¹ Influence of dispersal processes on the global dynamics of Emperor penguin,

² a species threatened by climate change.

³ **Running head**: Would dispersal act as an ecological rescue?

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Abstract. Species endangered by rapid climate change may persist by tracking their optimal habitat; this depends on their dispersal characteristics. The Emperor Penguin (EP) is an Antarctic seabird threatened by future sea ice change, currently under consideration for listing under the US Endangered Species Act. Indeed, a climate-dependent-demographic model without dispersion projects that many EP colonies will decline by more than 50% from their current size by 2100, resulting in a dramatic global population decline. Here we assess whether or not dispersion could act as an ecological rescue, i.e. reverse the anticipated global population decline projected by a model without dispersion. To do so, we integrate detailed dispersal processes in a metapopulation model—specifically, dispersal stages, dispersal distance, habitat structure, informed dispersal behaviors, and density-dependent dispersion rates. For EP, relative to a scenario without dispersion, dispersal can either offset or accelerate climate driven population declines; dispersal may increase the global population by up to 31% or decrease it by 65%, depending on the rate of emigration and distance individuals disperse. By developing simpler theoretical models, we demonstrate that the global population dynamic depends on the global landscape quality. In addition, the interaction among dispersal processes - dispersion rates, dispersal distance, and dispersal decisions - that influence landscape occupancy, impacts the global population dynamics. Our analyses bound the impact of between-colony emigration on global population size, and provides intuition as to the direction of population change depending on the EP dispersal characteristics. Our general model is flexible such that multiple dispersal scenarios could be implemented for a wide range of species to improve our understanding and predictions of species persistence under future global change.

Keywords: habitat selection — conspecific attraction — density dependence — distance of dispersal — dispersion rate — carrying capacity — emperor penguin — Antarctica

1 Introduction

Rapid climate change poses a fundamental threat to many species because it alters habitat suitability across their entire range. To preserve species in the face of rapid climate change, a new conservation paradigm involving a global spatial scale approach is warranted (Hannah, 2010). To inform conservation and management policy on future climate change impacts, quantitative global population projections including climate effects on population dynamics and forecasts of the future climate are required (Jenouvrier et al., 2014; Jenouvrier and Visser, 2011).

When the population decline is driven by climate changes that exceed species' tolerance or when acclimation and adaptation are insufficient to allow species persistence in a particular location (Visser, 2008), species' dispersal capabilities could be the key for persistence (Travis et al., 2012; Ponchon et al., 2015). Here, we study whether dispersal will act as an *ecological rescue* mechanism to reverse the global population decline of species endangered by climate change. We distinguish this ecological rescue from the local population rescue effect in source–sink dynamic models (Hanski, 1982). Here, ecological rescue focuses on species persistence, i.e. global population viability.

The Emperor Penguin (*Aptenodytes forsteri*, hereafter EP) is an Antarctic seabird endangered by future climate change (Jenouvrier et al., 2014), currently considered for listing under the Endangered Species Act (http://www.regulations.gov # FWS-HQ-ES-2016-0072). Previous studies have shown that EPs are very sensitive to change in sea ice, and local and global population declines are projected by the end of the century if sea ice concentration (SIC) decreases at the rates projected by climate models (Jenouvrier et al., 2012, 2014). EPs depend on sea ice to breed, feed, and molt (Ainley et al., 2010), and there is an optimal amount of sea ice for population growth (Jenouvrier et al., 2012). Because sea ice is projected to decline at geographically heterogeneous rates, some habitats will be more

favorable than others (Ainley et al., 2010). Without dispersion, at least two-thirds of known colonies are projected to decline by more than 50% from their current size by 2100 (Jenouvrier et al., 2014). As a result, the global population size is projected to decline dramatically by the end of the century.

Individual dispersal behaviors for EPs are poorly understood because EP have been marked at only one site (Pointe Géologie, Barbraud and Weimerskirch (2001)), and no recapture occurred at other colonies. Until recently, EPs were considered to be highly philopatric (Prevost, 1961). Recent studies have now shown a high degree of genetic homogenization for EP colonies from Adélie Land to the Weddell Sea, suggesting high connectivity in these populations via individual dispersal among colonies (Younger et al., 2015; Cristofari et al., 2016; Li et al., 2014). In addition, recent work suggests that EP colonies can move onto ice shelves and perhaps found new colonies (Fretwell et al., 2012, 2014; LaRue et al., 2015). Thus, there is a current debate on the impact of dispersal processes, and whether dispersion and habitat selection behavior could reverse the anticipated global population decline of EPs.

Dispersal is a process composed of three distinct behavioural stages: the decision to leave the resident patch (emigration), movement between patches (transfer), and settlement into a new patch (immigration) (Bowler and Benton, 2005). Furthermore, individuals may gather and exchange information during these different stages, a process defined as informed dispersal decisions by Clobert et al. (2009). Indeed individuals may preferentially leave unfavorable habitat (e.g climate deteriorated or exceeding carrying capacity) and settle in higher-quality habitat by relying on environmental cues or by assessing habitat quality through the breeding success or presence of conspecifics (Stamps, 2001).

Informed dispersers track environmental conditions closely and concentrate in few favorable patches, while random dispersers "spread their bets" across patches that experience contrasting environmental conditions (Armsworth and Roughgarden, 2005). Several studies

have found contrasted results of the effect of informed dispersal on the metapopulation dynamics. Informed dispersal decisions may concentrate the population within few favorable patches, lower the proportion of occupied patches, increasing the probability of extinction of the metapopulation (Ray et al., 1991; Anderson et al., 2009). Conversely informed dispersal decisions may allow the metapopulation population to persist longer at a larger size compared to random or no dispersal by concentrating the population in high-quality habitat (Ponchon et al., 2015). In addition, dispersal distance, landscape structure, local density, and local population dynamics influence species responses to climate change in complex ways (McRae et al., 2008; Anderson et al., 2009; Bennie et al., 2013; Altwegg et al., 2014). Thus, a metapopulation model is required to explore the consequences of various potentially realistic dispersal scenarios on EP persistence under future climate change.

Here, we develop a general metapopulation model that predicts species persistence in heterogeneous landscapes and non-stationary environments arising from climate change. It integrates, in a single framework, three dispersal stages, dispersal distance, informed or random movement, and density-dependent emigration and immigration rates within a structured habitat. Specifically, we incorporate putative dispersal behaviors, and study if the global population dynamics of emperor penguins depend on 1. the proportion of individuals emigrating from unfavorable quality habitat, 2. the dispersal distance, and 3. the existence of informed dispersal decisions. An 'informed decision' indicates that the decision to leave a colony and resettle is based on both a cue that conveys the climate-dependent quality of the habitat and on the local population density. We discuss how the influence of these climate-dependent dispersal behaviors is mediated by the quality of the whole landscape (measured as the global growth rate), with insights from theoretical models.

2   Materials and methods

We first describe our study species: the emperor penguin (EP). A metapopulation model is a perfect approach for the EP because they breed in large colonies (>100 individuals) on fast sea ice (sea ice that is fastened to the coastline), forming a set of discrete, yet potentially connected local populations over the entire species range along the Antarctic coast (Fretwell and Trathan, 2009) (Appendix A, Fig. A.1).

We develop a general metapopulation model including reproduction and dispersal phases that depend on various descriptors of the habitat. We parameterize this model using results of previous studies on the impact of sea ice on the life history of EP using the long-term capture-recapture data set collected at Pointe Géologie (Jenouvrier et al., 2010, 2012, 2014), and the spatial distribution of EP colonies observed from satellite imagery (Fretwell et al., 2012). Furthermore, we develop potential dispersal scenarios using information from studies on EP genetic (Cristofari et al., 2016; Younger et al., 2015), foraging ecology (Thiebot et al., 2013), and colonies movement (LaRue et al., 2015), as well as from studies on other birds using public information sources (Doligez et al., 2002), and relying on indirect cues to assess habitat quality (e.g. presence of conspecifics Stamps (2001)).

Finally, we conduct global sensitivity analysis (Aiello-Lammens and Akçakaya, 2016) to assess the respective impact of dispersal distance, dispersion rates and dispersal behaviors on the global population size and to account for high uncertainty in all parameters simultaneously.

2.1   A case study: the emperor penguin

They reproduce during winter (March through December) on fast sea ice and spend the non-breeding season at sea or on pack sea ice (ice that is not attached to the shoreline and drifts in response to winds, currents, and other forces) (Ainley et al., 2010). Little is known

about dispersal behaviors for the EP, thus we construct and compare two models, one which includes dispersal and one which does not. For many seabirds, fidelity to their natal colony and breeding site at adulthood is very high (Gauthier et al., 2010), thus we typically assume that the proportion of emigrant penguins from any favorable colony is zero; this is the basis for the no-dispersal model. We then model a scenario in which the EPs disperse during the non-breeding season. When a site becomes unfavorable, penguins may leave the colony with a probability proportional to their resident habitat quality (informed departure, Clobert et al., 2009). They may settle randomly in a new colony (random search) or in colonies that maximise their fitness (informed search) within their maximum dispersion range. Individuals may disperse over long or short distances using the aforementioned dispersal behaviors.

2.2   The metapopulation model

Our metapopulation model projects the population vector $\mathbf{n}$—comprising the population size n_i in each patch i—from time t to $t+1$. We write

$$\mathbf{n}(t + 1) = \mathbf{D}\big[\mathbf{x}(t), \mathbf{n}(t)\big]\mathbf{F}\big[\mathbf{x}(t), \mathbf{n}(t)\big]\,\mathbf{n}(t) \tag{1}$$

to indicate that the projection interval is divided into two main phases of possibly different duration: the reproduction phase ($\mathbf{F}$) followed by the dispersal phase ($\mathbf{D}$) [1]. The reproduction matrix $\mathbf{F}$ is constructed using the Ricker model, which includes the intrinsic population growth rate $\mathbf{r}$ $r_i(t)$, which may vary in time, and the carrying capacity of the patch, K_i, which is set to be constant over the entire time period. The dispersal phase ($\mathbf{D}$) combines various dispersal behaviors and dispersal events. The projection matrices $\mathbf{D}$ and $\mathbf{F}$ depend on both the current population density $\mathbf{n}(t)$ and the habitat characteristics, $\mathbf{x}(t)$, that vary among patches and over time, t. The global population size at time t is given by $N_t = \sum_i n_i(t)$.

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[1]Note on notation: In this paper, matrices are denoted by upper case bold symbols (e.g. $\mathbf{F}$) and vectors by lower case bold symbols ($\mathbf{n}$); f_{ij} is the (i, j) entry of the matrix $\mathbf{F}$, n_i is the *ith* entry of the vector $\mathbf{n}$.

2.3 Habitat descriptors

The habitat is described by three vectors $(\mathbf{x}_1, \mathbf{x}_2, \mathbf{x}_3)$ comprising the habitat component x_i in each patch i that may vary in time. Our first habitat descriptor is the quality of the habitat measured by the realized per capita growth rate $\mathbf{x}_1(t) := \mathbf{r}^*(SIC_t, \mathbf{K})$. The realized population growth rate depends both on the sea ice concentration (SIC, i.e. relative amount of area covered by ice, including both pack and fast ice), which influences the intrinsic growth rate $\mathbf{r}(SIC_t)$, and the carrying capacity of the patch, $\mathbf{K}$. $\mathbf{r}^*$ can differ from the intrinsic growth rate $\mathbf{r}$ from the Ricker model because when the sub-population, n_i, approaches its carrying capacity, the realized population growth rate is slower $(r_i^* < r_i)$. At time t, a habitat is favorable if $\mathbf{r}^*(SIC_t, \mathbf{K}) > 0$, and unfavorable if $\mathbf{r}^*(SIC_t, \mathbf{K}) \leq 0$. Thus a habitat can be unfavorable because *(i)* the colony experiences good SIC $(r(t)_i > 0)$ but exceeds carrying capacity $(n(t)_i > K_i)$ or *(ii)* the colony experiences poor SIC $(r(t)_i \leq 0)$.

The carrying capacity is our second descriptor: $\mathbf{x}_2(t) := \mathbf{K}$. It represents the maximum number of individuals that the habitat's resources can sustain without significantly depleting or degrading those resources.

The distance between the colonies is a spatial descriptor of the habitat structure that plays an important role in the dispersal process. It is represented by the matrix $\mathbf{x}_3 := (\text{dist}(i,j))$ which corresponds to the coastal distance between colonies i and j derived from the location of know EP colonies (Fretwell et al. (2012), Appendix A). Note, that $\mathbf{x}_3$ does not include potential novel habitats for EP and thus is not time-dependent.

2.4 Reproduction phase

The reproduction matrix, $\mathbf{F}$, is constructed using the Ricker model (Appendix B.1), whereby negative density-dependence effects occur within crowded favorable habitats $(r_i > 0)$ while populations tend to go extinct within poor habitat colonies $(r_i \leq 0)$. For each projection

8

interval t, we parameterize the intrinsic growth rate of each colony $r_i(t)$ using the median
of the stochastic population growth projected by a sea-ice dependent population model
without density dependence (Jenouvrier et al., 2014). The sea-ice dependent population
model integrates the whole life cycle of EP, specifically pre-breeders and non-breeders of
both sexes, as well as breeding pairs (Jenouvrier et al., 2010, 2014). The vital rates and their
response to sea ice included in this previous model are described in details in Jenouvrier et al.
(2012). The sea ice projections were obtained from a subset of atmosphere ocean general
circulation models (AOGCMs) forced with a middle range emissions scenario, which assumes
a future socio-economic development depending on fossil and non-fossil energy sources in
balanced proportions.

If we omit dispersion our mathematical model is

$$\mathbf{n}(t+1) = \mathbf{F}\big[\mathbf{x}(t), \mathbf{n}(t)\big]\,\mathbf{n}(t). \tag{2}$$

For EPs, estimating the carrying capacity of the environment is a daunting task because
population time-series are limited to a few colonies around Antarctica, and no study thus
far has reported the resources and breeding habitat availability. We estimate the carrying
capacity of each patch using the population projections from the stochastic sea-ice dependent
model that excludes density dependence (Jenouvrier et al., 2014). Our method results in
$K_i = 2N_0$, with N_0 the initial size of the population observed in 2009 (Appendix B.1).
Using other values of the carrying capacity does not qualitatively change our conclusions
(Appendix B.1, Fig. B.1, B.2).

2.5   The dispersal phase.

A dispersal event includes the three stages (Fig.1): (1) emigration from the resident patch,
(2) search for new patch among other patches with an average dispersal distance d (transfer),

9

and (3) settlement in a new patch. The duration of the transfer phase can vary, as the final settlement in a new patch may occur after several events (e.g., an individual may not settle in its first choice habitat if that habitat has reached its carrying capacity $n_i \geqslant K_i$.) In our model, movements of individuals among colonies are divided into two successive dispersal events to account for a time-limited search. Indeed for EPs the breeding season lasts 9 months, and thus the timing for prospecting other colonies during the non-breeding season is limited. During the first dispersal event ($\mathbf{D}^1$) individuals may select the habitat with highest quality (informed search) or settle in a random habitat. During the second dispersal event ($\mathbf{D}^2$) individuals that reached a saturated patch leave and settle randomly in a new patch (Fig.1). The later is a way to account for a dispersal cost of gathering information for the informed search (see discussion).

The dispersal projection matrix $\mathbf{D}$ is thus

$$\mathbf{D} := \mathbf{D}^2 \, \mathbf{D}^1. \tag{3}$$

and each dispersal matrix $\mathbf{D}^e$ is written

$$\mathbf{D}^e := \mathbf{S}^e[\mathbf{x}] \, \mathbf{M}^e[\mathbf{x}, \mathbf{n}_e] \tag{4}$$

to indicate that matrices for searching behavior, $\mathbf{S}^e$, and emigration, $\mathbf{M}^e$, depend on the population size at the start of the event (n_e) as well as the environment conditions $\mathbf{x}(t)$ (Appendix B.2).

The first dispersal event   The emigration rate for each patch i depends on the quality of the habitat, which is measured by the realized population growth r_i^*. The emigration rate increases linearly from $m^1 = 0$ at $r \geqslant 0$ to $m^1 = 1$ at critical value $r_c^* < 0$. The emigration

10

matrix thus only depends on the ratio $\mathbf{r}^*(t)/r_c^*$,

$$\mathbf{M}^1 := \mathbf{M}^1\left[\frac{\mathbf{r}^*(t)}{r_c^*}\right]. \tag{5}$$

A critical threshold r_c^* close to 0, corresponds to high dispersion scenario (red line on Fig.B.3), while a larger negative threshold reflects low dispersion (blue line on Fig.B.3; Appendix B.2, Eq. (B.4)).

Once individuals have left their colonies, we assume that they search for a new colony using two different behaviors: an informed searching behavior ($\mathbf{S}_I$) and a random searching behavior ($\mathbf{S}_R$).

The random search assumes that dispersers randomly seek a colony within the limits of the maximum dispersal distance. Thus the probability of selecting a colony depends on the mean dispersal distance of the EP, d, and the distance between colonies $\mathbf{x}_3 = (\text{dist}(i,j))$ (see Eq. (B.7)):

$$\mathbf{S}_R := \mathbf{S}_R[\mathbf{x}_3, d]. \tag{6}$$

Conversely, *the informed search* assumes that dispersers search for the most favorable habitat they can reach; we use $\mathbf{r}^*$ as a descriptor of the quality of the habitat. Thus the informed search matrix is also a function of r^*:

$$\mathbf{S}_I := \mathbf{S}_I[\mathbf{r}^*(t), \mathbf{x}_3, d] \tag{7}$$

(Eq. (B.8)).

If the selected colony is not at carrying capacity, individuals settle in this new habitat. However, individuals are not able to settle in colonies that have reached their carrying capacities after the first dispersal event, and will conduct a novel search during the second dispersal event.

241 **During the second dispersal event,** the surplus individuals leave and randomly settle

242 in another colony regardless of their dispersal strategy in their first event (see Fig.1). Thus

243 the emigration matrices depend on the carrying capacity $\mathbf{K}$, the population vector $\mathbf{n}$ at the

244 end of the first dispersal event, and a random search matrix:

$$\mathbf{M}^2 := \mathbf{M}^2[\mathbf{K}, \mathbf{n}] \ \ \text{and} \ \ \mathbf{S}^2 := \mathbf{S}_R. \tag{8}$$

245 where $\mathbf{M}^2$ is fully described by Eq. (B.6). Note that because of our random settlement

246 assumption during this second dispersal event, individuals may come back to their resident

247 patch if they first reached an overcrowded colony.

2.6 Global sensitivity analysis

249 Since dispersal characteristics of EPs cannot be quantified yet, we performed our analy-

250 sis using a wide range of parameters for the mean distance dispersal d, the emigration

251 rate $\overline{m}^1(r_c^*)$ (see Eq. (B.5)) and two contrasting dispersal behaviors (random and informed

252 search). To further quantify the effect of interactions among these dispersal characteristics

253 and model structure uncertainty, we perform a global sensitivity analysis (Aiello-Lammens

254 and Akçakaya, 2016); we compare the outcomes using the global population size percentage

255 difference relative to a scenario without dispersion, referred as $\triangle N_t$ (Appendix C). This

256 percentage difference is calculated as:

$$\triangle N_t = \frac{N_t^+ - N_t^0}{N_t^0} \tag{9}$$

257 where N_t^+ the global population size projected under different dispersal scenarios and N_t^0

258 is the size projected without dispersion. Specifically, we conduct two analyses for each year

259 from 2010 to 2100. The first focuses on the strength of the sensitivity for each parame-

12

ter, regardless of the sign of the impact. We compute the total-effect sensitivity index $\mathbf{s}_T$, using a variance-based sensitivity analysis with parameters sampled uniformly across their range (Saltelli, 2004) (Eq. (C.1)). The second analysis gives the direction of the impact of dispersal characteristics on the global population size, by computing the partial rank correlation coefficients (PRCC). If the PRCC is positive, the effect of the dispersal parameter increases $\triangle N_t$, while the opposite occurs for negative PRCC. By combining these two analyses for each year, we were able to fully assess the sensitivity of the global population size to our dispersal parameters and their interactions over the entire upcoming century (Saltelli, 2004; Marino et al., 2008).

3 Results

The trajectories of the global EP population size are depicted in Figure 2, and we compare our projection of global population size under different dispersal scenarios N_t^+ with the population projected by our reference model (Eq. (2)), N_t^0, in which dispersion does not occur (gray line on Fig. 2). Overall the global population size is larger when projected by a model including informed dispersion than a model without dispersion ($N_t^+ > N_t^0$), except for a scenario with a high proportion of long-distance emigrants at the end of the century.

Figure 3 details the percentage difference between N_t^+ and N_t^0, referred as $\triangle N$. Dispersion may induce at most a $\triangle N = 31\%$ increase in the global number of penguins relative to a case without dispersion, while it may cause up to 65% decrease (i.e. $\triangle N = -65\%$) when the emigration rate is extremely high and the dispersal distance is large. An informed search results in higher percent increases and lower percent decreases than a random search, especially at the end of the century.

Complex interactions arise between the effect of the emigration rate and the dispersion distance on $\triangle N$ that depend of the time period considered. We distinguish four periods

of contrasted patterns: [2010 2036], [2036 2050], [2050 2088] and [2088 2100]. During the first period from 2010 to 2036, the global population trajectories projected by various dispersal scenarios are similar to the global population trend anticipated without dispersion and slightly increase over time. However, during the period from 2036 to 2050, the inclusion of dispersal behaviors slows down or even reverses the population decline projected without dispersion. Specifically, a larger proportion of emigrants results in a larger percentage-increase in global population, $\triangle N$, as well as a positive population trend which contrasts with the declining trend projected without dispersion (Fig 2, 3), especially for long distance emigrants. For example, this ecological rescue effect lasts for 10 years with a small proportion of emigrants (Fig. 4). From 2050 to 2088 all population trajectories decline but dispersion may slow down the anticipated global population decline when penguins conduct an informed search, while it may accelerate the anticipated global population decline for the random search coupled with short distance dispersal. Finally, during the period from 2088 to 2100, dispersion may accelerate or slow down the anticipated global population decline. Indeed, if there is a large number of long-distance emigrants, the global population size is lower with than without dispersion ($\triangle N < 0$), showing a strong acceleration of the global population decline when dispersion occurs.

Finally, our global sensitivity analysis reveals that the global population size is more sensitive to a change in emigration rate than in the mean dispersal distance or the type of search behaviors – random versus informed (see Fig. 5). The magnitude of the sensitivity of $\triangle N_t$ – the percentage difference between N_t^+ and N_t^0 – measured by our total- effect sensitivity index $\mathbf{s}_T$, is small for the mean dispersal distance but increases by the end of the century (see Fig. 5(a)). The $\mathbf{s}_T$ is much larger for the emigration rate: it decreases during the period 2010-2060 and then increases during 2060-2100, especially with the random search. Except for the mean dispersal distance with an informed search, during the first half of the century, an increase of one of the dispersal parameters will positively increase $\triangle N_t$, while

14

during second half of the century, it will negatively increase $\triangle N_t$ (see Fig. 5(b)). Finally, the sensitivity of $\triangle N_t$ to emigration rates is usually smaller for informed than random search.

4 Discussion

By including dispersal in a model projecting species persistence under future climate change, we have shown that dispersion processes may accelerate, slow down, or reverse the anticipated global population decline of the EP projected by a population model without dispersion (Jenouvrier et al., 2014). The response of the global population size of EP to climate-dependent dispersal behaviors are complex and depend on the time-period considered, as the sea ice changes at different rates over time, as well as the interaction among dispersal processes: 1. the proportion of emigrants, 2. the dispersal distance, and 3. habitat selection behaviors. To better understand these results, we first discuss predictions from simpler theoretical models. Then, we propose a mechanistic explanation of our temporal patterns that are mediated by the quality and occupancy of the whole landscape. Finally we discuss the consequences of our dispersal scenario for EP conservation.

4.1 Theoretical insights

Complex interactions arise between the effect of the emigration rate and the dispersion distance on the percentage difference between N_t^+ (global population size with dispersion) and N_t^0 (global population size without dispersion) that depend on the time period considered (Fig. 2, 3). Overall, our global sensitivity analysis shows that the magnitude of the impact of dispersal processes on $\triangle N$ – the percentage difference between N_t^+ and N_t^0 – is larger at the beginning and at the end of the century, but the sign of the impact is reversed, except for the mean dispersal distance with the informed search (Fig. 5). Accounting for the effects of variation in multiple dispersal parameters simultaneously, $\triangle N$ increases at the beginning

of the century, while it decreases at the end of the century when the emigration rate or dispersal distance increases.

To understand the mechanisms behind this temporal pattern of the influence of dispersion, we develop simple and more general mathematical models of two heterogenous patches (Appendix D). In our first theoretical model, one patch is a good quality habitat with a positive local population growth rate ($r_1 > 0$) while the other is a poor quality patch ($r_2 < 0$). Emigration from the second patch occurs at rate α. Dispersion increases the global population size for short-time scales (i.e. transient dynamics before the population in the good quality patch reaches carrying capacity), if the landscape is globally of good habitat quality (case 1: $r_1 + r_2 > 0$) and emigration is low or if the landscape is globally poor (case 2: $r_1 + r_2 < 0$).

Our second theoretical model includes two poor patches (case 3: $r_1 \leq 0$ and $r_2 < 0$), but patch 1 is more favorable than patch 2 ($|r_1| < |r_2|$). Movements occur between the two patches at rate α_1 and α_2 respectively. In this case, the global population will go extinct, but dispersion slows down the global decline if massive emigration occurs from the patch of lower quality (case 3a: α_2 close to 1) while it will accelerate the global decline if emigration occurs from the patch of higher quality (case 3b: $\alpha_1 > 0$).

4.2 Mechanisms underlying emperor penguin global dynamics

These theoretical results shed light on the patterns observed in our complex and more realistic model for the EP. The Antarctic landscape in our model is composed of all known colonies of EP (Fretwell and Trathan (2009), Appendix A). The quality of the Antarctic landscape is described by the sum over all the colonies of the local growth rate (Eq. D.5, Fig. 6). It can be broken into three time periods that qualitatively correspond to the simple, theoretical cases (1-3): 1. from 2010 to 2036; 2. from 2036 to 2088, and 3. from 2088 to 2100.

During the first period from 2010 to 2036, most of the EP colonies have positive growth

16

conditions ($r^*(SIC, K) > 0$, blue color on 7), resulting in a globally favorable Antarctic landscape (case 1, Fig. 6). The effect of dispersion is small and positive ($N_t^+ > N_t^0$, Fig. 2, 3) on the global population dynamics because most of the colonies experiencing good SIC have not reached their carrying capacity and emigration rates are low (see Figs. 4, 7 and Fig.D.1(a) in Appendix D).

We divide the second period into two phases (i) 2036-2050, when dispersal processes have a positive impact on the global EP population size and (ii) 2050-2088, when the sign of the impact depends on dispersal processes. During the period from 2036 to 2050, dispersal processes have a larger, positive impact on the global EP population trajectory because the Antarctic is becoming a globally poor environment (case 2, Fig 6) but some colonies can still sustain increasing populations (blue color on Fig 7) and the proportion of emigrants from unfavorable colonies increases (Fig. 4, yellow and red colors on Fig 7). During this period, dispersion processes reverse the anticipated decline projected by a model without dispersion, i.e. the trend of N^+ is positive while the trend of N^0 is negative – especially with informed search behavior. The magnitude of this ecological rescue effect depends on the carrying capacity of the most favorable colonies, and is temporary because the colonies with good SIC quickly reach their carrying capacity (yellow color Fig. 7) and the overall landscape degrades as the climate changes (Fig 6). From 2050 to 2088, few colonies remain favorable (Fig. 6, few blue spots on Fig. 7), most of the colonies experiencing good quality habitat have reached their carrying capacity (yellow color Fig. 7), and all global population trajectories (with or without dispersion) decline (Fig. 2). The effect of dispersion depends on the probability of settlement in a better habitat than the resident patch. For example, the probability of settling in a better habitat is lower for the short distance dispersal using a random search, than informed search (Fig. 4). As a result, the global population decline is accelerated with the random search while it decelerates with the informed search.

At the end of the century—from 2088 to 2100— all colonies are unfavorable (case 3,

17

Fig. 6, red color on Fig. 7). The impact of the dispersion depends on the dispersal distance, the emigration rate, and the searching behavior which together set the strength and direction of individuals' movements between unfavorable patches. Specifically, dispersion to a higher quality patch will slow down the global population decline (case 3a). This pattern arises with the informed search behavior and short dispersal distance, because individuals will tend to settle in higher quality colony than their resident colony at the beginning of this period (Fig. 4). For the random search behavior, it is more likely that an individual will settle in lower quality patch than their resident patch—given that the quality of the colonies quickly decreases—eventually accelerating the global population decline (case 3b, Fig. 4 and red color on 7). A longer dispersal distance will decrease the settlement probability in a better quality colony (Fig. 4) and exacerbate the accelerated global population decline such that the global population size is lower than the size anticipated without dispersion by 2100 (Fig. 2). This strong acceleration of the global population decline also arises with the combination of informed search, long distance dispersal, and high dispersion rate, because most of the colonies experiencing good SIC have reached their carrying capacity and individuals randomly settle in phase 2 of the dispersion (Fig. 1).

To summarize, our projections for the EP suggest that the temporal dynamics of the population size of EP crucially depend on the presence of a non-stationary and heterogeneous quality habitat over Antarctica. Hence transient effects of climate change and spatial heterogeneity of the landscape are critical components when projecting species response to climate change (McRae et al., 2008). The temporal variations and the spatial heterogeneity of the landscapes combined with dispersal distance and emigration rate also determine the relative impact of informed versus random search. This echoes previous results, which show that the autocorrelation in environmental fluctuations determines the relative success of random versus informed dispersal (Armsworth and Roughgarden, 2005).

18

4.3 Implication for conservation

Antarctica offers a unique example of international policy collaboration with the Antarctic Treaty of 1959 coordinating relations among countries so that it is a continent reserved for peace and science. The United States is a party to the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR), a part of the Antarctic Treaty System that promotes conservation of marine resources and limits fishing in the Southern Ocean. Hence, the protection of EP under the ESA could play an influential role under these international conservation, management and policy decisions.

Many of the protections provided by the ESA apply to US species only, such as the development of species recovery plans and critical habitat designation. However, the listing of a foreign species such as the EP would trigger federal consultation (i.e., analysis) on the permitting of U.S. fishing vessels operating in the Southern Ocean and on importation of fish caught near Antarctica in the CCAMLR region into the US, in order to minimize impacts to EP. Furthermore, it may increase public attention on species threatened by climate change, motivate the implementation of crucial longitudinal individual-based studies, and highlight the need for a new global conservation paradigm involving international coordination and management (Hannah, 2010).

In a previous demographic study that did not include dispersal processes, Jenouvrier et al. (2014) proposed that "the emperor penguin is fully deserving of Endangered status due to climate change, and can act as an iconic example of a new global conservation paradigm for species threatened by future climate change". This Endangered status was based on the quantitative criteria of the IUCN applied at the end of the century, with the median of the global population growth rate declining by 3.2% per year and a projected global population decline of 78% over three generations, far exceeding the threshold for IUCN Endangered status.

The ESA has qualitative instead of quantitative listing criteria, and we propose here that

19

the EP is fully deserving of threatened status under the ESA due to climate change. The definition of threatened is "likely to become endangered" in the foreseeable future – that is, likely to become in danger of extinction throughout all or a significant portion of the range in the foreseeable future. There is no quantitative threshold for being in danger of extinction nor a formal definition of foreseeable future. The National Oceanic and Atmospheric Administration has defined foreseeable future as the period through 2100 for climate change and ocean acidification threats in recent listing decisions for marine species such as corals, ringed seal, and bearded seal.

By 2100, we showed that dispersal processes may increase the global population by 31% relative to a scenario without dispersion, while high emigration rates and long distance dispersal may accelerate the population decline decreasing the global population by 65% by 2100 compared to a scenario without dispersion. Informed dispersal decisions act as an ecological rescue for a short time from 2036 to 2046, but at the end of the century the global population is declining regardless of the dispersal scenario. Specifically, the median of the global population growth rate from 2090 to 2100 decline ranges from a rate of 1.1% per year under an informed search scenario with low emigration rates and short-distance dispersal to 11% with a random search, high emigration rates, and high-distance dispersal. This is a projected global population decline of 40% and 99% over three generations respectively. Thus, even idealistic dispersal processes will not rescue the EP by 2100.

The Ross Sea meta-population represents $\sim 25\%$ of the worldwide EP population (Kooyman and Ponganis, 2016), and most likely the last potential refuge by the end of the century (Jenouvrier et al. (2014); Ainley et al. (2010) but see some exception when dispersion occurs in Appendix F). Interestingly, the colonies in the Ross Sea are genetically distinct from the rest of the colonies for unknown reasons (Younger et al., 2015). Given that the Ross Sea is potentially the last refuge at the end of the century this isolation has potentially important conservation implications. Indeed, the global population size at the end of the century is

20

even more reduced compared to a scenario without dispersion if the Ross Sea colonies are isolated, especially for a high rate of emigration (Appendix G).

Our global sensitivity analysis reveals which aspects of dispersal processes the global population is most sensitive to, which could help prioritize future empirical research as well as conservation and management actions (Aiello-Lammens and Akçakaya, 2016). It shows that the global population size is more sensitive to change in emigration rates, regardless of the magnitude of climate change (i.e. the time period considered) and type of dispersal behaviors (random versus informed). Hence, researchers should prioritize data collection to assess emigration rates robustly. Novel genetic studies have made significant progress to that end by estimating that each EP colony could receive, on average, between 0.7% and 4.2% of its effective population size in migrants every generation (Cristofari et al., 2016). The generation time of the emperor penguin is approximately 16 years (Jenouvrier et al., 2014), hence these rates are small. It is important, however, to acknowledge that these dispersion parameters are averaged over many generations, and may not reflect the instantaneous dispersal rate relevant for demographic studies. The best approach to assess individual movements among penguin colonies, is to implement longitudinal monitoring program of individuals, such as for the Adélie penguin colonies in the Ross Sea (Dugger et al., 2010).

4.4 Dispersal scenarios

Although estimate of emigration and immigration rates and dispersal distance does not exist for the EP, our model permits to study the effect of various dispersal scenarios inspired from observations on EP life history, foraging behaviors, or colony dynamics, as well as habitat selection behaviors in other species. Here, we discuss our assumptions with respect to some important dispersal processes, and illustrate few modifications of our model framework for other species threatened by climate change.

21

4.4.1   Dispersal distance

The global population size is less sensitive to dispersal distance than other dispersal parameters, but some interesting local and regional population dynamics patterns appear for dispersal distance larger than 500 km (Appendix F). LaRue et al. (2015) reported the appearance and disappearance of some EP colonies and discussed examples of EP colonies or parts of colonies that may have moved within distance of more or less 200 km. Kooyman and Ponganis (2016) proposed that the EP colonies in the Ross Sea represent a meta-population system, with potential dispersal distance > 800 km. The inclusion of an even larger dispersal range may be realistic for the EP because foraging studies have shown that they can cover incredible distances during their migration routes (Kooyman et al., 1996, 2004; Thiebot et al., 2013); adults travel more than 2000 km to their colonies in the western Ross Sea (Kooyman et al., 2004) and one juvenile covered >7000km during the first 8 months after leaving his natal colony in Terre Adélie (Thiebot et al., 2013). In addition, populations around the Antarctic coast other than in the Ross Sea are panmictic (Younger et al., 2015), suggesting potentially large dispersal distance. A scenario in which all colonies are connected is not unlikely, as the maximum coastal distance between colonies is 8220 km. Our study reveals that long distance dispersal does delay the global population declines by 10 years for low rates of emigration, but may reduce the global population size at the end of the century for high emigration rates (compared to a scenario without dispersion).

4.4.2   Emigration rate

Massive emigration maybe an important element of EP life history (LaRue et al., 2015) and our global sensitivity analysis stresses that the global population size is more sensitive to a change in emigration rate than other dispersal processes (see Fig. 5). Our high emigration scenario reflects episodes of massive emigration when the local environmental conditions drive large population declines after 2050. Figure 4 shows that the proportion of emigrants

is higher than 30% after $\sim$ 2045, and reaches 100% by $\sim$ 2070. Whether these high emigration scenarios occur remain an open question, and will not reverse the anticipated global population decline by the end of the century.

4.4.3 Informed dispersal

In all models, we considered only informed emigration, whereby EPs only leave unfavorable habitats. In addition, we included an informed search, whereby EPs select for the most favorable habitat they can reach within their (potentially high) dispersal range. This ideal habitat selection is inspired by the behavior of colonial seabirds that prospect and assess habitat quality using the presence and reproductive success of residents (Doligez et al., 2002; Boulinier et al., 2008). In our model, the quality of the habitat is evaluated by the realized growth rate of the colony and consequently an individual will settle in the habitat that maximizes its fitness (Greene, 2003). Nonetheless, even such idealistic scenario acts as an ecological rescue for only few years and may allow little additional time to implement conservation strategies in the face of climate change. On the other hand, a scenario without informed dispersal decisions, such as random emigration and search (shown in Appendix E) projects a dramatic decline of the global population, even with a globally favorable Antarctic landscape. In that case, by the end of the century the global population is reduced by 39% to 80% compared to a scenario without dispersion.

Previous studies have stressed that the viability and dynamics of a metapopulation depend critically upon informed dispersal behavior (Greene, 2003; Ray et al., 1991; Anderson et al., 2009; Armsworth and Roughgarden, 2005; Clobert et al., 2009; Ponchon et al., 2015). In the context of climate change, our results highlight that informed emigration can result in lower or larger global population size than without dispersion – that depends on the spatial and temporal variations of the habitat quality, as well as the dispersal distance and emigration rate that influence landscape occupancy.

23

Ponchon et al. (2015) recently showed that informed dispersal maintains the global population size in a stationary environment, whereas random dispersal and no dispersion lead to extinction. Specifically, an ecological rescue effect appears in their simulations for an environment oscillating very slowly over time (their Fig. 2f), or when some patches are degrading quickly but the overall landscape is more likely favorable (their Fig. 2c). However, for an environment with fluctuations of high periodicity or a globally poor landscape the ecological rescue effect is limited (their Figs. 2e and 2c). For EP, we find that the effect of informed dispersal is small for most of our scenarios, probably because the sea ice environment is degrading very quickly over the century, resulting in a globally poor environment as soon as 2036.

4.4.4 Dispersal costs

Habitat fragmentation and climate change are likely to influence the costs of dispersal (Travis, 1999) and the ability of species to cope with these changes. Dispersal costs are diverse (energetics, time, risk such as predation) and may be direct or delayed (Bonte et al., 2012). Models including dispersal costs focus mostly on the causes and consequences of different dispersal strategies in an evolutionary context, and few incorporate costs during the various phases of dispersion (but see Travis et al., 2012). In our model, no additional cost of traveling or gathering information are included. However, during the second phase of dispersion, a deferred cost at settlement occurs because individuals have a limited search time and even with an informed search, the fitness of individuals may be reduced by settling randomly in a lower quality habitat than their resident one (Fig. 1).

4.4.5 New colony establishment

Polar species are less likely to colonize new habitats. For the EP we posit that no new colony is created with future climate change, as the Antarctic continent limits EP movements South

24

and new EP habitats – such as stable, long-lasting fast ice for breeding, and new polynyas (open area within sea ice for feeding) – are unlikely to appear under the future projections of Antarctic environmental conditions (Ainley et al., 2010). The benefits of dispersal may be different for species threatened by climate change that can colonize new favorable habitats. In our model framework, novel habitats can be included in the matrix $\mathbf{x}_3$ that describes the landscape structure.

Furthermore, founding a new breeding colony likely requires a group of emigrants as EPs need to huddle for warmth during the winter. To include such Allee effect in settling decisions in our model, one can use a critical density ρ_c in the searching matrix. Allee effects tend to increase the extinction probability of species endangered by climate change (Roques et al., 2008). Therefore, including Allee effect and new colony establishment are unlikely to reverse the anticipated global population decline by the end of the century.

4.4.6 Inter-individual differences in dispersal

Several studies have stressed the importance of variations in dispersal decisions among individuals related to for example, age, breeding stages (Ponchon et al., 2015) or thermal phenotype (Bestion et al., 2015). Our dispersal scenarios for EP, do not account for such individual heterogeneity. For seabirds, emigration rates are likely lower among adult than juveniles, and higher for failed adult breeders than successful breeders with consequences on the rate of the metapopulation recovery after an environmental change (Ponchon et al., 2015). Such individual heterogeneity will likely reduce our average emigration rates, hence increasing the effect of dispersal on the global population size at the end of the century (negative sensitivity of $\triangle N$ to emigration rates) but reducing the rescue effect during 2036–2046 (positive sensitivity of $\triangle N$ to emigration rates).

4.4.7 Environmental stochasticity

Our model includes a temporally variable and spatially heterogeneous landscape. However, it does not include stochastic environmental variations within patch i within season, such as random variations in the intrinsic growth rate of each colony $r_i(t)$. Such random variations will affect the predictability of the habitat quality and thus the benefits of an informed search dispersal (Armsworth and Roughgarden, 2005). Indeed, random emigration and search allow a species to spread its bets by distributing individuals broadly across a spatially heterogeneous landscape while informed emigration and search concentrate the population to the favorable habitats (Armsworth and Roughgarden, 2005). Therefore, if an unpredictable event occurs during the breeding season within a favorable patch reducing the local population growth rate, the global EP population may be greatly reduced for informed dispersal that concentrates most of the global population within such patch but not for a random dispersal. In our model framework, the intrinsic growth rate $r_i(t)$ could be perturbed by random variables to account for environmental stochasticity within patch such as in Armsworth and Roughgarden (2005).

4.5 Conclusion

Dispersal will affect how species persist and respond to rapid climate change and habitat fragmentation. However, the study of dispersal for most taxa is hindered by logistical difficulties and our approach— developing a wide range of dispersal scenarios and performing a global sensitivity analysis– could provide guidance on which behavioral and dispersal traits are critical to understanding the dynamics of real systems. In addition, it can permit evaluation of management strategies, such as relocation conservation programs.

Many previous modeling approaches that predict species response to global change have made simplistic assumptions regarding dispersal (but see Bocedi et al., 2014). Our metapopu-

lation model integrates multiple dispersal processes by considering informed behavior during three dispersal stages (emigration, transfer, and immigration) that depend on the spatial structure of the habitat, its quality, and its density. The model framework we have introduced here is sufficiently flexible for implementing multiple dispersal scenarios for a wide range of species to broaden our understanding of dispersal processes on population and species persistence under future global change.

5 Acknowledgements

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6   Supplementary material

A Information about the known colonies of the emperor penguin in Antarctica.

B Description of the metapopulation model

    B.1. Construction of the reproduction matrix **F**

    B.2. The dispersal model

C Global sensitivity analysis

D Baby models

    D.1. Case 1 and 2: Dispersion to the good patch is not always optimal

    D.2. Case 3: Random dispersion between poor habitats

    D.3. Implications of theoretical results for the emperor penguin

E Random departure and random search dispersal

F Local and regional population dynamics

G Isolating the colonies on the Ross Sea

Following the acceptance of this manuscript, data of this publication will be available online at: `http://www.datadryad.org`.

7   Figure Legends.

Figure 1.   Schematic description of the dispersal processes included in the metapopulation model.

Figure 2.   Global number of breeding pairs of emperor penguins from 2010 to 2100 projected by the metapopulation for various dispersal scenarios. Thick light gray line is the population trajectory without dispersion. Colored solid lines are population trajectories under high emigration rates ($\overline{m}^1(r_c) = 0.9$), while dashed lines show low emigration rates ($\overline{m}^1(r_c) = 0.1$). Green lines are trajectories under informed search, while red lines show the random search.

Figure 3.   Influence of emigration rate (y-axis), dispersal distance (d) and searching behaviors (panels) on the global number of breeding pairs of emperor penguins from 2010 to 2100. Percent difference between the size projected under different dispersal scenarios N_t^+ and the size projected without dispersion N_t^0 (gray line on Figures 2) from 2010 to 2100 (x-axis) is shown. Red (blue) colors show the parameter range for which the influence of dispersal is negative (positive), i.e $\triangle N_t < 0$ ($\triangle N_t > 0$). The gray color shows the case where dispersion has no effect, i.e. $\triangle N_t = 0$

Figure 4.   Mean proportion of emigrants (a)-(b), and the mean proportion of immigrants settling in a patch of better quality than their resident patch (c)-(d) from 2010 to 2100. Because the proportion of immigrants settling in a patch of better quality is equal to 1 minus proportion of immigrants settling in a patch of poorer quality from each colony, here we only illustrate the case for settling in a better quality patch. Colored solid lines are population trajectories under high emigration rates ($\overline{m}^1(r_c) = 0.9$), while dashed lines show low emigration rates ($\overline{m}^1(r_c) = 0.1$). Green lines are trajectories under informed search,

₇₈₂ while red lines show the random search.

Figure 5. Two time-varying global sensitivity analyses of the percentage difference ΔN_t between the global size population projected without dispersion N_t^0 and with specific dispersal scenario N_t^+: (a) total-effect sensitivity index $\mathbf{s}_T$ and (b) partial rank correlation coefficient $PRCC\rho$ for emigration rates $\overline{m}^1(r_c^*)$ (solid lines) and the mean-distance dispersal d (dashed lines) with random (red lines) and informed (green lines) search.

Figure 6. Projected habitat quality of Antarctic landscape through to 2100: the global growth rate of emperor penguin in Antarctica defined by Eq. (D.5) (blue line) and the maximal growth rate over the colonies (orange line).

Figure 7. Projected habitat quality and saturation of emperor penguin colonies from 2010 to 2100. The y-axis refers to the colony number fromTable A.1. The blue color shows a favorable habitat $(r^*(SIC, K) > 0)$, i.e. colony of good quality in term of sea ice conditions (SIC, $r > 0$) that is not saturated $(n < K)$; yellow is an unfavorable habitat $(r^*(SIC, K) < 0)$, i.e. good quality colony $(r > 0)$ but saturated $(n > K)$, and red is an unfavorable habitat, i.e. poor quality colony in term of SICs $(r < 0)$. The various panels correspond to the following scenarios: **(a)** Short-distance dispersion, low emigration and random search; **(b)** Short-distance dispersion, high emigration and random search; **(c)** Long-distance dispersion, low emigration and random search; **(d)** Long-distance dispersion, high emigration and random search; **(e)** Short-distance dispersion, low emigration and informed search; **(f)** Short-distance dispersion, high emigration and informed search ; **(g)** Long-distance dispersion, low emigration and informed search; and **(h)** Long-distance dispersion, high emigration, and informed search; where $d = 1000\,\text{km}$ for short-distance dispersion, $d = 6000\,\text{km}$ for long-distance dispersion, $\overline{m}^1(r_c) = 0.9$ for high emigration rate and $\overline{m}^1(r_c) = 0.1$ for low emigration rate.

36
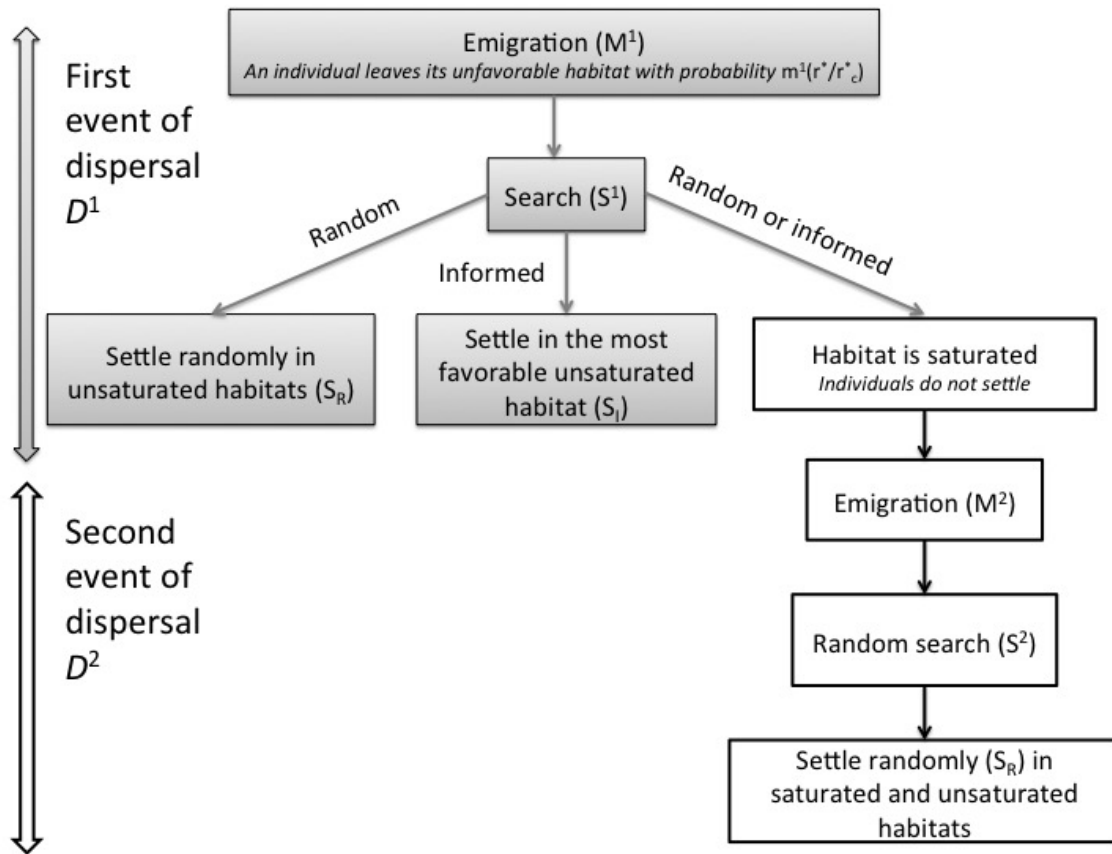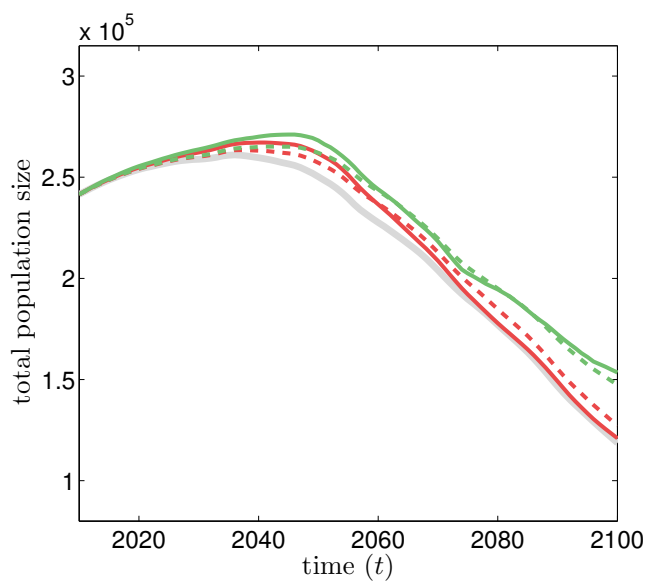
Figure 1:

(a) Short-distance dispersion ($d = 1000\,\text{km}$) (b) Long-distance dispersion ($d = 6000\,\text{km}$)
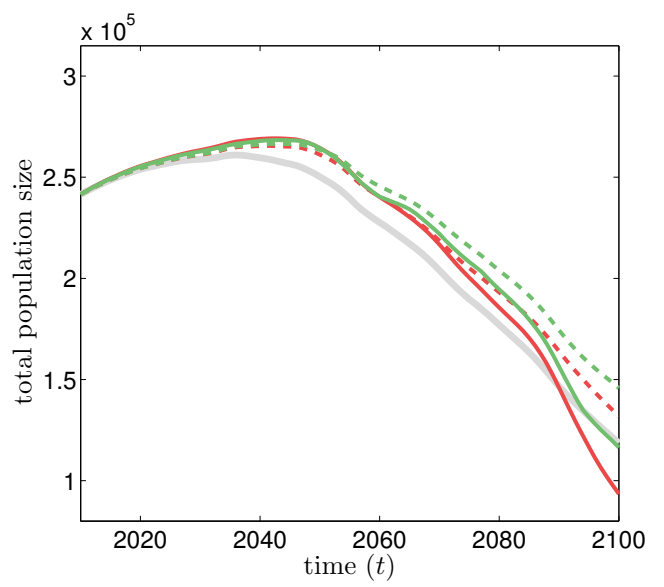
Figure 2:
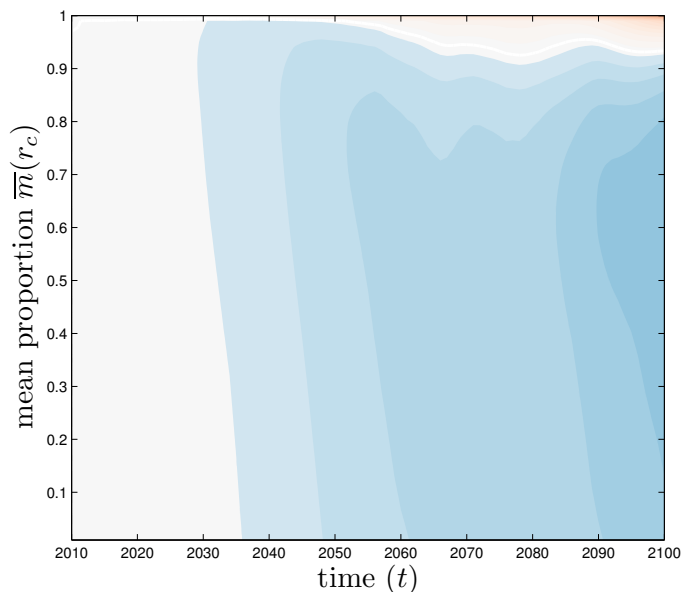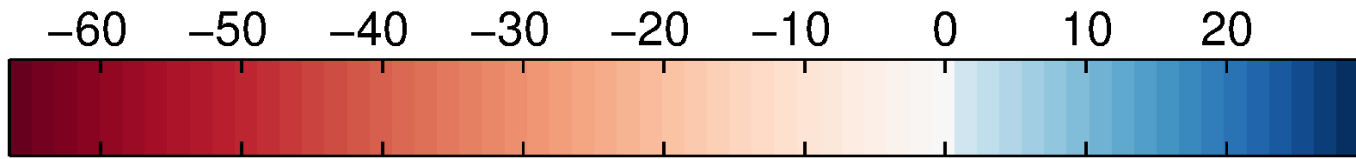
(b) Random and short-distance dispersion($d = 1000$) (c) Random and long-distance dispersion ($d = 6000$)
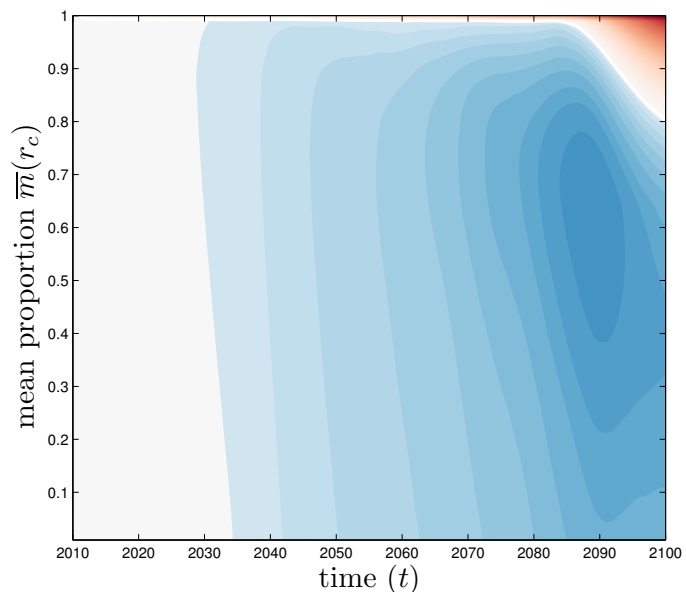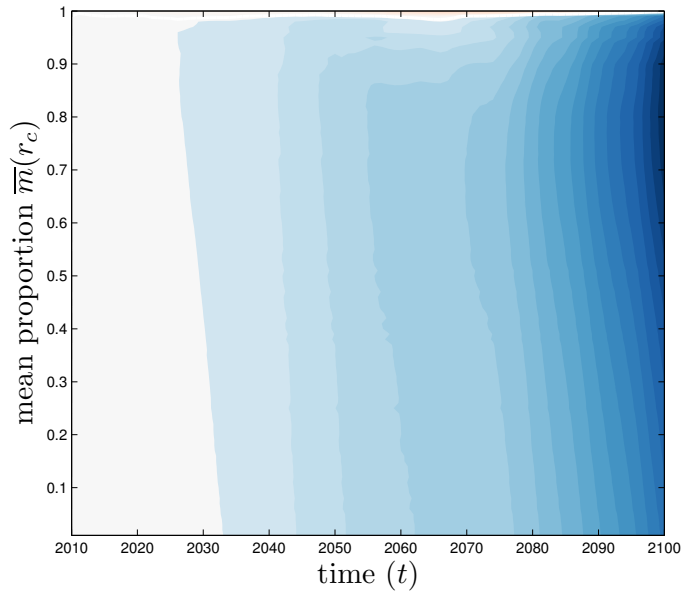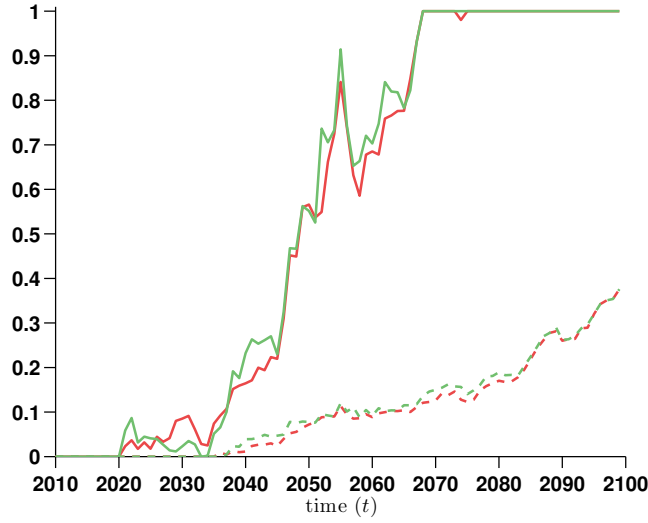
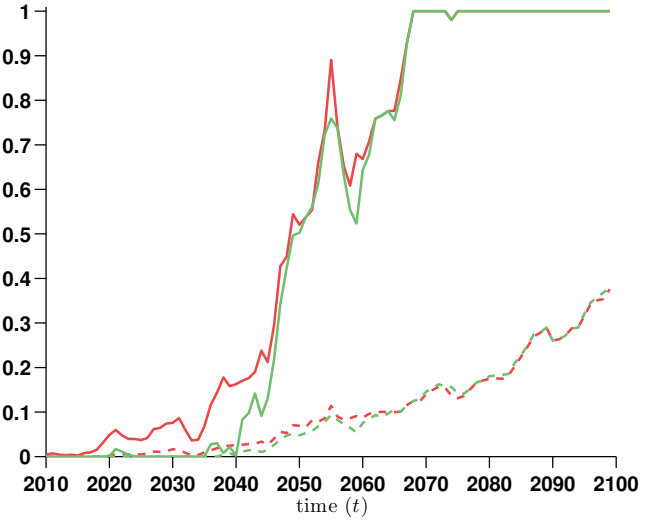(d) Informed and short-distance dispersion ($d = 1000$) (e) Informed and long-distance dispersion ($d = 6000$)
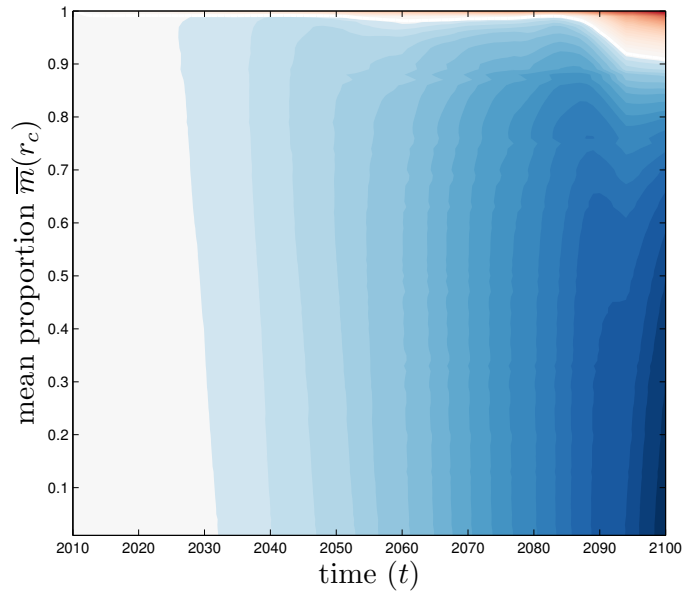
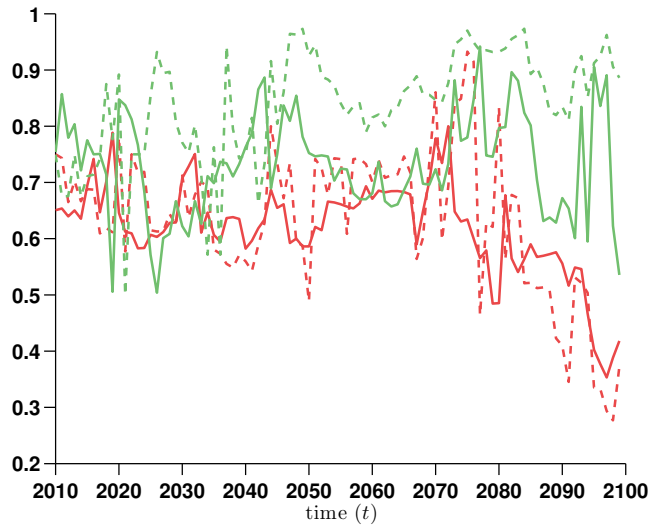Figure 3:

Mean proportion of emigrants
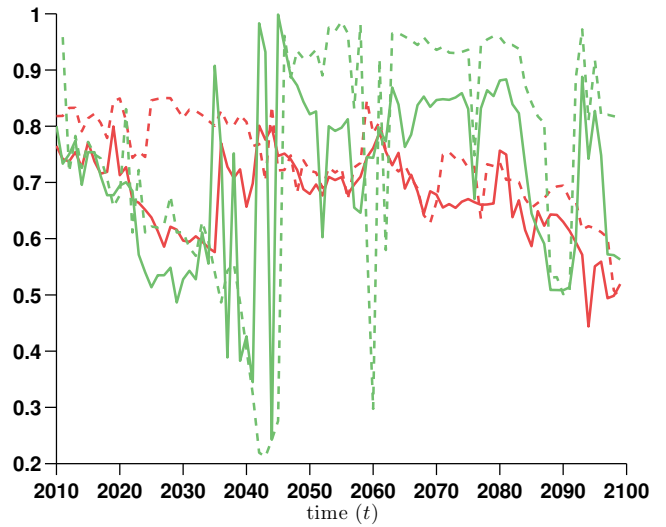

(a) Short-distance dispersion

(b) Long-distance dispersion

Mean proportion of immigrants settling in better quality patch than their resident patch

(c) Short-distance dispersion

(d) Long-distance dispersion

Figure 4:

40

(a) Total-effect sensitivity index

(b) PRCCs
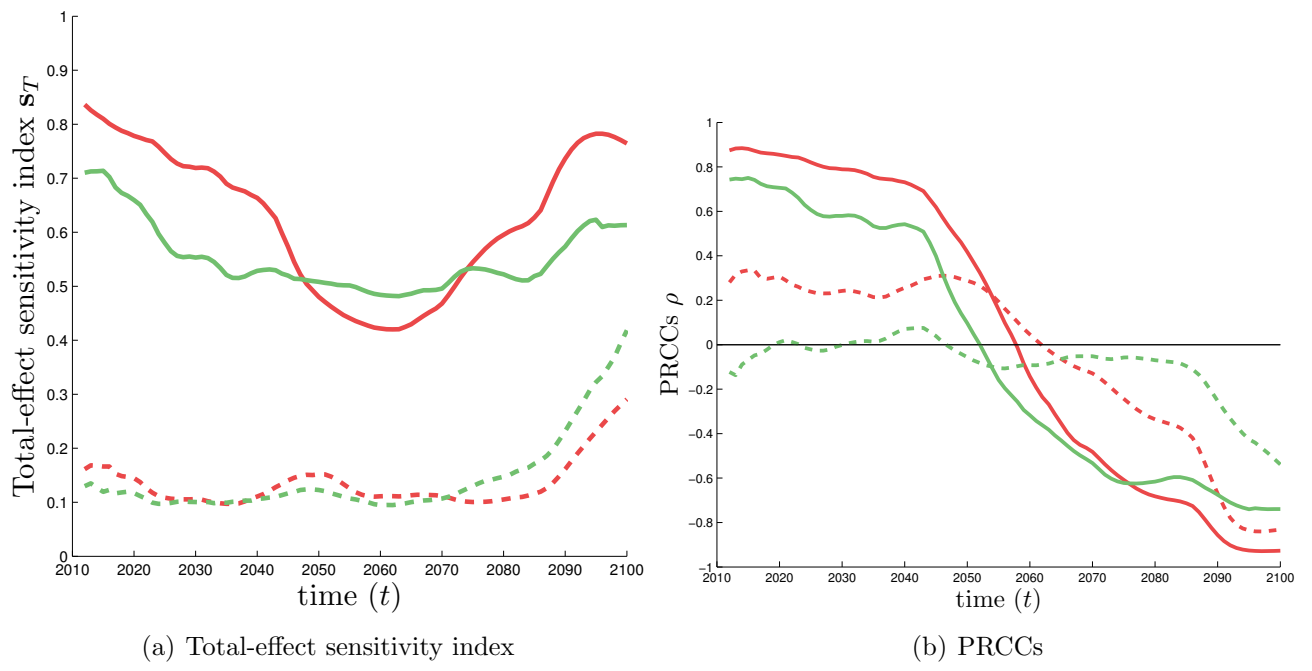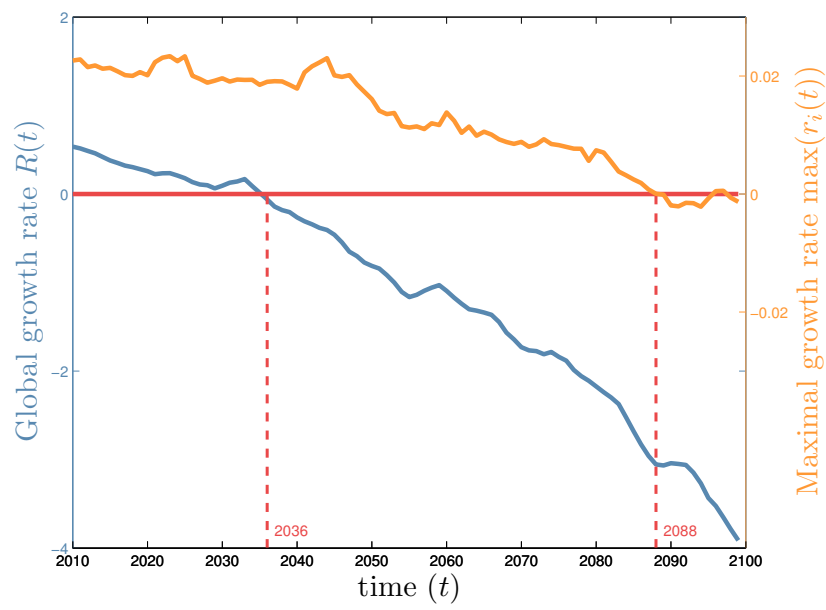
Figure 5:

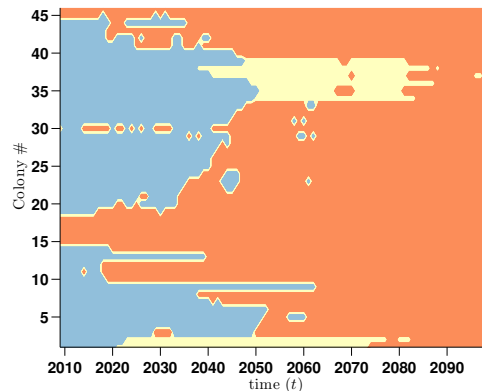Figure 6:

Short-distance dispersal

Long-distance dispersal
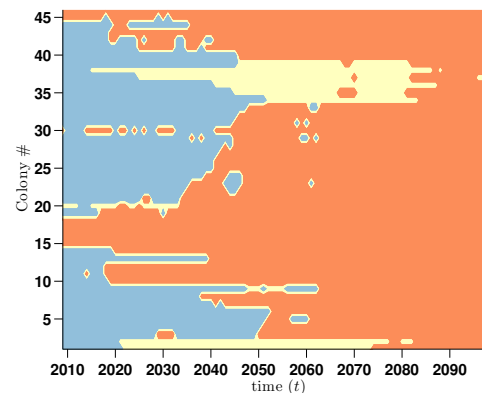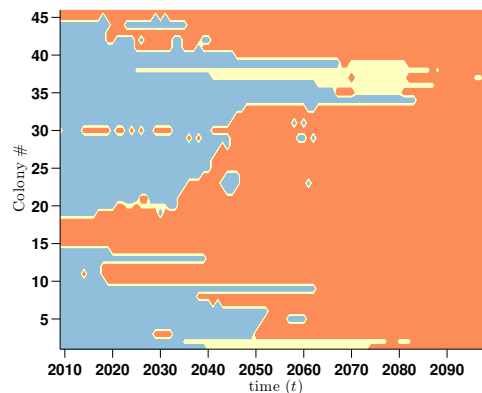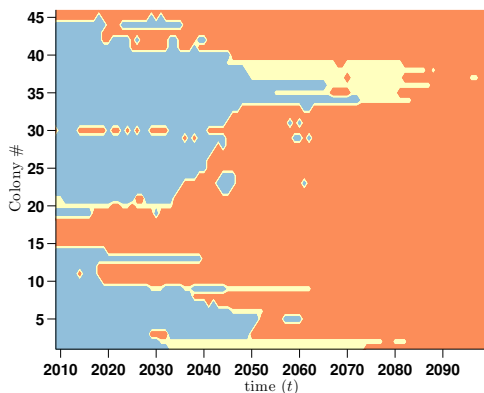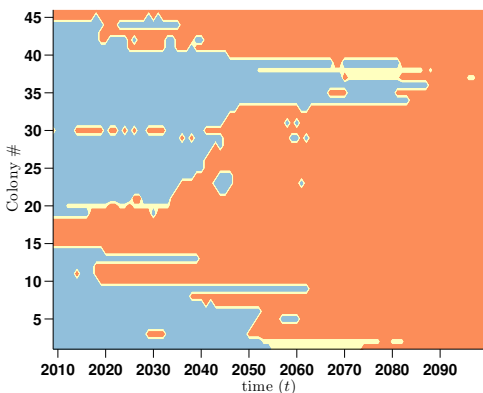
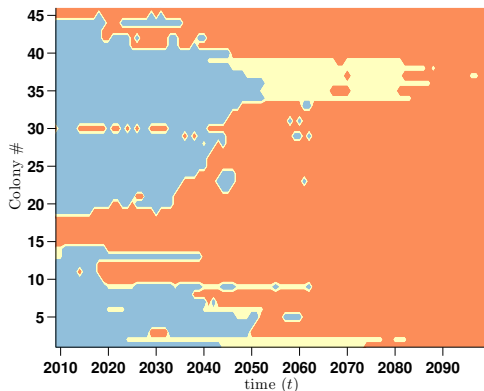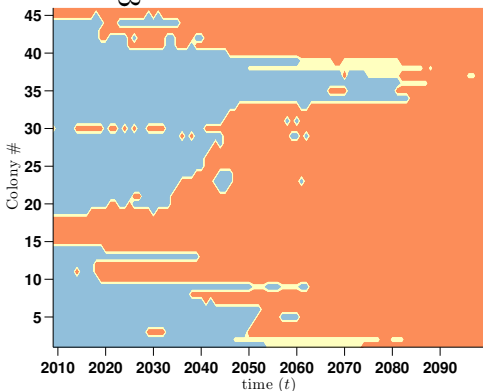(a) Low dispersion

(b) High dispersion

(c) Low dispersion

(d) High dispersion
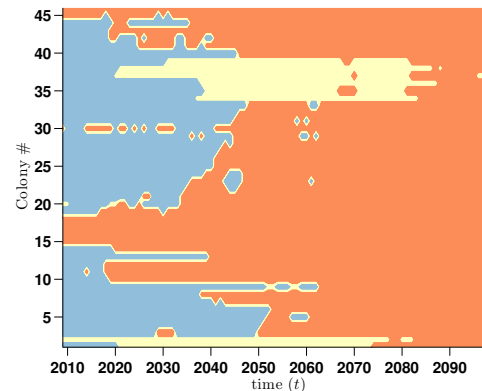
(e) Low dispersion

(f) High dispersion

(g) Low dispersion

(h) High dispersion

Figure 7:

43