

Modelling Ecosystem Adaptation and Dangerous Rates of Global Warming

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Abstract

We are in a period of relatively rapid climate change. This poses challenges for individual species and threatens the ecosystem services that humanity relies upon. Temperature is a key stressor. In a warming climate, individual organisms may be able to shift their thermal optima through phenotypic plasticity. However, such plasticity is unlikely to be sufficient over the coming centuries. Resilience to warming will also depend on how fast the distribution of traits that define a species can adapt through other methods, in particular through redistribution of the abundance of variants within the population and through genetic evolution. In this paper, we use a simple theoretical ‘trait diffusion’ model to explore how the resilience of a given species to climate change depends on the initial trait diversity (biodiversity), the trait diffusion rate (mutation rate), and the lifetime of the organism. We estimate theoretical dangerous rates of continuous global warming that would exceed the ability of a species to adapt through trait diffusion, and therefore lead to a collapse in the overall productivity of the species. As the rate of adaptation through intraspecies competition and genetic evolution decreases with species lifetime, we find critical rates of change that also depend fundamentally on lifetime. Dangerous rates of warming vary from 1°C per lifetime (at low trait diffusion rate) to 8°C per lifetime (at high trait diffusion rate). We conclude that rapid climate change is liable to favour short-lived organisms (e.g. microbes) rather than longer-lived organisms (e.g. trees).

1 Introduction

The geographical distribution and functioning of ecosystems is heavily dependent on aspects of the climate such as temperature, rainfall, soil moisture availability, and seasonality of the climate. This paper is specifically about the adaptation of ecosystems to warming, but the processes that we discuss and model are also more

generally relevant to other dimensions of climate and environmental change. Below we discuss the sensitivity of ecosystems to warming in the context of anthropogenic climate change.

1.1 Current Rates of Climate Change

Predictions for the rate of warming for the land surface and ocean range between 0.1-0.4°C per decade for the remainder of the 21st century [1]. Changes in ecosystem composition in previous periods of high rates of change can be used as reference to infer potential future changes. Examples include the Paleo-Eocene thermal maximum, where temperatures in the tropics were 5-10°C warmer than current, and the transition from the Pleistocene to the Holocene [2]. However, there is no exact climate analogue in the past, and both species and ecosystem compositions differed. Temperature data and the fossil record have limited spatial resolution [3]. Knowledge from the current period of warming can be used to inform predictions of future ecosystem response. The average global mean surface temperature between 2006-2015 was $\sim 0.9^\circ\text{C}$ higher than the period 1850-1900 [4], with measurable impacts on ecosystems. Combining this knowledge from the past with mechanistic understanding of underlying processes will lead to the most robust predictions of the future.

Climate variability on the spatial and temporal scales which ecosystems operate at must be taken into account. Over the course of recent climate change, topographic variation has offered refugia for plants and insects [5], and upwelling, strong currents and turbidity in the ocean has offered refugia for coral reefs [6]. Historically, plants have retreated to refugia during periods of maladaptation, and have then re-expanded when the climate became more optimal [2]. Rates also vary temporally, due to short and long term variability, such as the El Niño Southern Oscillation. Variability is expected to change in a warming world [7]. Short term extreme events also impact ecosystems, such as heat waves causing massive loss of ecosystem functioning in Australian seagrass meadows [8]. Increasing average temperatures mean that temperatures which would previously have been considered as extreme events are likely to be commonplace in the future [9], as can already be seen in the case of the increased frequency of bleaching of coral reefs [10]. Autocorrelation of temperature is expected to increase both spatially and temporally with the business as usual scenario [11], which means that extreme events will last longer and be more widespread spatially, and therefore have more of an impact on ecosystems [12].

1.2 Temperature and Organism Fitness

Temperature affects underlying biochemical rates of metabolism and therefore can influence fitness indirectly by changing how organisms acquire and allocate limiting resources. Extreme temperatures can also affect fitness directly by causing damage to cellular structures [13]. The combination of these effects yields the thermal tolerance curve [14]. Thermal tolerance curves measure the dependence of a fitness influencing trait on temperature, such as the growth rate. Rates increase up to the optimum temperature and then decline rapidly. The tolerance curve is the outcome of acclimation: plasticity in physiological traits. When acclimation can no longer adjust traits to a sufficient degree in the new environment, fitness declines. Over longer periods of time, genetic evolution can adjust the limits of plasticity. Thermal tolerances of species are usually measured in a laboratory environment, such as the sprint speed for ectotherms [15] or the growth rate for microbes [16]. The thermal tolerance is the underlying impact of temperature on the fitness of an organism. The geographic distribution of a species is then affected by many other biotic and abiotic factors.

1.3 Methods of Species Adaptation

Genetic evolution is usually thought to occur slowly over long timescales, but this is not necessarily the case. Rates of evolution depend on the population size, existing genetic diversity [17], turnover of the species and selection pressure. In high density populations with short generation times, there is the potential for large amounts of genetic variation to be generated quickly, upon which selection can act. This has been seen in both experiments [18] [19] [20] and natural populations [21]. Longer lived populations have also been shown to have potential for future adaptation through genetic evolution, by checking for existing heritable genetic variation [22] [23]. Rapid evolution under severe stress, or strong selection pressure, is known as ‘evolutionary rescue’ [24]. While higher rates of change reduce population size and therefore available genetic variation, this can be countered by increased selection pressure, resulting in the persistence of a few sufficiently adapted phenotypes. Quantitative genetics has been used to understand the potential for evolutionary rescue [25] [26], although these models can be challenging to parameterise. Modelling on an ecological scale can advance understanding of the relationship between rates of change, evolution and ecosystem functioning [27].

The same genotype can express itself as multiple different phenotypes. Known as phenotypic plasticity or acclimation when reversible, the phenotype is expressed based on environmental cues, taken during development, times of stress or the sea-

sonal cycle. The resulting change can be behavioural, physiological or morphological. Examples include changes to foraging behaviour and metabolic rates in salamanders [28] and changes to rates of photosynthesis in plants [29]. Plasticity can occur quickly, within the lifetime of the organism. This means it can be used for sharp changes in environment, and by long lived species which cannot adapt through genetic evolution. However the limits of plasticity may be insufficient to accommodate large shifts in climate [30]. Plasticity itself can be considered a trait that is under selection, with potential for the limits to shift through evolution. Traits that are expressed through phenotypic plasticity often covary with other traits. This leads to trade-offs that might impair fitness under certain environmental conditions [31]. Phenotypic plasticity has potential to impact both ecosystem functioning and future climate. Combining it with evolution in quantitative genetic models allows for improved predictions of species persistence [26], while inclusion in large scale Earth system models improves predictions for land-carbon storage [32].

Plastic adaptations are not usually passed between generations, but some can be. Epigenetic mechanisms include the binding of methyl groups or proteins to the DNA, which affect the way that the genome is expressed [33]. Some of the epigenetic modifications which occur during an organism's lifetime are heritable, and can be passed down to the next generation [34]. This is known as epigenetic inheritance or transgenerational plasticity. In experiments, coral reef fish have shown epigenetic responses to temperature over the course of two generations [35], and sheephead minnows responded over the course of one generation [36]. However, there are still too few studies to know whether epigenetic inheritance will be sufficiently widespread to play a key role in protecting species from rising temperatures.

Instead of adapting in situ, some species follow the climate. In general, under warming species move to higher latitudes [37] [38] and higher altitudes. Recent meta-analysis found species had shifted at rates of 17 km and 11 m per decade [39]. For polar and high altitude species, this leaves them with nowhere to go. Climate velocity provides a more robust measure, allowing for local variation in direction and magnitude of change [40]. Evidence in the fossil records suggests that for plants, movement was often the main response historically [2], although not necessarily for mammals [41]. Current distributions may not reach their full range limits, and may be restricted in the future, due to human land use [42]. On the other hand, humans may assist migration, both intentionally and unintentionally [43]. Limited dispersal potential may also restrict the rate of range shifts [44]. Species distribution models use correlations between distribution data and climate to define the habitat, or niche, of a species. Other models incorporate the underpinning physiological mechanisms [45]. Combining correlative and mechanistic methods gives the best insight into future species distributions and persistence [46]. While theoretical migration rates are easy to relate to rates of climate change, realised

rates are affected by a number of confounding factors. As a method of adaptation, migration is unlikely to act alone. Combining migration with genetic evolution [47], and phenotypic plasticity [28], reduced modelled extinction risk.

1.4 Methods of Ecosystem Adaptation

The response of ecological communities to environmental change depends on trait variation arising both within and among species; the processes of evolution and ecological species sorting respectively. Species sorting occurs when an environmental change results in the most abundant species being less well adapted to the current environment than another, less abundant species, causing a change in the dominant species [16]. Subsequent impacts on ecosystem functioning will reflect the phenotypes favoured in the new environment and the ways that they affect (and are themselves shaped by) species interactions.

The balance between evolution and species sorting determines the extent to which adaptation can buffer local extinctions and prevent species replacements. This is particularly important when traits covary. For example, body size and optimal temperature might be negatively correlated across species (i.e. small species are more tolerant of high temperature). Under a scenario with negligible evolution, replacement of species with higher optimum temperature under warming would also shift the body size distribution of the community towards smaller species. This would likely have marked impacts on ecosystem functioning. In contrast, if elevated optimum temperature evolves rapidly in response to warming and independently of body size, then shifts in community structure would be buffered by evolution.

2 Critical rates of change from a simple model

2.1 Introduction

Each method of adaptation occurs at a different rate, which is partly dependent on species or ecosystem. Phenotypic plasticity occurs quickly, whereas genetic evolution requires the turnover of multiple generations. Rates of adaptation can be related to rates of temperature change: under a low rate of temperature change, a system can adapt and survive, whereas under a higher rate, the system collapses. The critical rate of change divides these two states. To illustrate how the methods of adaptation discussed earlier could define a critical rate of change for a species or ecosystem, we have developed a process based model of evolution driven by an environmental stressor. Building on the resource based model presented in [48], which comprises of the standard ecological processes of growth, competition and

mortality, ‘trait diffusion’ is included to model the process of phenotypic evolution. Here, a trait is considered to be a fitness influencing physiological characteristic of a species, such as the optimum temperature for growth [49]. A phenotype is a particular physical value of this trait, such as an optimum temperature of $27.5^{\circ}C$. A trait is modelled as a continuous range of phenotypes, similar to quantitative genetics [50]. A distribution is formed according to the prevalence of each phenotype in the population. Trait diffusion models the potential for a member of the population to shift to a neighbouring phenotype, either through remixing of existing standing variation or new mutations. Through the inclusion of this term, the population also becomes diverse, as the process of trait diffusion pushes members away from the optimum phenotype. Diversity has been seen to increase through this process in experiments, for genes linked to thermal tolerance [51]. The model can be applied to a single species, in which case the trait diffusion models evolution within a species, known as microevolution. Alternatively, on a longer timescale, the model can be applied to assemblages of species, and evolution will occur between species. We will focus on framing the model for the case of intraspecies evolution. For simplicity we will use temperature as the environmental stressor, and optimum temperature as the trait. Other stressors such as moisture availability could be used instead.

2.2 The model equations

Growth is often used as a measure of the variation of organism fitness with temperature. The resulting thermal tolerance curves are usually close to gaussian [14][48] and can be measured in a laboratory environment [15][16]. In this model a quadratic form is used as a simplifying approximation. Members of the population are defined by their optimum temperature for growth, T_{opt} , with the trait axis running from low to high T_{opt} . Therefore, the growth rate, g , is defined by

$$g(T_{opt}) = g_{max} \left[1 - \frac{1}{2} \left(\frac{T - T_{opt}}{T_w} \right)^2 \right], \quad (1)$$

where T is the environmental temperature, T_{opt} is the optimum temperature for growth. The maximum growth rate, g_{max} , and the width of the quadratic growth curve, T_w , are the same for the entire population. The growth rate decreases as the environmental temperature moves away from the optimum temperature of the class.

The governing equations for the model are defined by the temporal rate of

change of the fractional area covered per unit T_{opt} ,

$$\frac{\partial \nu}{\partial t} = \nu \left(g(T_{opt}) \underbrace{\left(1 - \int \nu dT_{opt} \right)}_{N_{tot}} - \gamma \right) + \lambda \frac{\partial^2 \nu}{\partial T_{opt}^2}, \quad (2)$$

where ν is the fractional area covered per unit T_{opt} . In the first term, the growth rate is scaled by the amount of free space available in the system to be grown in. The total area covered by the population is N_{tot} . The maximum total area available is normalised to unity, and space is considered to be unitless. Space is treated as the limiting resource, and introduces competition into the system.

The mortality rate, γ , and the rate of trait diffusion, λ , are properties shared by all members of the population. To minimise the number of free parameters, the equations are rescaled by dividing through by the mortality rate. This means that time is in terms of number of lifetimes, τ . The maximum growth rate and the rate of trait diffusion are also rescaled, becoming $G_{max} = \frac{g_{max}}{\gamma}$ and $\Lambda = \frac{\lambda}{\gamma}$ respectively. Throughout this paper, $G_{max} = 10.0$ and $T_{\omega} = 10.0^{\circ}C$ are used. G_{max} was chosen so that at equilibrium with constant temperature and $\Lambda = 0.1^{\circ}C^2$ per lifetime, $N_{tot} \approx 90\%$.

Productivity is an important measure of ecosystem health and potential carbon uptake. The productivity of the system per unit T_{opt} , Π_{tot} , is the area-weighted sum of the growth rate of the distribution,

$$\Pi_{tot} = \int G \nu dT_{opt}. \quad (3)$$

The model can be solved analytically at equilibrium at a constant environmental temperature T_0 , when the population distribution in the phase space defined by T_{opt} is gaussian:

$$\nu(T_{opt}) = \left(\frac{\sigma^2 (G_{max} - 1) - \Lambda}{\sigma^3 G_{max} \sqrt{2\pi}} \right) \exp \left[- \frac{(T_0 - T_{opt})^2}{2\sigma^2} \right], \quad (4)$$

with standard deviation

$$\sigma = \sqrt{\frac{4T_{\omega}^2}{1 + \sqrt{1 + \frac{8T_{\omega}^2}{\Lambda}}}}. \quad (5)$$

A full derivation can be found in appendix A.1. The standard deviation of the population distribution, σ , is a measure of diversity, as it describes the range of phenotypes within the population. The variance increases with increasing trait

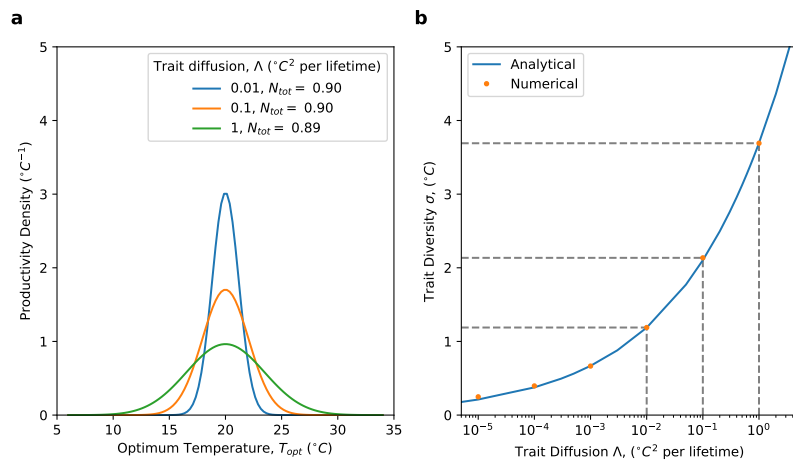


Figure 1: Characteristics of the model population at constant temperature. (a) Productivity density distribution defined by optimum temperature, at a constant environmental temperature $T_0 = 20^{\circ}\text{C}$ and a trait diffusion rate of Λ . (b) Higher rates of trait diffusion lead to more trait diversity. The three rates of trait diffusion used in (a) and their corresponding levels of diversity are marked with dashed grey lines.

diffusion, Λ . This equation provides an analytical relation between the rate of trait diffusion and diversity.

The analytical solution for the productivity distribution can be seen in figure 1a, at equilibrium at a constant environmental temperature $T_0 = 20^\circ C$. The most successful variant, best suited to the current environment, has the largest productivity and sits at the peak. The tails of the distribution are the phenotypes with lower productivity, resulting in competitive exclusion far from the optimum. Higher diversity leads to a decrease in area covered and productivity, as it leads to more of the species distribution being further away from the optimum phenotype. This is one of the key principles of trait-driver theory, where the traits of the most abundant species are more important for ecosystem functioning than the species richness [49]. Diversity increases strongly with trait diffusion rate, as seen in figure 1b. The model can also be solved numerically, using the Runge-Kutta 4th order algorithm (appendix A.3). The numerical and analytical solutions match well across a range of Λ .

2.3 The model in a changing environment

To explore the dependency on the rate of climate change, rather than the absolute warming between climate equilibria, we consider a linearly increasing temperature, $T(t) = T_0 + \epsilon t$, where ϵ is the rate of temperature change per time step. Starting from the equilibrium solution at constant temperature, two categories of behaviour emerge, seen in figure 2. A lower rate of change results in persistence of productivity, whereas a higher rate of change results in collapse. In both cases, the system behaves like a wave, changing shape and shifting rightwards, tracking the changing temperature as much as it can. The initial effect on the distribution is small. This is because mortality rate is independent of temperature, so the system has a delay while less adapted species die off to release free space, which is then filled by better adapted species.

For low rates of warming, the wave maintains an approximately gaussian form, with a skew to the right, seen in figure 2a. The population mostly adapts from redistribution of the population within the existing phenotypes, relying to a small extent on new phenotypes. There is a slight decline in productivity. After 25 lifetimes, the species covers 72.8% of the available space. When subjected to a higher rate of temperature change, as in figure 2b, the distribution loses its gaussian shape. The species is now relying mostly on the inclusion of new phenotypes to adapt, and cannot keep up with the fast rate of change, resulting in declining productivity. In this case, after 25 lifetimes the species covers 4% of the available area. An approximate analytical solution for trait diffusion at a low rate of temperature change can be seen in appendix A.2.

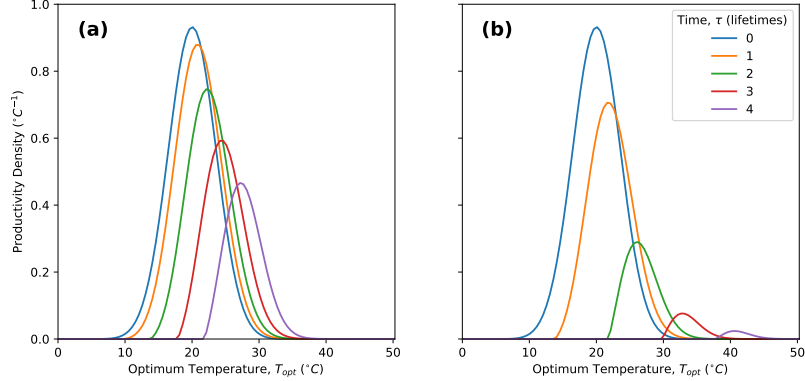


Figure 2: Evolution of the productivity density distribution under constant rates of climate change. Snapshots are taken at 0 – 4 lifetimes as the system experiences a constant rate of change from equilibrium: (a) $\epsilon = 4^\circ C$ per lifetime (b) $\epsilon = 8^\circ C$ per lifetime. In both cases $\Lambda = 1^\circ C^2$ per lifetime.

2.4 Separating the role of diversity and trait diffusion in population resilience to a changing environment

Diversity is often believed to confer resilience to a population in the face of a changing climate, and conservation goals tend to reflect this. However, in this model, trait diffusion (‘evolution’) is the sole driver of diversity, and therefore also plays a part in aiding species persistence. To compare the roles of diversity and trait diffusion, two different scenarios are analysed. To explore diversity without trait diffusion, the system is started with initial conditions corresponding to the equilibrium solution at a constant environmental temperature, T_0 , with non-zero trait diffusion, seen in figure 1a. Trait diffusion is then ‘turned off’ ($\Lambda = 0$), and a linear temperature change of $\epsilon = 1^\circ C$ per lifetime applied. To explore trait diffusion without diversity, the system is started from a single phenotype with optimum temperature equal to the initial temperature, T_0 . This initial condition has no diversity. The same temperature change of $\epsilon = 1^\circ C$ per lifetime is applied, with non-zero rates of trait diffusion.

Without trait diffusion, but with initial diversity, the system is productive at first, seen in figure 3a. On long timescales, once the environmental temperature moves beyond those which were included within the initial trait distribution, diversity cannot protect the system. Therefore, the environmental change results in the collapse of productivity. Without initial diversity, but with trait diffusion, the initial drop in productivity is slightly faster than a system protected by initial di-

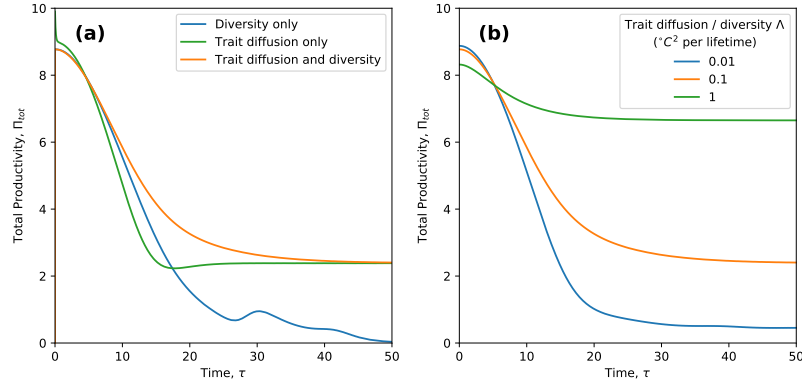


Figure 3: Separating the role of diversity and trait diffusion. (a) System resilience to warming under three scenarios: initial diversity and no trait diffusion; trait diffusion and no initial diversity; both initial diversity and trait diffusion. (b) Impact of different rates of diffusion, Λ , on system resilience to warming. In both cases, the total productivity of the system under a linear temperature change of $1^{\circ}C$ per lifetime is shown.

versity. On long timescales, trait diffusion allows the system to remain productive, although at lower levels than in a static environment. The system with initial diversity and trait diffusion performs the best, as it is protected by the initial diversity on short timescales, and by trait diffusion on long timescales.

Higher rates of trait diffusion drive higher levels of diversity, and higher diversity leads to lower productivity, seen in figure 1. This can also be seen in figure 3b. Although this might imply that higher trait diffusion and diversity are detrimental to the system, there is a trade-off involved. Higher initial diversity provides protection from a changing environment on a short timescale, and higher rates of trait diffusion provide protection on a long timescale. Therefore, in a changing environment, higher rates of trait diffusion are desirable.

2.5 Critical rates of temperature change

Under a low rate of temperature change, a population can adapt and remain productive, whereas under a higher rate, the productivity collapses, as seen in figure 2. The critical rate of change divides these two scenarios. We define the critical rate of change as the minimum rate at which the species covers less than 0.5% of the total area available, at dynamic equilibrium. This depends on the rate of trait diffusion, as seen in figure 4a. Dangerous rates of warming range from below $1^{\circ}C$

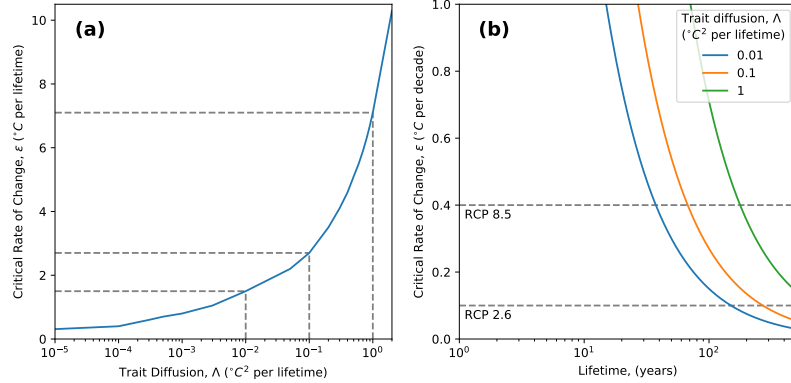


Figure 4: Critical rates of temperature change. (a) Dependence of the critical rate of temperature change per lifetime on the rate of trait diffusion, Λ . The three rates of trait diffusion used in (b) and their corresponding critical rates of temperature change are marked with dashed grey lines. (b) Critical rate of temperature change per decade in terms of species' lifetime. The minimum and maximum rate of change per decade from the IPCC AR5 [1] has been marked on.

per lifetime at low trait diffusion rates, to more than 8°C per lifetime at high trait diffusion rates [26]. The higher the rate of trait diffusion, the higher the critical rate of change.

Figure 4b shows the critical rate of change per decade for different species lifetimes. Also marked on are the predicted rates of temperature change per decade for the remainder of the 21st century [1]. Short-lived species such as microbes, with lifetimes from hours to days, are likely to be able to adapt through trait diffusion at a sufficient rate to keep up with climate change. This is backed up by evidence from both experiments [18] [19] [20] and natural populations [21]. Long-lived species such as trees, with lifetimes of decades to centuries, will require a potentially unrealistic rate of trait diffusion to maintain productivity.

2.6 Discussion

We use trait diffusion in an ecological model to act as the mechanism for evolution. Trait diffusion is neutral, occurring equally in both directions on a phenotypic trait axis. The ecological processes of growth, competition and mortality act as selection, meaning that better adapted phenotypes have higher fitness and are more successful. Trait diffusion also acts as a driver for diversity. Modelling evolution at an ecological scale means large scale processes can be included, such as the ef-

fect of competition on strength of selection. This however comes at the expense of small scale biological processes.

The addition of trait diffusion to a standard ecological model gives the system more potential to adapt in a changing environment. Without trait diffusion, a community can only adapt by redistributing the population among the existing phenotypes, making use of existing phenotypic diversity. In addition to this method, trait diffusion allows for the inclusion of new phenotypes, modelling the remixing of standing variation and fixation of new mutations. These two methods of adaptation hold different levels of importance, depending on the rate of environmental change. A low rate of change mostly leads to remixing of existing diversity and small changes to the community composition. At a high rate of change, the system mostly relies on adapting from new phenotypes leading to large changes to community composition.

One of the key factors that determines the behaviour of the system under an environmental change is the underlying timescale, the lifetime of the species. This affects the rate of change experienced, as a long lived species will experience a greater change per lifetime than a short-lived species. Diffusion occurs each time the species reproduces, therefore the rate of trait diffusion per lifetime is roughly constant. The lifetime is also linked to how the species will adapt. Initial diversity is a byproduct of trait diffusion, and acts on a shorter timescale, only able to protect the system from environmental change for the first few lifetimes. Trait diffusion is the main cause of resilience on any longer timescale. For a short-lived species, tens of lifetimes may pass in the space of one lifetime of a long-lived species. This means that species with a longer lifetime will rely more on high initial diversity to maintain their productivity, whereas species with a shorter lifetime will rely more on trait diffusion.

2.7 Conclusion

Species can respond to climate change in several different ways. Methods such as phenotypic plasticity occur quickly, but have distinct limits, beyond which species must find another way to adapt. Evolution and migration both have a maximum rate at which they can occur, which can be related to a critical rate of environmental change. High and low levels of productivity can be linked to the persistence and extinction of a species respectively. We define the critical rate as the minimum rate of temperature change which causes a collapse of productivity, and therefore the extinction of a species. This leads to a strong divide between the short and long lived. Current day rates of warming are between 0.1-0.4°C per decade [1]. For short-lived species, such as microbes, with lifetimes of hours to days, a change of less than 0.1°C per lifetime will be experienced, and any of the rates of trait-

diffusion presented will be sufficient for persistence. For long-lived species, such as trees, with lifetimes of decades to centuries, warming greater than 1°C is likely to be experienced in a lifetime. Although high initial diversity can act as a buffer, on long timescales a higher rate of trait diffusion will be needed to adapt. Otherwise, these processes of species-based adaptation may fail, resulting in extinctions and species replacement.

Summary

- Species face increasing pressure as continued global warming causes them to be maladapted to their environment. This has implications for the ecosystem services important to humans and the biosphere.
- Species can adapt to environmental change through phenotypic plasticity, evolution and migration.
- We find a theoretical critical rate of warming, below which a species can adapt and persist, above which a species will become extinct. This depends on the rate of adaptation and the species lifetime.
- The dominant method of adaptation will depend on a species lifetime. Long-lived species are likely to rely on redistribution of the abundance of existing diversity within the population, while short-lived species are likely to rely on genetic evolution.

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Author Contributions

R.C.M. carried out modelling, starting with a model initially developed by J.R.M.. R.C.M. drafted the paper, receiving comments and contributions from all of the authors, especially G.Y.D..

A Appendix

A.1 Solving the model analytically at constant temperature

The model can be solved analytically at equilibrium at a constant environmental temperature T_0 , when the population distribution in the phase space defined by T_{opt} is approximately gaussian. At equilibrium, the governing equation becomes

$$0 = \nu \left(G_{max} \left[1 - \frac{1}{2} \left(\frac{T_0 - T_{opt}}{T_w} \right)^2 \right] (1 - N_{tot}) - 1 \right) + \Lambda \frac{\partial^2 \nu}{\partial T_{opt}^2}. \quad (6)$$

For simplicity, the axes can be translated by setting $x = T_0 - T_{opt}$, and grouping constants by defining $C = G_{max}(1 - N_{tot})$. The governing equation becomes

$$\frac{\partial^2 \nu}{\partial x^2} = \frac{\nu}{\Lambda} \left(1 - C \left[1 - \frac{x^2}{2T_w^2} \right] \right). \quad (7)$$

Assuming the solution is a gaussian, then it can be written in the form $\nu_g = \frac{A}{\sqrt{2\pi\sigma^2}} e^{-\frac{x^2}{2\sigma^2}}$, where A and σ are constants. The second order derivative of ν_g is

$$\frac{d^2 \nu_g}{dx^2} = \left(-\frac{1}{\sigma^2} + \frac{x^2}{\sigma^4} \right) \nu_g. \quad (8)$$

The constant σ can be found by correlating the coefficients of the independent variables in the function multiplying ν and ν_g on the right-hand side of the two governing equations, 7 and 8.

Matching the x^2 coefficients gives

$$\sigma^2 = \sqrt{\frac{2\Lambda T_w^2}{C}}. \quad (9)$$

Matching the constant coefficients gives

$$\sigma^2 = \frac{\Lambda}{C - 1}. \quad (10)$$

σ^2 can be found by setting equations 9 and 10 equal to each other. Rearranging gives Λ in terms of C :

$$\Lambda = \frac{2T_w^2(C - 1)^2}{C}. \quad (11)$$

Finding C in terms of Λ gives

$$C = 1 + \frac{\Lambda \pm \sqrt{8\Lambda T_w^2 + \Lambda^2}}{4T_w^2}. \quad (12)$$

Substituting this into equation 10 gives

$$\sigma^2 = \frac{4T_w^2}{1 + \sqrt{\frac{8T_w^2}{\Lambda} + 1}}. \quad (13)$$

We take the positive root so that the variance is positive. A can be chosen so that the integral of the solution covers the correct total area, $A = N_{tot}$. Using $N_{tot} = 1 - \frac{C}{G_{max}}$ and equation 10 to eliminate C ,

$$A = \frac{\sigma^2(G_{max} - 1) - \Lambda}{\sigma^2 G_{max}}. \quad (14)$$

Therefore, the approximate analytical solution is given by

$$\nu(T_{opt}) = \frac{\sigma^2(G_{max} - 1) - \Lambda}{\sigma^3 G_{max} \sqrt{2\pi}} \exp \left[-\frac{(T_0 - T_{opt})^2}{2\sigma^2} \right]. \quad (15)$$

A.2 Solving the model analytically for a linear temperature change

An analytical approximation to the solution can be found for a linear temperature change of the form $T = T_0 + \epsilon t$. The population distribution in the phase space defined by T_{opt} remains close to gaussian for a low rate of temperature change, i.e. when ϵ is small. Therefore, an analytical solution can be found by approximating the distribution as a gaussian travelling wave. This solution holds for the dynamic equilibrium found after the initial stages of change seen in figure 2.

For a linear temperature change, the governing equation is

$$\frac{\partial \nu}{\partial t} = \nu \left(G_{max} \left[1 - \frac{1}{2} \left(\frac{T_0 + \epsilon t - T_{opt}}{T_w} \right)^2 \right] (1 - N_{tot}) - 1 \right) + \Lambda \frac{\partial^2 \nu}{\partial T_{opt}^2}. \quad (16)$$

For simplicity, constants can be grouped by defining $C = G_{max}(1 - N_{tot})$, and the independent variable can be grouped by defining $y(t, T_{opt} = T_0 + \epsilon t - T_{opt})$, leading to a simplified governing equation,

$$\frac{\partial^2 \nu}{\partial T_{opt}^2} - \frac{1}{\Lambda} \frac{\partial \nu}{\partial t} = \frac{\nu}{\Lambda} \left(1 - C \left[1 - \frac{y^2}{2T_w^2} \right] \right). \quad (17)$$

Assuming the solution is a gaussian travelling wave, then it can be written in the form $\nu_g = \frac{A}{\sqrt{2\pi\sigma^2}} e^{-\frac{(y-b)^2}{2\sigma^2}}$, where A , b and σ are constants. This solution can be substituted into the simplified governing equation to find the constants. The

derivatives of ν_g are $\frac{\partial \nu_g}{\partial t} = -\epsilon \frac{y-b}{\sigma^2} \nu_g$ and $\frac{\partial^2 \nu_g}{\partial T_{opt}^2} = \left(-\frac{1}{\sigma^2} + \frac{(y-b)^2}{\sigma^4}\right) \nu_g$. Substituting this into the left-hand side of equation 17 gives

$$\frac{\partial^2 \nu_g}{\partial T_{opt}^2} - \frac{1}{\Lambda} \frac{\partial \nu_g}{\partial t} = \nu_g \left(\frac{1}{\sigma^2} \left[\frac{\epsilon}{\Lambda} (y-b) - 1 \right] + \frac{1}{\sigma^4} (y-b)^2 \right). \quad (18)$$

The constants b and σ can then be found by correlating the coefficients of the independent variables in the function multiplying ν and ν_g on the right-hand side of the two governing equations, 17 and 18.

Matching the y^2 coefficients gives

$$\sigma^2 = \sqrt{\frac{2\Lambda T_\omega^2}{C}}. \quad (19)$$

Matching the y coefficients gives

$$b = \frac{\epsilon \sigma^2}{2\Lambda}. \quad (20)$$

Matching the constant coefficients gives

$$\frac{C-1}{\Lambda} - \frac{1}{\sigma^2} \left(\frac{\epsilon}{\Lambda} b + 1 \right) + \frac{b^2}{\sigma^4} = 0. \quad (21)$$

Use equations 19 and 20 to substitute expressions for b and σ in equation 21:

$$\frac{C-1}{\Lambda} - \sqrt{\frac{C}{2\Lambda T_\omega^2}} + \frac{\epsilon^2}{\Lambda^2} \left(\frac{1}{4} - \frac{1}{2} \right) = 0. \quad (22)$$

This is a polynomial in $C^{\frac{1}{2}}$. Finding $C^{\frac{1}{2}}$ in terms of Λ gives

$$C^{\frac{1}{2}} = \sqrt{\frac{\Lambda}{8T_\omega^2}} \pm \sqrt{\frac{\Lambda}{8T_\omega^2} + \frac{\epsilon^2}{4\Lambda} + 1}. \quad (23)$$

Substituting this into equation 19 gives a variance

$$\sigma^2 = \frac{4T_\omega^2}{1 \pm \sqrt{1 + \frac{2T_\omega^2 \epsilon^2}{\Lambda^2} + \frac{8T_\omega^2}{\Lambda}}}. \quad (24)$$

We take the positive root so that the variance is consistent with the form found for a constant environmental temperature. A can be chosen so that the integral of the

solution covers the correct total area, $A = N_{tot}$. Using $N_{tot} = 1 - \frac{C}{G_{max}}$ and equations 21 and 20 to eliminate C and b ,

$$A = 1 - \frac{1}{G_{max}} \left(\frac{\epsilon^2}{4\Lambda} + \frac{\Lambda}{\sigma^2} + 1 \right). \quad (25)$$

Therefore, the approximate analytical solution is given by

$$\nu(T_{opt}) = \frac{1}{G_{max}\sqrt{2\pi\sigma^2}} \left(G_{max} - \frac{\epsilon^2}{4\Lambda} - \frac{\Lambda}{\sigma^2} - 1 \right) \exp \left[\frac{-\left(T_0 + \epsilon\tau - T_{opt} - \frac{\epsilon\sigma^2}{2\Lambda} \right)^2}{2\sigma^2} \right]. \quad (26)$$

A.3 Solving the model numerically

To solve the model numerically, the governing equation, 2, must first be discretised. The model can be discretised along the trait axis, by dividing the axis up and sampling at n points. The second order derivative can then be written using a centred in space scheme. The governing equation for the i^{th} point is therefore

$$\frac{\partial \nu_i}{\partial t} = \nu_i \left(g_i(T_{opt,i}) \left(1 - h \underbrace{\sum_{i=0}^n \nu_i}_{N_{tot}} \right) - \gamma \right) + \frac{\lambda}{h^2} \left((\nu_{i+1} - \nu_i) - (\nu_i - \nu_{i-1}) \right), \quad (27)$$

where h is the spacing between T_{opt} of adjacent sampling points. A full solution can then be found using the Runge-Kutta 4th order algorithm.

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