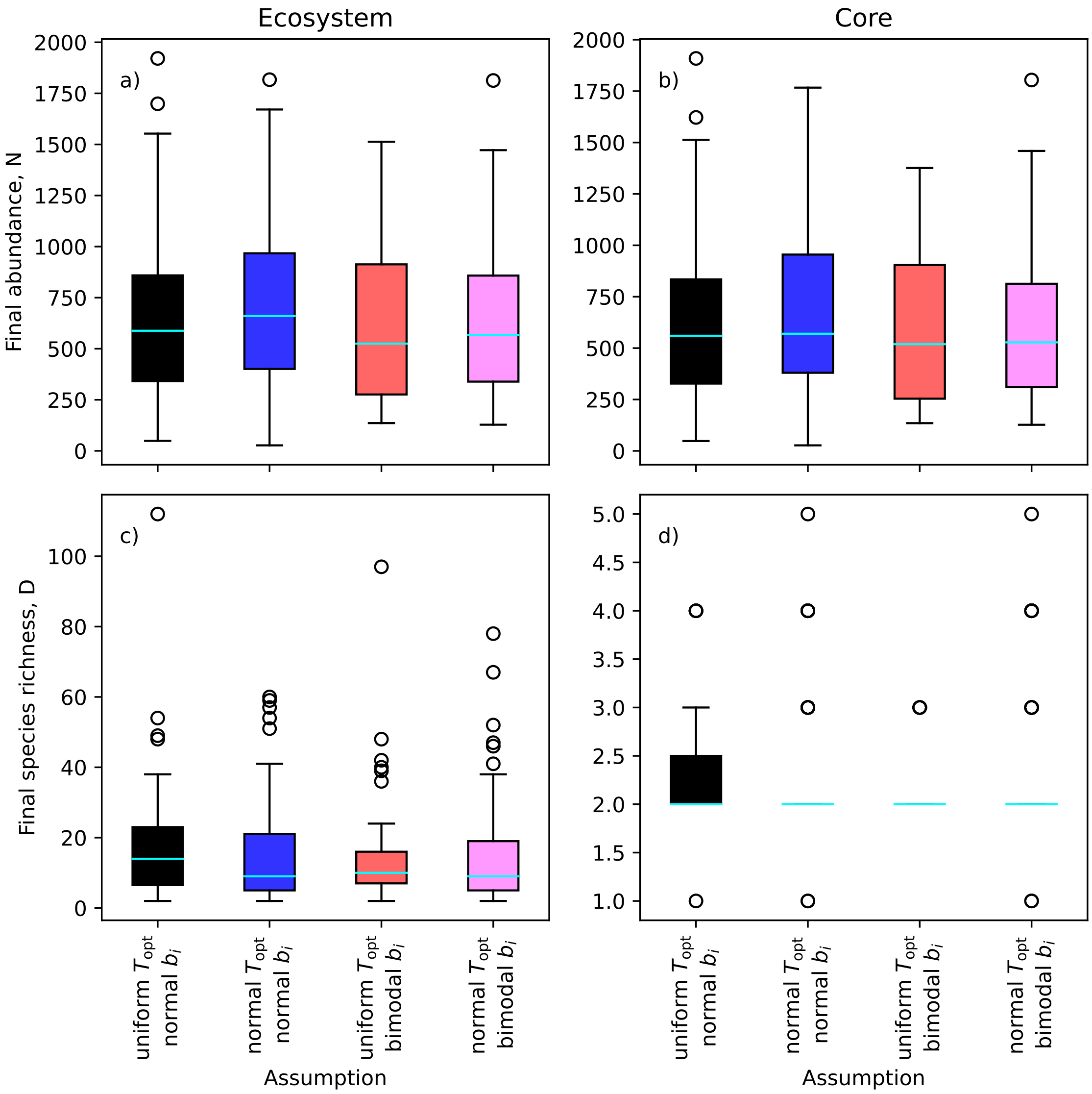


Figure 4.12: Boxplots of ecosystem (left) and core (right) abundance (top) and species richness (bottom) for ecosystems that survived 10,000 generations (10 million years). Cyan lines show the median values, boxes the quartiles, and whiskers the farthest point within 1.5 times the interquartile range from the median. Points beyond the whiskers are circled. (Invisible boxes indicate a narrow distribution. Missing sides of boxes indicate asymmetrical distributions.)

(Fig. 4.12c red). The configuration with the most core species, though, is the basic configuration (Fig. 4.12d black), probably because this is the warmest simulation and species richness is positively correlated with temperature (Chapter 2).

4.4 Discussion

The ways that species respond to and affect the environment are important factors in establishing eco-evolutionary feedbacks. Here, we test two key parameters controlling these feedbacks in the Tangled Nature + Climate (TaNC) model: the distribution of species' thermal optima ($T_{\mathrm{opt,i}}$) and the distribution of species' intrinsic impacts (b_i) on carbon.

4.4.1 Species with similar thermal optima do not produce climates near that shared optimum temperature

In Chapter 3, we assumed that species were equally likely to be adapted to any temperature between 263 and 330 K (-10 to 63°C), but in reality it may be thermodynamically favorable for species to survive and reproduce in more moderate temperatures (Costello et al., 2023). Therefore, in this chapter we investigate a normal distribution of species' thermal optima, making it more probable for species to be adapted to temperatures near 290K (17°C) than very warm or cold temperatures.

This enables us to investigate selection for similarity in species' thermal optima, and to test whether species with more similar thermal optima are more likely to bring the climate towards the universal optimum, where more species can reproduce more quickly. We find that ecosystems generally (regardless of the distribution of $T_{\mathrm{opt,i}}$) evolve towards more similarity in thermal optima, but as expected, species are better able to achieve this when thermal optima are normally distributed (Fig. 4.5). However, our simulations do not show that similarity in thermal optima brings the climate toward that shared optimum. In fact, simulations in which species' thermal optima are normally distributed may even cause slightly more cooling in the TaNC climate than ecosystems with a uniform distribution of thermal optima (Fig. 4.9). This contradicts our prediction that species with more similar thermal optima are more likely to bring the climate toward their shared optimum. Surprisingly, species also evolve to have larger thermal mismatches when there is more similarity in thermal optima (Fig. 4.3). As thermal mismatches reduce species' carbon fluxes (F_i) in addition to their reproduction rates ($p_{\mathrm{off,tot}}$), this suggests that minimizing environmental impacts is a stronger driver of ecosystem-level selection than is maximizing reproduction rates. Indeed, ecosystems are also more likely to survive when thermal optima are normally distributed.

Our results contrast the findings of Arthur and Nicholson (2023), in which species in the TaNa model that shared a universal optimum temperature were more likely to bring the climate toward the shared optimal temperature and maintain it there. The major methodological difference that can explain these diverging results is the implementation of species' responses to temperature. Here, species death and mutation rates increase monotonically with temperature, and birth rates peak at species' optimal temperature ($T_{\mathrm{opt,i}}$). In the work of Arthur and Nicholson (2023), by contrast, species' interaction strengths peak at the universal optimum temperature and decreases symmetrically at temperatures above and below that. The parameter exploration in Chapter 2 show that interaction strength affects ecosystem abundance, whereas death, birth and mutation rates do not. Therefore, species' impacts on the environment that feed back on ecosystem abundance may be necessary for ecosystems to evolve to maintain a shared universal temperature. However, in the real world, birth, death, mutation, and interaction strengths are all temperature-dependent (Brown et al., 2004; Dell et al., 2011), so it will be interesting in future work to see whether selection for cooler climates driven by the temperature-dependence of death, or selection for universally optimum temperatures driven by the temperature-dependence of interaction strengths, prevail in controlling ecosystem-climate co-evolution.

4.4.2 Species with opposite impacts on the climate are not more likely to reduce environmental impacts

The second assumption we test in this work is the assumption that species' intrinsic impacts on carbon are normally distributed (as in Chapter 3). Here, we make it impossible for species not to impact the climate by drawing species' intrinsic carbon impacts from a bimodal distribution. We investigate how this affects the rate of climate change in the model, and the probability of ecosystems driving themselves totally extinct. Unsurprisingly, we find higher extinction rates in simulations with a bimodal distribution of species' intrinsic carbon impacts, since species are more likely to cause climate change in this configuration (Fig. 4.10). We also find that species (Fig. 4.6c,d) and ecosystems (Fig. 4.7a) in which species have a bimodal distribution of intrinsic carbon impacts produce more rapid climate impacts than when species have a normal distribution of intrinsic carbon impacts. This suggests that it is harder for species and ecosystems to stabilize the climate if species' carbon impacts are bimodally distributed. However, in spite of species having a propensity for larger impacts on the climate, ecological steady states are not shorter in ecosystems with a bimodal distribution of intrinsic carbon impacts (Fig. 4.11).

Interestingly, we see that species in the TaNC model may be less likely to cancel out one another's carbon impacts when intrinsic carbon impacts are bimodally than normally distributed (Fig. 4.8). This suggests that ecosystems are unlikely to select for species with opposite impacts in the environment, even if intrinsic carbon impacts are bimodally distributed to begin with. Therefore, the TaNC is not likely to produce emergent rein control. This may be because rein control requires temperature-dependence of ecosystem abundance, which we show in Chapter 2 does not arise in the TaNa+T. This may support some criticism of the Daisyworld paradigm that questions how it could evolve in nature (Roberston & Robinson, 1998; Doolittle, 1981; Dawkins, 1982; Wood et al., 2008), or motivates further research to identify a realistic mechanism by which ecosystem abundance may respond to temperature.

4.4.3 Normally distributed thermal optima and bimodally distributed intrinsic carbon impacts work together to cool the climate

When both assumptions from Chapter 3 are changed together in the TaNC, there is more cooling than in any of the other configurations (Fig. 4.9). This is because both selection for species far from their thermal optima (which occurs when thermal optima are normally distributed) and selection for species with small negative rates of climate impact (which occurs when b_i are bimodally distributed) act as mechanisms of selection for cooler climates where death rates are reduced. Ecosystem survival probability also increases in this case relative to the case where thermal optima are uniformly distributed and intrinsic carbon impacts are normally distributed (Fig. 4.10), which is due to the normal distribution of thermal optima increasing ecosystem survival probability.

4.4.4 Future directions

Here we have tested two key assumptions about species' responses to, and impacts on, the climate. The main result from Chapter 3, that TaNC ecosystems evolve to cool the climate, holds in all three new cases tested here. However, there are still other ways that species' responses and impacts could be distributed which could affect our model results.

Here, we compare a normal distribution of species' thermal optima of reproduction to the uniform distribution used in Chapters 2 and 3. In both configurations, species' metabolic rates peak at one at their optimal temperature, regardless of what their optimal temperature is; so no temperature gives species an intrinsic advantage. However, Metabolic Theory suggests that species adapted to warmer climates have faster metabolic rates at their optimal temperature than species adapted to cooler climates (Gillooly et al., 2001; B. Chen, 2022). This means that species adapted to warmer climates may have greater fitness than species adapted to cooler climates, giving rise to a "hotter is better" hypothesis. Therefore, future research could consider whether scaling species' reproduction rates up in warmer climates might counteract the cooling tendency of the TaNC.

In this chapter we additionally compare a bimodal distribution of species' impacts on the climate to the normal distribution used in Chapter 3. However, both distributions are rather agnostic about how species actually affect the climate. In reality, every species respires while it is alive and then dies (leading to further respiration), so species in a different version of the TaNC could be assigned positive carbon fluxes in proportion to population size and death rates. Additionally, many of the most important impacts that species have on the environment are cooling, such as biotic enhancement of weathering (Schwartzman & Volk, 1991; Schwartzman, 2017), dimethyl sulfide production (Charlson et al., 1987; S. Wang et al., 2018), carbonate precipitation (Dupraz et al., 2009), and carbon burial (Falkowski, 2012; Isson et al., 2020). Species' random impacts on the environment could therefore be drawn from a negative distribution. Would this configuration, with more explicit positive and negative carbon fluxes, be more likely to enable species to stabilize the climate than the bimodal distribution we considered here?

4.5 Conclusion

The major aims of this study are to investigate selection on or by similar thermal optima and on or by opposite environmental impacts of species in ecosystems. We find that minimizing death rates is still the stronger driver of selection than maximizing reproduction rates, even when species agree on a $T_{\mathrm{opt,i}}$. We find selection for species far from their thermal optima, where their environmental impacts are smaller, suggesting that ecosystem-level selection can override species-level selection that might otherwise drive species toward their thermal optima.

A bimodal distribution of b_i acts as an obstacle in the TaNC, decreasing ecosystem survival probability and increasing species' impacts on the environment. Interestingly, ecosystems in which species' impacts on the environment are bimodally distributed are not more likely to have core species that cancel one another's impacts, which could reduce ecosystem-level climate impacts. This suggests that the strength of ecosystem-level selection for small environmental impacts is not dominant in shaping ecosystem characteristics.

Overall, we find that the distribution of species' thermal optima and intrinsic impacts on carbon affect the environment more strongly than they affect ecosystem characteristics. The finding that ecosystems tend to cool the climate and minimize their rates of climate impact is true in every distribution we tested. Future research should continue to unravel the general principles of ecosystem-level selection for different environmental impacts, and how these impacts and interactions evolve.

Chapter 5

How inheritance during speciation affects the co-evolution of ecosystems and climate in the Tangled Nature + Climate model

Abstract

Species' responses and impacts on their environments can be heritable traits which can affect the evolution of both organisms and the environment. However, the way that whole ecosystems co-evolve with their environments is still poorly quantified. Ecosystem and climate evolution might be shaped by selection on larger units of selection than organisms, but how this works is not entirely clear. Evolutionary theory suggests that both variation and inheritance are necessary for selection on a unit of selection to produce evolutionary changes; therefore, ecosystem-level selection and evolution may require that ecological traits associated with environmental interactions be heritable on long timescales.

Here, we investigate how ecosystem-climate co-evolution differs when ecosystems are able to inherit traits from ancestral ecosystems. To do this, we modify a model designed to investigate how ecosystems and their environments co-evolve, the Tangled Nature + Carbon (TaNC) model, to include inheritance of species' responses and impacts on the environment. This enables ecosystems to maintain similar characteristics even after mass extinction events eliminate the majority of species. We find that inheritance of species' thermal optima and carbon impacts each decreases the total number of surviving ecosys-

tems, causing more total extinctions early on in simulations. Over time, however, the rate of total extinctions loses its dependence on inheritance. Ecological steady states also last slightly longer with inheritance, and inheritance of thermal optima slightly increases abundance and species richness.

This work highlights that ecosystem-level selection is a much slower process than species-level selection, operating across and between mass extinction and total extinction events; however, ecosystem-level selection can operate simultaneously with species-level selection. We add clarity to how different units of selection, including species, ecological steady states, and entire lineages, interact. This research also shows how inheritance both helps and hinders ecosystem-level evolution.

5.1 Introduction

Ecosystem-level evolution, defined as changes in ecosystem characteristics over time, can arise from natural selection occurring at multiple biological levels (Stenseth & Maynard Smith, 1984; Maynard Smith, 1991). These different levels of selection manifest evolutionary changes on different timescales; for example, population sizes can change on the ecological timescale, the number of species and how they interact can change on the timescale of genetic mutations and gene flow, and the species present can change on the speciation-extinction (or macroevolutionary) timescale (Stenseth & Maynard Smith, 1984). The Tangled Nature + Climate (TaNC) model mainly relies on macroevolutionary changes through selection amongst species (Bell, 2016; Christensen et al., 2002). Some speciation (emergence of new species in the model) and species extinction occur within ecological steady states in the TaNC, but the most impactful speciation and extinction events are mass extinction events (in which the most abundance core species go extinct but some surviving species repopulate the ecosystem). Mass extinctions can cause shifts in the statistics of surviving ecosystems, since longer-lasting ecological steady states become more common simply by nature of lasting longer than short steady states (Lenton, Daines, Dyke, et al., 2018). Therefore, over time the statistics of ecosystems will reflect the properties of long-lasting ecosystems in a process called *sequential selection* (Betts & Lenton, 2008). Additionally, some lineages (i.e. realizations of TaNC simulations) experience total extinctions, leaving no surviving species, and as those lineages die off, the statistics of the remaining ecosystems shifts toward the properties of the surviving ecosystems. Selective total extinctions and differential survival of certain lineages is called *selection by survival*, and this can cause selection on entire ecosystem-environment systems, leading to the survival and persistence only of ecosystem-environment systems with “persistence-enhancing” traits (Doolittle, 2017; Lenton, Daines, Dyke, et al., 2018). In the previous chapters, we saw that sequential selection and selection by survival in the TaNC can drive ecosystem-level evolution toward ecosystems with small carbon fluxes (environmental stabilization), and colder climates (reduced death rates).

However, while natural selection on ecosystems via mass extinctions (sequential selection) and total extinctions (selection by survival) can shift the statistics of surviving ecosystems, it is still uncertain whether natural selection can produce lasting changes within surviving ecosystems. The biologist Maynard Smith (1991) writes that, for selection to cause lasting evolutionary changes in ecosystems, there must be differential survival or reproduction of units of selection with *heritable traits*; otherwise, selection does not produce lasting changes. Another influential biologist, Dawkins (1982), writes that “Differential lineage extinction, though technically a form of selection, is not enough in itself to generate progressive evolutionary change. Lineages may be ‘survivors’ but that does not make them replicators.” (Dawkins, 1982, p. 100). In other wors, both biologists stress that, for selection on a biological unit (e.g. a gene, organism, species, or ecosystem) to lead to lasting change at that level of selection, that biological unit must pass heritable traits to future generations.

The original Tangled Nature model (Christensen et al., 2002) and the TaNC both include inheritance *within* species: if a mutation does not occur during reproduction then offspring becomes an individual of the same species, inheriting all the traits of that species. This allows selection amongst species (macroevolution) to cause lasting changes in ecosystem properties. Arthur and Nicholson (2022) also argue that increasing species richness over time in the Tangled Nature model enables ecosystems to acquire evolutionary changes over the course of mass extinction events, because even if the traits of an ancestral ecosystem are not inherited by the next, an increasing pool of cloud species from each ancestral ecosystem increases the ecological possibilities in the next. However, since most species, including the core species, die during mass extinctions, new ecosystems forming in the TaNC after mass extinction events do not inherit the traits associated with ecosystem-environment interactions from their ancestral ecosystem. Therefore, the hypothesis echoed by both Dawkins (1982) and Maynard Smith (1991) would suggest that selection on ecosystems cannot produce lasting change in ecosystem characteristics.

Inheritance during speciation has been studied in a different Tangled Nature model configuration by making interspecific interactions heritable during mutation events (Laird & Jensen, 2006). Introducing inheritance at this level to the model increases the strength of selection for core species that have mutualistic interactions with one another, increases interspecific interaction strength, and increases network connectivity. The original Tangled Nature model already selects for these properties in ecosystems (Christensen et al., 2002), so enabling mutant species to inherit similar properties from their ancestral species seems to enhance the selective pressures already affecting the evolution of the system and their ability to cause lasting evolutionary change.

The TaNC focuses on ecosystem-climate interactions, and although previous configurations did not consider inheritance, in reality species' impacts and responses to the environment can also be heritable traits (El-Sabaawi, 2017). Species' ability to adapt to climate change is limited by their physiology, which is in part contributing to ecological crises today (Chown et al., 2010). Additionally, some evolutionary innovations can be maintained even after the original species is driven extinct (Maynard Smith, 1991; Falkowski, 2012). In particular, the traits controlling species' environmental impacts in the TaNC model are associated with carbon uptake and emission, which are generally associated with photosynthesis and respiration, and these traits evolve more slowly than interactions between species (Bell, 2016). As previously mentioned, heritability is also central to the theory of sequential selection: Doolittle (2017) hypothesizes that ecosystems that survive a mass extinction event are more likely to have, by chance, obtained "persistence-enhancing" traits than those ecosystems that went totally extinct, and they are thus more likely to continue to persist in the next ecological steady state if the persistence-enhancing traits exist in the next descendants of the lineage (Doolittle, 2017, 2019; Lenton, Daines, Dyke, et al., 2018). This means that if species' impacts and responses to the environment are associated with ecosystem persistence, then evolution towards persistence-enhancing traits may require inheritance of those traits.

Therefore, in this chapter we choose to introduce inheritance of species' thermal responses and intrinsic carbon impacts during mutation events in the TaNC. We propose that inheritance during mutation affects the unit of selection in the TaNC because it enables ecosystems to inherit properties of earlier ecosystems even if the core species of the earlier ecosystem all went extinct, since the surviving cloud species are more likely to have impact and response traits similar to the core of the previous ecosystem. Therefore, we suggest that inheritance enhances the possibility for ecosystems to act as a replicating unit of selection.

To investigate how inheritance of the traits associated with species-environment interaction affects the co-evolution of climates and ecosystems in the TaNC, we explore both how inheritance of response traits (thermal optima of reproduction) and impact traits (species' intrinsic impacts on carbon) affect the model, one at a time and then together. This enables us to determine whether inheritance of these key response and impact traits enhances or changes the direction of selection in model ecosystems, and to also compare the strength of selection between response and impact traits. We expect that incorporating inheritance of species responses and impacts on the environment will facilitate ecosystem-level selection and make it possible for surviving ecosystems to accumulate more persistence-enhancing traits than the TaNC without inheritance. We predict that these traits will be minimal thermal mismatches (which will maximize species' reproduction rates) and minimal environmental impacts (which should enable steady states to last longer given there are no abiotic drivers of climate change). We also expect to see more environmental cooling with inheritance, as cool climates have been shown in previous chapters to minimize death rates and prolong ecological steady states. Selection for these persistence-enhancing traits should involve all three mechanisms of selection: selection by survival (total extinctions of certain ecosystems), sequential selection (mass extinctions terminating ecosystems with large environmental impacts), and macroevolution (extinction of certain species — although we suspect selective species extinction is mostly driven by interspecific interactions rather than interactions between specific species and the climate).

5.2 Methods

Simulations are run with the Tangled Nature + Climate (TaNC) model introduced in Chapters 3 and 4. As in those chapters, the TaNC involves a coupling between the Tangled Nature model (Christensen et al., 2002) and a climate model (Chapter 3). The TaNC is initialized with 500 individuals evenly divided between 60 species, and then iterates between killing individuals with a temperature-dependent death probability (Eq. 2.6), reproducing them if they survive with a probability that depends on both temperature and interspecific interaction (Eq. 2.5), and mutating the offspring with a temperature-dependent "per-gene" probability (Eq. 2.7). Species are identified by their genome (a 20-bit binary number) and when mutations occur, one gene (a bit in the binary number) flips between 0 and 1, changing the identity of the species. The new species has new interactions with all other species, and in the versions of the TaNC without inheritance, the new species also has a new thermal optimum ($T_{\mathrm{opt,i}}$) of reproduction and a new intrinsic impact (b_i) on carbon.

Like the original Tangled Nature model, the TaNC produces emergent ecosystems called ecological steady states, characterized by the presence of at least two of the same core (most abundant) species for at least 100 generations. The abundance of ecosystems in ecological steady states generally fluctuates in the TaNC without trend, until a sudden ecological collapse called a mass extinction occurs. If all species go extinct, it is called a total extinction. However, some species often survive the mass extinction event and repopulate the model, producing a pattern called *Punctuated Equilibria* (Eldredge & Gould, 1972).

5.2.1 Introducing inheritance into the TaNC

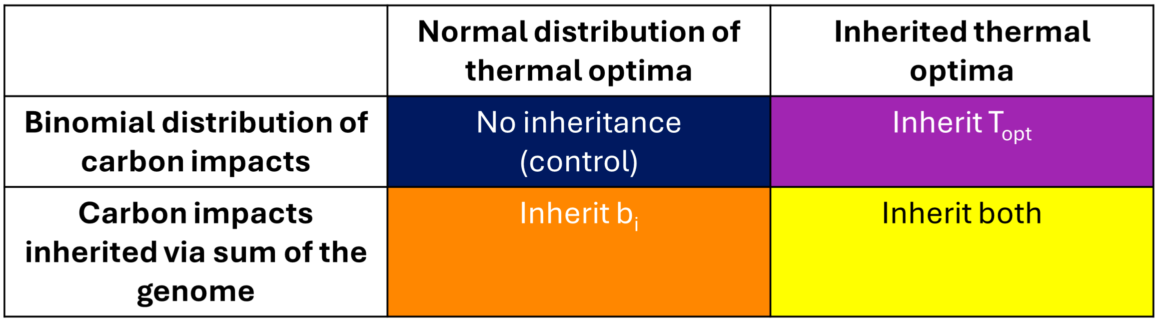
Here, we implement three new configurations in the TaNC: inheritance of only thermal optima ($T_{\mathrm{opt,i}}$) of reproduction, inheritance of only species' intrinsic impacts (b_i) on atmospheric carbon, and inheritance of both (Fig. 5.1). These three new configurations are compared to a case without inheritance (control). In Chapter 4, we found that the largest number of ecosystems survive when both thermal optima and carbon impacts are normally distributed, so we use this combination of distributions as our point of departure. However, as explained below, we replace the normal distribution of species' intrinsic carbon impacts with a binomial distribution in these configurations of the TaNC.

In all configurations, we initialize the model with a normal distribution of thermal optima. As in Chapter 4, the normal distribution of thermal optima is centered at 290K (17°C) with a standard deviation of 10K (10°C). In the two configurations in which thermal optima are inherited (Fig. 5.1 purple & yellow), a mutant species receives $T_{\mathrm{opt,i}}$ from its ancestral species plus a small modification drawn from a normal distribution centered at zero with a standard deviation of 1K (1°C).

In the two configurations where species' intrinsic carbon impacts are inherited during mutation (Fig. 5.1 orange & yellow), we calculate the strength of species' intrinsic carbon impacts to be the sum of their binary, 20-bit genome (G). We convert the sum of their genome to a carbon impact (b_i) using the transformation:

$$b_i = \Big(\sum(G) - 10\Big) \times s; \tag{5.1}$$

where s is a scaling factor which we set to 3×10^{-9}/year. The sums of all possible genomes in the model are binomially distributed, and with our scaling factor s, the shape of this binomial distribution is similar to a normal distribution with a standard deviation (σ_{bio}) of 6.7×10^{-9} (Fig. 5.2). When a mutation occurs during reproduction, the offspring has usually one (but possibly multiple) genes flip, altering the sum of their genome by a multiple of 5%. This makes it so that mutant species maintain intrinsic carbon impacts



	Normal distribution of thermal optima	**Inherited thermal optima**
Binomial distribution of carbon impacts	No inheritance (control)	Inherit T_{opt}
Carbon impacts inherited via sum of the genome	Inherit b_i	Inherit both

Figure 5.1: We run the TaNC with four configurations: no inheritance (intrinsic carbon impacts (b_i) drawn from a binomial distribution and thermal optima ($T_{\text{opt,i}}$) from a normal distribution; dark blue), inheritance of only $T_{\text{opt,i}}$ (b_i drawn from a normal distribution and inherited $T_{\text{opt,i}}$; purple), inheritance of only b_i (b_i from the sum of the genome and $T_{\text{opt,i}}$ drawn from a normal distribution, orange), and inheritance of both (b_i from the sum of the genome and inherited $T_{\text{opt,i}}$; yellow).

that are similar, but not identical, to their ancestral species. (Species' realized carbon fluxes are then calculated from Eq. 3.3, and the rate at which they impact the climate is $F_i/m_{\mathrm{CO}_2} = b_i r_i$, as explained in Chapter 3.)

In the two configurations in which intrinsic carbon impacts are not inherited (Fig. 5.1 blue & purple), b_i is assigned by summing a randomly drawn 20-bit binary number (not associated with the species ID) and then converting it to an intrinsic carbon impacts with Eq. 5.1. This makes the shapes of the two distributions of intrinsic carbon impacts — with and without inheritance – both binomial, facilitating more direct comparison of model results with and without inheritance of b_i. This does, however, make the control case without inheritance (Fig. 5.1 blue) slightly different from the previous chapters without inheritance.

5.2.2 Experimental design

For each of the four model configurations, we are running 250 simulations for 100,000 generations (100 million years in the climate model). However, only 30,000 generations have completed at the time of writing this dissertation, so here we present results from 30,000 generations — three times longer than the simulations in Chapters 2-4. Progress toward 100,000 generations is shown in the Appendix (Fig. D.1). Here we report findings thus far on the evolution of ecosystem survival probability, ecological steady state duration, temperature in the climate, ecosystem rates of climate impact, abundance, and species richness.

5.2.3 Statistical analysis

For each climactic and ecological metric, we calculate the median and standard deviation. Then, for each possible pair of experiments, we compare the statistical significance of differences between the medians using the Mann-Whitney U-test and the standard deviations using Levene's test, which are both applicable when data is not normally distributed. Those values and the significance of their differences are presented in Table ??.

5.3 Results

The results section is organized into subsections for: ecosystem survival probability and steady state duration, temperature and thermal optima, species and ecosystem climate

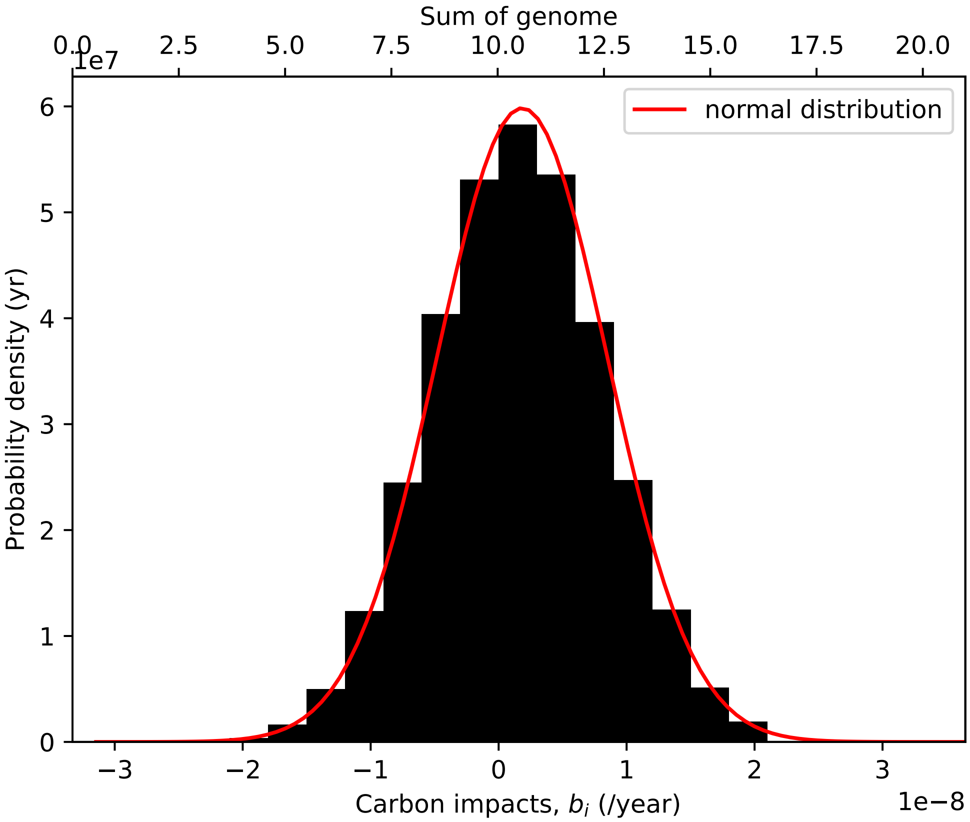


Figure 5.2: Species' intrinsic carbon impacts (b_i) are either drawn from a binomial distribution or taken from the sum of their 20-bit genome (top axis) and then converted to a carbon impact with Eq. 5.1 (bottom axis). In either case, b_i values have the binomial distribution shown in black. This binomial distribution of carbon impacts produces carbon impacts of similar scale to the normal distribution with a standard deviation of 6.7×10^{-9}/year (red curve).

impacts, and abundance and species richness. Statistical differences between outputs are presented in Table 5.1.

Distribution	Median	Significance				Standard deviation	Significance			
		1	2	3	4		1	2	3	4
Number of mass extinctions										
1 - No inheritance	6.5	–	**		***	30	–		*	**
2 - Inherit $T_{\mathrm{opt,i}}$	4.0	**	–			24		–		
3 - Inherit b_i	5.0			–	**	15	*		–	
4 - Inherit both	4.0	***		**	–	12	**			–
Final temperature										
1 - No inheritance	264.5	–				11.6	–			
2 - Inherit $T_{\mathrm{opt,i}}$	265.6		–		*	11.2		–		
3 - Inherit b_i	264.1			–		11.0			–	
4 - Inherit both	262.6		*		–	14.2				–
Thermal optima ($T_{\mathrm{opt,i}}$)										
1 - No inheritance	287.0	–	***	***	***	7.9	–	***	***	***
2 - Inherit $T_{\mathrm{opt,i}}$	288.7	***	–	***	***	6.1	***	–	***	***
3 - Inherit b_i	284.7	***	***	–	***	7.2	***	***	–	***
4 - Inherit both	287.5	***	***	***	–	6.9	***	***	***	–
Thermal mismatch ($T - T_{\mathrm{opt,i}}$)										
1 - No inheritance	-21.6	–	***	***	***	10.6	–	***	***	***
2 - Inherit $T_{\mathrm{opt,i}}$	-23.2	***	–	***	***	8.7	***	–	***	***
3 - Inherit b_i	-19.9	***	***	–	***	10.6	***	***	–	***
4 - Inherit both	-25.7	***	***	***	–	10.5	***	***	***	–
Species' intrinsic carbon impacts (b_i)										
1 - No inheritance	-2.3×10^{-9}	–	***	***	***	5.92×10^{-9}	–	***	***	***
2 - Inherit $T_{\mathrm{opt,i}}$	-2.6×10^{-9}	***	–	***	***	5.49×10^{-9}	***	–	***	***
3 - Inherit b_i	-3.0×10^{-9}	***	***	–	***	4.45×10^{-9}	***	***	–	***
4 - Inherit both	-3.8×10^{-9}	***	***	***	–	4.96×10^{-9}	***	***	***	–
Species' realized rate of climate impact ($F_i/m_{\mathrm{CO_2}}$)										
1 - No inheritance	-4.72×10^{-12}	–	***	***	***	1.25×10^{-9}	–	***	***	***
2 - Inherit $T_{\mathrm{opt,i}}$	-1.44×10^{-11}	***	–	***	***	9.31×10^{-10}	***	–	***	***
3 - Inherit b_i	-2.52×10^{-11}	***	***	–	***	8.00×10^{-10}	***	***	–	***

4 - Inherit both	-2.26×10^{-11}	***	***	***	–	9.14×10^{-10}	***	***	***	–
Final rate of ecosystem climate impact ($F_{\text{bio}}/m_{\text{CO}_2}$)										
1 - No inheritance	-2.98×10^{-9}	–				3.55×10^{-7}	–			
2 - Inherit $T_{\text{opt,i}}$	-1.95×10^{-9}		–			2.43×10^{-7}		–		
3 - Inherit b_i	-6.23×10^{-9}			–		2.25×10^{-7}			–	
4 - Inherit both	-4.30×10^{-9}				–	2.84×10^{-7}				–
Final rate of extinct ecosystem climate impacts ($F_{\text{bio}}/m_{\text{CO}_2}$)										
1 - No inheritance	-6.08×10^{-13}	–				2.26×10^{-7}	–			
2 - Inherit $T_{\text{opt,i}}$	-1.55×10^{-11}		–	*		2.91×10^{-7}		–	*	
3 - Inherit b_i	3.22×10^{-20}		*	–	*	9.26×10^{-8}		*	–	
4 - Inherit both	-5.85×10^{-11}			*	–	3.73×10^{-7}				–
Ratio of species to ecosystem carbon flux ($\lvert F_iN_i/F_{\text{bio}}\rvert$)										
1 - No inheritance	2.97×10^{-4}	–	*		*	5.71×10^{14}	–			
2 - Inherit $T_{\text{opt,i}}$	2.24×10^{-3}	*	–			1.95×10^{5}		–		
3 - Inherit b_i	3.86×10^{-4}			–		5.59×10^{10}			–	
4 - Inherit both	1.06×10^{-3}	*			–	7.74×10^{3}				–
Ecosystem abundance										
1 - No inheritance	601	–				456	–			
2 - Inherit $T_{\text{opt,i}}$	660		–			478		–		
3 - Inherit b_i	515			–		457			–	
4 - Inherit both	604				–	519				–
Ecosystem species richness										
1 - No inheritance	6	–				11	–			
2 - Inherit $T_{\text{opt,i}}$	7		–	*		13		–		
3 - Inherit b_i	6		*	–		11			–	
4 - Inherit both	6				–	19				–

Table 5.1: For all metrics except species' intrinsic rates of carbon impacts (b_i), the median and standard deviation of each of the four model configurations is presented, and then the significance of differences in medians is computed with the Mann-Whitney U-test and significance of differences in variance is computed with Levene's test. For b_i, a z-test is used to compare means since the distribution is binomial (and the mean is listed in the "Median" column; the median of all four is -3.00×10^{-9}). Statistical significance is reported as: * ($p < 0.05$), ** ($p < 0.01$), or *** ($p < 0.001$). (Dashes indicate that the comparison between a distribution and itself is irrelevant.) The four configurations are abbreviated as numbers 1-4 in the significance columns, and the same numbering is used in the Distribution rows.

5.3.1 Inheritance increases the frequency of total extinctions, but may reduce the frequency of mass extinctions

The fraction of ecosystems that survive 30,000 generations (30 million years) is largest when neither thermal optima nor intrinsic carbon impacts are inherited during speciation, suggesting that inheritance of anything decreases ecosystem survival probability (Fig. 5.3a). Without inheritance, about 70% of ecosystems survive 30,000 generations (30 million years). With inheritance of only thermal optima ($T_{\mathrm{opt,i}}$) or of only carbon impacts (b_i), the fraction of surviving ecosystems is reduced to a little less than 60% after 30,000 generations. With inheritance of both thermal optima and intrinsic carbon impacts, about 50% of ecosystems survive 30,000 generations.

However, in all cases, the rate of extinctions slightly decreases over time, showing that the instantaneous probability of an ecosystem going extinct decreases over time (Fig. 5.3b,c). The configuration without inheritance maintains the lowest extinction rate at almost all times, but the differences in extinction rates between configurations decrease over the course of simulations. After about 20,000 generations (20 million years), the extinction rates are similar in all four configurations, and by 30,000 generations (30 million years) the extinction rate in all configurations is around 1% of surviving ecosystems going to total extinction every 1000 generations (1 million years).

The rate of mass extinctions (extinctions of many species, including the core species, but survival of some species from the lineage) occurring in simulations is slightly smaller in the two cases where thermal optima are inherited than when thermal optima are randomly assigned to mutant species, suggesting that inheritance of thermal optima increases

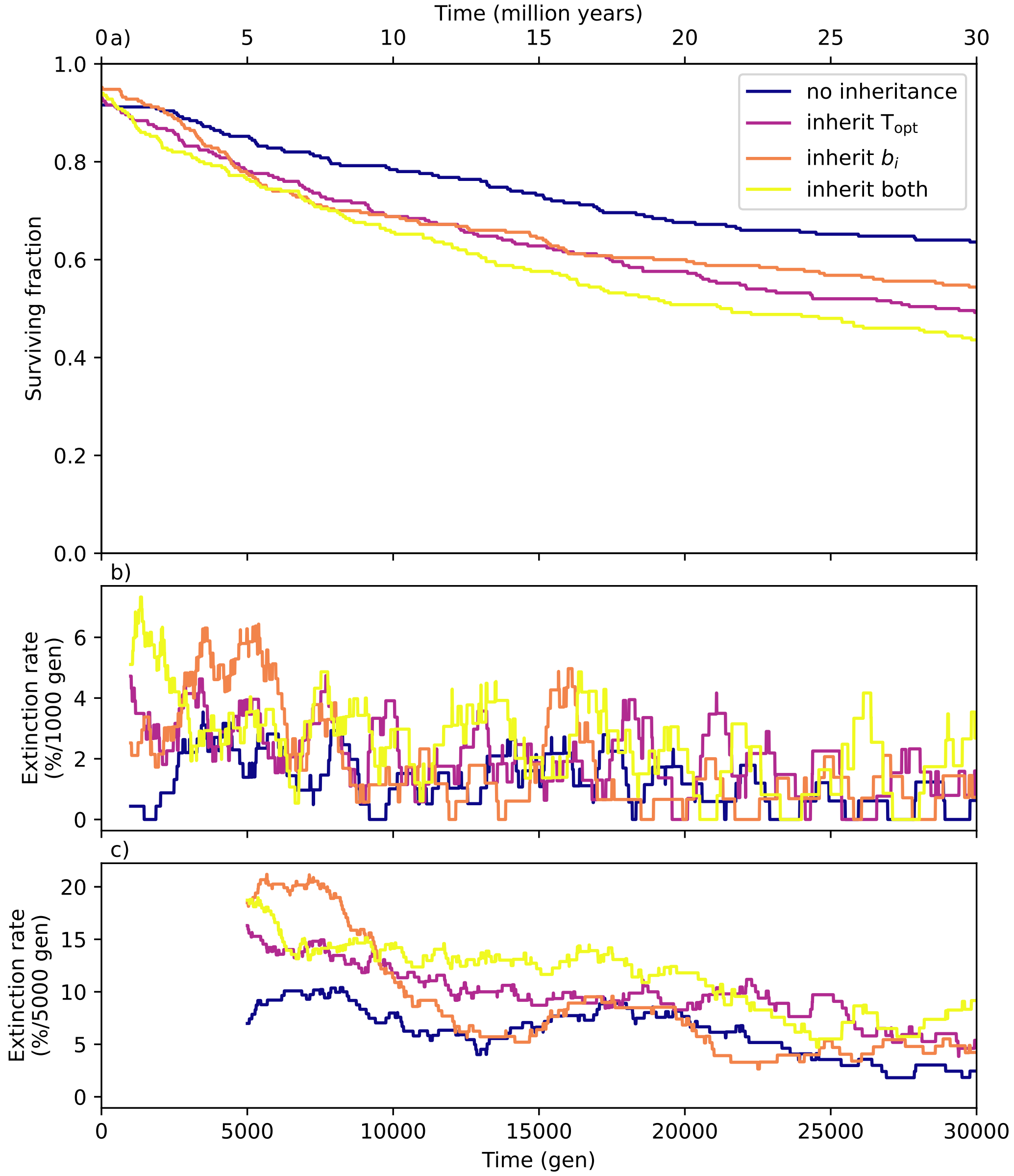


Figure 5.3: a) Surviving fraction of ecosystems out of 250 simulations over time for each of the four configurations: no inheritance (dark blue), inheritance of thermal optima ($T_{\mathrm{opt,i}}$) but not intrinsic carbon impacts (b_i) (purple), inheritance of b_i but not $T_{\mathrm{opt,i}}$ (orange), and inheritance of both $T_{\mathrm{opt,i}}$ and b_i (yellow). b,c) Ecosystem extinction rate, calculated as the number of total extinctions in 1000 (b) or 5000 (c) generations divided by the number of ecosystems at that time, of the four configurations over time.

the duration of ecological steady states (Fig. 5.4[1]; $p < 0.01$). The median number of mass extinctions in 27,000 generations (27 million years) is 4 without inheritance of thermal optima, and 3 with inheritance of thermal optima (Fig. 5.4b). Additionally, the range of the number of mass extinctions is larger without inheritance of anything: simulations with 10-12 mass extinctions are less common in the three cases with inheritance than without. With inheritance of only thermal optima, the 1st quartile is also smaller, showing that many simulations have just 1 mass extinction event, although the difference in variance is not statistically significant. The variance is significantly reduced in the two cases with inheritance of b_i, though ($p < 0.05$). The mean number of mass extinctions decreases in the three cases with inheritance as well, and the case with inheritance of both thermal optima and carbon impacts has the smallest mean number of mass extinctions. This all suggests that ecological steady states last a little longer with inheritance of b_i, $T_{\mathrm{opt,i}}$, or both than without inheritance.

The reduction in mass extinction frequency with inheritance could arise because mass extinctions are more likely to end in total extinction with inheritance than without it (selection by survival) or because ecosystems produce mass extinctions less frequently when thermal optima, and to a lesser extent carbon impacts, are inherited (ecosystem-level selection and evolution).

5.3.2 Inheritance of thermal optima increases thermal mismatches

The median temperature of surviving ecosystems in all configurations decays over the course of 30,000 generations, showing that surviving ecosystems generally evolve toward cooler climates in all cases (Fig. 5.5). After 30,000 generations of evolution, median temperature is around 265K (-8°C) in surviving ecosystems of all four configurations (Fig. 5.6a). The median and first and third quartiles of final temperature are each a few degrees cooler in the two configurations in which species' intrinsic carbon impacts are inherited, suggesting that inheritance of b_i enhances the cooling effect. When only thermal optima are inherited, the third quartile of final temperatures is also slightly cooler than without inheritance, and the lowest median temperatures are achieved with inheritance of both b_i and $T_{\mathrm{opt,i}}$. However, final temperatures vary by tens of degrees and differences in median final temperatures and variance of temperature are not statistically significance.

The temperature of ecosystems that suffered total extinctions before 30,000 genera-

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[1] Ecological steady states are defined by the continuous presence of at least two core species. In Fig. 5.4, we sort ecological steady states by length and count the number of steady states (starting with the longest) in 90% of simulation time in order to determine the number of long-lived ecological steady states.

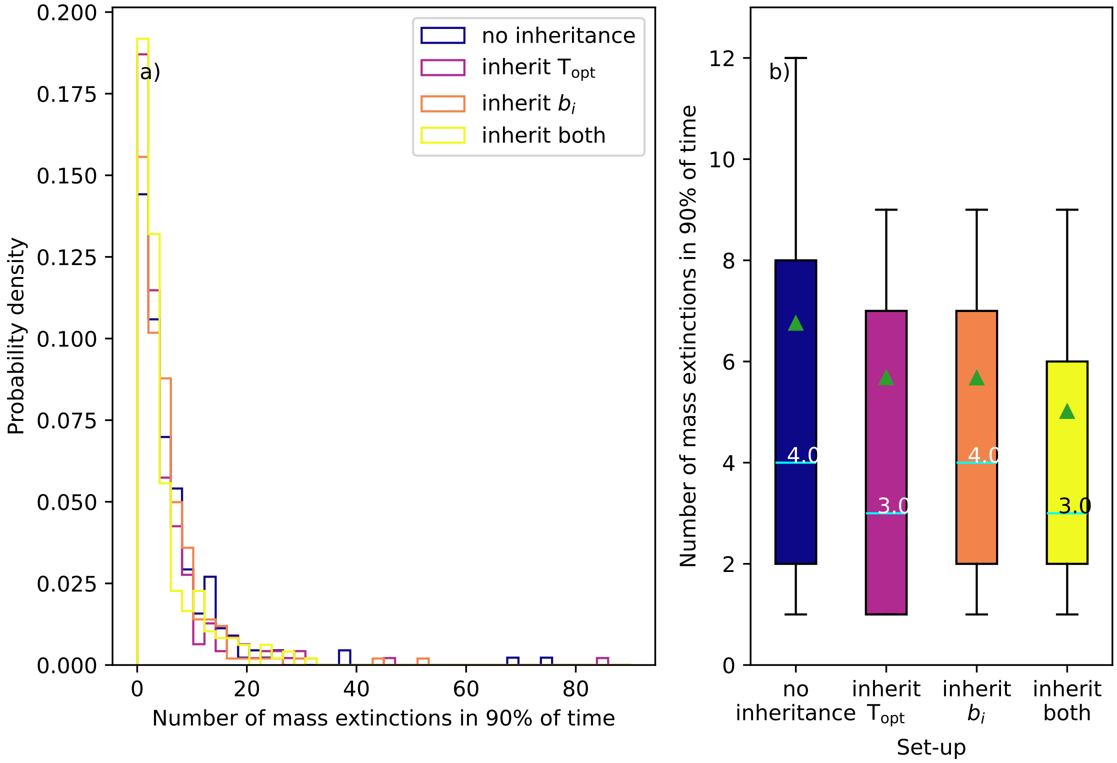

Figure 5.4: a) Histograms and b) boxplots of the number of mass extinction events taking up 90% of simulation time. (Mass extinction events are defined as extinctions of the two most abundant species from an ecological steady state — and are associated with an abrupt change in ecosystem abundance.) All values are shown in a), but outliers are omitted in b) to show the bulk of the values more clearly. In the boxplots (b), the median is printed on the boxplot and marked with a cyan line, and the mean with a green triangle. The edges of the boxes show the interquartile range, and the whiskers extend to the 15th and 85th quartiles.

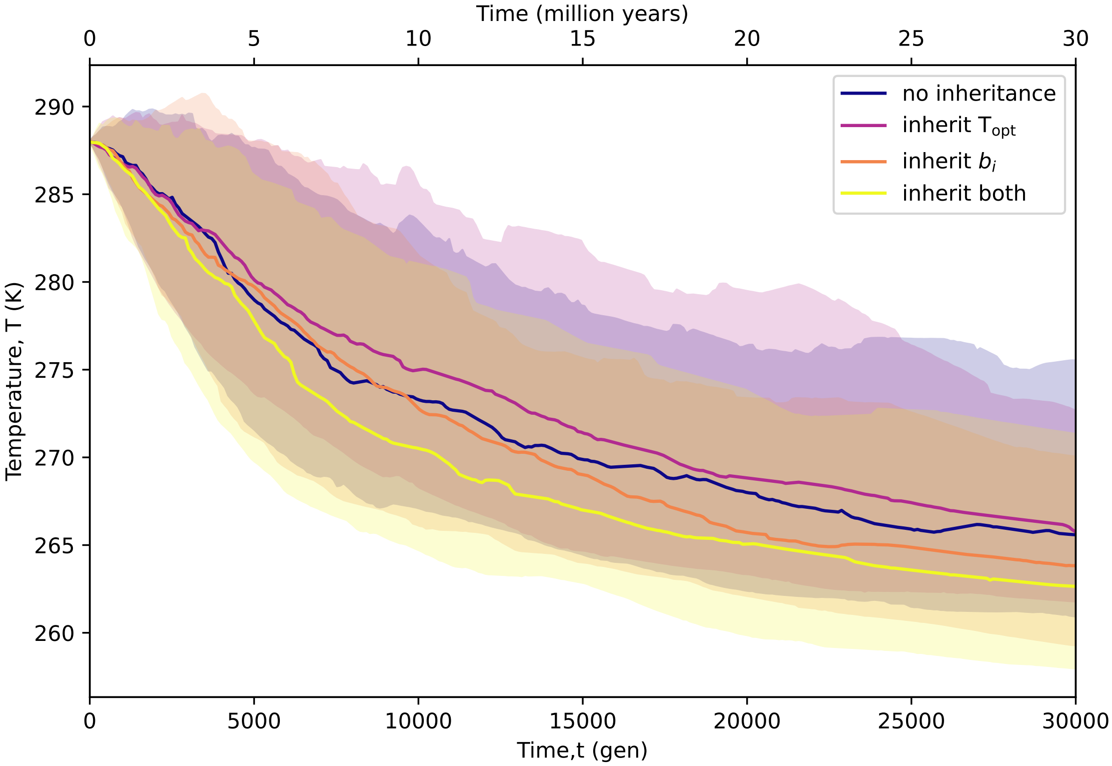

Figure 5.5: Timeseries of temperature of surviving experiments in the four inheritance experiments. The median temperatures are shown as lines, and the interquartile range is shaded in the corresponding color.

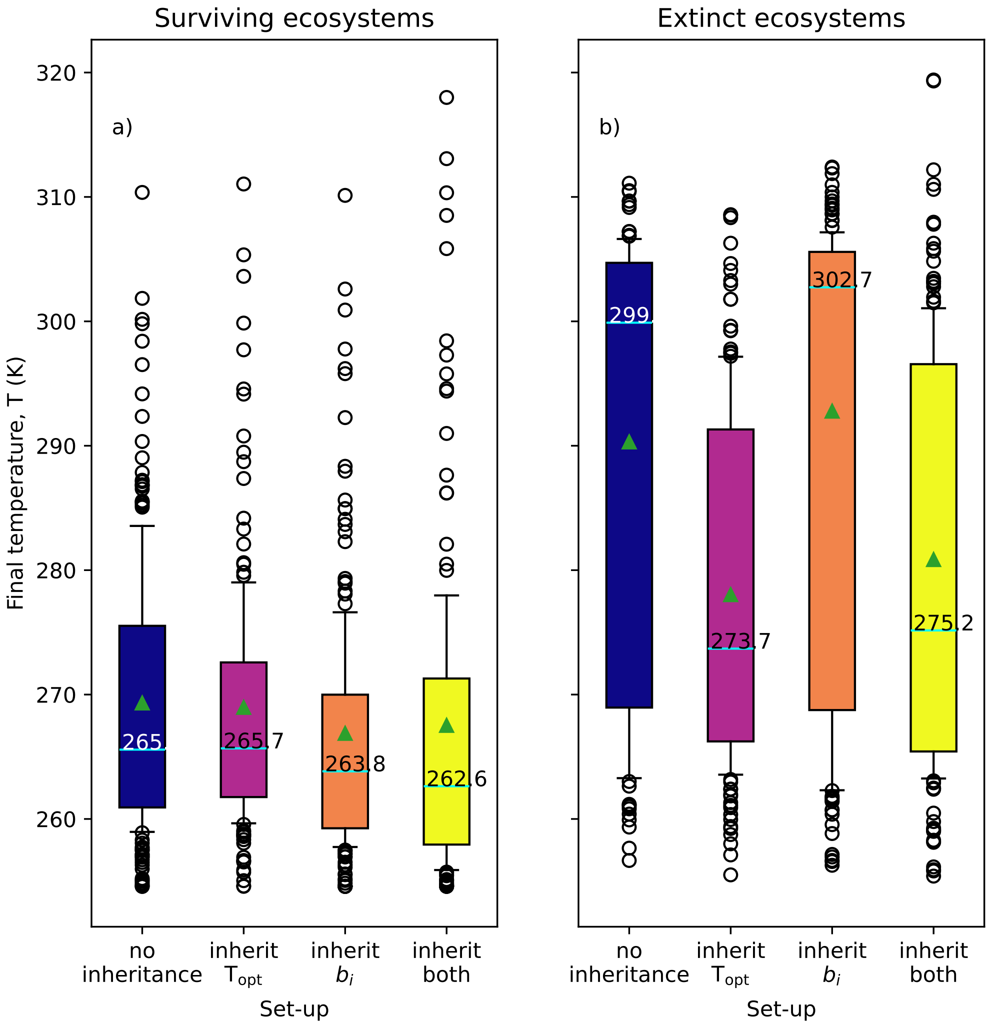

Figure 5.6: Final temperature of a) surviving and b) extinct ecosystems, at 30,000 generations (30 million years) or at the time of extinction, respectively. The number and cyan band in each boxplot indicates the median final temperature, the edges of the boxes indicate the upper and lower quartiles, and the whiskers extend to the 15th and 85th percentiles. Outliers are points beyond the whiskers and are marked with open circles. Green triangles indicate the mean value.

tions is generally warmer than the temperatures reached in surviving ecosystems, showing that ecosystems in warmer climates are more likely to go extinct in all cases (Fig. 5.6b). However, extinctions in the two configurations with inheritance of thermal optima occur at much cooler temperatures than the cases without inheritance of thermal optima, suggesting that inheritance of thermal optima either prevents ecosystems from ever warming as much as the other cases, or produces more total extinctions in cooler climates. More extinctions occur overall in the two cases with inheritance of $T_{\mathrm{opt,i}}$ than without (Fig. 5.3a), so either (or both) mechanism could be true.

After 30,000 generations (30 million years), median thermal optima of species in surviving ecosystems are around 285K in all four configurations; slightly cooler than both the center of the normal distribution from which thermal optima are originally drawn (290K) and the initial temperature (288K; Fig. 5.7a). Not surprisingly, the variance in species' thermal optima is smaller when thermal optima are inherited, showing more agreement between species around a central thermal optimum ($p < 0.001$). Interestingly, though, species also generally have a larger magnitude of thermal mismatch (difference between the environmental temperature, T, and a species' thermal optimum, $T_{\mathrm{opt,i}}$) in the two configurations in which thermal optima are inherited ($p < 0.001$), with median thermal optima around 26K (26°C) warmer than the environment in those cases, compared to about 20K (20°C) warmer than the environment when thermal optima are not inherited (Fig. 5.7b). This suggests that species that inherit thermal optima are generally worse-adapted to their environments (producing fewer offspring, Eq. 2.5) than species whose thermal optima are randomly assigned at the time of mutation. In other words, inheritance of thermal optima does not increase — and actually decreases — species' reproductive fitness.

5.3.3 Inheritance slightly increases ecosystem cooling impacts on the climate

In all configurations, median species' intrinsic impacts (b_i) on carbon are negative ($b_i < 0$) in surviving ecosystems after 30,000 generations (30 million years) of evolution, making species more likely to reduce atmospheric carbon (Fig. 5.8a). Inheritance of species' thermal optima and of intrinsic carbon impacts each enhances this effect ($p < 0.001$), shifting the distribution of species' intrinsic carbon impacts slightly more negative by shifting the third quartile of intrinsic carbon impacts from positive (without inheritance) to near zero in all three cases with inheritance (Fig. 5.8a). This shows that species with positive intrinsic carbon impacts are relatively common without inheritance, but in the three cases with

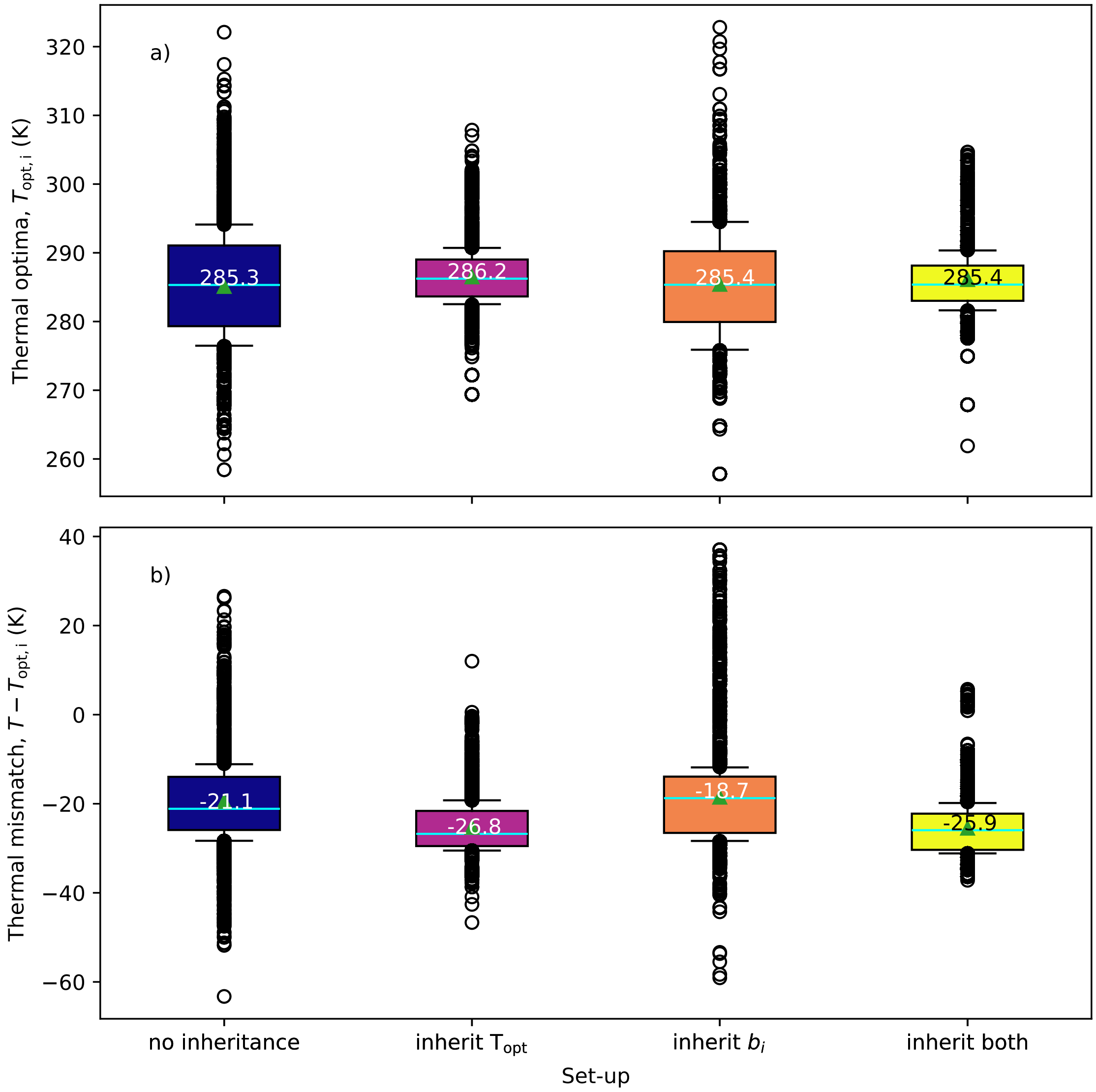

Figure 5.7: a) Species' thermal optima ($T_{\mathrm{opt,i}}$) after 30,000 generations (30 million years) in surviving ecosystems. b) Thermal mismatches ($T - T_{\mathrm{opt,i}}$) of species in surviving ecosystems after 30,000 generations. The number and cyan band in each boxplot indicates the median thermal optimum (a) or thermal mismatch (b), the edges of the boxes indicate the upper and lower quartiles, and the whiskers extend to the 15th and 85th percentiles. Green triangles indicate the mean value.

inheritance, species with positive intrinsic carbon impacts become much more rare. With inheritance of only intrinsic carbon impacts, the range of b_i is smaller than the other cases ($p < 0.001$), indicating selection against species with the largest carbon impacts effectively leading to evolution of the b_i distribution (Fig. 5.8a). Interestingly, though, when thermal optima are inherited in addition to species' intrinsic carbon impacts, the wide range of b_i is not reduced as drastically over the course of simulations.

The rate at which species impact the climate is determined by species' carbon fluxes divided by the mass of carbon in the atmosphere ($F_i/m_{\mathrm{CO_2}}$) (as CO_2 is logarithmically related to temperature; Eq. 3.2). In all cases, the median rate at which species affect the climate is near zero, with an interquartile range much smaller than the original interquartile range of b_i (Fig. 5.8c). This suggests that species are very likely to have small impacts on the climate, and that the rates at which species actually impact the climate have evolved to be smaller than species' intrinsic carbon impacts (which can be achieved by species living at temperatures away from their thermal optimum; Eq. 3.3). The distribution of the rate at which species impact the climate is also much sharper than the distribution of species' intrinsic carbon impacts in all cases, which also shows that the rates at which species actually impact the climate are reduced relative to their intrinsic carbon impacts (Fig. 5.8d). More species produce negative than positive impacts on the climate in all cases, additionally showing selection for species that cool the climate rather than warm it (Fig. 5.8c). Selection for species with negative climate impacts is stronger with inheritance ($p < 0.001$), and in the three cases with inheritance, almost no species within the 85th percentile produce positive impacts on the climate. The range and variance of the rates at which species impact the climate is furthermore reduced with inheritance of species' thermal optima ($p < 0.001$), which importantly shows that species are more likely to produce small-magnitude climate impacts with inheritance of thermal optima than with inheritance of carbon impacts (Fig. 5.8c,d). The combination of these results with the results of b_i and thermal mismatches suggests that inheritance of $T_{\mathrm{opt,i}}$ increases the magnitude of species' thermal mismatch (Fig. 5.7b) which reduces their impact on climate (Fig. 5.8c), so selection against species with large, positive b_i is not as important (Fig. 5.8a).

As for species, the rate at which ecosystems affect the climate is the flux of carbon (F_{bio}) divided by the mass of CO_2 in the atmosphere ($F_{\mathrm{bio}}/m_{\mathrm{CO_2}}$ is also proportional to the instantaneous rate of climate change since $dC/dt = F_{\mathrm{bio}}; Eq.3.5$). The magnitude of the rate at which ecosystems affect the climate ($|F_{\mathrm{bio}}/m_{\mathrm{CO_2}}|$) decays over time in all four configurations, showing that ecosystem impacts on the climate evolve closer to zero over time (Fig. 5.9). Ecosystems that warm the climate are only observed in the first

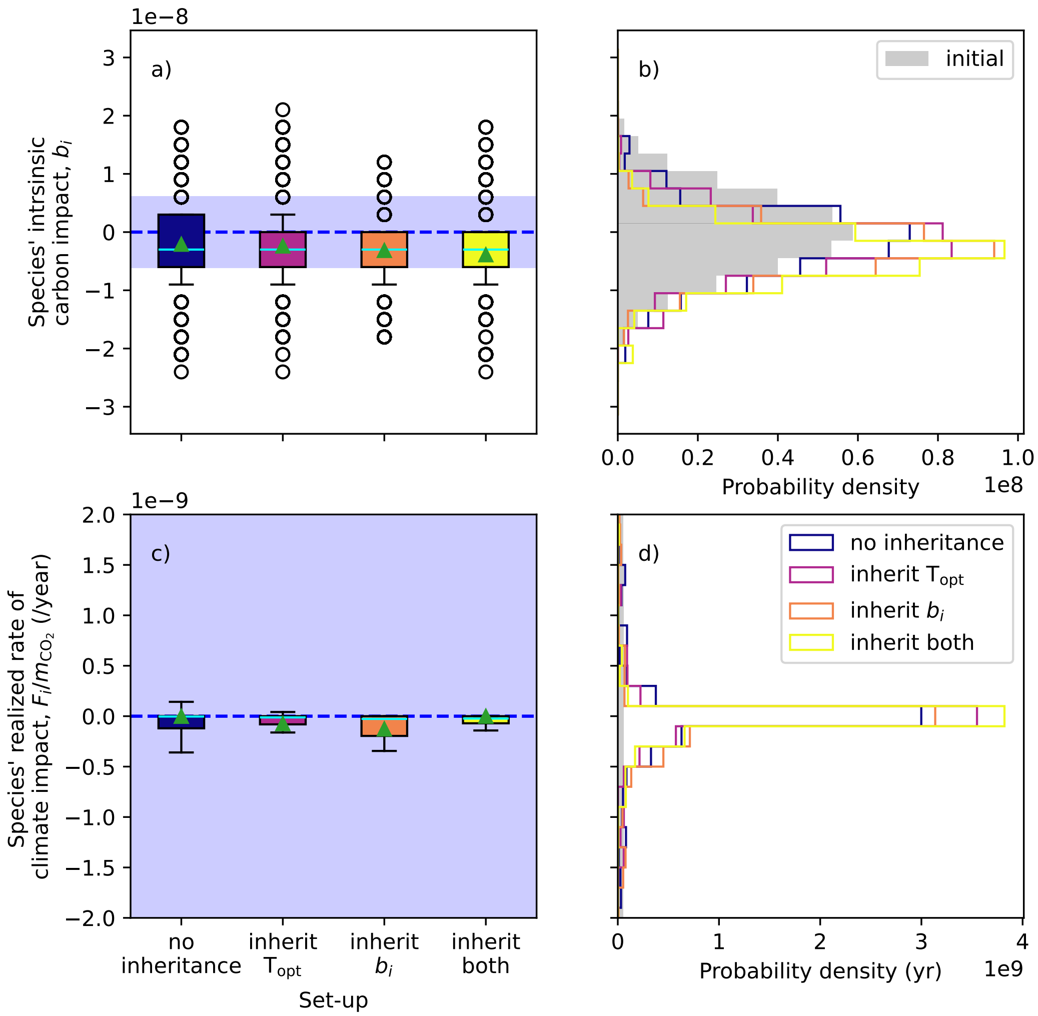

Figure 5.8: a,c) Boxplots and b,d) histograms of a,b) species' intrinsic carbon impacts (b_i) and c,d) the rates at which species actually impact the climate ($F_i/m_{\mathrm{CO}_2} = b_i r_i(T, T_{\mathrm{opt,i}})$), in surviving ecosystems after 30,000 generations (30 million years). In the boxplots (a,c), the cyan horizontal lines inside boxes indicate the median, box edges show the first and third quartiles, and the whiskers extend to the 15th and 85th percentiles. The blue dashed line is at zero and the blue shaded region shows the interquartile range of the initial distribution of b_i. Outliers (points beyond the whiskers) are circled in a) and omitted in c) because the range is very large (but are shown in Fig. D.2, in addition to a zoom-in on panel c)). Green triangles indicate the mean value. In the histograms (b,d), the initial distribution of b_i is shown in grey (but in (d) the initial distribution is hard to see because it is much wider than the final distribution).

$\approx$2,000 generations (2 million years), and then the interquartile range of ecosystem climate impacts remains almost entirely negative for the rest of simulations. This shows strong selection for cooling, rather than warming, ecosystems.

Without inheritance, the median annual rates at which entire ecosystems affect the climate after 30,000 generations (30 million years) is only slightly larger than the size of the original standard deviation ($\sigma_{\text{bio}} = 6.7 \times 10^{-9}$) of species' per-capita intrinsic carbon impacts (Fig. 5.10). Mean ecosystem impacts on climate are much more negative, indicating the presence of a few very cooling, outlying ecosystems in all cases, and especially with inheritance of both $T_{\text{opt,i}}$ and b_i (Fig. 5.10, D.3). The ecosystems with the most warming impacts occur in the configuration without inheritance, whereas in the three cases with inheritance, the distribution and median rates of ecosystem impacts on the climate are more negative. Differences in median ecosystem climate impacts are not statistically significant, though. However, the interquartile range of ecosystem climate impacts is larger, including more negative ecosystem climate impacts, in the two cases with inheritance of $T_{\text{opt,i}}$, but the difference in variance in not statistically significant. Overall, this suggests that differences in species-level evolution (in terms of $T_{\text{opt,i}}$, $T - T_{\text{opt,i}}$, b_i, and F_i) do not significantly affect ecosystem-level climate impacts.

Interestingly, in every case except with inheritance of only b_i, ecosystems that go extinct have a similar probability of warming or cooling the climate at the time at which they go extinct (Fig. 5.10b). With inheritance of only b_i, on the other hand, it is almost exclusively warming ecosystems that go extinct. This suggests that selection by survival (selective total extinctions of warming ecosystems) is a more important driver of ecosystem evolution when only species' intrinsic carbon impacts are inherited.

Species almost always produce smaller carbon fluxes than their ecosystem, suggesting that multiple species with the same sign of carbon impacts (i.e. many warming species or many cooling species) often co-exist in ecosystems (Fig. 5.11a). However, the configurations in which species are most likely to have larger impacts than their ecosystems are the cases with inheritance of b_i, and especially with inheritance of only b_i (Fig. 5.11a,b; $p < 0.05$). This suggests that inheritance of b_i makes it more likely for species with opposite impacts on the climate to co-exist in ecosystems, canceling out one another's climate impacts.

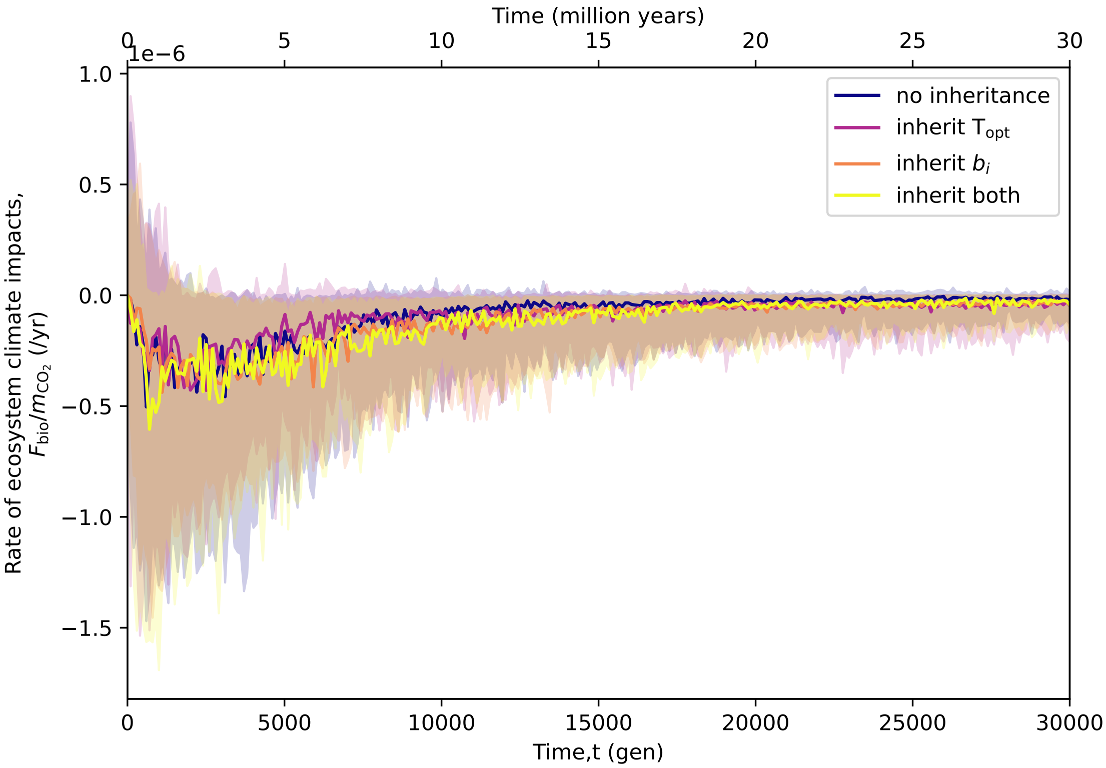

Figure 5.9: Timeseries of rates of ecosystem climate impacts (ecosystem carbon fluxes, F_{bio}, divided by the mass of carobn in the atmosphere, $m_{\mathrm{CO_2}}$) for surviving ecosystems in the four inheritance experiments. The median rates are shown as lines, and the interquartile ranges are shaded in the corresponding color.

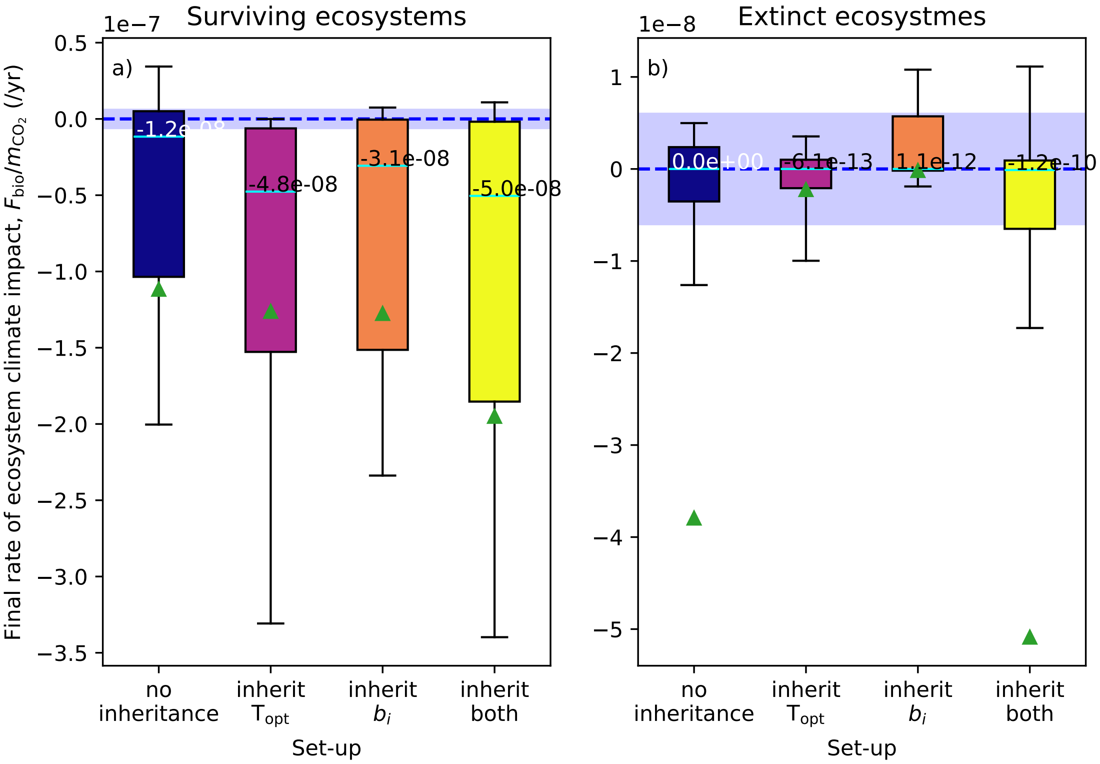

Figure 5.10: Boxplots of annual rates of climate impacts of surviving ecosystems ($F_{\mathrm{bio}}/m_{\mathrm{CO_2}}$) after 30,000 generations (30 million years). The number and cyan band in each boxplot indicates the median ecosystem climate impact rate, the edges of the boxes indicate the upper and lower quartiles, and the whiskers extend to the 15th and 85th percentiles. Outliers are omitted as they are very wide-ranging, but are shown in Appendix D.3. The blue dashed lines are at zero and the blue shaded region shows the interquartile range of the initial distribution of b_i. Green triangles indicate the mean value.

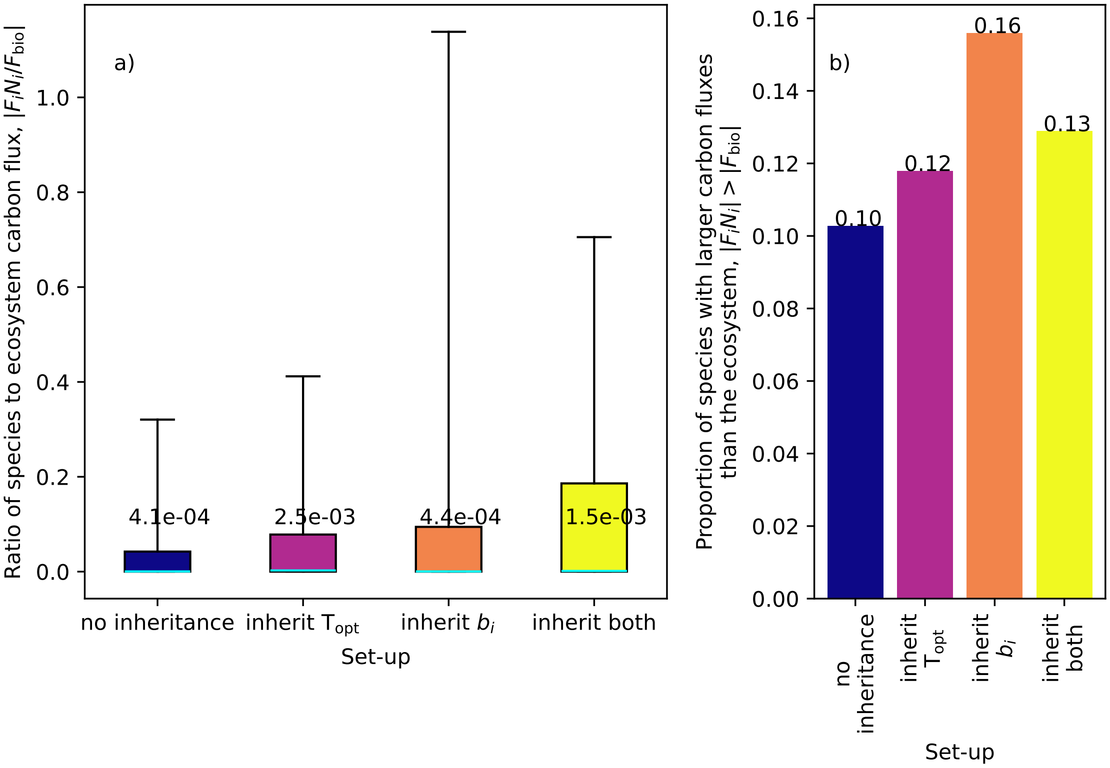

Figure 5.11: a) Magnitude of the ratio of each species' total carbon flux (the species' per-capita carbon flux, F_i, times the population of the species, N_i) to the ecosystem carbon flux (F_{bio}). This indicates the relative size of species' carbon fluxes compared to the carbon flux produced by the whole ecosystem. The number and cyan band in each boxplot indicates the median value, the edges of the boxes indicate the upper and lower quartiles, and the whiskers extend to the 15th and 85th percentiles. Outliers are omitted as they are very wide-ranging, but are shown in the Appendix (Fig: D.4) Proportion of species with larger carbon fluxes than the ecosystem ($|F_iN_i/F_{\text{bio}}| > 1$), indicating that species' carbon fluxes cancel out with other species in the ecosystem, leading to smaller ecosystem than species carbon fluxes.

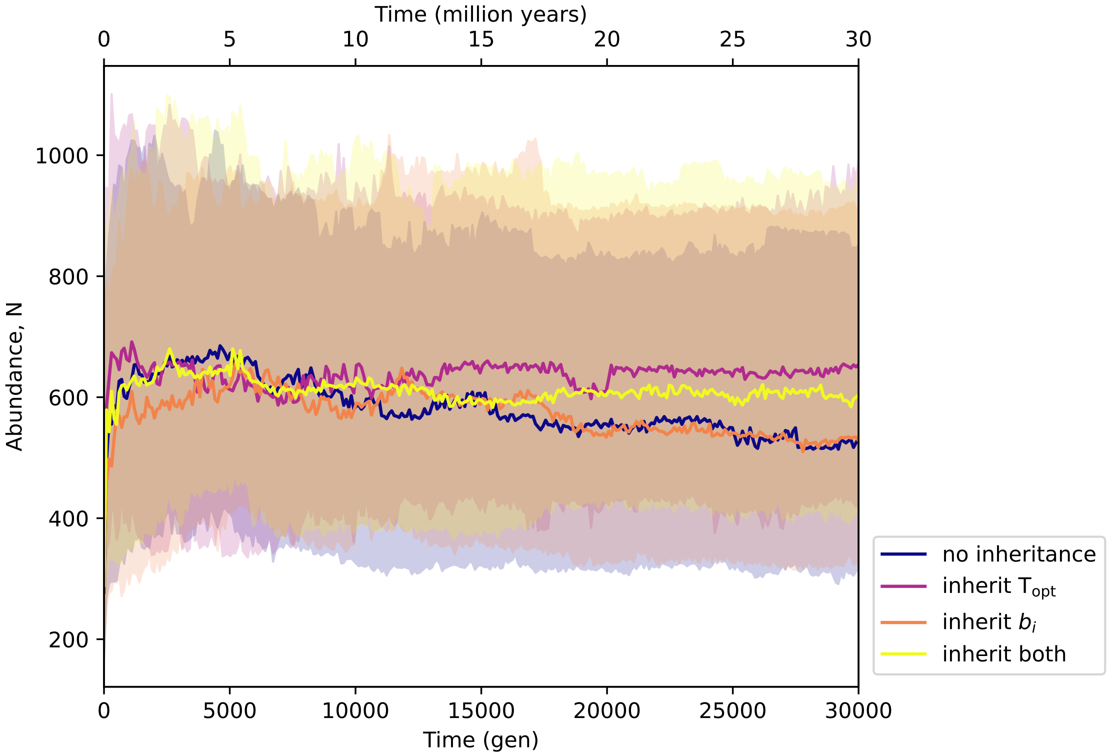

Figure 5.12: Median (lines) and interquartile range (shaded areas) of ecosystem abundance of surviving ecosystems over 30,000 generations (30 million years).

5.3.4 Inheritance has minimal effects on abundance and species richness

In all four configurations, median ecosystem abundance is around 600 individuals throughout the entire simulation, with an interquartile range of ecosystem abundance from about 300 to 1000 individuals (Fig. 5.12). In the two configurations without inheritance of thermal optima, median abundance declines slightly over time, reaching about 550 individuals after 30,000 generations. In the two configurations in which thermal optima are inherited, on the other hand, median abundance stays more constant throughout simulations, with larger values than the other two cases at all times after about 15,000 generations (15 million years). The difference in ecosystem abundance is also apparent in the interquartile ranges, with the first and third quartile ecosystems containing about 100 more individuals in the two cases with inheritance of thermal optima than without. However, differences in final median abundance and final variance are not statistically significant.

Median species richness decays from 60 to around 25 in the first 100 generations, and

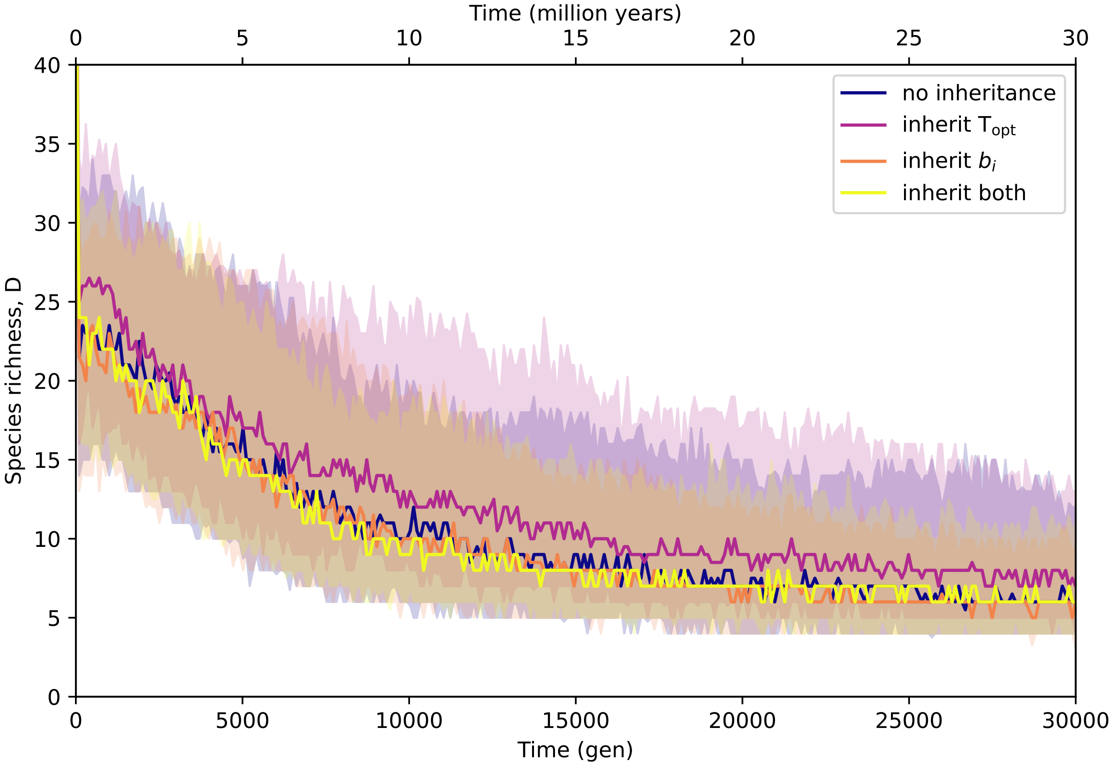

Figure 5.13: Median (lines) and interquartile range (shaded areas) of species richness of surviving ecosystems over 30,000 generations (30 million years). (Median species richness rapidly decreases from the initial value of 60 to around 25 species in the first 100 generations (100,000 years) of simulations, but the axis limits are adjusted to make the bulk of the values visible.)

then to about 6 over the course of the next 30,000 generations (30 million years) in all four configurations (Fig. 5.13). The low values of species richness reached are consistent with values of species richness expected at very low temperatures from in Chapter 2. The configuration with inheritance of only $T_{\mathrm{opt,i}}$ maintains slightly larger median species richness than the other configurations by one or two species at almost all times, and the upper quartile contains 1-5 more species than the two configurations with inheritance of b_i, but differences in median species richness and variance are not statistically significant at the end of simulations.

5.4 Discussion

5.4.1 Summary

In this chapter we aim to investigate how inheritance of traits associated with ecosystem-climate interactions affects ecosystem and climate evolution. We run the Tangled Nature + Cliamte (TaNC) model in four different configurations: one in which nothing is inherited when new species enter the model, one in which thermal optima ($T_{\mathrm{opt,i}}$) are inherited with a small modification from the ancestral species, one in which species' intrinsic carbon impacts (b_i) are inherited with a small modification from the ancestral species, and one in which both $T_{\mathrm{opt,i}}$ and b_i are inherited. These modifications make new species more similar to existing species, and also make new ecosystems similar to the old ones after mass extinction events. We expected that inheritance of species responses and impacts on the environment would enable ecosystem to act as a unit of selection, and that ecosystems should thus acquire "persistence-enhancing" traits, as predicted by (Doolittle, 2019). We hypothesized that these traits would be minimal thermal mismatches (maximizing species' reproduction rates; Eq. 2.5), minimal environmental impacts (producing longer steady states, as seen in Chapter 3), and cooling (minimizing death rates; Eq. 2.6 and prolonging ecological steady states, as seen in Chapter 3). We also hypothesized that these persistence-enhancing traits would increase ecosystem survival probability and the duration of ecological steady states in configurations of the TaNC that include inheritance.

Surprisingly, we find that more ecosystems survive to 30,000 generations (30 million years) without inheritance of thermal optima or intrinsic carbon impacts than in any of the cases with inheritance, suggesting that inheritance of thermal optima and of intrinsic carbon impacts each causes more total extinctions (Fig. 5.3a). This can be explained because when thermal optima are inherited, species are less able to adapt to a new climate, and when species' intrinsic impacts on carbon are inherited, the climate is more likely to warm or cool continuously. Both aspects of inheritance therefore make it difficult for species to adapt to new climates. This suggests that ecosystems are better able to adapt to changes in the climate, or minimize environmental change, when their responses and impacts are not constrained by being similar to their ancestors, because they have more opportunity to innovate.

While the total number of extinctions is greater in the cases with inheritance than without, the rate at which total extinctions occur decreases over time in all model configurations, and by about 20,000 generations (20 million years), ecosystems that have survived thus far have a similar probability of continuing to survive with inheritance or without it (Fig. 5.3b,c). Additionally, we find that ecosystems that survive with inheritance of anything, especially thermal optima, have slightly less frequent mass extinctions (Fig. 5.4). In conjunction with the finding that more ecosystems suffer total extinctions with inheritance, ecosystem evolution could arise because mass extinctions are more likely to end in total extinction with inheritance than without it, leading to a higher proportion of ecosystems with less-frequent mass extinctions persisting. The cases with inheritance of thermal optima produce the most total extinctions (Fig. 5.3a) in addition to the least frequent mass extinctions, which supports the interpretation that mass extinction are more likely to end in total extinctions with inheritance of thermal optima, which could in turn be because species adapt to new climates more slowly with inheritance of thermal optima than without. In other words, selection by survival (selective total extinctions of ecosystems) could more effectively cause ecosystems to evolve long-lasting steady states when new species are able to inherit thermal responses or intrinsic carbon impacts from their ancestral species.

As in the previous chapters, surviving ecosystems in all configurations of the TaNC tend to cool the climate, with median final temperatures after 30,000 generations (30 million years) around 265K ($-8°$C) both with and without inheritance (Fig. 5.5; note that we do not account for the freezing of water in this model). Inheritance of thermal optima and intrinsic carbon impacts each enhance this cooling, with median temperature 1-2K (1-2°C) cooler after 30,000 generations (30 million years), and about 3K (3°C) cooler with inheritance of both (Fig. 5.6), but these impacts are very minimal. This provides limited support for our prediction that inheritance increases the ability of selection for low-death environments to cause lasting evolutionary change.

The rate at which ecosystems affect the climate decreases over time in all cases, suggesting that evolution always drives ecosystems toward minimizing their climate impacts (Fig. 5.9). However, neither inheritance of species' thermal optima nor of their intrinsic carbon impacts enhances this trend (Fig. 5.10), contradicting our prediction that minimizing climate impacts is a persistence-enhancing trait which can be selected at the level of the ecosystem when ecosystems inherit properties of ancestral ecosystems.

Interestingly, while inheritance does not decrease the magnitude of ecosystem carbon fluxes, the mechanisms that could drive selection for smaller ecosystem climate impacts are operating. When thermal optima are inherited, species evolve larger thermal mismatches (Fig. 5.7b) which reduce the magnitude of the rates at which species impact the climate (Fig. 5.8c). On the other hand, when species' intrinsic carbon impacts are inherited, species becomes more likely to cancel out their fluxes with other species, (Fig. 5.11a), but this does not successfully reduce ecosystem carbon fluxes relative to the case without inheritance (Fig. 5.10). Therefore, although inheritance does not decrease the magnitude of ecosystem climate impacts relative to the case without inheritance, it does seem to enhance selection for species with small impacts on the climate.

Finally, we see that inheritance of thermal optima produces ecosystems with slightly larger abundance (Fig. 5.12) and species richness (Fig. 5.13). The TaNa+T (Chapter 2) suggested that ecosystem abundance is not temperature-dependent, and that cooler ecosystems generally have smaller species richness, so temperature is not the driver of this response. Instead, this may arise here because inheritance of thermal optima increases species' thermal mismatches ($|T - T_{\mathrm{opt,i}}|$) and thus decreases their reproduction rates (Eq. 2.5), and this may enable more species and individuals to co-exist. However, the increases to abundance and species richness are very minimal.

5.4.2 Interpretations

Illustrating how ecosystem-climate trajectories differ when species' ecosystem-climate interaction traits are heritable is one core aim of this chapter. Another important aim is to use these simulations to gain insight into how ecosystem-climate evolution works, and how variation and inheritance at different levels of selection shape evolutionary trajectories. In particular, both variation and reproduction with inheritance are often considered necessary components for natural selection to cause lasting evolutionary change in a unit of selection (Maynard Smith, 1991; Dawkins, 1982). These experiments allow us to compare ecosystem evolution when different units of selection produce offspring with similar traits to their own.

In the original Tangled Nature (TaNa) model, individuals inherit the traits of their species unless a mutation/speciation event occurs. This means that natural selection can act at the level of species, promoting certain species above others. Successful species in the original TaNa model generally benefit from interactions with other species, and in the TaNC, successful species must also be sufficiently adapted to the prevailing climate. In this chapter, though, enabling mutant species to inherit certain traits from their ancestral species adds another layer of complexity. Now, successful species (those with larger populations) produce mutant species that more closely resemble their own thermal preferences and/or impacts on the climate. This means that selection amongst species has the potential to produce more lasting changes in species and ecosystem characteristics than in the other versions of the Tangled Nature and TaNC models.

We see in this chapter that inheritance of thermal optima puts more stress on ecosystems initially, causing more mass extinction events to end in total extinction as mutant species have a harder time adapting to new climates. It additionally drives species away from their thermal optima, reducing their reproduction rates. However, surviving ecosystems last longer, reach slightly cooler temperatures, and obtain larger abundances and species richness. As cooler temperatures, larger abundance, and larger species richness can all be considered "persistence-enhancing" traits, this would suggest that selection by survival (and possibly sequential selection) indeed promotes ecosystem-level persistence.

Increased thermal mismatches in simulations with inheritance of thermal optima result in species with smaller impacts on the climate, but surprisingly does not reduce ecosystem-level impacts on the climate compared to the case without inheritance. Large thermal mismatches may, however, be responsible for allowing more individuals and species to co-exist in ecosystems, since species' reproductions rates are generally smaller. Therefore, inheritance of thermal optima may cause selection at the ecosystem-level (increasing steady state duration, abundance, and species richness) to override selection at the species level (for larger reproduction rates). Importantly, inheritance of thermal optima limits all species' ability to adapt to new climates similarly, which may be one reason that higher-level selection can be effective.

Inheritance of species' intrinsic impacts on carbon has similar, but not identical, impacts on ecosystem-climate evolution. Like inheritance of thermal optima, inheritance of carbon impacts increases the number of total extinctions but slightly increases steady state durations and slightly increases climate cooling. Inheritance of carbon impacts does not affect abundance or species richness, though. As with inheritance of thermal optima, the inverse relationship between total extinctions and mass extinctions suggests that selection by survival is harsher with inheritance of carbon impacts than without, and successfully weeds out ecosystems with frequent mass extinction events (and thus short ecological steady states).

At the species level, inheritance of carbon impacts weeds out the species with the largest intrinsic carbon impacts (as long as thermal optima are not also inherited), but this does not produce a strong reduction in the magnitude of species' rates of climate impact. This surprisingly suggests that inheritance of thermal optima is more effective at reducing the rates at which species affect the climate than is inheritance of species' intrinsic impacts on carbon. Inheritance of carbon impacts also increases the proportion of species' whose climate impacts cancel out, but this does not successfully reduce the magnitude of ecosystem climate impacts. As with inheritance of thermal optima, inheritance of carbon impacts produces more cooling, rather than smaller climate impacts (which would enable more stable climates). This either suggests that selection for cooling ecosystems is stronger than selection for stable climates, or that ecosystems are unable to drive strong enough selection for minimal climate impacts that could override selection at other levels. (This could arise because selection for positive interactions between species feeds back on species reproduction rates more quickly than selection on species' impacts on the climate feed back on the duration of the ecological steady state.) If it is the case that selective pressures driving ecosystems toward cooling are stronger than selective pressures driving ecosystems toward stable climates, it would seem to suggest that species have relatively high chances of adapting to change (both in climate and in ecosystem structure if a mass extinction occurs) in cooler climates, and this ability to adapt is more important than a long-lasting stable climate.

Disentangling which level of selection causes evolution, and which level reacts to the changes produced at other levels, is challenging. However, we interpret our results to suggest that at least three levels of selection act simultaneously. First, there is selection amongst species for positive interactions with one another. This produces the ecological stable states characteristic of Tangled Nature models. Second, there is selection for species that are sufficiently well-adapted to the climate. Species that are initially well-adapted to their thermal environment are also relatively robust to climate changes since species' impacts on the climate are often reduced throughout the course of climate change, especially if the climate is cooling, enabling stable ecosystems to persist. Inheritance of species' thermal optima makes new species more likely to maintain the warmer thermal optima of the ancestral climate, which inadvertently reduces their impacts on the climate and enables ecosystems to persist. Therefore, inheritance of thermal optima does not drive selection for thermally well-adapted species, but for poorly-adapted species with small climate impacts. When species' thermal optima are not inherited, on the other hand, new species are more likely to be better-adapted to newer climates. Therefore, with inheritance of carbon impacts, there is stronger selection on species' intrinsic carbon impacts, selecting for species with explicitly small impacts on the climate. Third, there is selection at the level of ecosystems for cooler climates. Warmer climates are more likely to have both mass and total extinction events, and this yields more cool and cooling climates in surviving simulations. Selection for cooling seems to be a major driver of ecosystem and climate evolution, even though it occurs at the level of ecosystem. Inheritance has the weakest impacts on these large-scale properties though, with statistically insignificant increases in cooling and steady state durations arising in the cases with inheritance. This highlights the selection hierarchy, in which smaller levels evolve more quickly the larger levels.

5.4.3 Future directions

An important aim of this study is to bridge different levels of selection by enabling speciation with inheritance. So far, our results suggest that this enhances some aspects of ecosystem-level selection more than others. In particular, inheritance in the TaNC drives more cooling and less minimization of climate impacts. However, selection by survival is a very slow driver of evolution, and only small differences in ecosystem traits are noticeable with and without inheritance after 30,000 generations (30 million years). Therefore, finishing our longer (100,000 generation) simulations, or running simulations even longer (since TaNa dynamics are slow down logarithmically) could help determine how different timescales of evolution interact and affect ecosystem evolution in the long run. It will be interesting to see if long run times will enable ecosystems with inheritance to accumulate more measures of ecosystem-level fitness: for example, decreasing extinction rates, increasing steady state durations, or increasing abundance or species richness. If so, the time required for ecosystems with inheritance to outperform those without inheritance will be very interesting to quantify relative to species and ecosystem turnover rates.

To continue to probe into the interactions between different units of selection in ecosystems, future work could also consider inheritance of species interactions with one another; the main driver of ecological stability in the Tangled Nature model and its variants. Stable interactions between core species lock the impacts of that ecological steady state on the environment, and in the configurations of the TaNC considered here, mutant species can only change the effects of the ecosystem on the climate by causing a mass extinction and core re-configuration. However, interspecific interactions are the main traits that define species, so introducing inheritance of these traits during mutation would further blur species boundaries and enable microevolution to participate in affecting model dynamics. Inheritance of interspecific interactions could make more similar species form ecosystem cores from one ecological steady state to the next, which could increase mutualistic interactions between species (Laird & Jensen, 2006). This could also increase ecosystem abundance, which is dependent on interaction strength (Appendix A.3, Arthur and Nicholson (2023)). Therefore, incorporating inheritance of ecological interactions would be a very interesting next step in investigating how inheritance affects the co-evolution of climate and ecology on multiple timescales.

Another interesting direction of future study would be to investigate selection on ecosystem characteristics when there are external forcings on the climate (such as variable rates of volcanic outgassing of CO_2 or weathering (due to the position of the continents for example) (Isson et al., 2020), or due to increasing solar luminosity (Sagan & Mullen, 1972)). Variable climates could exert stronger pressure on ecosystems to counteract perturbations to the climate. If selection by survival is the strongest mechanism of selection, variable climates might drive more ecosystems to extinction early on, but ultimately produce ecosystems that counteract abiotic climate perturbations. For this to arise, selection for species with larger climate impacts might be necessary, which would change the direction of selection previously observed in the TaNC. It would be very interesting to see whether this is the case.

Continuing to test this model and its sensitivity to different assumptions, and continuing to build in more realistic elements of ecology and geochemical cycles, will be crucial to relate these results to Earth history, climate evolution, and macroecology.

5.5 Conclusion

Overall, this chapter illustrates how ecosystem-level selection may operate, and shows how inheritance both helps and hinders ecosystems in achieving persistence-enhancing traits. Inheritance causes harsher selection by survival — meaning it drives more ecosystems to total extinction. In surviving ecosystems it is a weak driver of evolution, selecting for ecosystems with very slightly cooler climates (which minimizes death rates and increases steady state durations). We do not see enhanced selection for ecosystems with smaller impacts on the climate, though, in contrast to one of our main hypotheses. Overall, inheritance of environmental impacts and responses may enhance the ability of natural selection to cause lasting change in ecosystem characteristics, but ecosystem-level selection is a very slow process.

Chapter 6

Conclusions

6.1 Summary

In this dissertation, I investigate how ecosystem properties, the climate, and the interactions between them evolve over geologic timescales. To do this, I modify an evolving ecosystem model called the Tangled Nature (TaNa) model (Christensen et al., 2002) to give species physiological thermal response curves in the Tangled Nature + Temperature (TaNa+T) model (Chapter 2, Febvre et al., 2024). Then I allow species to affect the environment with randomly drawn impacts on atmospheric carbon in the Tangled Nature + Climate (TaNC) model (Chapters 3-5). Here, I briefly summarize the findings from this modeling work.

6.1.1 Chapter 2: Thermal performance of ecosystems: modeling how physiological responses to temperature scale up in communities

In Chapter 2, I investigate how species' responses to temperature in terms of reproduction, death, and mutation scale up to produce ecosystem-level thermal responses in the TaNa+T model. I find that different ecosystem characteristics respond differently to temperature, each depending on different underlying thermal response curves. This produces a wide variety of ecosystem-level thermal responses. Ecosystem survival probability depends on species' fitness threshold, related to the ratio between species' reproduction and death rates. The shape of the thermal response of ecosystem survival probability depends on the constraints on species' ability to adapt to new temperatures. Importantly, ecosystem survival probability is the only ecosystem metric that is sensitive to interspecific variation in species' thermal optima of reproduction. Species richness increases exponentially with temperature, scaling up from the thermal response of mutation rates, while population sizes and interspecific interaction strengths are inversely related to mutation rates. Abundance does not respond to temperature at all, though this could relate to scaling of parameters.

6.1.2 Chapter 3: Ecosystem-level niche construction in the climate: modeling co-evolution of ecosystems and temperature

In Chapter 3, I investigate how species' impacts on the environment evolve, and how this affects the evolution of both the climate and ecosystem characteristics. To do this, I enable species to increase or reduce the amount of carbon in the atmosphere, thereby affecting environmental temperature in our new variation of the TaNa model called the Tangled Nature + Climate (TaNC) model. I find that ecosystems generally cool the climate when the standard deviation of biotic impacts on atmospheric carbon is large enough for species to affect the climate. Cooling arises both as a result of lower death and mutation rates in cooler climates, and because the asymmetry of the thermal response of reproduction allows species to reproduce in a wider range of temperatures below their thermal optimum than above it. Selection for species with smaller intrinsic impacts on the climate and for species combinations whose climate impacts cancel out also arises with strong enough biotic impacts. Additionally, the strength of selection for small ecosystem-level climate impacts increases as the standard deviation of species' impacts on carbon is increased in the model. I find that stable ecosystems generally do not stabilize the climate. However, the amount of climate change within surviving ecosystems does not increase in proportion to the standard deviation of biotic impacts, showing that selection for smaller ecosystem-level impacts on the climate successfully reduces climate change when ecosystems have large standard deviations of biotic impacts. I also find that ecosystem survival probability, species richness, and abundance all decline when the model is run with large standard deviations of biotic impacts, which I attribute to increased extinction rates due to climate change, and reduced abundance species richness in the colder temperatures reached in simulations with larger biotic impacts (as Chapter 2 shows that species richness decreases in colder temperatures).

Overall, this chapter shows that asymmetry of species' thermal responses can produce asymmetrical impacts on the environment, even if species' intrinsic impacts on the climate are symmetrically distributed. This work furthermore shows that species' impacts on the climate can feed back on ecosystem properties such as ecosystem survival probability, species' intrinsic carbon impacts, species richness, and abundance. Importantly, this demonstrates that niche construction occurring at the ecosystem level can drive environmental conditions toward reducing death probabilities, with minimal assumptions about ecology, evolution, and climate.

6.1.3 Chapter 4: Shared preferences and opposite effects: how similarity in thermal optima, and opposition of impacts, affect the co-evolution of climate and ecology

In Chapter 4, I examine how the distributions of species' thermal optima and intrinsic carbon impacts affect the co-evolution of ecosystems and the climate. I specifically ask two main questions: 1. Are species with more similar thermal optima more likely to produce a climate near their shared optimal temperature? and 2. Are species more likely to cancel out their impacts with other species in the ecosystem if species are forced to affect their environment?

In response to my first question, I find that species with more similar thermal optima are not more likely to bring the climate toward their shared optimal temperature. Instead, they actually tend to cause more cooling in the model. Interestingly, species generally have larger thermal mismatches in this configuration than when thermal optima are uniformly distributed. This reduces species' reproduction rates, but it also reduces their metabolic rates and thus their carbon fluxes, which may help more ecosystems survive in this configuration than when thermal optima are uniformly distributed.

In response to my second question, I find that forcing species to affect the climate increases the strength of selection for species with small intrinsic carbon impacts, but does not make it more likely for species' impacts on the climate to cancel out with other species. Fewer ecosystems survive overall, but the duration of ecological steady states in surviving ecosystems is not affected. Thus, a bimodal distribution of environmental impacts does not promote complementarity of environmental impacts — suggesting that any selection for species to cancel their impacts is too weak to guide ecosystem evolution.

In all cases, TaNC ecosystems tend to cool the climate, as in Chapter 3. In fact, cooling increases with both new distributions of thermal optima and intrinsic carbon impacts tested in this chapter.

6.1.4 Chapter 5: How inheritance during speciation affects the co-evolution of ecosystems and climate in the Tangled Nature + Climate model

In Chapter 5, I investigate how ecosystem-climate co-evolution changes when new species, and thus whole ecosystems, can inherit their responses to and intrinsic impacts on the climate. I find that when species inherit similar thermal optima to their ancestors, intrinsic impacts on the climate, or both, fewer ecosystems survive overall. However, the rate of total extinctions decreases over time in all cases, and extinction rates with and without inheritance begin to converge. Additionally, ecosystems that survive with inheritance tend to have slightly longer steady states than those that survive without inheritance. Inheritance of thermal optima also increases abundance and species richness. This suggests that, while inheritance decreases ecosystem survival probability overall, total extinctions may cause lasting change in ecosystem characteristics that promote the longevity of ecological steady states. This exemplifies the concept of selection by survival: total extinctions of certain ecosystems leave only ecosystems with persistence-enhancing traits surviving, and they thus have better chances of continuing to survive in the future. While selection by survival produces evolutionary changes in the TaNC without inheritance, this chapter suggests that inheritance enhances this process of ecosystem-level evolution.

Interestingly, inheritance increases the magnitude of ecosystem-level carbon fluxes, showing that inheritance shifts evolution toward cooling rather than ecological stability. Additionally, inheritance of species' impacts on the climate increases the proportion of species whose carbon fluxes cancel with other species, but this does not effectively decrease ecosystem-level carbon fluxes. This suggests that selection for stable climates is not as strong a driver of ecosystem evolution as selection for cooling when ecosystems inherit climate-interaction characteristics.

We also find that inheritance of thermal optima is more beneficial for ecosystems than inheritance of intrinsic carbon impacts in terms of abundance and species richness. Interestingly, inheritance of thermal optima is also more effective for reducing species' carbon fluxes (by reducing species' metabolic rates) than inheritance of intrinsic carbon impacts. However, inheritance of thermal optima and of carbon impacts each increase the duration of ecological steady states and increase cooling, and each has a similar impact on ecosystem survival probability, so inheritance of either trait affects ecosystem-climate co-evolution similarly.

Overall, this chapter shows that ecosystem-level selection enhances ecosystem accumulation of persistence-enhancing ecosystem traits, but it is a very weak evolutionary force which requires many mass extinctions, and thus very long timescales.

6.2 Overarching interpretations

The results of the TaNC help formulate and illustrate the selective pressures experienced by different units of selection, including both species and whole ecosystems. Additionally, the TaNC provides insight into how selective pressures at different levels cause changes in ecosystem and climate characteristics over time. In this section, I provide an overview of the different interacting units of selection in the TaNC, and then summarize our key findings related to the directions of evolution that result from selection on these units.

6.2.1 Units of selection

The TaNC contains three main units of selection: species, ecological steady states, and entire lineages. This captures an aspect of the complexity of ecology that remains mysterious in Evolutionary Biology. In considering the emergence of evolution at higher levels of selection, Maynard Smith (1991) asks "If the transition involved the joining together in a single evolutionary unit of previously independent entities, how did it come about that selection between these lower-level entities did not disrupt integration at the higher level?" In other words, what determines which level of selection dominates evolutionary changes? Maynard-Smith then proposes that compartmentalization is necessary for an assemblage to act as a single unit of selection. If compartmentalization is essential for a unit of selection to drive evolution, evolution can act on ecosystems as a whole in the TaNC because the survival of each species is linked with the survival of the ecosystem as a whole — providing compartmentalization. Additionally, the temperature of the ecosystems is experienced by all species, with all species experiencing the same death and mutation rates as a result.

But how do ecosystems experience natural selection in the TaNC? Maynard Smith (1991) writes, "many entities are selected but do not reproduce and hence do not evolve." In other words, reproducing entities must produce offspring with inherited traits for selection on those entities to cause lasting changes in their characteristics. The TaNC includes both heritable and non-heritable components in both the configurations without and with inheritance. I consider these components in the next subsection.

Species-level selection

Species are replicating units in the TaNC which experience several different selective pressures. The fundamental ecosystem model (the TaNa model) is largely driven by selection on interactions between different species (Christensen et al., 2002; Arthur et al., 2017). Because there is a universal carrying capacity in the model, species must compete for larger population sizes, which depend on interactions with other species (and also historical population sizes). Stable ecosystems generally form between a few species with mutualistic interactions between one another and who are then able to dominate in terms of population sizes. As in the original TaNa model, selection on interactions is a major feature of the TaNC. Punctuated Equilibria always emerge in the TaNC, again characterized by relatively stable community compositions dominated by a few core species. This is probably the strongest selective pressure in the model.

Species in the TaNa+T and TaNC also experience selection based on their thermal adaptations, as we fleshed out in Chapter 2. Temperature affects species' reproduction rates, and so species' must be sufficiently well-adapted to a certain climate in order to persist. When model species can adapt to different temperatures, ecosystems are more likely to survive in colder climates because of the asymmetry of reproduction thermal response curves and because death rates are reduced in cooler temperatures. Consequently, when species can also affect the climate through their carbon fluxes (Chapters 3-5), we see climate evolution toward cooler climates.

When species affect the climate (sufficiently strongly), there is also selection on species' climate impacts. To a small extent, this takes the form of selection for species with small intrinsic carbon impacts (b_i). However, there is even stronger selection for species far from their thermal optima, as species' carbon fluxes are reduced when they are far from their thermal optima. Selection for large thermal mismatches is seemingly at odds with selection for species that are well-adapted to the climate. However, species' thermal adaptation can change over the course of ecological steady states, so species that were originally well-adapted to the temperature may become worse-adapted as the climate changes away from their thermal optimum. While species become less adapted, their carbon fluxes decrease, thus decreasing the rate of climate change. In this case, ecosystem-level selection (for a stable core and a cool climate with low death rates) may override species-level selection for larger reproduction rates.

Selection by survival

Ecosystem level selection can arise in two main forms in the TaNC; selection by survival (via selective total extinctions) or sequential selection (via differential durations of ecological steady states). These two forms of selection cause changes in the statistics of ecosystem and climate properties, and although new species in the TaNC without inheritance do not inherit traits of ancestral species, some of these changes can still be heritable. Other changes, though, are not heritable, and thus natural selection must constantly weed out ecosystems with similar characteristics.

Selection by survival can cause non-heritable changes in ecosystems if descendants of a lineage do not share any traits with their ancestors. This non-heritable selection may occur in the TaNC if ecosystems with large carbon fluxes, for example, cause rapid climate change and drive themselves extinct, but surviving ecosystems are no less likely to later produce large carbon fluxes than the original distribution of ecosystems. If this is the case, we should expect ecosystems to die out at a constant rate determined by the unchanging probability of species producing large carbon fluxes.

However, the rate of total ecosystem extinctions decreases over time in the TaNC even without inheritance, so some aspects of ecosystem evolution must be heritable even when new species bear no resemblance to their ancestors. Differences in the statistics of surviving compared to extinct ecosystems, especially in terms of climate, suggest that surviving ecosystems are indeed acquiring different traits from those that went extinct. In Chapter 5, we additionally see that ecosystem extinction rate decreases more markedly with inheritance of species' thermal optima or intrinsic carbon impacts than without inheritance, but as extinction rate decreases even without inheritance of thermal optima or intrinsic carbon impacts, ecosystems must evolve persistence-enhancing traits within lineages even without inheritance during speciation events. When ecosystem evolution occurs without total extinctions, it may partially be due to the process of sequential selection.

Sequential selection

In sequential selection, ecosystems that disrupt their environments terminate their ecological steady states more quickly (Betts & Lenton, 2008). By contrast, ecosystems that do not disrupt their environments have a possibility of lasting longer, and so over time, they become more common (Lenton, Daines, Dyke, et al., 2018). As with selection by survival, if an ecological steady state emerging after a mass extinction terminated a previous, long-lasting steady state is no more likely to last a long time than an ecosystem emerging after a short steady state, sequential selection does not cause heritable change, even if lineages spend a disproportionate amount of time in long rather than short ecological steady states.

However, it has already been shown that steady state durations increase over time in the TaNa model, even without inheritance, due to the emergence of increasingly positive interactions between species (Christensen et al., 2002). Roach et al. (2017) also showed that biological order increases over time in the TaNa model without inheritance. Arthur and Nicholson (2022) suggest that an "entropic ratchet" operates across mass extinction events, based on increasing species richness providing more possibilities for each subsequent ecosystem. As species richness represents the diversity of the genetic pool of an ecosystem, this can be considered a heritable change in ecosystem properties. Doolittle (2019) additionally suggested that ecosystems with larger species richness would be more likely to persist, and so considered species richness to be a persistence-enhancing trait which, if acquired within a lineage, promotes the probability of that lineage continuing to persist.

In the TaNC, the same aspects of sequential selection as in the original TaNa models are operating. Additionally, sequential selection drives evolution of surviving ecosystems' interactions with the environment in the TaNC, which is most clearly seen when the statistics of surviving and extinct ecosystems are similar (and therefore selection by survival is not acting), and when there is still evolution of their ecological traits. For example, the distributions of species' thermal mismatches in Chapter 3 are only slightly wider in extinct compared to surviving ecosystems, but species successfully adapt to the climate in surviving lineages, suggesting that total extinctions of ecosystems are not solely responsible for driving species to adapt to the climate. Species' intrinsic carbon impacts are also distributed around a negative value in both surviving and extinct ecosystems in Chapter 3, suggesting that there is effective selection for species with negative climate impacts even without total ecosystem extinctions.

While sequential selection appears to produce heritable changes in model ecosystems over time without inheritance, inheritance of species' traits associated with climate interactions also enhances some aspects of heritable ecosystem-level evolution, as the rate of total ecosystem extinctions decreases more drastically over time with inheritance than without, increases the duration of ecological steady states, and increases cooling in the TaNC. Additionally, inheritance seems to shift the balance of selection pressures away from stabilizing and toward cooling climates. This could be because inheritance is ineffective at enabling ecosystems to minimize their environmental impacts, or because cooling is more strongly selected for than environmental stabilization. On the other hand, this shift in evolutionary pressures could be because ecological inheritance — ecosystems "inheriting" their abiotic environments (rather than species inheriting certain genes) — is an even stronger driver of evolution than genetic inheritance.

Ecological inheritance

Ecosystems in the TaNC inherit the climates produced by their predecessors, even if they do not inherit their predecessors' environmental preferences or impacts, and this can affect the selective pressures experienced by species in later generations. Inheritance of the physical conditions created by earlier organisms is called ecological inheritance (Odling-Smee et al., 1996; Bonduriansky & Day, 2009), and the TaNC illustrates how this can play out. In the TaNC, cooler climates reduce the death and mutation rates of all species in the model, and therefore extends ecological steady states and decreases the probability of total ecosystem extinctions. Species are also more likely to have thermal optima greater than the environmental temperature in cooler temperatures, which both gives them a wider range of temperatures at which they can reproduce, and reduces their carbon flux. This seems to be the most important feature of heritable change in the TaNC: not the traits associated with species' responses or impacts, but environmental traits external to organisms.

Interactions between different units of selection

Overall, species-level selection (on interspecific interactions and thermal adaptation) may drive ecosystem evolution initially. Over the course of mass extinction events, however, ecosystem-level selection — through total extinctions, mass extinctions, and changes in the abiotic environment (all leading to selection for cool climates and small environmental impacts) — becomes strong enough to affect ecosystem and climate characteristics.

One early criticism of ecosystem-level evolution (in the form of the Gaia hypothesis) was that feedback on species whose impacts are detrimental to a shared environment would be too slow and too late to stop those species from causing total catastrophe and driving all species — their own species included — extinct (Doolittle, 1981). This is similar to the concept of selection by survival — ecosystems that by chance evolve species with very large impacts on the environment may have no chance to evolve mechanisms that reduce those impacts, and so only "lucky" ecosystems that never evolve harmful species persist. However, sequential selection suggests that if some species survive a catastrophic mass extinction, ecological lineages get another chance. If any ecosystem characteristics (including species richness and environmental temperature) are heritable, then ecosystems can additionally acquire persistence-enhancing traits.

6.2.2 Key findings about the directions of evolution

Selection on species, selection by survival, sequential selection, and ecological inheritance drive evolution in the TaNC toward cooler climates and smaller environmental impacts. Here I explain the outcomes of the selective pressures discussed above, and then apply the TaNC results to our understanding of ecosystem-level selection for beneficial environments — the central concept of the Gaian paradigm.

Selection for cool climates

The main result of the TaNC model is that evolutionary pressures can drive ecosystems toward cooling their environments. Every configuration of the TaNC, under every set of assumptions we have tested in this dissertation, produces cooling more frequently than climate warming, suggesting that cooling is a general result of the TaNC. This arises partially because death and mutation rates are much lower at colder temperatures. However, cooling also arises in the TaNC when death and mutation rates are held constant, indicating that the asymmetry of species' thermal response curves of reproduction alone can drive ecosystems toward cooler climates (Chapter 3).

The fact that it is easier for species to exist below than above their thermal optimum is well-documented, even today on human timescales (Martin & Huey, 2008; Amarasekare & Savage, 2012). However, the TaNC does not only highlight the importance of ecosystem-level response to temperature, but also suggests that ecosystems have the ability to drive the climate toward the conditions where species are more likely to survive. The mechanism that ecosystems could use to do this is at the heart of our exploration and is a fundamental question in this research. One option is that total extinctions could selectively kill off ecosystems in warm climates through the process of selection by survival, and while this does occur in the TaNC, it does not seem to be the only mechanism operating. Sequential selection is also at play because ecological steady states last longer in cooler temperatures. In warm temperatures, by contrast, mutation rates, and possibly birth rates and climate impacts are all higher, leading to more rapid climate change in addition to more rapid ecosystem evolution, shorter steady states, and a higher probability of total extinction when a mass extinction occurs. It is important to recognize, therefore, that mass extinction events may terminate ecological steady states that do not have persistence-enhancing characteristics, but as long as they do not cause a total extinction, they give rise to another chance for ecosystems to promote better conditions for ecosystem survival, as proposed in the paradigm of sequential selection (Betts & Lenton, 2008; Lenton, Daines, Dyke, et al., 2018). Mass extinction events can act as “resets” that give ecosystems sequential chances to produce favorable conditions for life. This results in ecosystems that cool the climate in every configuration of the TaNC: regardless of the assumptions about the distributions of species’ thermal optima and carbon impacts (Chapter 4) and whether or not new species inherit their thermal responses and carbon impacts from ancestral species (Chapter 5), suggesting that this is a widespread result in the TaNC.

Our finding that ecosystems evolve to cool the climate contrasts the results of another TaNa modification in which species are enabled to both respond to and affect a model climate (Arthur & Nicholson, 2023). As explained in the Conclusions of Chapter 3, Arthur and Nicholson (2023) make TaNa model species’ fitness temperature-dependent by scaling interaction strength with a symmetrical, unimodal thermal response curve with a peak at a universal optimum temperature. They additionally assign species random impacts on the model. In this configuration, surviving ecosystems evolve toward the universal optimum temperature, which does not occur in our configurations of the TaNC, even when TaNC species’ thermal optima are drawn from a normal distribution. Therefore, the shared thermal optimum in the Arthur and Nicholson (2023) version of the TaNa model is probably necessary, but not sufficient, for ecosystems to evolve to stabilize the climate. The other key ingredient must be the temperature-dependent interaction strengths, which make ecosystem abundance peak at the optimum temperature in their model, and decline at temperatures above and below (as we also show in Appendix Fig. A.2). Generally, we believe that the assumptions we make about species’ thermal responses in the TaNC are more realistic than those used in Arthur and Nicholson (2023), as our assumptions are founded in the Metabolic Theory of Ecology, which has ample evidence supporting both the thermodynamic mechanisms (Gillooly et al., 2001; Arroyo et al., 2022; Amarasekare & Savage, 2012) and the ecological outcomes (Brown et al., 2004). However, the sensitivity of ecosystem-climate co-evolutionary trajectories to assumptions about which physiological rates respond to temperature and how is an essential take-away from the comparison of these two studies.

Turning to the fossil record to analyse our results, species extinction rates are found to increase at temperatures above 293K (20°C) (Costello et al., 2023). Additionally, Earth’s biosphere has survived multiple global glaciations (e.g. Hoffman & Schrag, 2002; Casado, 2021). This evidence that life can survive cool climates, possibly better than warm climates, is compatible with our finding that ecosystem survival probability is high at colder temperatures.

Additionally, some of the most important biotic impacts on the climate today and throughout Earth history are cooling: biotic enhancement of weathering (Schwartzman & Volk, 1991; Lenton & Watson, 2004), dimethyl sulfide production (Charlson et al., 1987; S. Wang et al., 2018), carbonate precipitation (Dupraz et al., 2009), and carbon burial (Falkowski, 2012; Isson et al., 2020). Many species' carbon-releasing activities are also constrained by earlier organisms having removed that carbon from the atmosphere, creating biomass or carbonate reservoirs (Archer, 2010, Ch. 1, 4): biotic warming can therefore outpace cooling only after a long time of biotic carbon burial has accumulated. Even though these biotic impacts are largely cooling, it would be a stretch to suggest that Earth's biogeochemical cycles evolved as a mechanism of selection for cooler environments. However, it is interesting that our model suggests that ecosystems should both be motivated to, and possibly capable of driving the climate cooler. As mentioned above, the mechanisms that could drive ecosystems to cool their climates are also not far-fetched, but grounded in the thermodynamics of chemical reaction rates and protein denaturation (Gillooly et al., 2001; Brown et al., 2004). This work therefore suggests, at the very least, that these basic facts of life could have non-trivial impacts on the evolution of ecological interactions with the climate.

Importantly, while the TaNC almost always produces very cold climates, the climate record of Earth has not remained glaciated or at minimum non-glacial temperatures throughout the time that life has existed. However, there are many abiotic pressures which were not included in the TaNC that prevent Earth from remaining glaciated. For example, volcanic outgassing causes CO_2 to build up in the atmosphere during glaciations, causing warming (Hoffman & Schrag, 2002). Additionally, solar luminosity has steadily increased over the course of Earth history, leading to an increasing warming forcing (Sagan & Mullen, 1972). The TaNC isolates biotic pressures on the climate and how they evolve, and suggests that ecosystems experience selective pressures to cool the climate, but in the real world, the climate responds to a complex combination of both biotic and geological pressures (Falkowski, 2012).

Abiotic climate forcings are an intriguing next direction to investigate in the TaNC, not only because they could help explain some of Earth's warmer climates, but also because they could change the selective pressures experienced by ecosystems in the TaNC. In all the versions of the TaNC considered in this dissertation, the most stable climates could be produced by ecosystems with minimal impacts on the climate since there were no abiotic climate forcings. However, variable climates might increase selection for ecosystems that dampen climate perturbations, which would therefore require stronger biotic impacts on the climate. In future work, it would be very interesting to see if ecosystems would evolve to resist abiotic climate forcings if there were any.

Selection for small carbon fluxes

In all versions of the TaNC in which ecosystems produce noticeable impacts on the climate, there is species and ecosystem evolution toward smaller climate impacts than the initial distribution. This arises through multiple mechanisms. The most effective mechanism of selection for small climate impacts in the TaNC seems to be selection for species with relatively large thermal mismatches, as they have smaller metabolic rates and thus drive smaller carbon fluxes. We also observe selection for species with small intrinsic carbon impacts (the parameter b_i) in all cases, but this does not affect ecosystem carbon fluxes as strongly as thermal mismatch. Additionally, species sometimes cancel out their carbon fluxes with other species with opposite impacts, especially when the standard deviation of biotic impacts is large, or when species' intrinsic carbon impacts are inherited.

Importantly, we find that ecological stability is not always paired with climate stability. Additionally, Chapter 5 shows that inheritance enhances selection for climate cooling more than for small ecosystem impacts on the climate. This could suggest that cooling is a stronger driver of ecosystems selection than is climate stability. Even in the Daisyworld model, which was originally designed to exemplify ecosystems that stabilize the climate, when species can freely adapt to the climate, they will do so instead of regulating it (Roberston & Robinson, 1998).

Selection for beneficial environmental impacts?

One of the major gaps in the literature motivating this research is the contrast between the Gaia hypothesis, which proposes that species' impacts on the environment have a beneficial impact on life in general (Lovelock, 1972; Lovelock & Margulis, 1974; Doolittle, 2017; Lenton, Daines, Dyke, et al., 2018; Doolittle, 2019), and the more agnostic study of niche construction that observes species' environmental modifications but does not claim that they should necessarily benefit ecosystems (Matthews et al., 2014; Hendry, 2016). Both fields are related to the interactions between organisms and the environment, but the bridge between examples of ecosystem engineers and the general properties of how species' impacts on the environment evolve remains underdeveloped.

The Daisworld model was a crucial formulation of how species' impacts on the environment could lead to environmental stabilization (Watson & Lovelock, 1983), but whether something similar exists or can evolve on Earth remains uncertain. The key feature of the Daisyworld model is that species with opposite impacts on the environment each suffer from their own environmental impacts but benefit from the impacts of the other. In this way, no single species can out-compete the other, and the populations of each species remain in a balance that keeps the environmental temperature between the optima of the different species. This process, called rein control, does not generally arise in the TaNC, even when species are pre-disposed to have opposite impacts on the climate (Chapter 4). Therefore, in this dissertation I have not identified a mechanism by which rein control can arise through natural selection in the TaNC.

However, surviving ecosystems in the TaNC almost always cool the climate. Since this reduces the death rates of all species, we consider this to be a form of ecosystem-level adaptation or acquisition of persistence-enhancing traits at the level of the ecosystem. This suggests that, although ecosystem-level selection for environmental impacts may not necessarily take the form of rein control suggested by Watson and Lovelock (1983), it may still affect ecosystem evolution and progressively increase ecosystem persistence over time. However, ecosystem-level selection is a slow process that involves both total and mass extinction events.

6.3 Future directions

The model and model findings I present in this dissertation illustrate a range of possible outcomes of ecosystem-environment co-evolution. At the end of each chapter, I outline some enticing next steps to continue testing the assumptions of the model and building in more realistic components. The experiments analyzed in Chapter 5 are also continuing to run, and will provide insight into ecosystem-level evolution on longer timescales.

Here, I briefly summarize some of the advantages of the TaNC as a tool for future investigations, and some of the main directions that I think future work should pursue.

6.3.1 The TaNC as a tool for future work

The most essential aspect of the TaNC model is its coupling of an evolving ecosystem with an evolving environment. Earth scientists are interested in understanding how evolutionary responses of the biosphere will affect the climate (Moorcroft, 2006), and ecologists recognize the importance of feedbacks with other species and the environment in directing species evolution (Odling-Smee et al., 1996; K. Laland et al., 2014; Dawkins, 1982; Pausas & Bond, 2022), but very few models have attempted to tackle this problem. The most famous model to attempt this is the Daisyworld model (Watson & Lovelock, 1983). The Daisyworld model is built around the assumption that species can regulate (maintain stable, habitable conditions in) the environment, but it has been problematic to show that Daisyworld-like conditions evolve on Earth. Many variations of the Daisyworld model have investigated different spatial distributions and assumptions about evolution and tested whether regulation is a robust model result (reviewed by Wood et al., 2008). However, the applicability of the Daisyworld model to Earth remains very unclear, and so aside from a few exceptions (e.g. Bagdassarian et al., 2007), the Daisyworld paradigm has largely not participated in ecological theory.

The TaNa model provides a much more general model of ecosystem evolution, being constructed from a model of ecology and evolution based on the generalized Lotka-Volterra model and the logistic model of population growth rates (Christensen et al., 2002; Arthur & Nicholson, 2017). It also reproduces Punctuated Equilibria, which are widely observed in the fossil record (Eldredge & Gould, 1972; Gould & Eldredge, 1977). This makes it a good point of departure for studying how ecosystems evolve. The TaNa model has been modified to investigate species' impacts on the specific environments of other species, showing that species in ecosystems evolve beneficial impacts on other species' environments (Arthur & Nicholson, 2017). The TaNa model was also modified to investigate ecosystem-level impacts on temperature with basic assumptions about species' thermal responses (Arthur & Nicholson, 2023). The assumptions we subsequently build into the TaNa+T model about species' responses to temperature are based on the metabolic theory of ecology (Brown et al., 2004; Gillooly et al., 2005; Amarasekare & Savage, 2012), and therefore broaden the applicability of model results to real ecosystems. In the TaNC, we have also tested the sensitivity of the model to assumptions about how species' thermal optima and carbon impacts are distributed (Chapter 4). For all these reasons, the TaNC is a flexible model based on well-developed ecological theory that can be used to probe further into ecosystem-climate and ecosystem-environment interactions and co-evolution and compared to a variety of other work.

Like every model, the TaNC captures some essential features of reality and allows us to investigate how they interact. Therefore, in the next section I highlight some of the modeling choices I have made in the TaNC, and how future research could expand upon this work in order to further the applicability of these results, deepen an understanding the complexity of nature, and continue disentangling the interactions between ecosystems and the environment.

6.3.2 Modeling the environment

In this dissertation, I investigate ecological impacts on environmental temperature as an example of an aspect of the environment which species can affect and respond to. Importantly, the background climate in the TaNC is constant — meaning that the model temperature does not change without biotic impacts. However, in the real world there are many abiotic processes that both perturb and also stabilize the climate. In Chapter 3 I find that ecosystems experience stronger selection to minimize their carbon fluxes when species have stronger impacts on the climate, and so an interesting direction of future research would be to investigate how species impacts on the climate evolve when the background climate is intrinsically variable. Would species be more likely to evolve impacts that dampen perturbations in that case?

Ecosystems could also have different co-evolutionary trajectories when they interact with other aspects of the environment than temperature. For example, if species interacted with pH, there might be some environmental buffering which could allow species to have larger impacts without consequence. When organisms in the real world evolved to calcify crusts, for example, it provided unprecedented stability of ocean pH and facilitated diversification (Eichenseer et al., 2019). Ecosystems could also interact with nutrient or water availability, which could feed back on the carrying capacity of ecosystems. The parameter exploration in Chapter 2 suggests that this could change the ways that ecosystems respond to the environment, and therefore the feedbacks that arise.

6.3.3 Modeling ecosystems

In the TaNa+T and TaNC, abundance does not respond to the environment, which could be an important control on ecosystem-environment feedbacks. This contrasts two models of ecosystem-climate interactions in which ecosystems do regulate the climate: the Daisyworld model (Watson & Lovelock, 1983) and the version of the Tangled Nature model modified by Arthur and Nicholson (2023) to include species thermal responses and climate impacts. Our parameter exploration of the Tangled Nature + Temperature model (Appendix A.2) shows that ecosystem abundance depends on ecosystem carrying capacity (the parameter μ in the Tangled Nature model) and on the strength of ecological interactions (C). For species in the real world to affect these parameters, species' ability to extract or use up resources, or their ecological interaction strengths, would need to be temperature-dependent. Indeed, some research suggests that both carrying capacity (Vasseur, 2020) and interaction strengths (Dell et al., 2011) may be temperature-dependent, so incorporating this into the TaNC would be a very interesting next step.

In addition to temperature, another important control of species' metabolic rates — and thus both their responses and impacts on the environment — is their mass (Gillooly et al., 2001; Brown et al., 2004). The impact of species' mass on metabolic rate is a fundamental part of metabolic theory of ecology, and has also been considered in evolving ecosystem models by Loeuille and Loreau (2005). Body size is also correlated with trophic level in that model, and trophic level is another important factor in determining ecosystem-level responses to temperature (Bideault et al., 2021). Stegen et al. (2009) later modified the Loeuille and Loreau (2005) model to include temperature dependence and to investigate temperature dependence of species richness. In contrast to our work, that work suggests that the temperature dependence of species richness is transitory. Therefore, a more thorough investigation of the complimentary roles of temperature, mass, and trophic levels in controlling ecosystem characteristics would be very interesting.

Another important aspect of the TaNa model that warrants further investigation is its predisposition to produce ecosystems characterized by core species with mutualistic interactions (Christensen et al., 2002; Laird & Jensen, 2006). Some modeling work studying the gut microbiome — diverse, resistant, and sometimes resilient ecosystems — suggests that competitive interactions between species may be essential for stability of diverse ecosystems (Coyte et al., 2015) — which is opposite to the TaNa model. An important difference between the TaNa model and the gut mircobiom models is that Coyte et al. (2015) assume an external resource supply, which enables species to survive without benefiting from other species in the ecosystem. Species in the TaNa model, on the other hand, must derive their resources from interactions with other species, so competitive-only interactions could never be sustainable. Therefore, it would be very interesting to probe into the ways that interactions between species affect the interactions between ecosystems and their environments.

Another aspect of species interactions that I did not consider in the TaNC is the association between interspecific interactions and environmental impacts. Species in the TaNC are randomly assigned intrinsic impacts on atmospheric carbon, but many species that absorb carbon in the real world are primary producers, and many species that emit carbon are consumers. Therefore, it could be interesting to investigate a scenario in which carbon-reducing species benefit the carbon-increasing species in the TaNC, and carbon-increasing species have negative effects on the carbon-reducing species. Similarly to this idea, Bagdassarian et al. (2007) link species' impacts with their trophic level, making two species of primary producers act like the daisies in the Daisyworld model. They find that when these primary producers stabilize the temperature, a larger richness of other species can be maintained in a foodweb. However, environmental impacts of consumers are not considered, and the environmental impacts of primary producers are not allowed to evolve.

6.3.4 Applying the TaNC to real ecosystems

Another direction of potential future study is to apply the TaNC to real ecosystems. McKay et al. (2020) and Coyte et al. (2015) estimate species interaction strengths from ecosystem data. B. Chen (2022) measure the parameters associated with different physiological and ecological thermal responses for phytoplankton. These methods could be used to estimate more realistic values of species interactions and species thermal responses to apply the TaNC to a specific ecosystem of study. For example, the TaNC could be applied to the gut microbiome, providing comparison to the work of Coyte et al. (2015). Investigating soil ecology would be another very interesting application of the TaNC, as soil bacteria are sensitive to temperature and have important impacts on soil carbon, nutrients, and other properties, and these impacts affect other species such as plants in addition to the climate (Davidson & Janssens, 2006; Domeignoz-Horta et al., 2020; Schimel, 2023).

6.4 Conclusion

In this dissertation, I show that species' responses to the environment can guide ecosystem-level impacts on the environment, generally pushing ecosystems toward conditions that minimize death rates. This demonstrates a process we call ecosystem-level niche construction. Our results suggest that minimizing death rates is the primary driver of selection for ecological impacts on the environment, and ecological inheritance is a key tool that ecosystems can use to ratchet environmental conditions over the course of many mass extinction events.

This work helps piece together how eco-evolutionary feedbacks manifest in environmental and ecological evolution. We bridge the gap between ecology and Earth system evolution in our investigation of how both the climate and ecological properties evolve when each affects the other. The TaNC also provides a tool that can be used in future research to both expand upon the assumptions about ecology and the environment and to use for comparison to other approaches to studying ecosystem-level niche construction. I hope this work inspires future studies to continue probing into the ways that species interacting with one another and with their abiotic environment co-evolve.

Appendix A

Appendix to Chapter 2

A.1 Example TaNa model output

The first 4000 generations of 4 TaNa model simulations are shown in Fig. A.1.

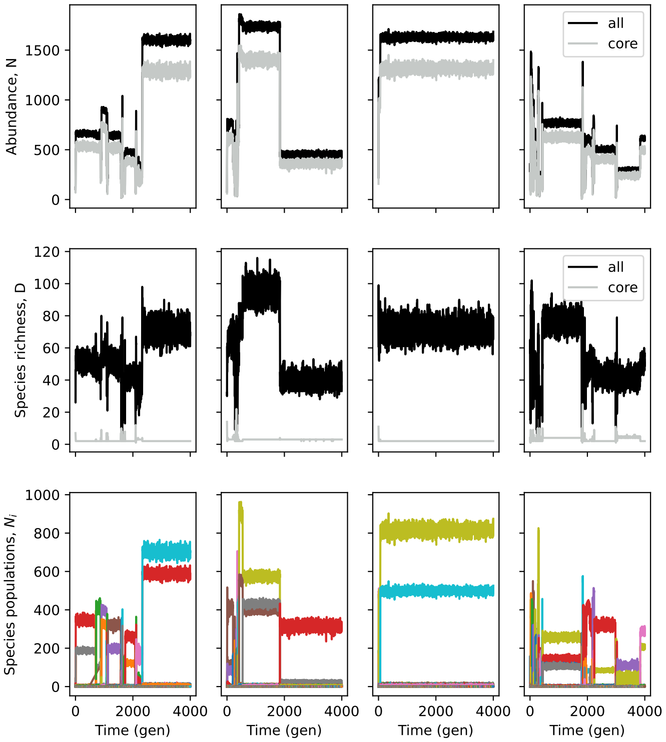

Figure A.1: Each column shows a single TaNa model simulation for its first 4000 generations. Rows illustrate ecosystem characteristics; from top to bottom: 1. abundance (number of individuals) in ecosystems (black) and cores (grey); 2. species richness (number of species); and 3. populations of each species (colors).

A.2 Parameters used in reproduction TRC

Reproduction rate in the TaNa+T is approximated with a left-skew normal curve such that the shape of the skew-normal curve matches the second term in Eq. 11 in Amarasekare and Savage (2012). That equation gives a general TRC derived from temperature-dependence of fecundity (the reproduction rate of an individual), development (the rate at which fecundity changes with an organism's age) and mortality (Amarasekare & Savage, 2012). The TRC of reproduction rate is defined as

$$b(T) = \frac{1}{\alpha(T)} W \left[b_{\alpha_{\text{peak}}}(T)\alpha(T) \exp\left[\left(d(T) - d_{\text{juv}}(T) \right) \alpha(T) \right] \right], \tag{A.1}$$

Parameters for reproduction and mortality rates		
A_a	Activation energy of development	-8000 eV
$A_{\mathrm{d,j}}$	Activation energy of death of juveniles	7500 eV
A_{d}	Activation energy of death of adults	6000 eV
$\alpha_{\mathrm{T_r}}$	Development rate at T_r	60
$b_{\mathrm{T_r}}$	Birth rate at T_r	50
$\bar{b}_{\mathrm{T_r}}$	Average birth rate at T_r	295
$d_{\mathrm{j,T_r}}$	Death rate of juveniles at T_r	0.03
$d_{\mathrm{T_r}}$	Death rate of adults at T_r	0.05
T_r	Reference temperature	294 K
T_{opt}	Optimum temperature for reproduction	298 K

Table A.1: Parameter values used for Eqs. A.1 & 2.6 (Fig. 2.1 birth rate: black solid line, death rate: grey solid line).

where T is temperature, $\alpha(T)$ is age at first reproduction, $W(\cdot)$ is the Lambert W function (arising in the solution to the temperature-dependence of the Euler-Lotka equation for fecundity), $b_{\alpha_{\mathrm{peak}}}(T)$ is maximum fecundity (expected number of offspring at the age of first reproduction, assuming fecundity decreases thereafter), and $d(T)$ and $d_{\mathrm{juv}}(T)$ are death rates of adults and juveniles, respectively ($b(T)$ and $d(T)$ shown as solid black and grey lines, respectively, in Fig. 2.1). Development and mortality are modelled as Boltzmann-Arhhenius exponential equations, and fecundity is given a Gaussian shape (Amarasekare & Savage, 2012). Parameter values used in the TaNa+T are listed in A.2. The shape of Eq. A.1 is the typical TRC: a unimodal, left-skew curve. The parameters we used in Eq. A.1 are listed in Table A.1 (Fig. 2.1, black solid line).

A.3 1-D exploration of all 7 TaNa parameters

A.3.1 Testing ecological sensitivity to TaNa model parameters

We vary each of the 7 TaNa model parameters along one dimension (holding all other parameters constant) in fifty simulations at each parameterization. Ecosystem survival probability, abundance, species richness, and core species richness are measured after 10,000 generations (Fig. A.2).

Ecosystem survival probability is sensitive to 4 of the 7 parameters: temperature-dependent scaler of reproduction probability ($p_{\mathrm{off,T}}$), death probability (p_{death}), mutation probability (p_{mut}), and damping factor of carrying capactity (μ) (Fig. A.2, top row). Ecosystem survival decreases from 1 to 0 as $p_{\mathrm{off,T}}$ decreases or p_{death} increases. For values of p_{mut}

greater than the control value (0.01 mutations per gene per timestep), survival remains near 1, but decreases toward 0.8 for p_{mut} values below that. Survival also decreases for values of μ greater than the control (0.1), which are associated with relatively small carrying capacities (less than about 700 individuals, Fig. A.2) and species richness less than about 60. The other parameters do not affect survival probability for the range of parameter values sampled.

Abundance is sensitive to μ and interaction strength scaler (C) (Fig. A.2, second row). μ scales the carrying capacity of the model, so its effect on abundance is expected. C affects the fitness equaiton, Eq. 2.3, by scaling the positive term, so increasing C has the same effect as decreasing μ, and it is therefore not surprising that these two parameters have similar effects on the model. No other parameter affects abundance in the TaNa model.

Species richness is affected by p_{mut}, μ, and genome length (L) (Fig. A.2, third row). Increasing mutation rate enables more species to enter the model per unit time, contributing to a larger equilibrium species richness. Increasing L has a similar effect as increasing p_{mut}, because each individual gets L chances for a mutation to occur during reproduction. Increasing μ does not affect speciation rate but enables more individuals to coexist in the model, and thereby allows more different species to coexist.

Core species richness responds only to p_{mut} (Fig. A.2, bottom row). This is interesting because even though μ increases abundance and species richness, it does not affect the number of stable core species — only the number of cloud species.

A.3.2 Temperature dependence of TaNa model parameters

The three physiological parameters in the TaNa model (birth, death, and mutation probabilities) reflect intrinsic, organism-level rates which are all predicted to increase exponentially with temperature according to the Arrhenius curve due to their dependence on metabolic rate (Gillooly et al., 2001; Brown et al., 2004; Gillooly et al., 2005). We vary these three rates with temperature in the model, and keep the other parameters constant in order to test how physiological properties propagate upward through ecological networks. However, some discussion of the temperature dependencies of the other parameters is warranted.

Interaction strength is not explicitly encompassed by MTE, but some empirical measures of activities associated with interaction strength or trophic interactions, such as attack or escape velocity, increase with temperature according to the Boltzmann-Arrhenius

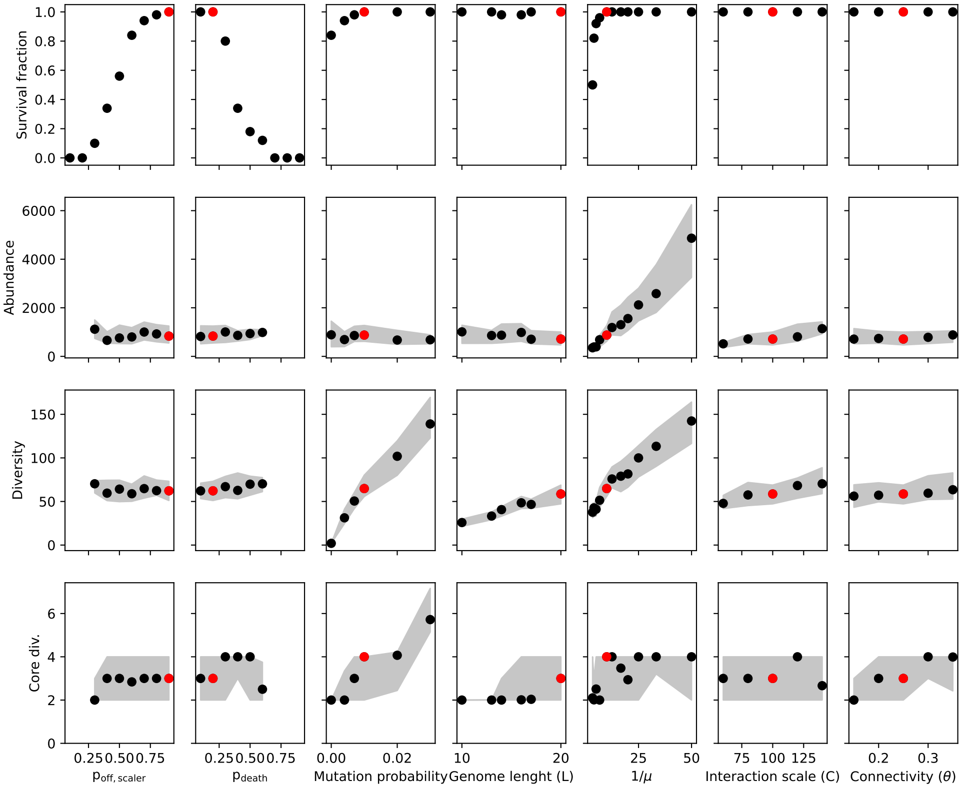

Figure A.2: Seven TaNa model parameters are varied independently while holding all values constant. The first column shows how reproduction probability was scaled ($p_{\text{off},\text{T}}$), which is a parameter we introduce to scale ecological reproduciton probability ($p_{\text{off},\text{f}}$, Eq. 2.2). The other six columns show variation of the six intrinisc TaNa model parameters: death probability (p_{death}), mutation probability (p_{mut}), genome length (L), carrying capacity scaler ($\frac{1}{\mu}$), interaction scale (C), and connectance (θ). Each dot corresponds to 50 experiments: in the top row, the fraction of those 50 experiments that survived for 10,000 generations is shown, and for the other rows, the dot sows the median and the shaded grey region shows the interquartile range. The red dots in all plots indicate the control value of the parameter.

equation (Dell et al., 2011). Network connectance (θ) was also found to increases in warmer temperatures in some studies (Yuan et al., 2021). However, for both interaction scale and network connectance, the connection between individual physiology and traits affecting these network-level characteristics is not obvious. We choose to test whether either response may emerge secondarily from other physiological TRC, rather than being direct physiological responses to temperature themselves.

Carrying capacity (scaled by μ) could vary with temperature for a number of reasons. For example, productivity could be higher in warmer or more optimal temperatures, or the temperature-dependence of nutrient recycling by microbes could affect nutrient availability (either positively or negatively). On weathering timescales, primary nutrients come from weathering bedrock, and weathering rates generally increase in warmer climates (R. A. Berner, 1990). Future research should continue to investigate the responses of resourece availability to temperature, but currently, it is standard in MTE not to assume that resources vary with temperature, and empirical patterns seen in trees support this prediction (Allen et al., 2002; Brown et al., 2004).

The last parameter in the TaNa model is genome length (L), and we do not know of any evidence that L is affected by temperature. However, Stegen et al. (2009) assume that genome length increases with mass (which they admit is a rough approximation) in their eco-evolutionary model of MTE. As both their model and ours utilize per-gene mutation rates, increasing L has the effect of increasing the mutation rates of larger organisms in their model. Here, we do not treat mass, and to keep the complexity to a minimum in our model, we hold genome length constant for organisms in our model. However, varying genome length between model species could be an interesting area of further investigation.

Appendix B

Appendix to Chapter 3

B.1 Temperature change in steady states

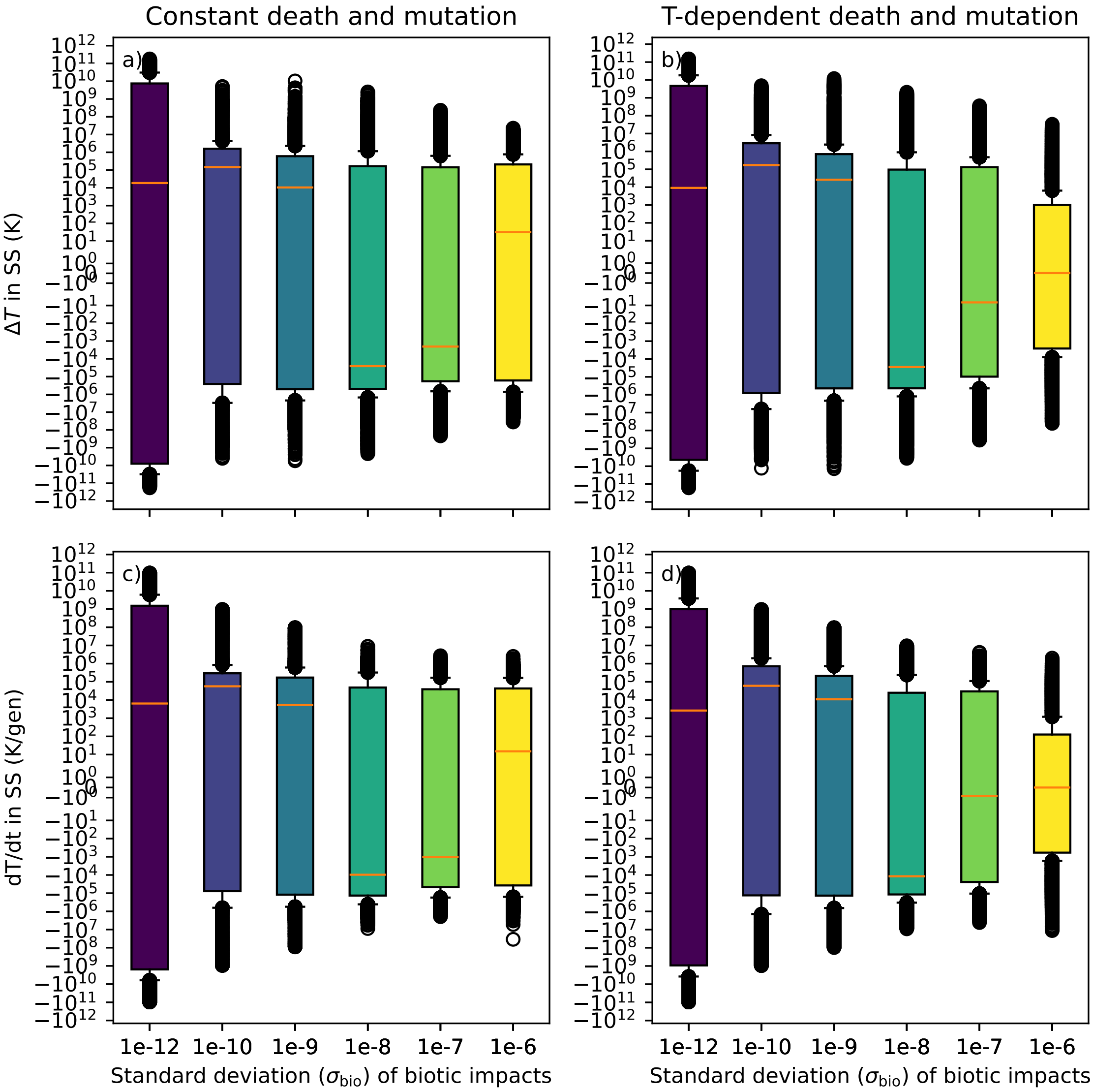

Figure B.1: Boxplots of total (a,b) and rate of change (c,d) of temperature divided by the standard deviation (σ_{bio}) of biotic impacts during ecological steady states, relative to σ_{bio}. Note that if ΔT or dT/dt were proportional to σ_{bio}, then the boxplots of $\Delta T/\sigma_{\text{bio}}$ and $dT/\sigma_{\text{bio}}dt$ would have similar magnitudes on a linear vertical axis, but here a logarithmic vertical axis is necessary for the results to be visible. Orange lines in boxes show the median values, the box edges show the first and third quartiles, and whiskers extend to the farthest point within 1.5 times the interquartile range.

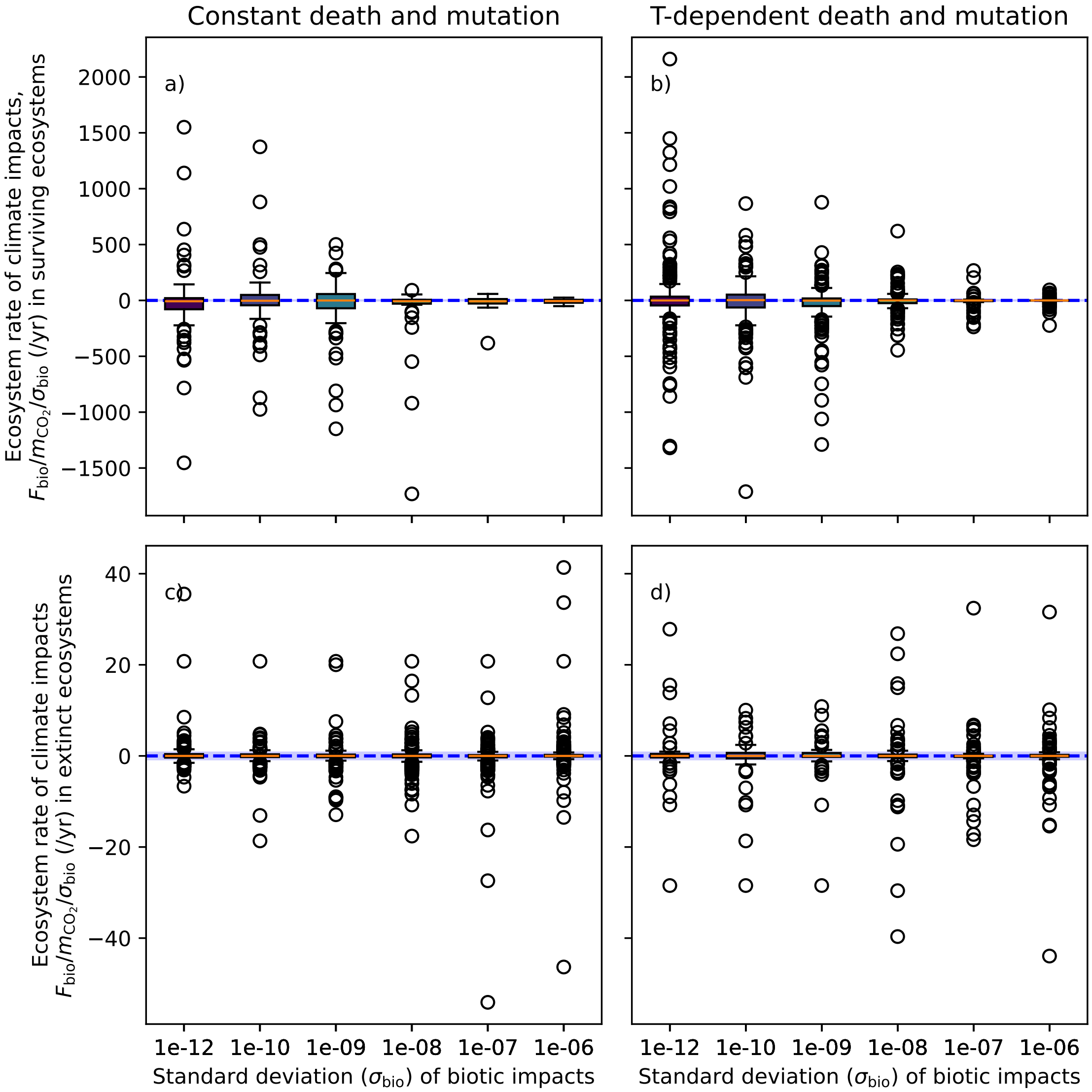

Figure B.2: Boxplots of rates at which ecosystems affect the climate ($F_{\text{bio}}/m_{\text{CO}_2}$) at different standard deviations (σ_{bio}) of biotic impacts for a,c) constant and b,d) temperature-dependent death and mutation, in a,b) surviving and c,d) extint ecosystems. Orange lines in boxes show the median values, box edges show the quartiles, whiskers extend to 1.5 times the interquartile range, and points outside the whiskers are circled. The same plot with outliers omitted is shown in Fig. 3.17.

Appendix C

Appendix to Chapter 4

C.1 Species' and ecosystems' intrinsic and realized rates of carbon impacts depending on distributions of thermal optima and carbon impacts

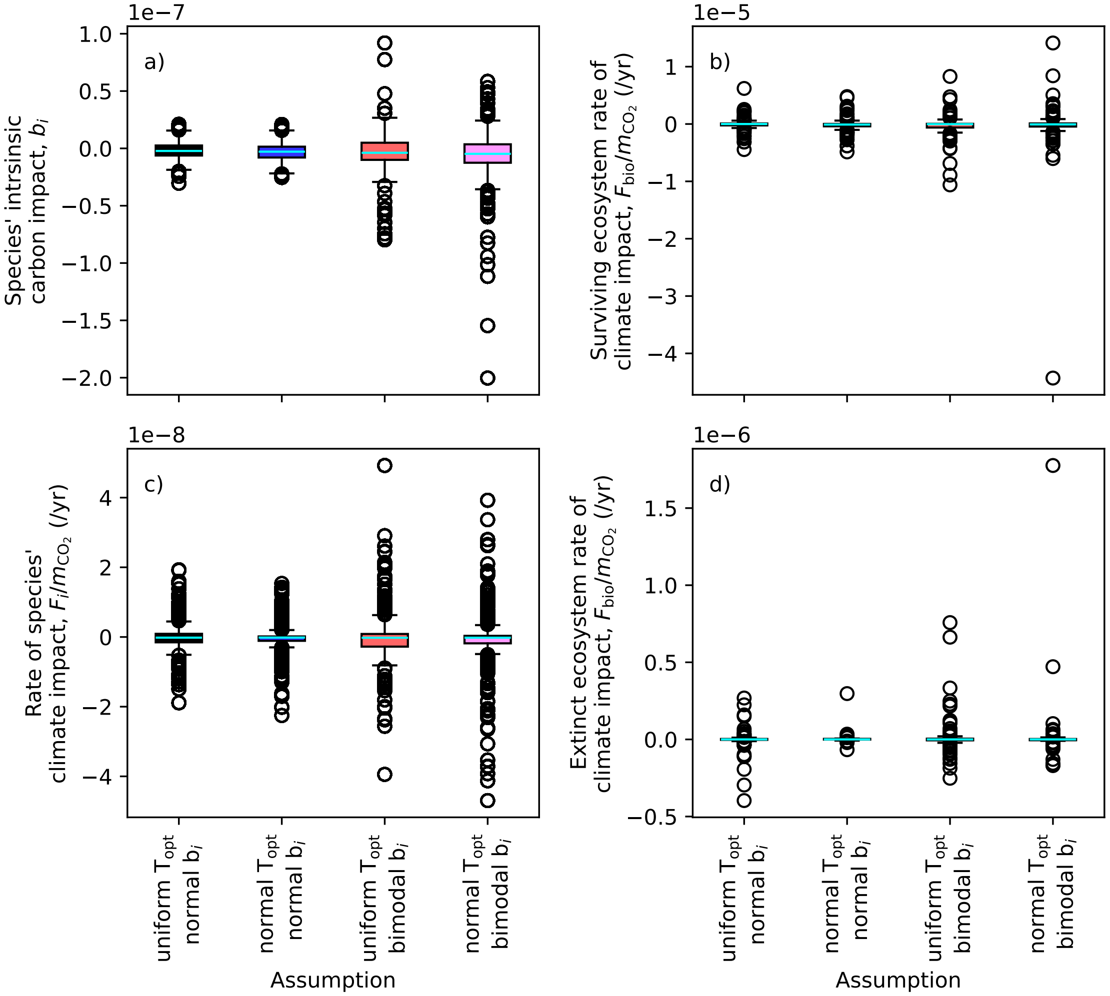

Figure C.1: Boxplots of a) species' intrinsic carbon impacts (b_i), c) the rates at which species actually impact the climate ($F_i/m_{\mathrm{CO_2}}$), and b,d) ecosystem carbon fluxes (F_{bio}) for b) surviving and d) extinct ecosystems, all at 10,000 generations or the time of extinction. The median is shown in cyan, the boxes extend to the first and third quartiles, the whiskers extend to the farthest point within 1.5 times the interquartile range from the median, and points beyond the outliers are shown as empty circles. (Fig. 4.6 and 4.7 show the same information with outliers omitted.)

Appendix D

Appendix to Chapter 5

D.1 Progress of inheritance experiments toward 100,000 generations

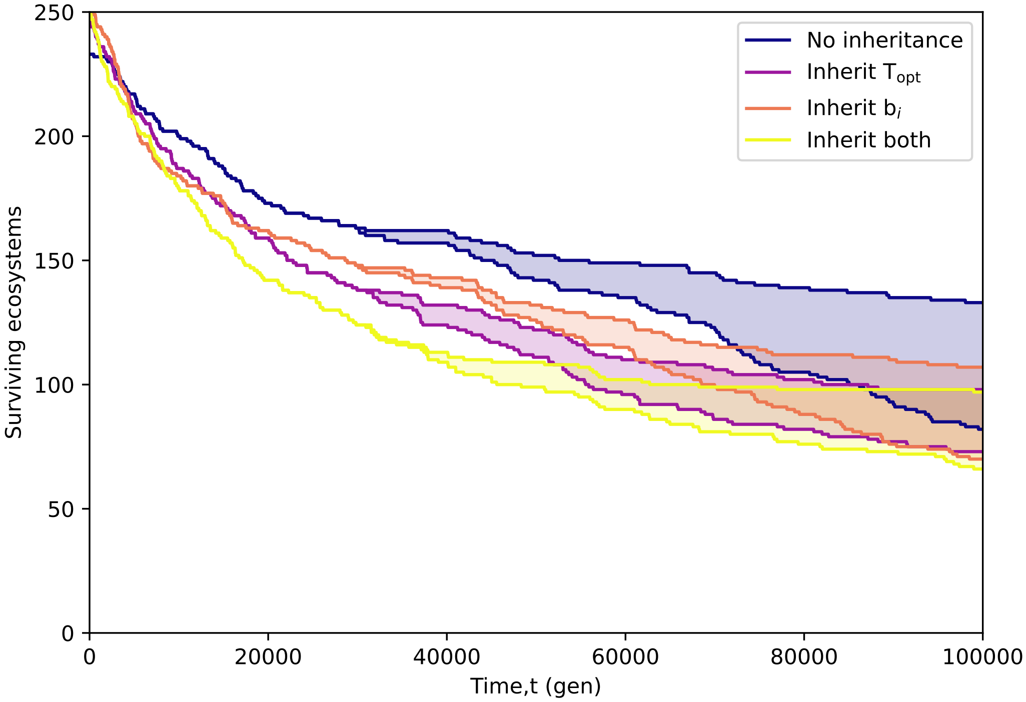

Figure D.1: For each of the inheritance experiments, the number of surviving ecosystems is shown assuming all unfinished experiments survive (upper line) and assuming all unfinished experiments go extinct at the generation at which the simulation has stopped running (lower line). The shaded region shows the range of possible ecosystems that could survive, and will shrink to zero once all simulations have finished running. Progress as of April 9, 2025.

D.2 Carbon fluxes in the inheritance experiments

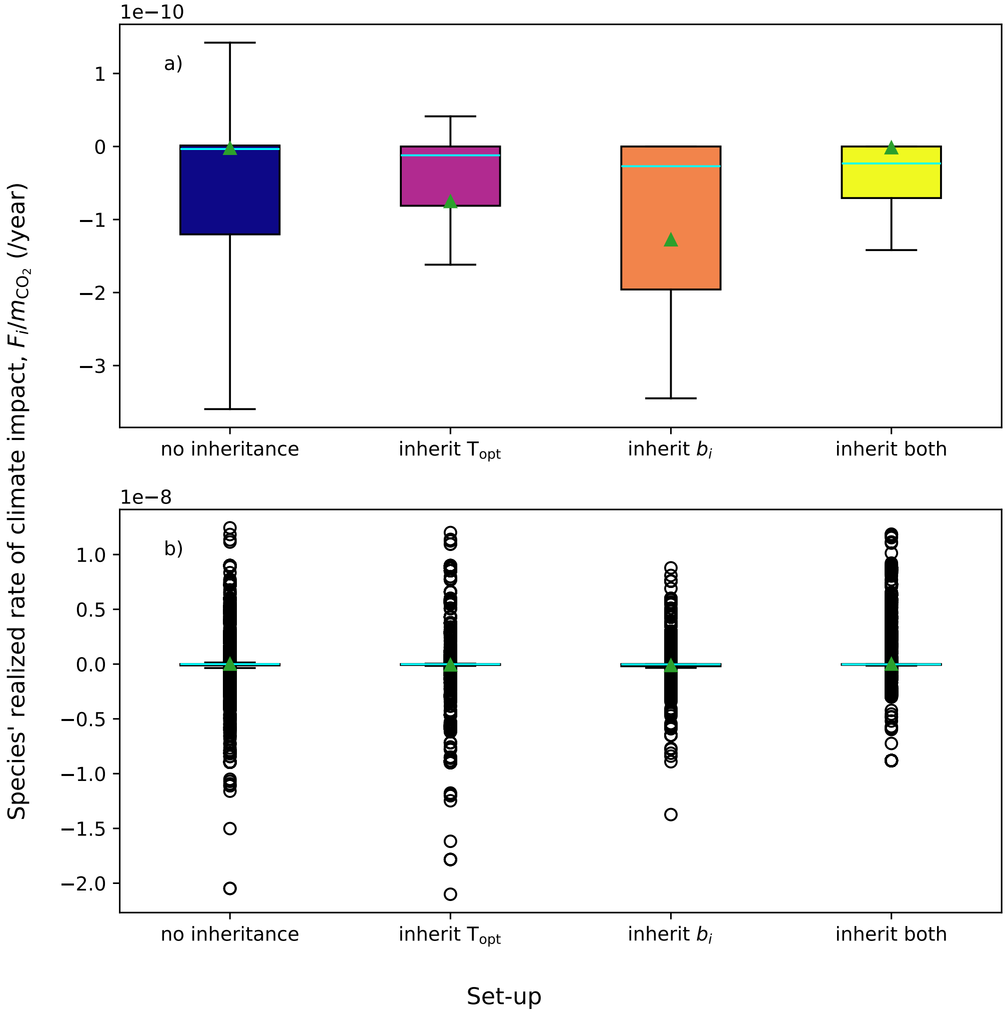

Figure D.2: Species carbon fluxes (F_i), divided by the mass of carbon in the atmosphere (m_{CO_2}) to show the strength of species' climate impacts. Outliers are omitted in a) to show the bulk of the values, and shown in b) to exhibit the full range of values. Compare to Fig. 5.8c,d.

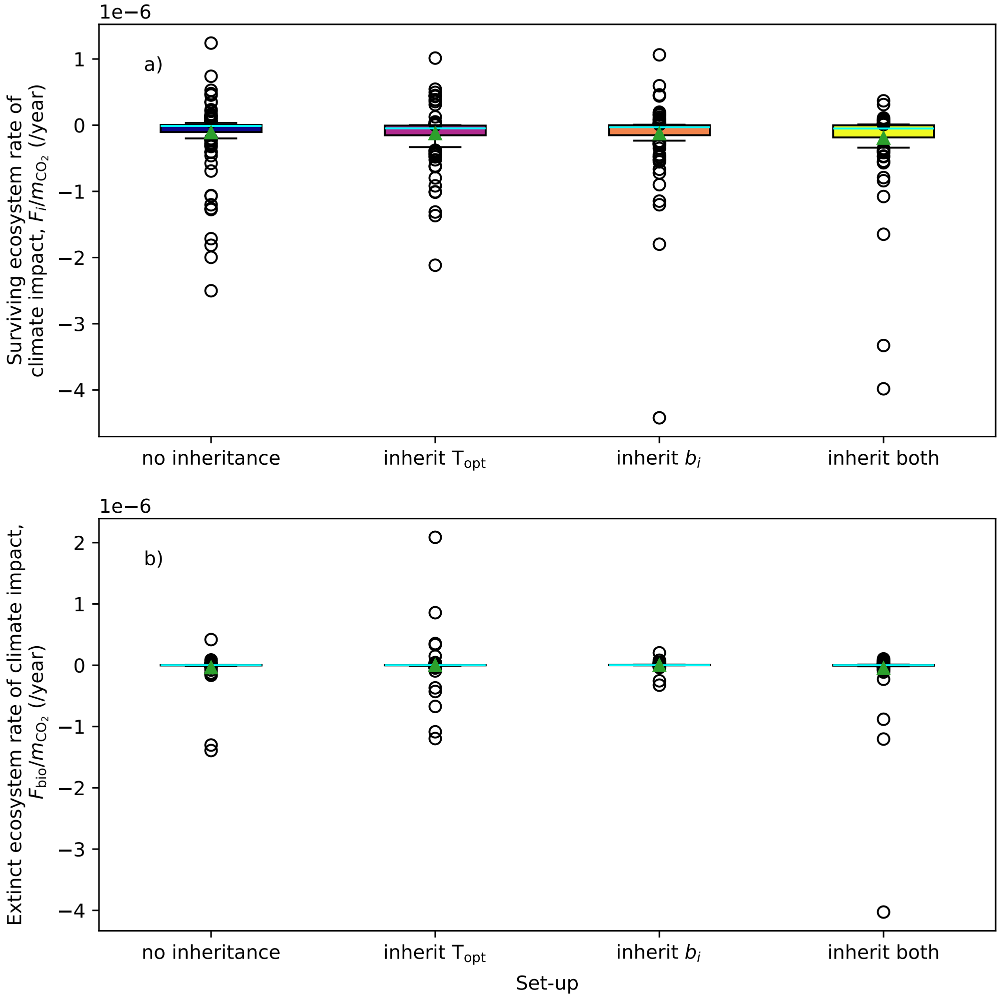

Figure D.3: a) Surviving and b) extinct ecosystem carbon fluxes (F_{bio}), divided by the mass of carbon in the atmosphere (m_{CO_2}) to show the strength of ecosystems' climate impacts. Outliers are shown here, as compared to Fig. 5.10, which zooms in on the bulk of the values.

D.3 Canceling of species' carbon fluxes in ecosystems with and without inheritance

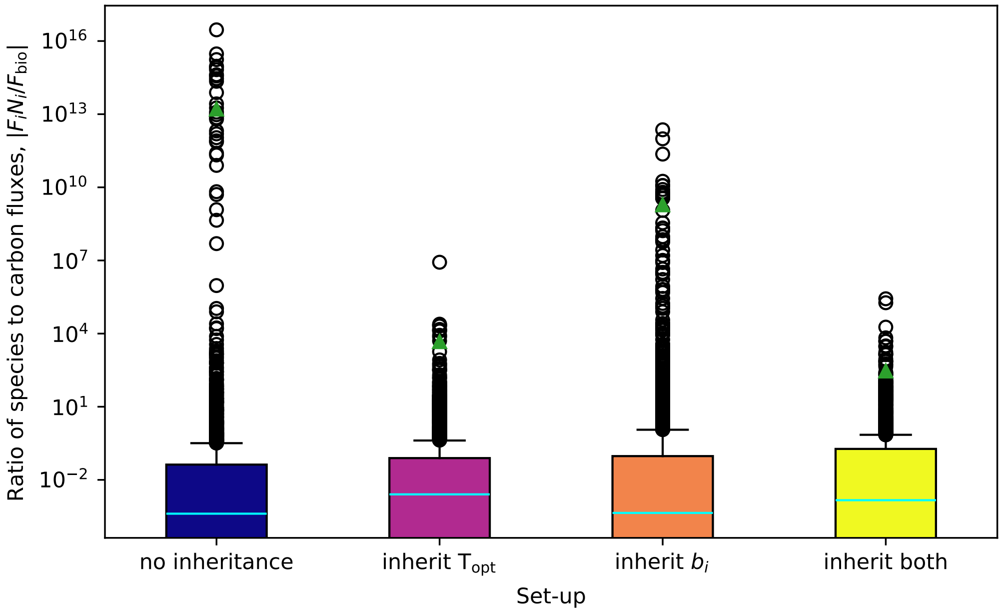

Figure D.4: Ratio of species' to ecosystem carbon fluxes ($|F_i N_i / F_{\text{bio}}|$). The blue band in each boxplot indicates the median ecosystem carbon flux, the edges of the boxes indicate the upper and lower quartiles, and the whiskers extend to the 15th and 85th percentiles. Points beyond the whiskers are shown as empty circles. To see just the boxes, see Fig. 4.8.

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