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Working paper

# Single species dynamics under climate change

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## Abstract

We propose a general mathematical model describing the growth and dispersal of a single species living in a 1-D spatially discrete array of habitat patches affected by a sustained and directional change in climate. Our model accounts for two important characteristics of the climate change phenomenon: 1) Scale dependency: different species may perceive the change in the environment as occurring at different rates because they perceive the environment at different scales, and 2) Measure dependency: different species measure the environment differently in the sense that they may be sensible to or cue in on different aspects of it (e.g. maximum temperature, minimum temperature, accumulated temperature) which is associated with their physiological, ecological and life history attributes, which renders some characteristics of the environment more biologically relevant than others. We show that the deterioration in the quality of habitable patches as a consequence of climate change drives the species to

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extinction when dispersal is not possible; otherwise, we proof and provide a numerical example that, depending on the velocity of climate change, the scale at which a species measures it, and the particular attribute of the environment that is more biologically relevant to the species under analysis, there is always a migration strategy that allows the persistence of the species such that it tracks its niche conditions through space, thus shifting its geographic range. Our mathematical analysis provides a general framework to analyze species' responses to climate change as a relational property of a given species in interaction with a change in climate. In particular, we can analyze the persistence of species by taking into account the ways in which they measure and filter the environment. Indeed, one of our main conclusions is that there is not a single climate change but many, as it depends on the interaction between a particular species and climate. Thus the problem is more complex than assumed by analytically tractable models of species responses to climate change.

**keywords:** Climate change, Species dynamics, Temporal scale dependency, Allee effect threshold, Species' fundamental niche, Migration strategies, Threshold migration rate.

## 1 Introduction

It is well established that since the mid-20th century the earth surface and oceans have warmed, that human influence has been the dominant cause of the observed warming, and that temperature will continue to increase in 1 to over 4 Celsius degrees approximately, by the end of century [40]. This sustained global warming or climate change have already had an impact upon biodiversity, affecting ecosystem services and leaving clear fingerprints upon the distribution and abundance of the species (see [16], [46], [1], [42], [32], [31], [30], [18], [23] and [27], among others).

There is evidence that species have changed their altitudinal and latitudinal distributions at a median rate of 11 to 30 meters and 16,9 km per decade, respectively (see [23] and [8]). Although these rates seem large enough to track temperature changes, there is large variation across species' responses such that warming, especially if abrupt or rapid might cause extinction of some species unless they are able to adapt. But several other causes could impact upon the ability of a species to migrate fast enough to track their niche across space. It may happen that the combinations of temperature, humidity and key resources for a given species disappear (their niche is lost) or that while suitable conditions may still exist they cannot be reached from the species' present position due to dispersal limitation and/or barriers created by human-driven landscape changes (e.g. native habitat transformed into settlements or use in agriculture or forestry).

The traditional approach to infer the response of species to climate change is to use distribution or niche models ([36], [42]), which can be characterized as mostly phenomenological, static, and statistical and suffer from several limita-

tions such as not considering biotic interactions and evolution (e.g., [10]). An alternative to model the impact of climate is to use process oriented models that estimate the direct and/or indirect impact of climate change upon populations by fitting statistical models to time series data at particular locations in space (e.g., [38], [13], [17]). While this approach is of great value to understand the impact of both density dependent and independent factors, as well as their interaction upon population dynamics, it has the limitations of being data intensive and difficult to scale up from local sites to regions. Fortunately, these limitations are slowly being overcome (see [44]), however we still miss a general theoretical framework to model and project the response of species to climate change and the potential effect of other components of global change (e.g. land use change, habitat loss and fragmentation) in their response. In this contribution we attempt to provide a general mathematical framework that could be later expanded to address these issues.

Recent mathematical models of the impact of climate change upon species persistence, using integro-difference equations (e.g., [48], [22]) or reaction-diffusion models (e.g., [39], [5], [24], [26]) have been important in highlighting the impact of patch size and climate change velocity, as well as the role of dispersal in determining persistence. These models typically assume the existence of a uniformly suitable patch or domain of constant size, inside of which species disperse and grow at a fix rate and outside of which the conditions do not allow for the persistence of the species. Our formulation builds upon these efforts to model climate change and does so by linking growth and dispersal explicitly to changes in climate. That is, how a change in climate conditions affects natality mortality and immigration rates. The explicit consideration of this link, however, may be critical to understand the response of species to climate change (e.g. [11], [28]). Further, since different species may perceive their environment at different scales [25], and cue in on different aspects of it depending on their size, thermal physiology and other traits (see, e.g., [20]), it is desirable for a general model of species' response to climate change to deal with this diversity of scales problem. Indeed, for microbial species responsible for key ecosystem level processes, such as decomposition and nitrogen fixation, the relevant scale could be days and the relevant measure could be the average temperature, meanwhile for some species of annual plants a year could be the relevant scale and temperature extremes could be the most important signals that affect species persistence, while for some tree species, the relevant scale could be years as well, but the relevant measure could be the growing degree days accumulation (i.e. the number of days above a threshold temperature. See [43]). Thus different species within a community are likely to experience and be sensible to changes in climate in a different way (e.g., [6]) and measure it in different time windows or scales. This is likely one of the most significant aspects of the complexity of climate change; it will not be the same change for everyone.

In this contribution we propose a general model to account for both the link between climate change, growth and dispersal, as well as for the fact that different organisms perceive and measure the environment in different ways. To do this we consider a single focal species living within a 1-D hypothetical region

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divided in discrete patches and subjected to a change in its climate conditions.

Our main motivation is to characterize the migration strategies that would allow for the persistence of species under a sustained environmental change. We find that regions that do not allow for dispersal (like extremely isolated fragments or oceanic islands) are a bad omen for the species persistence under rapid and sustained environmental changes. Further, we show that depending on the velocity of the environmental change and the scale and the way at which the focal species measures the environment, there are migration strategies that allow for the species persistence. Such migration strategies are based on the paradigm that a species migrates to maximize its fitness.

In Section 2 we present the mathematical model and describe our results. In Section 3 a numerical example is given and Section 4 is devoted to discussion.

## Notations

Let us start by defining some of the most used mathematical terms and their meaning.

Table 1: Definition of frequently used mathematical notation.

Notation	Meaning
$\mathcal{O}$	Focal region divided in countable patches $1, 2, 3, \dots$ along a 1-D array.
$z^i$	$z^i = \{z_t^i\}_{t \in \mathbb{R}_+}$ , $\mathbb{R}_+ = \{t \in \mathbb{R} : t \geq 0\}$ , is a continuous environmental process in patch $i \in \mathcal{O}$ .
$\Delta$	Species-dependent parameter representing the time window or temporal scale that a given species use to assess and respond to changes in its environment. For simplicity we refer to this as the scale at which the species measures the environment.
$\mathcal{U}_\Delta$	Set of all possible measures (attributes) of the environment that could affect species fitness at a given scale $\Delta$ . Any $\mu_\Delta \in \mathcal{U}_\Delta$ is assumed to be a continuous measure on $\mathbb{R}$ . For example, a species could measure the average of temperature in each time window of size $\Delta$ or the minimum temperature or the maximum. All these correspond to different $\mu_\Delta$ . Thus different species ‘filter’ the environment by using a particular $\mu_\Delta$ .
$x_{\eta(\cdot)}^i$	$x_{\eta(\cdot)}^i = \{x_{\eta(t)}^i\}_{t \in \mathbb{R}_+} = \{x_{\eta(t)}^i(\mu_\Delta)\}_{t \in \mathbb{R}_+}$ is a $\mu_\Delta$ -filtered environmental process in patch $i \in \mathcal{O}$ . For any $i \in \mathcal{O}$ and $t \in \mathbb{R}_+$ , $x_{\eta(t)}^i$ is assumed to belong to a bounded open set $E \subset \mathbb{R}$ . That is, $E$ is the state space of the environment.
$\rho_\star$	$\rho_\star = \inf_{i \in \mathcal{O}, t \in \mathbb{R}_+} [x_{\eta(t)}^i - x_{\eta(t)}^{i+1}]$ is the smallest difference in a $\mu_\Delta$ -filtered environment between adjacent patches.
$\rho^\star$	$\rho^\star = \sup_{i \in \mathcal{O}, t \in \mathbb{R}_+} [x_{\eta(t)}^i - x_{\eta(t)}^{i+1}]$ is the largest difference in a $\mu_\Delta$ -filtered environment between adjacent patches.
$\tilde{p}$	$\tilde{p} = \sup_{j \in \mathcal{O}, t > 0} [x_{\eta(t)}^j - x_{\eta(t-)}^j]$ is the largest possible jump in a $\mu_\Delta$ -filtered environment within a patch.
$y^i$	$y^i = \{y_t^i\}_{t \in \mathbb{R}_+}$ is the species biomass dynamics in patch $i \in \mathcal{O}$ .
$\gamma$	The biomass threshold below which the growth rate of the species is negative (i.e. Allee effect threshold).
$M$	Carrying capacity ( $0 < \gamma < M < \infty$ ).
$H(\cdot, \cdot)$	$H : \mathbb{R} \times \mathbb{R} \rightarrow \mathbb{R}$ is the growth function of the focal species. It depends on the species biomass on its first component and on the environment on its second component. Also, for all $x \in \mathbb{R}$ , $H(\cdot, x)$ has a unique maximum point at $\tilde{y} \in (\gamma, M)$ , independent of $x$ .
$\Phi$	Represents the largest open set in $E$ such that $H(\tilde{y}, \cdot) < 0$ on it. Since in the long-term the environment, of a given patch and for a given species, will deteriorate because of climate change, the environmental conditions within it will be attracted to this set.
$\Psi^i$	Represents the dynamical set $\Psi^i = \{i' \in \psi^i : x_{\eta(\cdot)}^{i'} \notin \Phi \text{ and } y^{i'} < M\}$ , where $\psi^i = \{i' \in \mathcal{O} :  i' - i  = 1\}$ . That is, the neighboring patches to patch $i$ that are potentially habitable by the species.
$\lambda(\cdot, \cdot)$	$\lambda : \mathbb{R} \times \mathbb{R} \rightarrow \mathbb{R}$ is a function that specifies the migration rate expressed as a proportion of the biomass in a patch that migrates to neighboring patches. $\lambda$ depends on the species biomass on its first component and on the environment on its second component.
$\mathcal{C}^{i \rightarrow i'}$	$\mathcal{C}^{i \rightarrow i'} = \{\mathcal{C}_t^{i \rightarrow i'}\}_{t \in \mathbb{R}_+}$ accounts for how much of the emigrating biomass from patch $i \in \mathcal{O}$ will move to neighboring patch $i' \in \psi^i$ . It takes values in $[0, 1]$ .

Also, for a set  $A \subset \mathbb{R}$ , denote by  $\bar{A}$  for its closure, by  $\text{int}\{A\}$  for its interior and by  $\partial A$  for its boundary. An important set considered in this work is the set  $(y_*, y^*) \times (x_*, x^*)$ , which represents the largest open rectangle in  $\mathbb{R} \times \mathbb{R}$  such that  $H(\cdot, \cdot) > 0$  on it. In ecological terms, this set corresponds to the realized niche of the species or those combinations of biotic effects (i.e. intraspecific in a 1-species model) and environments where growth is positive [7].

## 2 The mathematical model

Our model envisions a sustained and unidirectional environmental change along a region  $\mathcal{O}$  and its influence on one focal species. We follow a macroscopical approach and consider  $\mathcal{O}$  to be a large landscape undergoing an unidirectional change in environmental conditions (e.g. temperature) implying an unidirectional movement response (modeled as discrete biomass jumps between adjacent patches) of the species inhabiting it. Accordingly, we are going to consider  $\mathcal{O}$  to be a 1-D arrangement of  $N \in \mathbb{N}$  patches of the same size undergoing climate change. In practical terms,  $\mathcal{O}$  represents the portion of land on which our focal species will be able to track its niche.

In what follows we will present our model. We will start by describing the dynamics of the abiotic environment, and how this is measured and “filtered” by the species, in the sense that the biological attributes of species, such as life span, dispersal distance, among others, make some scales and attributes of the environment (e.g. median, mean or extreme values of temperature) more biologically relevant than others. Then we will describe how the environment affects the growth and dispersal of the species. Finally, we will explore the conditions for species persistence and provide some numerical examples.

### 2.1 Dynamics of the abiotic or environmental process

For every patch  $i \in \mathcal{O}$ , let  $z_t^i \in \mathbb{R}$  be a process accounting for some abiotic or environmental characteristic in  $i$  at time  $t \in \mathbb{R}_+$ . We consider  $z_t^i$  homogeneous within each  $i$  (i.e. all individuals within patch  $i$  experience the same  $z_t^i$ ), continuous and taking values in a bounded open set.

Since temperature is a key variable associated to climate change and has important fitness effects (see [40], [15], [27] and [3]), driving changes in growth and distribution of species across gradients (e.g., [23]), we can think of  $z_t^i$ 's as representing temperature in the corresponding patches within  $\mathcal{O}$ . The process  $z_t^i$  could also represent a function of more than one environmental characteristic, as for example, rainfall and temperature (see [27]). This will depend, however, on the species under study.

For the sake of simplicity, we will model a single species whose niche is invariant such that no evolutionary change is possible in response to climate change (see Discussion), but in a framework that would allow us to assess the response of different species that perceive changes in their environment at different scales. To do this, we will hypothesize the existence of a species-dependent parameter

$\Delta$  with respect to the  $z^i$ 's, whose absolute value will be dependent on the time units we are working on. It will represent the time span or time window at which the species "evaluates" the environment, in terms of how it affects its population growth rate and migration potential. Thus, different species will measure, and be affected by the environment in different ways.

The mathematical structure associated to the way that each species measures the environment will be characterized as follows: First, each species measures the environment according to a fixed temporal partition  $0 = t_0 < t_1 < t_2 < \dots$  such that for all  $k \in \mathbb{N}$ ,  $t_k - t_{k-1} = \Delta$ , where  $\Delta$  has the interpretation given above and can be different for different species. Secondly, let  $\mathcal{U}_\Delta$  be the set of  $\Delta$ -dependent continuous measures.

Finally, for all  $i \in \mathcal{O}$ , we define a new environmental process  $x_{\eta(\cdot)}^i$  that is the result of transforming the original one ( $z^i$ ) by some measure that captures a characteristic of the environment that is biologically significant (i.e. accrues fitness effects) for the species under analysis in the time window  $\Delta$ , as (see definitions in Table 1):

$$\left\{ \begin{array}{l} x_{\eta(t)}^i = x_{\eta(t)}^i(\mu_\Delta) = \sum_{k \in \mathbb{N}} \int_{(t_{k-1}, t_k]} z_s^i d\mu_\Delta(s) \mathbf{1}_{\{t \in [t_k, t_{k+1})\}} + x_0^i \mathbf{1}_{\{t \in [t_0, t_1)\}} \\ \mu_\Delta \in \mathcal{U}_\Delta \end{array} \right. , \quad (1)$$

where  $x_0^i$  is the starting environmental state for patch  $i$ , according to the species environmental measure, and  $\eta(t) = \sum_{k \in \mathbb{N}} k \mathbf{1}_{\{t \in [t_k, t_{k+1})\}}$  for all  $t \in (t_1, \infty)$ , where the indicator function  $\mathbf{1}_{\{t \in [t_{k-1}, t_k)\}} = 1$  if  $t \in [t_{k-1}, t_k)$  and 0 otherwise. That is, the behavior that the species is performing at time  $t \in [t_k, t_{k+1})$  will depend on the measure of the environment over the previous time interval  $[t_{k-1}, t_k)$ . We are going to assume that the  $x_{\eta(\cdot)}^i$ 's do not exhibit a cyclic or an almost cyclic behavior. Note that for any fixed  $\mu_\Delta \in \mathcal{U}_\Delta$ , the  $x_{\eta(\cdot)}^i$ 's also take values in a bounded open set and as they are piecewise constant functions (i.e., they can switch their values every  $\Delta$  times), and then only right-continuous, we will write  $\lim_{s \uparrow t} x_{\eta(s)}^i = x_{\eta(t-)}^i$  for all  $t > 0$ .

So far, we have defined  $\Delta$  and the  $x_{\eta(\cdot)}^i$ 's, that is, the extent or temporal window at which the species measures and the relevant aspect of the environment that the species cue in on within that window, respectively. Let see a concrete example.

### Example

Consider a region  $\mathcal{O}$  divided in patches where  $z_t^i$  is the temperature ( $^\circ\text{C}$ ) of patch  $i$  at time  $t \in \mathbb{R}_+$  (years). Suppose that we have a focal species living in  $\mathcal{O}$ , whose physiological and life-history attributes are such that the relevant characteristic of the environment or "filter" is  $x_{\eta(\cdot)}^i$ , which represents the mean annual temperature. That is,  $\Delta = 1$  year,  $t_{k-1} = k - 1$  for all  $k \in \mathbb{N}$  and  $d\mu_\Delta(s) = d\mu_1(s) = ds$ . Assume that the dynamics for the continuous temperature is:



$$z_t^i = z^i + \varphi\left(t + \frac{1}{2}\right) + D_1 \cos(\varrho_1 t + h_{1,0}) + D_2 \cos(\varrho_2 t + h_{2,0}), \quad (2)$$

where  $z^i$  sets the mean trend at  $t = 0$ ,  $\varphi > 0$  is a drift parameter and the last two terms represent a  $2\pi/\varrho_1$  and a  $2\pi/\varrho_2$  periodic variations respectively, such that  $D_1$  and  $D_2$  are constants representing the daily and seasonal range or amplitude of variation in temperature. The parameters  $h_{1,0}$  and  $h_{2,0}$  are deviations from the mean trend associated to the initial conditions. The above terms allow us to capture the typical cyclic behavior of temperature during a year (e.g., with daily and seasonal cycles), and its corresponding amplitudes. If the species under analysis measures the environment by cueing in on the mean annual value of (2) we obtain:

$$\begin{aligned} x_{\eta(t)}^i &= \sum_{k \in \mathbb{N}_{k-1}} \int_0^k z_s^i ds 1_{\{t \in [k, k+1)\}} + x_0^i 1_{\{t \in [0, 1)\}} \\ &= \sum_{k \in \mathbb{N}} \varphi k 1_{\{t \in [k, k+1)\}} + x_0^i 1_{\{t \in [0, 1)\}}, \end{aligned} \quad (3)$$

where  $x_0^i = z^i$ . Notice that the species-filtered temperature changes linearly in time (due to the constant drift parameter  $\varphi$ ) implying that all jumps in the species-filtered temperature are of the same magnitude.

## 2.2 Dynamics of the species driven by the environmental process

For our focal species living in  $\mathcal{O}$ , consider that the environmental process follows (1) with respect to a fix  $\Delta$ -dependent measure  $\mu_\Delta \in \mathcal{U}_\Delta$ , and let  $E$  be the state space of the  $x_{\eta(\cdot)}^i$ 's or the set of all possible values that the  $x_{\eta(\cdot)}^i$ 's could take.

Let  $y_t^i$  be the biomass of the focal species in patch  $i \in \mathcal{O}$  at time  $t \in \mathbb{R}_+$ . Its dynamics will consist of two main parts: A growth function  $H : \mathbb{R} \times \mathbb{R} \rightarrow \mathbb{R}$  and a dispersal function  $\lambda : \mathbb{R} \times \mathbb{R} \rightarrow \mathbb{R}_+$ . Both parts have a first component depending on the species biomass and a second one depending on the environment. Also, all the functions involved are species-dependent; that is, the specific structure of such functions and their parameters can vary according to species functional traits and life history.

The general structural conditions on  $H$  are:  $H$  is a  $C^2(\mathbb{R}) \otimes C(\mathbb{R})$  function, that is, twice continuously differentiable with respect to the first component and continuous with respect to the second component. In addition, we define two constants  $M$  or carrying capacity and  $\gamma$  or Allee threshold, such that  $0 < \gamma < M < \infty$  and  $H^*(\cdot) = \sup_{x \in E} H(\cdot, x)$  is negative on  $[0, \gamma) \cup (M, \infty)$ . Further, for all  $x \in E$ ,  $H(\cdot, x)$  on  $[0, M]$  has a unique maximum point  $\tilde{y} \in (\gamma, M)$  independent of  $x$  ( $H(\cdot, x)$  is concave on  $[0, M]$ ).

### 2.2.1 The general case

In the Supplementary Material we show that the particular case where there is no migration, the species will go extinct. In what follows we will explore the general scenario when migration is possible, and show that the migration rate that allows survival depends upon the scale as well as the way species measure the environment.

Migration may be an effective adaptive response to a changing climate as long as it is possible and at an adequate pace. In this regard, our main result (Theorem 2 below) establishes a migration strategy that assures species persistence under some environmental conditions, if there are no barriers to migration. In a region affected by an increase in temperature and with no barriers to migration, species will change their spatial patterns of occupation as a consequence of dispersal and differential persistence across patches. This case, which we call the general case, will be developed in what follows.

The mathematical abstraction for this case will be to consider  $\mathcal{O}$  as an unlimited region, that is  $\mathcal{O} = \mathbb{N}$  (i.e., patch 1 is half-fenced since  $\mathcal{O}$  starts in patch 1) but with a finite number of habitable patches, where growth is positive, but whose environmental conditions are being gradually attracted into some specific “deteriorated environment”. The main challenge for species persistence in this region is to migrate from habitable patches before they become attracted to a such environmental condition. To do this, individuals have “to keep running” away from the deteriorating environment to keep their fitness unchanged, similar to the Red Queen Hypothesis by Van Valen.

To develop the general case we need to consider the following definitions and assumptions:

(G.1) Let us define a *Deteriorated Environment* (DE) as a set that belongs to  $\Phi = \{\mathcal{E} \in \mathcal{B}(E) : H(\tilde{y}, \cdot) < 0 \text{ on } \mathcal{E}\} \neq \emptyset$ , where  $\mathcal{B}(E)$  is the set containing all the open subsets of  $E$ . Additionally, we assume that  $E \cap \Phi^c$  is connected, that is,  $\text{int}\{E \cap \Phi^c\} \neq \emptyset$  cannot be represented as the union of two or more disjoint nonempty open subsets of it.

(G.2) We assume that  $\Phi$  is an attracting set for  $x_{\eta(\cdot)}^i$ , for all  $i \in \mathcal{O}$ . Further, since  $\Phi$  is a disconnected set, we should specify to which subset of  $\Phi$  is  $x_{\eta(\cdot)}^i$  attracted to, for all  $i \in \mathcal{O}$ . To do this, denote by  $\mathcal{V} \in \Phi$  the open connected set representing the specific DE to which the environment is attracted to. Once the environment of patch  $i$  enters in  $\mathcal{V}$  it becomes immediately uninhabitable or “destroyed” for the focal species.

(G.3) We assume that the environment changes along a latitudinal-altitudinal gradient in  $\mathcal{O}$ : For all  $i, i' \in \mathcal{O}$  and  $t \in \mathbb{R}_+$  such that  $x_{\eta(t)}^i, x_{\eta(t)}^{i'} \in \mathcal{V}^c$ , with  $i' > i$ , define  $\tau_i^D = \inf\{t' > t : x_{\eta(t')}^i \in \mathcal{V}\}$  and  $\tau_{i'}^D$  analogously. Then  $\tau_i^D \leq \tau_{i'}^D$ .

Thus, (G.3) implies a directionality in how the environment changes across  $\mathcal{O}$ , which captures the essential empirical fact that temperature decreases towards higher latitudes and higher altitudes, which implies that along the gradient some sites will change before others in an ordered sequence.

Now, we need to specify a key assumption regarding the velocity at which the

environmental change is advancing along  $\mathcal{O}$  and the time at which the species is affected by it. It will be a crucial assumption for the species persistence because it differentiates the time at which the species measures its environment  $\Delta$  from the time at which the environment deteriorates the patch potentially occupied by the species (in the sense of (G.1)). It will make possible to establish two different time scales and the way that they interact. Consider first the following definitions:

Let  $(y_*, y^*) \times (x_*, x^*) \subset (\gamma, M) \times \text{int}\{E \cap \Phi^c\}$  be the largest open rectangle such that for every  $(y, x) \in (y_*, y^*) \times (x_*, x^*)$ ,  $H(y, x) > 0$  (which makes sense because of  $E \cap \Phi^c$  is connected). As  $E \cap \Phi^c \cap (x_*, x^*)^c$  consists in the union of two disjoint closed sets, consider  $\mathcal{T}_*$  and  $\mathcal{T}^*$  as pictured in Fig. 1. That is, the set of values outside of  $(x_*, x^*)$  that lie outside of  $\Phi$ .

$$\underbrace{\Phi \cap \mathcal{V}^c \longrightarrow \mathcal{T}_* \longrightarrow (x_*, x^*) \longrightarrow \mathcal{T}^* \longrightarrow \mathcal{V}}_E$$

Figure 1: Division of the state space  $E$  according to the growth function  $H$ . Arrows indicate directionality of the environmental change according to (G.3); that is, for any  $x_1 \in \Phi \cap \mathcal{V}^c$ ,  $x_2 \in \mathcal{T}_*$ ,  $x_3 \in (x_*, x^*)$ ,  $x_4 \in \mathcal{T}^*$  and  $x_5 \in \mathcal{V}$  we have  $x_1 < x_2 < x_3 < x_4 < x_5$ . For any  $y$  within  $(y_*, y^*)$ ,  $H(y, \cdot)$  will be always positive on  $(x_*, x^*)$  and always negative on  $\Phi$ . The positivity or negativity of  $H(y, \cdot)$  on  $\mathcal{T}_*$  or  $\mathcal{T}^*$  will depend upon the value of  $y$  and the functional form chosen for  $H$ .

Thus, according to (G.3) and Fig. 1, for any  $t \in \mathbb{R}_+$ , we will have that the species-filtered environmental process along the landscape patches will follow the strictly ordered sequence:  $x_{\eta(t)}^1 < x_{\eta(t)}^2 < x_{\eta(t)}^3 < \dots$ . Further, for any  $i \in \mathcal{O}$  and  $t \in \mathbb{R}_+$  such that  $x_{\eta(t)}^i \leq x_*$ , we can define a time at which the species-filtered environmental process at patch  $i$  enters and exits the set of environmental conditions  $(x_*, x^*)$  as  $\tau_i^{\text{in}} = \inf\{t' > t : x_{\eta(t')}^i > x_*\}$  and  $\tau_i^{\text{out}} = \inf\{t > \tau_i^{\text{in}} : x_{\eta(t)}^i > x^*\}$ . Additionally, we can define the largest possible difference in the species-filtered environment between adjacent patches as  $\rho^* = \sup_{i \in \mathcal{O}, t \in \mathbb{R}_+} [x_{\eta(t)}^i - x_{\eta(t)}^{i+1}]$ . Finally we assume:

(G.4) For an  $i \in \mathcal{O}$  and  $t \in \mathbb{R}_+$  as above,  $\tau_{i+1}^{\text{out}} > \tau_i^{\text{out}}$  and  $\rho^* < x^* - x_*$ .

This assumption guarantees the existence, since a point in time, of at least one environmentally suitable patch in  $\mathcal{O}$  where the focal species could grow. Indeed, let  $i \in \mathcal{O}$  and  $t \in \mathbb{R}_+$  such that  $x_{\eta(t)}^i \in (x_*, x^*)$ . Let  $\tau_i^{\text{out}}$  be the first exit time from  $(x_*, x^*)$  after  $t$ . Then,  $x_{\eta(\tau_i^{\text{out}})}^{i+1} \in (x_*, x^*)$ , because  $\tau_{i+1}^{\text{out}} > \tau_i^{\text{out}}$  and  $x_{\eta(\tau_i^{\text{out}})}^i - x_{\eta(\tau_i^{\text{out}})}^{i+1} < x^* - x_*$ .

Assumption (G.4) also encompasses assumptions (G.1)-(G.3). Thereby, if (G.4) is assumed to be true, (G.1)-(G.3) hold true as well.

Even under these conditions, the rate at which the environment changes can be variable as has been observed and predicted to occur across the globe [27].

For any  $i \in \mathcal{O}$  and  $t \in \mathbb{R}_+$  we can now write our general model as:

$$\left\{ \begin{array}{l} y_t^i = y_0^i + \int_0^t H(y_{s-}^i, x_{\eta(s-)}^i) y_{s-}^i ds \\ + \sum_{\{s \in (0, t] : \eta(s) \neq \eta(s-)\}} \left[ \sum_{i' \in \psi^i} \mathcal{C}_{s-}^{i' \rightarrow i} \lambda(y_{s-}^{i'}, x_{\eta(s-)}^{i'}) y_{s-}^{i'} - \lambda(y_{s-}^i, x_{\eta(s-)}^i) y_{s-}^i 1_{\{\Psi_{s-}^i \neq \emptyset\}} \right] \\ y_0^i \in [0, M], \{i \in \mathcal{O} : y_0^i > 0\} \subset \{i \in \mathcal{O} : x_0^i \in E \cap \Phi^c\} \neq \mathcal{O} \end{array} \right. , \quad (4)$$

where  $\psi^i = \{i' \in \mathcal{O} : |i' - i| = 1\}$  and  $\Psi^i = \{i' \in \psi^i : x_{\eta(\cdot)}^{i'} \notin \Phi \text{ and } y^{i'} < M\}$ . The migration function ( $\lambda$ ) specifies the proportion of the biomass that will migrate at the end of the current time window  $\Delta$ . The functions  $\mathcal{C}_{s-}^{i' \rightarrow i}$ 's specify the proportion of migrating biomass from patch  $i'$  that is allocated to patch  $i$ . These functions satisfy  $\mathcal{C}_{s-}^{i' \rightarrow i} = 0$  if  $i \notin \Psi^{i'}$ , and for  $\Psi^{i'} \neq \emptyset$ ,  $\sum_{i'' \in \Psi^{i'}} \mathcal{C}_{s-}^{i' \rightarrow i''} = 1$ . That is, a patch can receive biomass only from its neighbors, and only if its environment is not already deteriorated or saturated at its carrying capacity. Also, the model assumes that at  $t = 0$  the biomass of the focal species is allocated only to non-DEs patches.

This general model involves two different time scales: The first one, described in the right-hand side of the first line of (4), accounts for the continuous growth within patch  $i$ ; and the second one, described in the second line of (4), accounts for the migration regime of the species in response to climate change and according to what it experienced during the last time window  $\Delta$ . In our framework, biomass migration is a jump in time and space. In time because it applies after  $\Delta$  units of time have elapsed, and in space because the spatial discretization of  $\mathcal{O}$  makes migration to be seen as a ‘‘jump’’ from a patch towards a contiguous one. Such jumps can occur just before the end of the corresponding  $\Delta$  time period, i.e., after measuring and responding to the environmental conditions in the patch.

Notice that the model assumes that the continuous dynamics of the whole biomass of the species is affected in each synchronized non-overlapping  $\Delta$  time periods. This envisions the biomass dynamics as a continuous flow along  $\mathcal{O}$ .

The process  $\Psi^i$  denotes the ‘‘potentially habitable  $i$ -neighborhood’’, that is, the model assumes that the species avoid sending immigrants to DEs and saturated patches (i.e., patches whose biomass is at its carrying capacity).

With respect to the migration function, we are going to assume that  $\lambda(\cdot, \cdot)$  is a right-continuous function. This is because it acts each  $\Delta$  time periods and not continuously in between. As  $\lambda$  represents the proportion of biomass that will migrate, it takes values in  $[0, 1]$ .

Regarding the functions  $\mathcal{C}_{s-}^{i \rightarrow i'}$ 's they can also be interpreted as a measure of how much of the biomass leaving a patch  $i$  is sent to a neighboring patch  $i'$ . As such measures will depend exclusively upon the quality of the neighboring patches, we are going to assume that  $\mathcal{C}_{s-}^{i \rightarrow i'}$ 's can be written as:

$$\mathcal{C}^{i \rightarrow i'} = \frac{f(x_{\eta(\cdot)}^{i'}) 1_{\{i' \in \Psi^i\}}}{\sum_{i'' \in \Psi^i} f(x_{\eta(\cdot)}^{i''})} \quad (5)$$

where  $f$  is a species-dependent positive continuous function, that describes the quality of a given patch to sustain biomass of the focal species; and the indicator function  $1_{\{i' \in \Psi^i\}} = 1$  if  $i' \in \Psi^i$ , and 0 otherwise. The function  $f$  describes the species' fundamental niche [19] or the combination of species-filtered environments where the species might maintain biomass. We further assume that there exists a species-dependent parameter  $\nu \in (x_*, x^*)$  such that  $f(\nu) > f(x)$ , for all  $x \in E \cap \{\nu\}^c$ . This parameter can be interpreted as the “ideal or best environment” for our species. The functions  $\mathcal{C}^{i \rightarrow i'}$ 's assume that the focal species is able to evaluate the quality of the neighboring habitat patches through  $f$ . Thus implying that individuals of the focal species are constantly moving within patches where they effectively have the possibility of “evaluating” the environments in the adjacent patches. Our coarse-grain approach assumed, for the sake of simplicity, that patches are internally homogeneous in environment. In reality, however, patches will likely have gradients, that albeit small, can be used by species as directional cues for movement.

As an example, consider  $f$  as:

$$f(x) = f(x; \nu, \sigma) = \exp \left\{ -(x - \nu)^2 / (2\sigma^2) \right\}, \quad (6)$$

where  $\nu \in (x_*, x^*)$  and  $\sigma > 0$ . That is,  $f$  is a normal density-like function with location parameter  $\nu$  and scale  $\sigma$ . If the relevant characteristic of the environment for some species is the mean annual value of temperature, then  $\nu$  will represent the “ideal mean annual temperature” because  $\sup_{x \in \mathbb{R}} f(x) = f(\nu) = 1$ , and  $\sigma$  will represent how plastic or tolerant the species is in terms of environmental temperature.

In Theorem 1 (see Supplementary Material) we proof that (4) has a unique solution.

### Some important concepts

We saw that  $\nu$  represents the “ideal or best environment” for the focal species, therefore it is expected that if a certain patch has an environment valued in  $\nu$ , the species therein will maximize its fitness. Translated into a mathematical language, for all  $x', x \in E$  and for all  $y \in (y_*, y^*)$ ,  $f(x') > f(x) \Leftrightarrow H(y, x') > H(y, x)$ , which will imply that the species maximum growth is reached at  $H_{\max} = H(\tilde{y}, \nu)$ . Further, we will assume that the species looks for its ideal environmental conditions and once it finds them it will remain there unless the conditions change. Thus the species will migrate its biomass in proportion to its relative fitness in the available patches. This is essential to keep in mind when defining a functional form for  $\lambda$  in (4). Thus, according to the above, we will say that  $\lambda$  is a *Migration Strategy for Persistence* (MSP) if it satisfies:

$$\lambda(y, x) \begin{cases} = 0, & H(y, x) = H_{\max} \\ = 1, & H(y, x) \leq 0, (y, x) \notin (y^*, \infty) \times (x_*, x^*) \\ \in (0, 1), & \text{otherwise} \end{cases}, \quad (7)$$

and is such that the species persists. Notice that all the biomass found in a habitat patch will migrate whenever  $H \leq 0$  and the environmental conditions are outside the region  $(x_*, x^*)$  or the biomass is  $\leq y^*$  or both. The case  $H(y, x) \leq 0$  when  $(y, x) \in (y^*, \infty) \times (x_*, x^*)$ , may occur when immigrants crowd into a good habitat and make the resident population to go above  $M$  and become a pseudo-sink [47].

**Theorem 2**

Assume that (G.4) holds. Additionally, consider the following conditions:

1. There exists  $i \in \mathcal{O}$  such that  $(y_0, x_0) \in (y_*, \infty) \times (x_*, x^*)$ ,
2.  $\{x \in \mathcal{T}^* \cup \mathcal{V} : x + \rho_* \notin \mathcal{V}\} = \emptyset$ , where  $\rho_* = \inf_{i \in \mathcal{O}, t \in \mathbb{R}_+} [x_{\eta(t)}^i - x_{\eta(t)}^{i+1}]$ , and
3.  $\nu + \tilde{p} \leq x^*$ , where  $\tilde{p} = \sup_{j \in \mathcal{O}, t > 0} [x_{\eta(t)}^j - x_{\eta(t-)}^j]$ , that is, the largest possible

jump in the species-filtered environment within a patch.

Then there exists at least one MSP.

Condition 1 in the preceding theorem says that, at the beginning, the species occupies at least one patch of the dynamics and it is not doomed to extinction; condition 2 says that once the environment of some patch  $i + 1 \in \mathcal{O}$  exits from  $(x_*, x^*)$ , then the environment of patch  $i$  is in  $\mathcal{V}$  (i.e., the length of  $\mathcal{T}^*$  is small compared to  $\rho_*$  or the smallest possible difference in the species-filtered environment between adjacent patches). If that condition does not hold, then the species might go towards an opposite direction to the one followed by its niche; in other words, with a positive probability the species might prefer to go to an unsuitable patch for its growth instead of the suitable one. Condition 3 says that patches in the ideal environment  $\nu$  for the species growth cannot completely ruin in a single  $\Delta$  period. This condition sets a specific relationship between the rate of the environmental advancement and the migration function (see Proof below). Further, the MSP considers that the migration function maximizes fitness, hence individuals will not leave a patch where the species population is at  $H_{\max}$ .

The proof of this theorem can be found in Supplementary Material.

*Remark:* The procedure used in the above proof is applied repeatedly many times as the species advances in  $\mathcal{O}$ , hence surviving individuals will live far away from its historic geographic range. Given the conditions specified in Theorem 2, we know that there exists at least one  $\lambda$  that satisfies (7) and is in fact a MSP. To find this  $\lambda$  pose a challenge for the numerical implementation of the model as we show in the next section.

### 3 Numerical example

In order to answer how the extent and the way a species measures the environment affect its persistence it is necessary to develop a model for how its demography or population dynamics is affected. We will do this in what follows.

We are going to consider a focal species living in a region  $\mathcal{O}$ , whose environmental dynamics is described in the example before Section 2.2, where the continuous temperature is given by (2) and the species filtered environment is given in (3).

Regarding the species biomass dynamics, we will use the logistic-type model with Allee effect and with an explicit mortality term. Let  $\{\tau_i^k\}_{k \in \mathbb{N}}$  be the sequence of the  $x_{\eta(\cdot)}^i$ -jumps. For all  $k \in \mathbb{N}$  our model is described by:

$$\begin{cases} \frac{dy_t^i}{dt} = [r(x_{\eta(t)}^i)(\frac{y_t^i}{\gamma} - 1)(1 - \frac{y_t^i}{M}) - \beta(x_{\eta(t)}^i)]y_t^i, \\ t \in [\tau_i^{k-1}, \tau_i^k) \end{cases} \quad (8)$$

Here,  $y_{\tau_i^0}^i = y_0^i$  and the growth function is given by  $H(y, x) = r(x)(y/\gamma - 1)(1 - y/M) - \beta(x)$ , where  $H(\cdot, x)$  reaches a maximum at  $\tilde{y} = (M + \gamma)/2$ ,  $0 < \gamma < M < \infty$ , with  $M$  and  $\gamma$  as the carrying capacity and the Allee threshold respectively.  $H$  belongs to the family of logistic growth functions with Allee effect, but where rates instead of being constant vary according to the environment:  $r$  is the linear birth rate function and  $\beta$  the death rate function, which are assumed to be in  $C(\mathbb{R})$  and are such that  $\Phi = \{x \in E : r(x)(\tilde{y}/\gamma - 1)(1 - \tilde{y}/M) < \beta(x)\} \neq \emptyset$ . So,  $\Phi$  is the largest DE representing extreme temperatures for the species growth.

#### Specific values/functions

To describe the allocation of the migrating biomass among neighboring patches, as in (5), we need to define the function  $f$  or the species fundamental niche function that describes the quality of a given patch to sustain a population of the focal species based upon the environment  $x$  at patch  $i$ . We will assume  $f$  as in (6); that is,  $f$  is a normal density-like function with location parameter  $\nu$  and scale  $\sigma$ , such that  $\nu$  represents the “ideal mean annual temperature” and  $\sigma$  represents how plastic the species is, or its environmental tolerance.

As pointed out above (see Some important concepts before Theorem 2), the niche function is related to the species population growth function  $H$ . We will represent this by linking  $\nu$  and  $\sigma$  with the species-dependent birth rate:

$$r(x) = a_r + \frac{b_r}{1 + \exp\{\frac{(x-\nu)^2}{\sigma}\}} \quad \text{and} \quad \beta(x) \equiv \beta > 0$$

To present our numerical example, we choose the following parameter values:

Function/Parameter	Value
$x_0^i - x_0^{i+1}, \forall i \in \mathcal{O}$ Initial difference in temperature between adjacent patches	$1 \times 10^{-1} \text{°C}$
$\varphi$ Magnitude of the change in the mean annual value of temperature	$4 \times 10^{-2} \text{°C}$
$\nu$ and $\sigma$ Optimal temperature and temperature tolerance	$20 \text{°C}$ and $1 \text{°C}$ respectively
$a_r$ and $b_r$ Parameters of the birth rate function	$0$ and $1$ respectively
$\beta$ Death rate	$1$
$\gamma$ and $M$ Allee threshold and carrying capacity	$100 \text{kg}$ and $10.000 \text{kg}$ per patch, respectively
$\partial\{E \cap \Phi^c\}$ Values of temperature delimiting the region outside DE	$\{1822 \times 10^{-2} \text{°C}; 2178 \times 10^{-2} \text{°C}\}$

The greatest open rectangle  $(y_*, y^*) \times (x_*, x^*)$  such that  $H(\cdot, \cdot) > 0$  turned out to be  $(331230 \times 10^{-2} \text{kg}; 678770 \times 10^{-2} \text{kg}) \times (1826 \times 10^{-2} \text{°C}; 2174 \times 10^{-2} \text{°C})$ .

Given the above values, we are going to set a time horizon of 100 years, where the temperature over  $\mathcal{O}$  will increase at most  $4 \text{°C}$  within it. Actually, this increase is predicted to be in the range of  $1 \text{°C}$  to over  $4 \text{°C}$  approximately (depending on the scenario considered) by the end of century ([40]), although not necessarily this can occur in a linear way as in this example (thus, notice that  $\tilde{p} = \varphi$ ). Also in this example, there is no species individuals living in environments whose mean annual values are less than  $1822 \times 10^{-2} \text{°C}$ , so it is enough to take  $E$  as any open set containing the interval  $[1822 \times 10^{-2}, x_0^1 + 4]$ .

Note that, under (8) and using the values of the table above, the maximum and minimum difference in temperature between adjacent patches are equal  $\rho^* = \rho_* = 1 \times 10^{-1} \text{°C}$ , and the length of  $\mathcal{T}^*$ , as defined in Fig. 1, is equal to  $|\mathcal{T}^*| = 4 \times 10^{-2}$ . Thus, condition 2 of Theorem 2 is immediately satisfied. Also, we can show that (G.4) holds. First, since jumps of the  $x_{\eta(\cdot)}^i$ 's are equal to  $4 \times 10^{-2} \text{°C}$  and patches are environmentally separated by  $1 \times 10^{-1} \text{°C}$ , exit times from  $(x_*, x^*)$  of the environment of adjacent patches  $i$  and  $i + 1$  are separated by  $3\Delta = 3$  years. Second,  $3480 \times 10^{-2} \rho^* \approx x^* - x_*$  in agreement with the conditions specified under (G.4).

Assumption (G.4) widely holds, so it is also clear that condition 3 of Theorem 2 will be as well. Further, this also means that we will have a very wide number of potential MSPs, which are important especially in the leading margins of a species geographic range, where conditions are by definition critical as they demarcate areas where the species persist from areas where the species does not. In practice, to identify a MSP we will choose a critical initial condition (near the points defined by  $\{y_*, x^*\}$ ) satisfying condition 1 in Theorem 3, which in this example corresponds to  $\{y_0^1, x_0^1\} = \{331240 \times 10^{-2} \text{kg}; 2173 \times 10^{-2} \text{°C}\}$ ,  $y_0^i = 0 \text{kg}$  for  $i > 1$ . To illustrate this, we are going to simulate two slightly different migration strategies, where just one of these is a MSP, represented by fixed values in  $(0, 1)$  of the migration function  $\lambda$  ( $\lambda \equiv \bar{\lambda}$  and  $\lambda \equiv \underline{\lambda}$  respectively), in the corresponding cases posed in (7) (i.e. except when  $H(y, x) = H_{\max}$  and  $H(y, x) \leq 0$  for  $(y, x) \notin (y^*, \infty) \times (x_*, x^*)$ ). Using the first migration strategy the species will persist (i.e., it is a MSP), and using the second one the species



## Growth Function

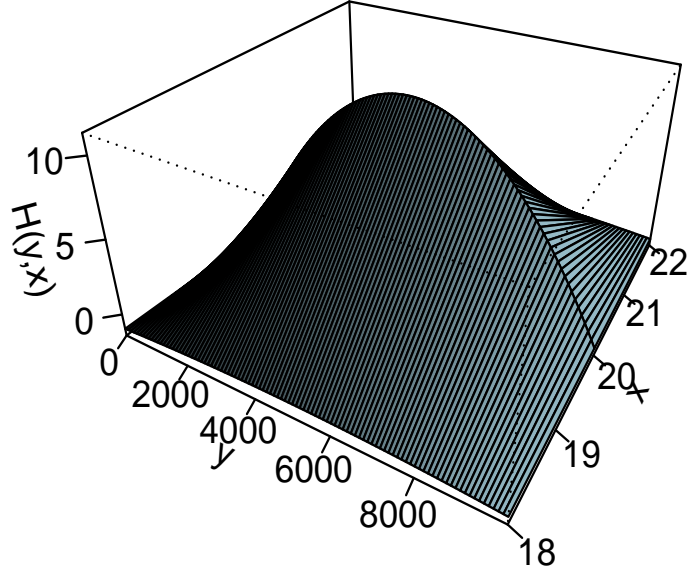


Figure 2: The 3-D growth function. In our numerical example  $H_{\max} = H(\tilde{y}, \nu)$  is reached at (5050kg, 20°C).

will die out (see Fig. 3 and Fig. 4 below). This numerical example indicates that if we consider such migration values, there exists a threshold value  $\lambda_{\text{th}}$  such that the species will persist if  $\lambda \geq \lambda_{\text{th}}$  and will die out otherwise. This is because of at the end of the first time period  $\Delta$  the species has to move enough biomass from patch 1 towards patch 2 to ensure its persistence. However, multiple, maybe infinite, MSPs could exist if we consider dynamic migration functions.

Using a constant migration rate function (except when  $H(y, x) = H_{\max}$  and  $H(y, x) \leq 0$  for  $(y, x) \notin (y^*, \infty) \times (x_*, x^*)$ , as indicated before) and a species' fundamental niche  $f$ , as a probability density-like, allowed us to find a critical or threshold migration rate. This critical migration rate (in this example

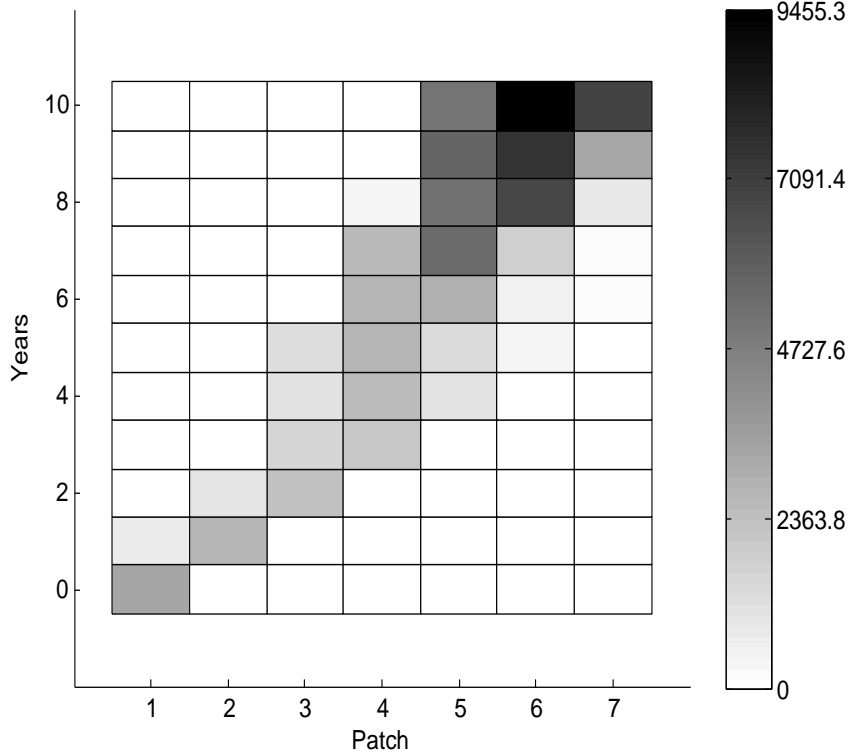


Figure 3: Species biomass dynamics during ten years and over the first seven habitat patches in response to climate change. In this example  $\lambda \equiv \bar{\lambda} \approx 81 \times 10^{-2}$  is a Migration Strategy for Persistence (MSP) and the biomass of the species grows.

$\lambda_{\text{th}}$ ) determines persistence and is usually shown to exist in models of species responses to climate change using integrodifference or reaction-diffusion equations (see, e.g., [48], [22], [39], [5], [24], [26]). We stress, however, that our model considers that a species could choose among several strategies for persistence (maybe infinite) if the conditions specified in Theorem 3 hold, resulting in a migration function instead a fixed dispersal rate. Nevertheless, a numerical or analytical analysis of functional MSPs is beyond the scope of this paper.

Our model also contemplates that different species can perceive environmental changes in different ways. Following this, it may be interesting to explore persistence under different  $\Delta$ 's, or the temporal scales that a given species uses to assess and respond to changes in its environment, and under different measures  $\mu_{\Delta}$ 's, and study the behavior of the corresponding  $\lambda_{\text{th}}$ 's. To do this, let us consider different measures  $\mu_{\Delta}$ 's as members of a family of weighted means:

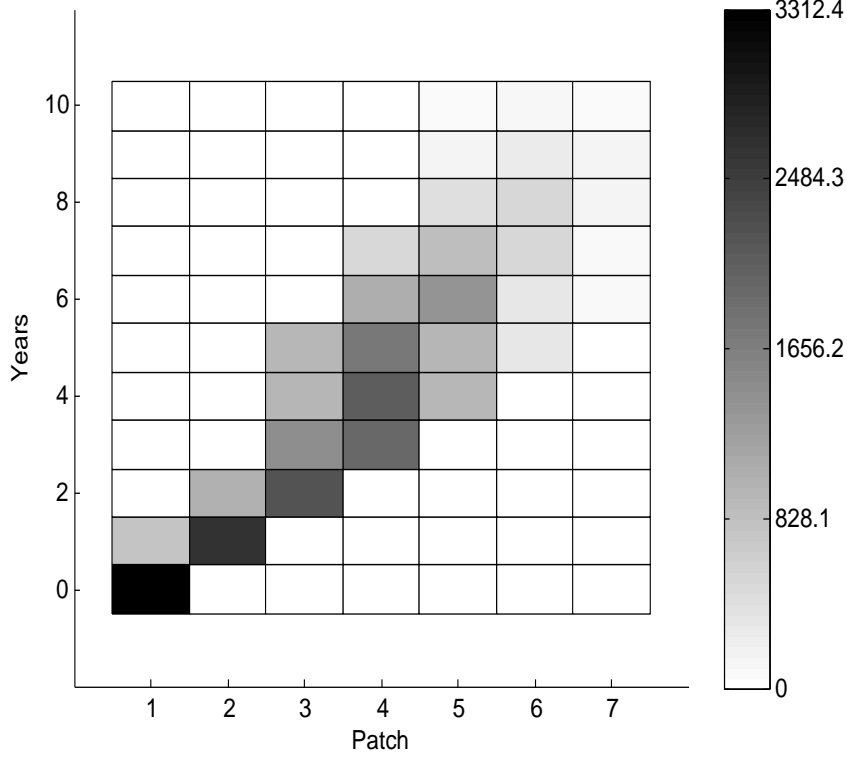


Figure 4: Species biomass dynamics during ten years and over the first seven habitat patches in response to climate change. In this example  $\lambda \equiv \underline{\lambda} \approx 80 \times 10^{-2}$  is not a Migration Strategy for Persistence (MSP) and the biomass of the species decays to extinction.

$q \max\{z_t^i, k - 1 \leq t < k\} + (1 - q) \min\{z_t^i, k - 1 \leq t < k\}$ ,  $q \in [0, 1]$ , where the measure used in the example above (i.e., mean annual temperature as described in (3)) corresponds to  $q = 1/2$  in the above expression. The question now is How does  $\lambda_{th}$  changes as we change  $q$  and/or  $\Delta$ ? As our context is the warming of  $\mathcal{O}$  and the initial conditions are critical, the case  $q > 1/2$  (i.e., the species is more sensitive to maximum temperatures than to average ones) probably results in an initial situation where the initial patch becomes unsuitable for the species growth, condemning it to extinction (in particular, condition 1 of Theorem 3 may not be satisfied). Therefore, only the case when  $q \leq 1/2$  deserves attention. Also, we are going to consider two cases:  $\Delta = 1$  year and  $\Delta = 2$  years, under the same family of measures, which also satisfy all the conditions/assumptions for the existence of a MSP. One of the consequences of changing  $\Delta$  is that the change of the filtered-environment through time will be perceived differently by

the different species:  $\tilde{p} = 4 \times 10^{-2}\text{°C}$  and  $\tilde{p} = 8 \times 10^{-2}\text{°C}$  respectively. Notice, however, that even though the change in the filtered environmental change is larger for  $\Delta = 2$ , it is small with respect to how much the species grows during  $\Delta = 2$  years as compared to  $\Delta = 1$  year (since both species grow with the same growth function  $H$ ), and hence the corresponding threshold value for persistence  $\lambda_{\text{th}}$  is lower for  $\Delta = 2$ , as shown in Fig. 5. Certainly a critical scale  $\Delta$  above which  $\tilde{p}$  does not satisfy condition 3 of Theorem 2 exists, maybe implying the nonexistence of a MSP. Biologically speaking, this means that the species will respond so slowly to environmental changes, that the environment will change from being suitable to be deteriorated, and thus having no place to escape before a response is possible. This may explain why some species characterized by fast life histories (like herbs) move faster in response to climate change than trees in the same region (see [23]).

Finally, Fig. 5 shows that as  $q$  becomes smaller (i.e., as the focal species is more sensitive to changes in the minimum temperature rather than mean or maximum ones), so does  $\lambda_{\text{th}}$ , since the filtered temperature of patch 1 does not go out immediately of the region where population growth is positive, with respect to temperature or  $(x_*, x^*)$ , as in the case with  $q = 1/2$ , hence the species can grow for a longer time and accumulate more biomass in the patch before it leaves the region with positive growth, thus requiring a lower proportion of migrating biomass to persist.

## 4 Discussion

In this contribution we presented a mathematical model that explicitly accounts for two important characteristics of the climate change phenomenon: 1) Scale dependency: different species may perceive the change in the environment as occurring at different rates because they perceive the environment at different scales, and 2) Measure dependency: different species may be sensible to or cue in on different aspects of the environment (e.g. maximum temperature, minimum temperature, accumulated temperature); that is they measure the environment differently. For example, an increase in minimum temperatures can negatively affect the survival of overwintering rust fungi (*Puccinia graminis*) [37] and rice grain yield [34]. More tellingly, an increase in minimum temperature during spring can negatively affect the biomass of some species (e.g. the C4 grasses) but have positive impacts upon the biomass of exotic C3 forbs in the same site [2]. Similarly, a decrease in the number of frost days may foster the invasion of exotic species over natives [45]. Scale dependency is also important as it affects the rate at which species respond to climate change. Lenoir et al [23] report that in general larger distributional shifts of plant species in west Europe were correlated with faster life histories such as shorter life cycle, faster maturation and smaller sizes at maturity, as well as with life forms; herb, ferns and mosses will likely move faster than shrubs and trees. Similar patterns have also been reported for the response of vertebrates to climate change [35]. This variability and scale dependency could be amplified by biotic factors such as changes in

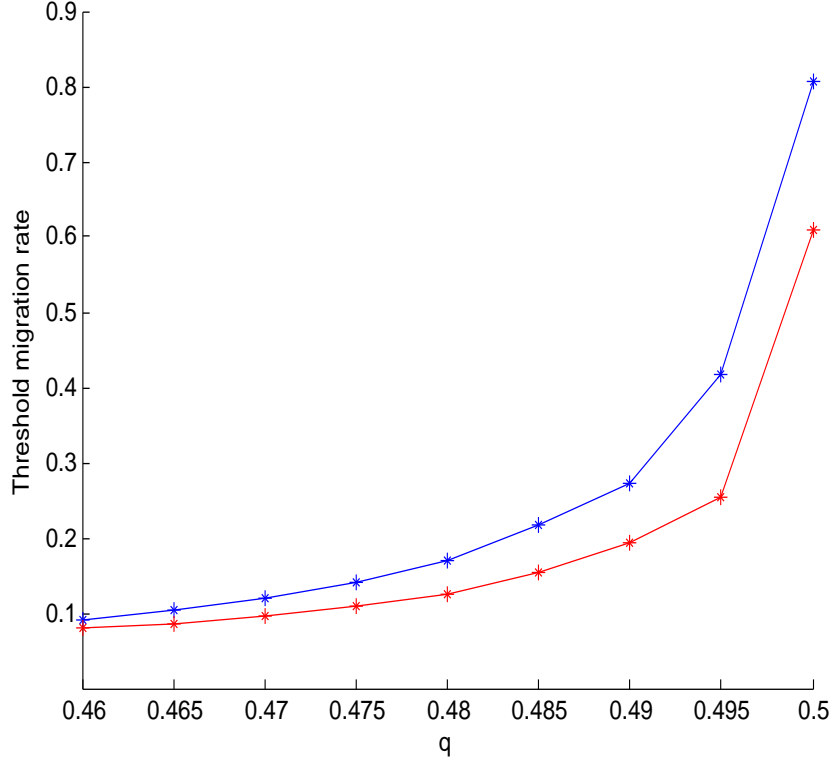


Figure 5: Behavior of the threshold migration rate  $\lambda_{\text{th}}$  under different measures from the family  $q \max\{z_t^i, k-1 \leq t < k\} + (1-q) \min\{z_t^i, k-1 \leq t < k\}$ ,  $q \in [0, 1]$ ,  $i, k \in \mathbb{N}$ , and different scales at which the species measures the environment: in ‘continuous line’  $\Delta = 1$  and in ‘dashed line’  $\Delta = 2$ .

the intensity of biotic interactions [14].

In the worst case scenario, the species living in a given region could be rapidly impacted by a changing climate and can not disperse or adapt fast enough to the environmental change, increasing their extinction risk ([16], [46], [42], [1], [32], [18] and [27]). While evolution and adaptation can be an important component of a species’ response to a changing climate (e.g., [33], [9], [12]) in this work we assumed that the environmental changes in our focal region  $\mathcal{O}$  was such that no species was able to evolve and adapt fast enough to the changing conditions. Thus, the species niche is fixed, there is no evolution and the only possible response to a changing climate is dispersal.

To our knowledge, under the no evolution assumption, this is the first model that accommodates in the same framework both phenomena: scale dependency and measure dependency, as defined above. Further, we show that both are

important in affecting the existence of what we call a Migration Strategy for Persistence (MSP). As illustrated in our numerical example (Fig. 3 and Fig. 4), the potential existence of a MSP, which depends on the function  $\lambda$ , does not guarantee the persistence of a given species since its  $\lambda$  may not be in the region where MSP exist. The analytical and numerical characterization of this region is an open problem, since it depends upon many factors. For example  $\lambda$  may be dynamic, instead of a fixed parameter as in our numerical example, and depend upon the quality of a given habitat or upon how the species measures the environment as exemplified in Fig. 5. This figure shows that under the same growth function  $H$  the corresponding migration values for persistence is affected by the scale at which the species measures its environment. In the numerical example, the  $\lambda_{\text{th}}$ 's associated to the MSP is smaller for species measuring the environment at a time scale  $\Delta$  equal to 2 years than for species measuring it at the time scale  $\Delta$  of 1 year (i.e. the species with  $\Delta$  equal to 2 requires less migration for persistence). Nevertheless, in our numerical example species with larger  $\Delta$  will not always be better off in terms of migration, since for some large enough value of  $\Delta$  condition 3 in Theorem 3 will not be satisfied. For example, for  $\Delta = 50$  years,  $\bar{p} = 2^\circ\text{C}$ , and a patch inhabited by the species whose environmental conditions are close to reach the ideal one ( $\nu = 20^\circ\text{C}$ ) will change so much that it will become inhabitable in one  $\Delta$ , and thus a MSP may not exist. A similar situation may occur regarding measure dependency. Fig. 5 shows that in general, for our numerical example, as  $q$  becomes larger (i.e. as species become more sensible to higher temperatures) larger  $\lambda_{\text{th}}$ 's are required in order to persist in the context of a warming climate. Indeed, one of our main conclusion is that there is not a single climate change but many, as its effects depend on the interaction between a particular species and climate. This interaction is not only affected by the length or temporal scale relevant to the species, but also for what is the change important for the species (i.e. what climatic signal is the species more sensible to). Thus, the problem is more complex than assumed by analytically tractable models of species responses to climate change (e.g. [24], [22]).

Another important feature of our model is that it can accommodate different types of population growth dynamics. For example, we chose to include an Allee effect (i.e.,  $\gamma > 0$ ) because they are paramount in affecting the movement of species across landscapes and in setting the boundaries of their spatial distribution ([21], [41], [4]). Also, our model can be extended to a two dimensional landscape and/or using more realistic dispersal kernels (see [29] for a review). In its current version, our dispersal kernel corresponds to the function  $\mathcal{C}^{\rightarrow}$  (see Eq. (3)) that expresses the proportion of biomass that the focal species will move to one of adjacent patches around the focal patch. In future extensions this proportions could be made to apply to larger neighborhoods, and include stochastic effects.

Finally, it is worth emphasizing that the numerical implementation of our model, could accommodate the existence of patches that are not habitable because of land use changes (e.g., transformed to urban or agriculture), as well as a more realistic dispersal functions that accommodates stochasticity, to as-

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sess their impact upon species' persistence and responses to climate change in human dominated landscapes. We expect to explore these possibilities in the future with the aim of helping to build a quantitative framework to assess the response of biodiversity to climate change in interaction with other drivers of global change.

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## Supplementary Material

### The particular case of climate change but no migration is allowed

Assume that our species is fenced in some patch  $i \in \mathcal{O}$ , i.e., the species cannot escape from  $i$  neither receive immigrants thereof. For a fixed  $x_{\eta(\cdot)}^i \equiv x \in E$ , our model will be represented by the ordinary differential equation (ODE)

$$\begin{cases} \frac{dy_t^i}{dt} = H(y_t^i, x)y_t^i \\ y_0^i \in [0, M] \end{cases}, \quad (9)$$

which has a unique solution for any finite time horizon  $[0, T]$  by the Picard–Lindelöf theorem. Moreover, its solution is non-negative and belongs to  $[0, M]$ , which implies that the solution of (9) is actually well-defined on  $\mathbb{R}_+$ .

Now, we can add the dynamics of the environment by considering  $x_{\eta(\cdot)}^i$  to be dynamical in (9) and obtain a piecewise ODE:

$$\begin{cases} \frac{dy_t^i}{dt} = H(y_t^i, x_{\eta(t)}^i)y_t^i \\ y_0^i \in [0, M] \end{cases} \quad (10)$$

It is “piecewise” because (10) is defined between the jumps of  $x_{\eta(\cdot)}^i$ ; between them we have a well-defined ODE as in (8). Note that the time range between jumps is fixed and equal to  $\Delta$ , as presented in (1). Thus, a solution of (10) can be constructed by joining the solutions between the jumps of  $x_{\eta(\cdot)}^i$ , knowing that the boundedness of the solution does not depend on the values taken by  $x_{\eta(\cdot)}^i$ .

Note that the process  $y_t^i$  is also right-continuous, where analogously we write  $\lim_{s \uparrow t} y_s^i = y_{t-}^i$  for all  $t > 0$ . Nevertheless, to avoid theoretical complications with derivatives over such discontinuities it would be convenient to use the notation

$$\begin{cases} dy_t^i = H(y_t^i, x_{\eta(t)}^i)y_t^i dt \\ y_0^i \in [0, M] \end{cases} \quad (11)$$

instead of (10), where  $y_t^i = y_0^i + \int_{(0,t)} H(y_{s-}^i, x_{\eta(s-)}^i)y_{s-}^i ds$ .

The following lemma will be employed repeatedly throughout this special case, whose proof follows from [1], Lemma 1.1 in Chapter 1.

**Lemma**

Let  $\theta_t$  be a process satisfying, for  $t \geq t_{in}$ ,

$$d\theta_t \leq (\xi_t \theta_t + \zeta_t) dt,$$

where  $\xi_t$  and  $\zeta_t$  are integrable functions over every finite time horizon. Then

$$\theta_t \leq \theta_{t_{in}} \exp\left\{\int_{t_{in}}^t \xi_{s-} ds\right\} + \int_{t_{in}}^t \exp\left\{\int_s^t \xi_{u-} du\right\} \zeta_{s-} ds$$

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Given the general structural conditions assumed for  $H$  in Section 2.2, the species always goes extinct when  $y_0^i \in [0, \gamma)$ , that is when the initial biomass is below the Allee threshold and regardless of the state of the environment. In fact, we have that:

$$dy_t^i = H(y_t^i, x_{\eta(t)}^i) y_t^i dt \leq H^*(y_t^i) y_t^i dt \leq H^*(y_0^i) y_t^i dt,$$

since  $H^*(\cdot)$  is negative and increasing on  $[0, \gamma)$ ; and by the previous lemma we obtain,

$$y_t^i \leq y_0^i \exp\{tH^*(y_0^i)\} \xrightarrow[t \uparrow \infty]{} 0$$

But when  $y_0^i \in [\gamma, M]$  is possible for the species to grow positively. Nevertheless, such an increase could be reversed if the environment becomes progressively worst for the species such that  $H$  becomes always negative.

Henceforth, we are going to consider that the environment, as experienced by the focal species, is becoming increasingly less suitable for its persistence. In order to explicitly define it with respect to (11), and study its future behavior, we need additional definitions and assumptions:

(S.1) Let us define a *Deteriorated Environment* (DE) as a set that belongs to  $\Phi = \{\mathcal{E} \in \mathcal{B}(E) : H(\tilde{y}, \cdot) < 0 \text{ on } \mathcal{E}\} \neq \emptyset$ , where  $\mathcal{B}(E)$  is the set containing all the open subsets of  $E$ . Additionally, we assume that  $E \cap \Phi^c$  is connected, that is,  $\text{int}\{E \cap \Phi^c\} \neq \emptyset$  cannot be represented as the union of two or more disjoint nonempty open subsets of it.

(S.2) We assume that  $\Phi$  is an attracting set for  $x_{\eta(\cdot)}^i$ .

In (S.1) we consider  $E \cap \Phi^c$  connected because we think of  $\Phi$  as a set of extreme values for the species within the state space  $E$  that are outside of the range where the species could grow. Also, as  $\Phi$  is open,  $\Phi$  is reached by  $x_{\eta(\cdot)}^i$  in finite time.

Unfortunately, in this particular case, independently of the starting point  $(y_0^i, x_0^i)$  of (11), the species unavoidably goes extinct. Indeed, let  $\tau = \inf\{t \geq 0 : x_{\eta(t)}^i \in \Phi\}$ , or equivalently  $\kappa = \inf\{k \in \mathbb{N} \cup \{0\} : x_k^i \in \Phi\}$ , where  $\tau = \Delta\kappa < \infty$  by (S.2). So, the extinction of the species can be shown by observing that:

$$dy_t^i = H(y_t^i, x_{\eta(t)}^i) y_t^i dt \leq H(\tilde{y}, x_{\eta(t)}^i) y_t^i dt,$$

and given that the inequality is true for all  $t \in [\tau, \tau + \ell\Delta]$ , for all  $\ell \in \mathbb{N}$ , by applying the previous lemma again, over  $t \in [\tau, \tau + \ell\Delta]$ , we get:

$$y_{\tau+\ell\Delta}^i \leq y_{\tau}^i \exp\left\{ \int_{(\tau, \tau+\ell\Delta]} H(\tilde{y}, x_{\eta(s-)}^i) ds \right\} = y_{\tau}^i \exp\left\{ \sum_{\ell'=1}^{\ell} H(\tilde{y}, x_{\kappa+\ell'-1}^i) \Delta \right\}$$

By (S.1) and (S.2)  $H(\tilde{y}, x_{\eta(\cdot)}^i) < 0$  on  $(\tau, \infty)$  and hence,  $y_{\tau+\ell\Delta}^i \xrightarrow[\ell \uparrow \infty]{} 0$ .

Under this simple reasoning we can further conclude that the species will die out if fenced. Nevertheless, if the species can move away from the deteriorating

conditions from one patch into another through dispersal, thus escaping from DEs at a large enough rate, the species might survive.

### Theorem 1

(4) has a unique solution.

#### Proof

We can proceed similarly as in the case of no migration: we consider first a “fixed environment” (i.e. for any window of size  $\Delta$ , which are by definition non-overlapping) and prove its well-posedness; finally, the general solution is obtained by joining the solutions between the jumps of the  $x_{\eta(\cdot)}^i$ 's.

Without loss of generality, assume that the set  $\{i \in \mathcal{O} : x_0^i = x^i \in E \cap \Phi^c\}$  are the  $n$  first patches, that is  $\{i \in \mathcal{O} : x_0^i = x^i \in E \cap \Phi^c\} = \{1, \dots, n\}$ , for some  $n \in \mathbb{N}$ . As those processes jump together at the same time, let  $\{\tau^k\}_{k \in \mathbb{N}}$  be the sequence of its jump times.

For  $\mathbb{R}^n$  vectors  $\mathcal{Y} = (y^{(1)}, \dots, y^{(n)})^T$  and  $\mathcal{X} = (x^{(1)}, \dots, x^{(n)})^T$ , where T is the matrix/vector transposition, let  $\mathcal{H}(\mathcal{Y}, \mathcal{X})$  be an  $n \times n$  diagonal matrix whose elements are  $(H(y^{(i)}, x^{(i)}))_{i=1, \dots, n}$ , and consider the following matrix norms for real  $n \times n$  matrices  $Q = (q_{i,j})_{i,j=1, \dots, n}$ :

$$\|Q\|_{\text{F}} = \left( \sum_{1 \leq i, j \leq n} (q_{i,j})^2 \right)^{1/2}$$

and

$$\|Q\|_{\text{max}} = \max_{1 \leq i, j \leq n} |q_{i,j}|,$$

and let  $\|\cdot\|$  the usual  $\mathbb{R}^n$  Euclidean norm. We have the following relation among these norms:

$$\|\mathcal{H}(\mathcal{Y}, \mathcal{X})\mathcal{Y}\| \leq \sqrt{n} \|\mathcal{H}(\mathcal{Y}, \mathcal{X})\|_{\text{max}} \|\mathcal{Y}\| \leq \sqrt{n} \|\mathcal{H}(\mathcal{Y}, \mathcal{X})\|_{\text{F}} \|\mathcal{Y}\|$$

Thus, assumptions made for  $H$  can be expressed as follows: for each  $R > 0$  there exist non-negative functions  $\mathcal{M}_R(\mathcal{X}, n)$  and  $\mathcal{N}_R(\mathcal{X}, n)$  such that:

$$\|\mathcal{H}(\mathcal{Y}, \mathcal{X})\mathcal{Y}\| \leq \mathcal{M}_R(\mathcal{X}, n),$$

$$\|\mathcal{H}(\mathcal{Y}', \mathcal{X})\mathcal{Y}' - \mathcal{H}(\mathcal{Y}'', \mathcal{X})\mathcal{Y}''\| \leq \mathcal{N}_R(\mathcal{X}, n) \|\mathcal{Y}' - \mathcal{Y}''\|,$$

if  $\|\mathcal{Y}\|, \|\mathcal{Y}'\|$  and  $\|\mathcal{Y}''\|$  are less or equal to  $R$ .

Then, the following system has a unique solution:

$$\begin{cases} \frac{dy_t^i}{dt} = H(y_t^i, x_0^i)y_t^i, & t \in (0, \tau_1) \\ y_0^i > 0, \quad i = 1, \dots, n \end{cases} \quad (12)$$

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(see [1], Theorem 1.2, Chapter 1). To construct the general solution, define for every  $i = 1, \dots, n$ :

$$\Delta y_{\tau_1}^i = \lim_{\epsilon \downarrow 0} [y_{\tau_1}^i - y_{\tau_1 - \epsilon}^i] = \lim_{\epsilon \downarrow 0} \left[ \sum_{i' \in \psi^i} \mathcal{C}_{\tau_1 - \epsilon}^{i' \mapsto i} \lambda(y_{\tau_1 - \epsilon}^{i'}, x_0^{i'}) y_{\tau_1 - \epsilon}^{i'} - \lambda(y_{\tau_1 - \epsilon}^i, x_0^i) y_{\tau_1 - \epsilon}^i 1_{\{\Psi_{\tau_1 - \epsilon}^i \neq \emptyset\}} \right]$$

Thus, we consider that

$$y_{\tau_1}^i = y_{\tau_1 -}^i + \Delta y_{\tau_1}^i,$$

where  $y_{\tau_1 -}^i = \lim_{\epsilon \downarrow 0} y_{\tau_1 - \epsilon}^i$ . If  $x_{\eta(\tau_1)}^{i+1} \in E \cap \Phi^c$ , define:

$$y_{\tau_1}^{i+1} = \lim_{\epsilon \downarrow 0} \mathcal{C}_{\tau_1 - \epsilon}^{i \mapsto i+1} \lambda(y_{\tau_1 - \epsilon}^i, x_0^i) y_{\tau_1 - \epsilon}^i$$

Therefore, we can define an analogous system as (12):

$$\begin{cases} \frac{dy_t^i}{dt} = H(y_t^i, x_{\eta(\tau_1)}^i) y_t^i, & t \in (\tau_1, \tau_2) \\ i \in \mathcal{O}, y_{\tau_1}^i > 0 \end{cases}$$

Finally, we can proceed similarly as above to construct the solution of (4) over the disjoint sequence of time intervals  $\{[\tau_i, \tau_{i+1}]\}_{i \in \mathbb{N}}$ .  $\square$

## Proof of Theorem 2

Let  $i \in \mathcal{O}$  satisfying condition 1 and let  $\tau_i^{\text{out}} = \inf\{t > 0 : x_{\eta(t)}^i > x^*\}$ . Note that there exists  $\kappa_i^{\text{out}} \in \mathbb{N}$  such that  $\tau_i^{\text{out}} = \kappa_i^{\text{out}} \Delta$ , where  $\kappa_i^{\text{out}} - 1 \in \mathbb{N} \cup \{0\}$  by (G.4). Consider the following cases.

(a)  $\kappa_i^{\text{out}} - 1 = 0$ . By (G.4),  $x_{\kappa_i^{\text{out}}}^{i+1} \in (x_*, x^*)$ , and we have that,

$$\begin{aligned} y_{\tau_i^{\text{out}}}^{i+1} &\geq \lim_{\epsilon \downarrow 0} \mathcal{C}_{\tau_i^{\text{out}} - \epsilon}^{i \mapsto i+1} \lambda(y_{\tau_i^{\text{out}} - \epsilon}^i, x_{\kappa_i^{\text{out}} - 1}^i) y_{\tau_i^{\text{out}} - \epsilon}^i = \mathcal{C}_{\tau_i^{\text{out}} -}^{i \mapsto i+1} \lambda(y_{\tau_i^{\text{out}} -}^i, x_{\kappa_i^{\text{out}} - 1}^i) y_{\tau_i^{\text{out}} -}^i \\ &> \lambda(y_{\tau_i^{\text{out}} -}^i, x_{\kappa_i^{\text{out}} - 1}^i) y_{\tau_i^{\text{out}} -}^i, \end{aligned}$$

because  $\mathcal{C}_{\tau_i^{\text{out}} -}^{i \mapsto i+1} = 1$  by condition 2. Now define  $\lambda$  as:

$$\lambda(y, x) = \begin{cases} 0, & H(y, x) = H_{\max} \\ 1, & H(y, x) \leq 0, (y, x) \notin (y^*, \infty) \times (x_*, x^*) \\ \frac{1}{2}^{1/\ell(y, x)}, & \text{otherwise} \end{cases}, \quad (13)$$

with  $\ell : [0, M] \times E \rightarrow \mathbb{R}_+ \cap \{0\}^c$  a right-continuous function. Notice that it satisfies (7). We have that  $\lambda(y_{\tau_i^{\text{out}} -}^i, x_{\kappa_i^{\text{out}} - 1}^i) \neq \lambda(\tilde{y}, \nu) = 0$ , since by condition 3,  $x_{\kappa_i^{\text{out}} - 1}^i > \nu$ . Note that there exists  $\ell_0 > 0$  such that  $y_{\tau_i^{\text{out}} -}^{i+1} > y_*$ , if we define the function  $\ell$  in (13) such that  $\ell(y, x) \leq \ell_0$ , for all  $(y, x) \in (y_*, \infty) \times (\nu, x^*)$ .

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(b)  $\kappa_i^{\text{out}} - 1 > 0$ . We have that,

$$\begin{aligned}
y_{\Delta}^i &\geq y_0^i + \int_{(0,\Delta]} H(y_{s-}^i, x_0^i) y_{s-}^i ds - \sum_{\{s \in (0,\Delta] : \eta(s) \neq \eta(s-)\}} \lambda(y_{s-}^i, x_0^i) y_{s-}^i \\
&= y_0^i + \int_{(0,\Delta]} H(y_{s-}^i, x_0^i) y_{s-}^i ds - \lim_{\epsilon \downarrow 0} \lambda(y_{\Delta-\epsilon}^i, x_0^i) y_{\Delta-\epsilon}^i \\
&= y_0^i + \int_{(0,\Delta]} H(y_{s-}^i, x_0^i) y_{s-}^i ds - \lambda(y_{\Delta-}^i, x_0^i) y_{\Delta-}^i \\
&= y_{\Delta-}^i (1 - \lambda(y_{\Delta-}^i, x_0^i)),
\end{aligned}$$

because  $y_{\Delta-}^i = \left( y_0^i + \int_{(0,\Delta]} H(y_{s-}^i, x_0^i) y_{s-}^i ds \right)$ . Consider the following strategy: in patch  $i$  maintain the species biomass over  $y_*$  until  $x_{\eta(t)}^i > \nu$ , and thereafter proceed analogously as in (a) above. This can be done by choosing  $\ell_1 > 0$  such that:

$$\lambda(y, x) < 1 - \frac{y_*}{y},$$

if we define the function  $\ell$  in (13) such that  $\ell(y, x) \geq \ell_1$ , for all  $(y, x) \in (y_*, \infty) \times (x_*, \nu]$ .

Finally, by defining  $\tau_{i+1}^{\text{out}} = \inf\{t > \tau_i^{\text{out}} : x_{\eta(t)}^{i+1} > x^*\}$ , we can proceed in an analogous way as above. Thus, the proof is finished.  $\square$

## References

- [1] Khasminskii, R. *Stochastic Stability of Differential Equations*. Applications of Mathematics. Springer-Verlag, 2012. ISBN 9783642232794.