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Hällfors, Maria Helena; Aikio, Sami Aslak; Schulman, Leif Edvard

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Quantifying the need and potential of assisted migration.

Hällfors MH[a], Aikio S[a], Schulman LE[a]*

[a] Botany Unit, Finnish Museum of Natural History, P.O. Box 7, FI-00014 University of Helsinki, Finland

[*] **corresponding author**: Leif Schulman, Finnish Museum of Natural History, P.O. Box 7, FI-00014 University of Helsinki, Finland; leif.schulman@helsinki.fi, tel. +35850 54 87 692

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Abstract

Assisted migration is recognized as a possible method for species conservation under climate change. Predicted decrease in range size and emergence of new suitable areas due to climate change are the main reasons for considering assisted migration. The magnitude of such changes can be used to guide decisions on the applicability of this conservation method. However, it has not been formalized how predictions acquired, e.g., with the help of species distribution models or expert assessments, should translate into recommendations or decisions. Climate change threat indices concentrating on predicted loss of habitat are not directly applicable in this context as they do not define whether a species has the potential to expand its range compared to the area that remains suitable. Here we present a conceptual framework for identifying and quantifying situations in which predictions indicate that a species could benefit from assisted migration. We translate predicted changes in suitable area into separate metrics for migration need and migration potential on the basis of the amount of lost, remnant, and new area. These metrics can be used as part of decision-making frameworks in determining the most suitable conservation method for a specific species. They also hold potential for coarser screening of multiple species to estimate the proportion of species that could benefit from assisted migration within a given time frame and climate change scenario. Furthermore, the approach can be used to highlight time frames during which assisted migration or, alternatively, other conservation actions are the most beneficial for a certain species.

Key words: adaptive management, assisted colonization, climate change, ecological niche modelling, managed relocation, translocation

1. Introduction

Observed and potential effects of climate change on biodiversity are becoming evident (Dawson et al. 2011, Brommer et al. 2012, Urban 2015). A concern that traditional conservation methods may not be enough to safeguard species from decline has led to proposals of new proactive methods, such as actively moving species to new areas in pace with the changing climate (Peters & Darling 1985; Hunter 2007, Schwartz et al. 2012). Although rarely implemented to date, this approach has been extensively discussed. It has variously been called assisted migration, assisted colonization, and managed relocation, among others, and also defined in different ways (Hällfors et al. 2014). In the strict sense, however, it is a type of conservation translocation (*sensu* IUCN 2012) in which species are moved from their indigenous range to areas where they would be predicted to move as climate changes, were it not for anthropogenic dispersal barriers or lack of time (see Hällfors et al. 2014 for a thorough discussion); here we refer to the method in this sense and call it assisted migration (AM). We use 'conservation' in the broad sense, i.e., include in it all actions aimed at safeguarding biodiversity, both preserving approaches and conservation management.

To begin with, it should be noted that wide consensus on the acceptability of AM has not been reached (Hewitt et al. 2011; Maier & Simberloff 2016; Siipi & Ahteensuu 2016). Nevertheless, AM has already been conducted for the conifer *Torreya taxifolia* in the USA (Barlow & Martin 2004; Marris 2009) and for two butterfly species in the UK (Willis 2009), and is being considered, e.g., for the butterfly *Euphydryas editha quino* (Marris 2009). Hence, it is important to develop best-practice guidelines for the possible future implementation of the method even if their application, in the end, may not turn into mainstream conservation practice. Indeed, several frameworks have been presented for guiding decisions on whether and when a species needs AM, for risk evaluation, and

for planning the process if deemed feasible (Hoegh-Guldberg et al. 2008; Richardson et al. 2009; McDonald-Madden et al. 2011; Perez et al. 2012; Schwartz & Martin, 2013).

Predictions of future changes in suitable areas have repeatedly been suggested as aids in evaluating the need of AM (Chauvenet et al., 2012; Schwartz, 2012; Guisan et al., 2013; Gallagher et al 2014). Such predictions can be derived at least through expert evaluation, mechanistic niche models, or species distribution models (SDMs). All these approaches contain uncertainties and caveats, such as biases in expert judgement, and assumptions on ecological equilibrium and local adaptation in niche models. These have been extensively discussed in the literature (Heikkinen et al. 2006; Araújo & Peterson, 2012; Martin et al. 2012). However, the prediction methodology is continuously developing (Morin & Thuiller 2009; Martin et al. 2012, Braunisch et al. 2013) and holds clear potential in this context as long as predictions are interpreted in the light of the limitations of the applied methodology. Nevertheless, it has not been established how the information obtained from predictions should be translated into decisions on whether or not to apply AM.

The absence of a recognized method for utilizing the information on range change predictions means that managers wishing to evaluate the appropriateness of AM are left with a recommendation on what tool to use but with no instructions on how to use it. This lack of guidance may result in subjective decisions and thereby inconsistent policy, or even in a status quo where no decisions are made, leading to a high risk of losing biodiversity in a rapidly changing world. A formal and rigorous way of utilizing range change predictions for the specific purpose of AM evaluations and decisions is therefore needed.

In evaluating species' vulnerability to and threat from climate change, formalizations of the use of modelling outputs have been put forward (e.g., Thomas et al. 2011, Maggini et al. 2014). Although

the proposed frameworks may be suitable for evaluating general threat from climate change, being vulnerable to climate change because of anticipated loss of distribution area does not necessarily mean that AM would be a suitable conservation method for the species. Instead, a combination of expected loss and gain of area is required for AM to be an appropriate response. A species that is not losing suitable habitat does not need to migrate and a species that will not have new climatically suitable area outside its current distribution area will not benefit from migration (with migration we mean the processes of dispersal, colonization, and establishment, which in the case of AM are aided by humans; Fig. 1). Hence, vulnerability assessments concentrating on species' sensitivity to climate change (see, e.g., Pacifici et al. 2015 for a review) are not sufficient to inform decisions regarding AM. Instead, both estimates on climate change exposure and on availability of new suitable area for translocations are necessary when deciding on and planning AM.

On the basis of our conceptualization of when a species would benefit from AM (Fig. 1), we present a straightforward method for converting predictions of changes in suitable area into metrics describing AM benefit. These metrics can be utilized in decision-making frameworks to answer those questions that concern range change. The predictions themselves can be constructed through a variety of methods, including not only correlative SDMs but also mechanistic models and expert evaluations, and be based on various data sources. Likely data include known species occurrences, climate variables, dispersal abilities, habitat requirements, habitat availability, and biotic interactions among species. The data needed for calculating the metrics we propose are readily obtainable from the range change predictions, provided these are quantifiable into spatial units, such as grid cells. The reliability of the results of predictions would largely depend on the degree of expert knowledge, the quality of the data, and other assumptions made in the process of obtaining the predictions. However, in this paper we do not attempt to test the usability of different prediction methods for range changes nor how different input data or modelling assumptions affect the

predictions. Instead, the aim is to describe a process that can be used for supporting decisions in conservation once sufficiently reliable predictions on changes in suitable area are available (see Hällfors et al. 2016 for a real-life application of the method described here).

2. Methods

2.1. Derivation of the AM metrics

Assisted migration, i.e., human-mediated dispersal to and establishment in new areas, may be applicable as a conservation method for species that meet the following criteria:

1. Migration need: Climate change, e.g.., changes in temperature and precipitation regimes, is predicted to render (part of) the species' current distribution area unsuitable.
2. Migration potential: Climate change is predicted to bring about new suitable area for the species.
3. Migration inability: The species either has poor intrinsic dispersal ability or faces anthropogenic dispersal barriers.

Criteria 1 and 2 can be quantified using predictions of changes in climatic conditions and corresponding changes in suitable area, in addition to information on current distribution and habitat preferences. In this paper and in the simulations we present, we treat suitable and unsuitable area in a binary fashion. However, the suitability of the area could also be weighted by the probability of suitability, or by some metric of habitat quality or carrying capacity, resulting in a correspondingly

scaled measure of suitable area. For the purpose of introducing our method, however, we here use a simple binary approach with either suitable or unsuitable cells.

The metrics presented here are defined under the assumption of complete dispersal inability within the considered time frame. Although this may be the worst case scenario of Criterion 3 for most species, we consider it a suitable starting point and assessment background. When the approach presented here is applied, information on dispersal ability, if available, can be incorporated into the development of range change predictions to obtain more realistic estimates.

The first metric is migration need, which we define as the relative need to compensate for the loss of range caused by climate change. We quantify migration need at a given time t ($M_{Need,t}$) as the proportion of a species' current distribution area that is projected to be lost due to climate change:

Eq. 1 $$M_{Need,t} = \frac{A_{Original} - A_{Remnant,t}}{A_{Original}}$$

$A_{Original}$ is the size of the distribution area at the time (t = 0) selected as the initial point of the assessment (e.g., current distribution; preferably observed and verified occurrences, but alternatively modelled depending on species, method, and available data). $A_{Remnant,t}$ is the part of $A_{Original}$ that remains climatically suitable at a time t in the future.

$M_{Need,t} = 0$ means that the entire current distribution area is covered by projected future suitable area, i.e., $A_{Original} = A_{Remnant,t}$, which indicates no need for migration because of climate change (other reasons, such as habitat destruction, may cause migration need, but in that case a possible management intervention would be a conservation translocation other than AM; see definitions in IUCN 2012 and Hällfors et al. 2014). The higher the value of $M_{Need,t}$, the more of the current

distribution area is projected to no longer be suitable, and at $M_{Need,t} = 1$ none of the species' current area remains climatically suitable.

The second component, migration potential ($M_{Potential,t}$), we define as the prospect of migration at time t when new area becomes suitable with changes in climate. We model $M_{Potential,t}$ as the proportion of new suitable area from the total suitable area at a certain point in time:

Eq. 2 $$M_{Potential,t} = \frac{A_{New,t}}{A_{New,t}+A_{Remnant,t}}$$

$A_{New,t}$ is the area that was previously unoccupied but is projected to become suitable due to climate change according to the predictions. We scale $A_{New,t}$ by the prospective future suitable area ($A_{New,t}$ + $A_{Remnant,t}$), so that $M_{Potential,t}$ represents the potential for range expansion that a species has after the loss of its original area, i.e., what its potential is in relation to what it has left (the prospect of migration).

A small value of $M_{Potential,t}$ indicates that there is little possibility for range expansion under climate change compared to what the species has left ($A_{Remnant,t}$). The species will therefore benefit only marginally from migrating to the new area, as most of the available suitable area covers its original distribution. Conversely, a high $M_{Potential,t}$ value indicates that the species could increase its range considerably compared to what is left of $A_{Original}$ if it were able to disperse.

For species that have limited ability to disperse fast enough on their own, the need for and potential of migration correspond to the need for and potential of AM. We therefore create a single metric with the name $I_{AM,t}$ (AM index) composed of the geometric mean of its components $M_{Need,t}$ and $M_{Potential,t}$:

Eq. 3 $$I_{AM,t} = \sqrt{M_{Need,t} \cdot M_{Potential,t}}$$

We calculate the root of the product of $M_{Need,t}$ and $M_{Potential,t}$ to arrive at a constant rate of change of $I_{AM,t}$ across low and high values of its components (when the components are in a constant ratio). This makes the index more sensitive to changes when at least one of the components is low. These properties facilitate comparison of the index across different species and climate change scenarios and the detection of small changes in $M_{Need,t}$ and $M_{Potential,t}$. High values of $I_{AM,t}$ indicate that a species has both the need of AM and the potential to benefit from it. Hence, on the basis of range change evaluation, AM might be an appropriate approach in the conservation of this species.

$M_{Need,t}$, $M_{Potential,t}$ and $I_{AM,t}$ are all unitless metrics between zero and one. This facilitates their interpretation, and comparison between different species, future time periods, and climate change scenarios.

2.2. Simulations

We illustrate the behaviour of the metrics with simulated cases of possible changes in $A_{New,t}$ and $A_{Remnant,t}$. The focus is on qualitatively different cases that are representative of possible changes in suitable area of species, and on the response of $I_{AM,t}$ to these changes. Although real-life predictions would normally include climate change projections into only a few future time windows or time steps (e.g., the situation after three, five, and eight decades; see Hällfors et al. 2016) we use 50 time steps to showcase in greater detail how the metrics change through time.

In simulation group 1, changes in $A_{New,t}$ and $A_{Remnant,t}$ are modelled as simple but qualitatively differing functions. In accordance with criteria 1 and 2 above, we assume that climate change decreases $A_{Remnant,t}$ and increases $A_{New,t}$ over time. We allow $A_{Remnant,t}$ and $A_{New,t}$ to change at different rates, and present different combinations with changes being initially fast or slow. We also consider a case of retrogression in $A_{New,t}$, where A_{New} first increases and later decreases, becoming zero by the end of the simulation (signifying that no more A_{New} appears, which in real life could happen when the climatically suitable area moves northwards until the edge of a continent is reached, or up a mountain until the top is reached).

The temporal decrease in $A_{Remnant,t}$ (Fig. 2a) was modelled as $A_{Remnant,t} = 1 - (t/t_{max})^{\alpha}$, where t is the time (arbitrary units) from current, t_{max} is the time at which the simulation ends, and α is a shape parameter that defines whether the initial rate of change in $A_{Remnant,t}$ is faster ($\alpha > 1$) or slower ($0 < \alpha < 1$) than linear. We used the values $\alpha = 2$ and $\alpha = 0.5$ for fast and slow initial change, respectively. The temporal increase of $A_{New,t}$ (Fig. 2b) was modelled as $A_{New,t} = (t/t_{max})^{\alpha}$, with parameters as in $A_{Remnant,t}$, except for the retrogression case that was modelled as $A_{New,t} = \max(0, -0.0005 \cdot t^2 + 0.04 \cdot t)$.

In simulation group 2, we mimic a possible progress of climate change by letting $A_{Remnant,t}$ and $A_{New,t}$ change over time depending on different patterns of viable landscape (Fig. 3). The simulation landscapes consist of 101 × 50 cell lattices, where the black and grey cells constitute the viable landscape where different parts are, have been, or will become suitable (see caption of Fig. 3), while the white cells remain non-viable throughout the simulations signifying habitat types that are unsuitable regardless of the climatic conditions. Suitable climate at each time step is represented as a square frame. It moves over the landscape, representing the change in climate, at a constant rate. Depending on its location, the sliding frame will cover a different part of the simulated landscape

and therefore contain a different number of viable cells, which will be made up from Remnant and New cells in different proportions. The direction of the movement represents the direction of climate change, which in real-life is typically towards the poles or upwards along an elevational gradient. The number of suitable landscape cells that fall within the square frame constitute the climatically (and otherwise) suitable area for the species at each time step. We can now simulate different scenarios of increase and decrease in $A_{New,t}$ and $A_{Remnant,t}$ by varying the pattern of viable landscape cells.

We generated different patterns of viable landscape with a first order autoregressive process (AR1), where the viability of a cell at the row *i* and column *j* of a landscape depends on the viability of its four neighbouring cells at the previous iteration step. This is calculated as $X'_{i,j} = \varphi \cdot (X_{i-1,j} + X_{i+1,j} + X_{i,j-1} + X_{i,j+1})/4 + \varepsilon_{i,j}$, where X is the initial spatial configuration with a normally distributed random state ε (zero mean, unit variance), and φ is the autoregression coefficient (values $\varphi \leq 1$ are feasible). Cells with $X'_{i,j} > 0$ are considered viable.

We used different values of φ to generate patterns of different spatial autocorrelation. The first case (Fig. 3a, $\varphi = 0$) represents complete spatial randomness, where the probability of a cell being viable is spatially independent ($p = 0.5$). This represents a landscape that is uniform at a large scale but randomly patterned as viable or non-viable at a smaller scale. For instance, an insect specialised on living on pine trees could see a large tract of uniform boreal forest like this. The case also serves as a reference point for perhaps more common landscape patterns, where patches of suitable habitat are interspersed in a matrix of non-suitable habitats. These kinds of patterns are positively autocorrelated, i.e., a viable cell in our simulation landscape is more likely to have another viable cell as an immediate neighbour than an unviable one.

We modelled such cases with increasing values of the autoregression coefficient that result in intermediate (Fig. 3b, $\varphi = 0.900$) and high (Fig. 3c, $\varphi = 0.999$) spatial autocorrelation. The increasing size of landscape patches allows large variation in climatically suitable area between sampling intervals. Each value of φ was replicated 100 times to investigate the effect of a random spatial pattern on $I_{AM,t}$ (Fig. 3d) and on the difference between $M_{Potential,t}$ and $M_{Need,t}$ (Fig. 3e) in relation to $A_{Original}$. The state of the replicated systems was investigated at $t = 25$, which corresponds to the climatic frame having moved half of its length from the original position and allows for the highest variance in original, remnant, and new areas.

We measured the degree of autocorrelation in the simulated landscape patterns using global Moran's *I* calculated with first degree neighbourhoods (Fortin and Dale 2005). The metric has been used for quantifying the degree of habitat fragmentation (e.g., Gao and Li 2011) and it facilitates the comparison of our simulated landscapes to patterns in nature. The value of global Moran's $I \approx 0$ represents complete spatial randomness in large samples, while $I = 1$ results from the landscape being divided in two: a viable and an unviable half.

All computations were carried out using Matlab 8.5. (Release 2015a, The MathWorks Inc.). The scripts for generating the simulations and figures 2, 3, and 4 are distributed as Supplementary Data (Appendix A, B, and C).

2.3. Assisted migration threshold

There is no inherent threshold value of $I_{AM,t}$ that would indicate range-change-associated benefit of AM for the species. Such thresholds could, however, be explored based on other widely applied

298 thresholds, e.g., those used in the Red List (IUCN, 2001) or the Climate Change Vulnerability
299 Index (CCVI; Young et al., 2010). Thomas et al. (2011) presented an evaluation framework for
300 incorporating Red List -inspired decadal losses and increases in species' ranges under climate
301 change, with the purpose of recognizing threats and benefits of climate change. In their evaluation,
302 a species receives a score of 0–3 depending on the percentage of decline or increase in distribution
303 per decade (1–4% → score of 1, 4–7.5% → 2, >7.5% → 3). We calculated the values of $I_{AM,t}$ that
304 correspond to these categories to use as thresholds for deciding how beneficial, in terms of range
305 change, AM would be as a conservation method for a species. If both $M_{Need,t}$ and $M_{Potential,t}$ are
306 above a certain threshold, AM could be a relevant method to consider in the conservation of the
307 species in question.
308
309 To arrive at the thresholds, we first investigated a special case where $I_{AM,t}$ only depends on $A_{Remnant,t}$
310 and its rate of decline over a number of decades. We ignore Eq. 2 for the moment, substitute
311 $M_{Potential,t} = 1$ in Eq. 3, and assume that a species loses a constant proportion p_{Loss} of its range in each
312 decade. $A_{Remnant,t}$ and the corresponding $M_{Need,t}$ after t decades then become:
313
314 Eq. 4 $$A_{Remnant,t} = A_{Original} \cdot (1 - p_{Loss})^t$$
315 Eq. 5 $$M_{Need,t} = 1 - (1 - p_{Loss})^t$$
316
317 The minimum requirement for a species to be recognized as climate change threatened, and to
318 receive the score of 1 in Thomas et al.'s (2011) scaling, equals losing 1% of its range per decade
319 (i.e., $p_{Loss} = 0.01$) over the projected time span t = 1. Consequently, $M_{Need,1} = 0.01$ and $I_{AM,1} =$
320 $(0.01 \cdot 1)^{1/2} = 0.1$. In a similar way, 4% and 7.5% declines over a decade correspond to $I_{AM,1} = 0.2$
321 and $I_{AM,1} \approx 0.27$, respectively.
322

We next considered how the formation of $A_{New,t}$ affects $I_{AM,t}$. Following Thomas et al. (2011), we assume that $A_{New,t}$ is formed as a proportion p_{Gain} of $A_{Original}$ and that the amount of $A_{New,t}$ is zero at t = 0. The size of $A_{New,t}$ and the corresponding $M_{Potential,t}$ then become:

Eq. 6 $$A_{New,t} = A_{Original} \cdot [(1 + p_{Gain})^t - 1]$$

Eq. 7 $$M_{Potential,t} = \frac{(1+p_{Gain})^t - 1}{(1+p_{Gain})^t + (1-p_{Loss})^t - 1}$$

By substituting relevant factors in Eq. 3 with Eqs. 5 and 7, $I_{AM,t}$ becomes a function of p_{Gain} and p_{Loss}, and the number of decades investigated. The time t is known from the point in time for which the prediction was made, and we can present the threshold values for one decade (t = 1) as $I_{AM,1}$ = [0.1, 0.2, 0.27] in a parameter space of p_{Loss} and p_{Gain} (Fig. 4a). The loss rates are restricted to $0 \leq p_{Loss} \leq 1$, because $A_{Original}$ cannot decrease by more than 100%, but no such restriction applies to the rate of increase in area (i.e., $p_{Gain} \geq 0$). With increasing p_{Gain}, the corresponding value of p_{Loss} approaches the threshold values $I_{AM,1}$ = [0.1, 0.2, 0.27]. With decreasing p_{Gain}, the corresponding value of p_{Loss} approaches unity.

3. Results

As climate change causes progressive changes in $A_{New,t}$ and $A_{Remnant,t}$ for a species (simulation group 1; Fig. 2a,b), the corresponding values of $M_{Need,t}$ and $M_{Potential,t}$ form trajectories in the parameter space (Fig. 2d,e), where the value of the combined metric increases towards the top-right corner (Fig. 2c). Depending on the rate of change in $A_{Remnant,t}$ and $A_{New,t}$, the relative magnitude of $M_{Need,t}$ and $M_{Potential,t}$ can vary, and the trajectories move above or below the diagonal that divides the parameter space.

When $A_{Remnant,t}$ decreases faster than $A_{New,t}$ increases, $M_{Need,t}$ is large relative to $M_{Potential,t}$, and trajectories move below the diagonal (Fig. 2d). Slow reduction in $A_{Remnant,t}$ combined with fast increase in $A_{New,t}$ results in large $M_{Potential,t}$ in relation to $M_{Need,t}$, and trajectories progress above the diagonal (Fig. 2e). A fast decrease in $A_{Remnant,t}$ combined with equally fast increase in $A_{New,t}$ leads to a trajectory that follows the diagonal (Fig. 2d). A slow decrease in $A_{Remnant,t}$ and slow increase in $A_{New,t}$ leads to a similar trajectory, but $I_{AM,t}$ increases at a slower rate (Fig. 2e). $I_{AM,t}$ can also decrease if $A_{Original,t}$ and $A_{New,t}$ do not change at an even rate. For example, if $A_{New,t}$ first increases and then decreases, $I_{AM,t}$ similarly first increases and then decreases (Fig. 2e).

Under complete spatial randomness of viable and non-viable cells (simulation group 2; Fig. 3a), $M_{Need,t}$ and $M_{Potential,t}$ increase at the same rate, owing to equally many new cells becoming suitable at the leading edge (top) of the sliding sampling frame (i.e., the 'changing climate') as originally suitable cells become unsuitable at the trailing edge (bottom) of the frame. At each advancing simulation step, $A_{Remnant,t}$ therefore decreases by the same amount as $A_{New,t}$ increases, with slight variation coming from the randomness in the distribution of viable cells. As a consequence, there is little variation in $A_{original}$ and $I_{AM,t}$ between replicates of the pattern-generating process (Fig. 3d), and M_{Need} and $M_{Potential}$ are nearly equal (Fig. 3e). This indicates that the trajectory of $I_{AM,t}$ would follow the diagonal of the M_{Need} vs. $M_{Potential}$ parameter space (cf. Fig. 2c).

When the degree of spatial autocorrelation takes intermediate (Fig. 3b) or high (Fig. 3c) values, $A_{original}$ and $I_{AM,t}$ vary more, and there is more variation in the relative magnitudes of $M_{Need,t}$ and $M_{Potential,t}$ (Fig. 3e). If this was presented in the parameter space of $M_{Need,t}$ vs. $M_{Potential,t}$ (Fig. 2c), the trajectory of $I_{AM,t}$ would in many cases be far from the diagonal and could also move from one side of the diagonal to the other. Increasing spatial autocorrelation also brings about a negative

relationship between $A_{original}$ and $I_{AM,t}$ (Fig. 3d), and the value of $M_{Potential,t}$ decreases in relation to $M_{Need,t}$ when $A_{original}$ increases (Fig. 3e). The first relationship shows that species already occupying most of the viable cells in the landscape do not benefit from AM. The second relationship shows that the decrease in $I_{AM,t}$ with increasing proportion of viable cells in $A_{original}$ results from a decrease in $M_{Potential,t}$. The values of the autoregression coefficient φ used for simulating landscape patterns resulted in large differences in degree of autocorrelation as measured by Moran's *I*. Complete spatial randomness (φ = 0) led to Moran's *I* = -0.0023 ± 0.0066 (mean ± SD), while the autoregressive process with φ = 0.9 and φ = 0.999 corresponded to *I* = 0.35 ± 0.01 and *I* = 0.73 ± 0.03, respectively.

Our translation of Thomas et al.'s (2011) climate change threat scores into critical values of $I_{AM,t}$ can be interpreted so that, when $I_{AM,t}$ is calculated based on predictions extending one decade into the future, a species with $0.1 < I_{AM,1} < 0.2$ is a possible candidate for AM, a species with $0.2 < I_{AM,1} < 0.27$ is a probable candidate for AM and a species with $I_{AM,1} > 0.27$ is a strong candidate for AM (Fig. 4a). For a prediction 100 years into the future (10 decades) the corresponding thresholds for $I_{AM,10}$ are 0.31, 0.58, and 0.74 (Fig. 4b).

4. Discussion

The parameter space formed by all possible values of $M_{Need,t}$ and $M_{Potential,t}$ shows the nonlinear relationship between $I_{AM,t}$ and its components (Fig. 2c). At the combined low $M_{Need,t}$ and low $M_{Potential,t}$ (Fig. 2c: lower left corner of the parameter space), the low value of $I_{AM,t}$ indicates that a species is neither losing its current range nor gaining new migration opportunities (Fig. 1a). This could happen in reality, e.g., when a species has a wide distribution area to start with

(geographically or as regards climatic variation), or when it occurs in an area that is climatically relatively stable even in the face of global change, such as refuge areas during Pleistocene climatic oscillations. Alternatively, a species may be so strongly limited by other factors than climate that a change in climate does not lead to a marked change in its distribution. Examples include some plant species adapted to serpentine soils (Damschen et al. 2012).

When one of the components ($M_{Need,t}$ or $M_{Potential,t}$) is very small, $I_{AM,t}$ may not exceed the threshold for the species to be considered a candidate for AM even if the other component is substantially larger. This implies that AM is likely a poor conservation choice, since there is either little threat of losing area or little new area available to translocate the species to. Therefore, a low $I_{AM,t}$ for a certain species would support a decision of no intervention, if there is no threat of losing area, or the application of actions other than AM in the conservation of the species, if there is loss of current area but no emerging new area. If only $M_{Need,t}$ is high (Fig. 1b; Fig. 2c: lower right-hand part of parameter space), the need for conservation is certainly more urgent than if only $M_{Potential,t}$ is high (Fig. 1c; Fig. 2c: upper left-hand part), but AM is not an applicable method, as there would be no suitable area to which the species could be assisted to migrate. Alternative conservation strategies might then involve increased *in situ* management, *ex situ* conservation, or even conservation introduction (IUCN 2012), i.e., translocating the species to any environmentally suitable area outside of its indigenous range, where the species could not move on its own even with time, such as another continent.

Only a species that gains new suitable area at the same time as it loses previously suitable area (Fig. 1d; Fig 2c: centre to upper right part of parameter space), but has difficulties in dispersing on its own, is a clear candidate for AM. Changes in climatically suitable area of this kind are likely to occur in settings lacking an elevational gradient and where an edge of a continent is not

immediately reached (for an example of a dispersal-limited desert tree in Africa, see Foden et al. 2007).

Spatial autocorrelation increased variance in $A_{Original}$ of the modelled hypothetical species, and led to variation in the value of $I_{AM,t}$ and the relative magnitude of its components (Fig. 3d,e). The variance allows us to see the negative correlation between $A_{Original}$ and I_{AM}. When most of the viable cells are within the original area, the result is a low $I_{AM,t}$ (Fig. 3d) and a relatively low $M_{Potential,t}$ (Fig. 3e). In the opposite case, where most of the viable cells in the landscape are outside the original area (small $A_{Original}$), climate change will result in a high proportional loss of the original area and a large proportional gain of new area in comparison to remnant area, which leads to a high I_{AM} (Fig. 3d) and a relatively high $M_{Potential,t}$ (Fig. 3e). We can therefore expect a negative relationship between $A_{Original}$ and $I_{AM,t}$ to arise from the spatial distribution of viable landscape cells. This pattern emerged in a study where the method presented here was applied to real-world species using range change predictions derived through SDMs (Hällfors et al. 2016). Based on the present simulation results, the relationship between $A_{Original}$ and $I_{AM,t}$, or the relative magnitude of its components should not automatically be attributed to biological processes or species characteristics without additional evidence, as the relationship can simply result from landscape patterns. Nevertheless, in real-life situations a large $I_{AM,t}$ for a species with a small $A_{Original}$ can also reflect an ecologically relevant process for rare species: as climate change makes large parts of the original area unsuitable, even if not much new area is gained, the proportional importance of the new area increases, since remnant area is scarce. In such cases a high $I_{AM,t}$ value correctly reflects the need and potential of AM, even though focal translocation areas may be limited.

Natural landscapes have values of Moran's *I* that correspond to our simulated landscapes. The intermediate landscape ($\varphi = 0.9$; Moran's $I = 0.36$) falls in the range of values estimated for urban

448 landscape of Shenzhen in Guangdong Province in South China (I = 0.28-0.55; Gao and Li 2011)
449 and the estimated I = 0.44 for the pattern of architectural landscape in Jinan, China (Xue et al.
450 2015). These urban landscapes represent a higher degree of fragmentation than the protected areas
451 in northern New England (Meyer et al. 2015), where the highest values of Moran's $I > 0.70$ are
452 similar to the landscapes we simulated with the highest autoregression coefficient ($\varphi = 0.999$).
453
454 We harmonized our conceptualization and metrics with the climate change threat scale of Thomas
455 et al. (2011) by using the same percentage rates of change in $A_{Remnant,t}$ and $A_{New,t}$ as they did for loss
456 and gain, and by calculating the corresponding combined values of the metrics for these thresholds.
457 Applying this framework in evaluating AM suitability for real species should provide useful
458 experience and insight into the functionality of this approach and the suggested thresholds. It is
459 important to note, however, that placing species in these categories does not alone determine how
460 appropriate AM would be in each case. Species recognised as strong AM candidates based on the
461 $I_{AM,1} > 0.27$, will additionally have to be subjected to more detailed analyses on the ecological,
462 economic, societal, legal, and ethical applicability of AM (e.g., IUCN 2012, Peréz et al. 2012,
463 Maier & Simberloff 2016; Siipi & Ahteensuu 2016). But without a rigorous measure of the need
464 and potential for migration, suggesting whether AM could be the appropriate method, when it
465 comes to geographical shifts in the species' suitable area, such further considerations are premature.
466
467 We see the formalization of migration need and potential presented here as a useful tool in two
468 main situations:
469 (1) Determining the most suitable conservation method and, in particular, evaluating the spatial
470 applicability of AM in conservation planning for a specific species.

(2) Screening of large numbers of species to gain understanding about what proportion of a regional biota might be in need of AM within a given time frame under a certain climate change scenario.

In the first situation, the formalization can be used as part of decision-making frameworks (e.g., Perez et al. 2012; Schwartz & Martin 2013) to provide objective, quantitative answers to questions concerning future decline and increase of suitable area. Here, its novelty comes from specifically relating predictions in range change to the ecological usefulness of AM. The approach thus provides instructions on how to apply previously identified tools, such as correlative species distribution models and expert predictions of range change, in the context of decision-making concerning AM. Obviously our method does not, however, represent a statement regarding how generally recommendable AM of the species is.

An additional benefit of the AM index calculations is that they can provide guidelines on the applicability and timing of application of other conservation methods too. If, for instance, $M_{Need,t}$ rapidly increases within the coming decades, while $M_{Potential,t}$ remains low, it may be advisable to opt for designing and carrying through an *ex situ* conservation programme for the species. Since the development of I_{AM} is non-linear, predictions further into the future may suggest that eventually new climatically suitable area will appear, and then the *ex situ* population of the species could be used for an introduction of the species into the newly emerged suitable area, should it be deemed otherwise acceptable. This could be described as a delayed AM procedure, where the calculation of I_{AM} and its components gave impetus to the intermediate *ex situ* conservation stage. Alternatively, if $M_{Need,t}$ increases only gradually, while the increase in $M_{Potential,t}$ is delayed, more intensive *in situ* management in the current distribution area may be the best option. This could help a population

stay viable until new climatically suitable area appears where the population can migrate (or be assisted to migrate).

In the second situation, screening large numbers of species, formalized metrics make it possible to calculate comparable percentages of species that could benefit from AM for different points in time, e.g., after two, five, or eight decades. Here, the important aspect of our AM metrics is that their values are likely to change non-linearly over time as climate change progresses in real-world settings (see Hällfors et al. 2016). Hence they have the potential of highlighting time frames during which specific conservation actions are the most beneficial, or even at all possible, for a certain species. For instance, if the proportion of the biota needing AM increases considerably after five decades, it is probably advisable to strive for avoiding that situation, e.g., through investing in enhancing natural dispersal by increasing connectivity between habitat patches, since large-scale AM is likely to be considerably challenging and costly, and may be challenged on other grounds too (Maier & Simberloff 2016). Hence, the metrics introduced here can highlight resource need for conservation under different climate change scenarios and help resource managers to plan ahead. Moreover, scenarios like this can further emphasize the need to mitigate climate change, rather than relying on adaptation to it.

The approach presented here can thus be used in a similar manner as the Red List Index (Butchard et al. 2007). The Red List Index describes observed changes in species' threat status, and serves as an evaluative and political tool for assessing conservation trends. However, our metrics concern anticipating future challenges, rather than evaluating past changes. It is therefore important to recognize the many uncertainties involved in methods for predicting change in suitable area (Heikkinen et al. 2006; Martin et al. 2012). These include epistemic uncertainties regarding our incomplete knowledge on the environmental requirements of species as well as uncertainty in

human decisions ranging from expert judgments to climate change mitigation. Although some of this uncertainty can be handled or at least apprehended through ensemble modelling (Araújo and New 2007; for application in the context of the method described here, see Hällfors et al. 2016), the reliability of predictions will continue to depend on the quality and validity of the data and theory used to develop them. However, because our metrics are based on explicit data and formalized calculations, they have the advantage of being comparatively easy to update and re-evaluate as new data and refined prediction methods become available.

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Glossary

Assisted migration = safeguarding biological diversity through the translocation of representatives of a species or population harmed by climate change to an area outside the indigenous range of that unit where it would be predicted to move as climate changes, were it not for anthropogenic dispersal barriers or lack of time (Hällfors et al. 2014).

Migration = the processes of dispersal, colonization, and establishment, which in the case of assisted migration are aided by humans.

$\mathbf{A_{Original}}$ = current distribution (observed or modelled depending on the species and available occurrence data) of a species (measured in number of grid cells, km^2, or similar).

$\mathbf{A_{Remnant,t}}$ = the part of $A_{Original}$ that remains suitable at a certain point of time in the future (measured in number of grid cells, km^2, or similar).

545 $\mathbf{A_{New,t}}$ = the area (number of grid cells, km^2, or similar) that was previously unoccupied or
546 unsuitable but has become suitable due to climate change.
547 $\mathbf{M_{Potential,t}}$ = Migration potential, the prospect of migration when new area becomes suitable with
548 change in climate, calculated as the proportion of new suitable area ($A_{New,t}$) from the total suitable
549 area ($A_{Remnant,t} + A_{New,t}$) at a certain point in time. A high value of $M_{Potential,t}$ indicates that climate
550 change offers the species relatively large potential for range expansion compared to what it has left.
551 $\mathbf{M_{Need,t}}$ = Migration need, the relative need to compensate for the loss of range by climate change,
552 calculated as the proportion of a species' original distribution area ($A_{Original}$) that will be lost due to
553 climate change ($A_{Original,t} - A_{Remnant,t}$). A high value of $M_{Need,t}$ indicates that climate change turns a
554 relatively large part of the original area unsuitable wherefore the species has a high need for range
555 expansion to maintain a distribution area of the same size.
556 $\mathbf{I_{AM}}$ = the geometric mean of $M_{Need,t}$ and $M_{Potential,t}$, indicating, on a scale between 0-1, how relevant
557 assisted migration might be for the species.
558
559 **Appendix A. Supplementary data**
560 **Appendix B. Supplementary data**
561 **Appendix C. Supplementary data**
562 Supplementary data associated with this article can be found, in the online version, at http:
563 //dx.doi.org/10.1016/…
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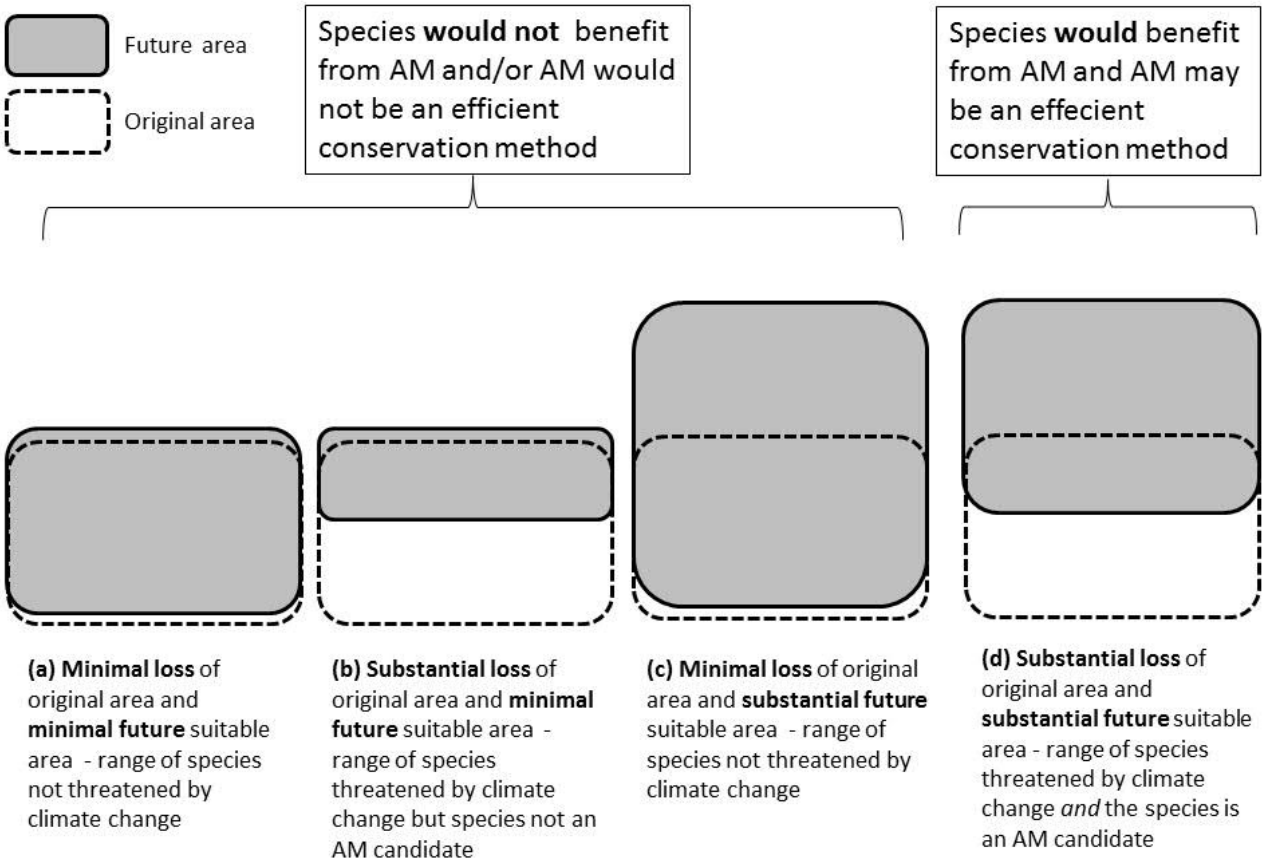
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724 Fig. 1. Conceptualization of assisted migration (AM; *sensu* Hällfors et al. 2014) candidacy
725 interpreted in the context of predictions about a species' future suitable area. If predictions suggest
726 any of the three future scenarios (a-c), the species in question either does not need AM or does not
727 have the potential of shifting its distribution because new area does not become available. The
728 fourth scenario (d) suggest that AM could be an appropriate conservation method for this species.

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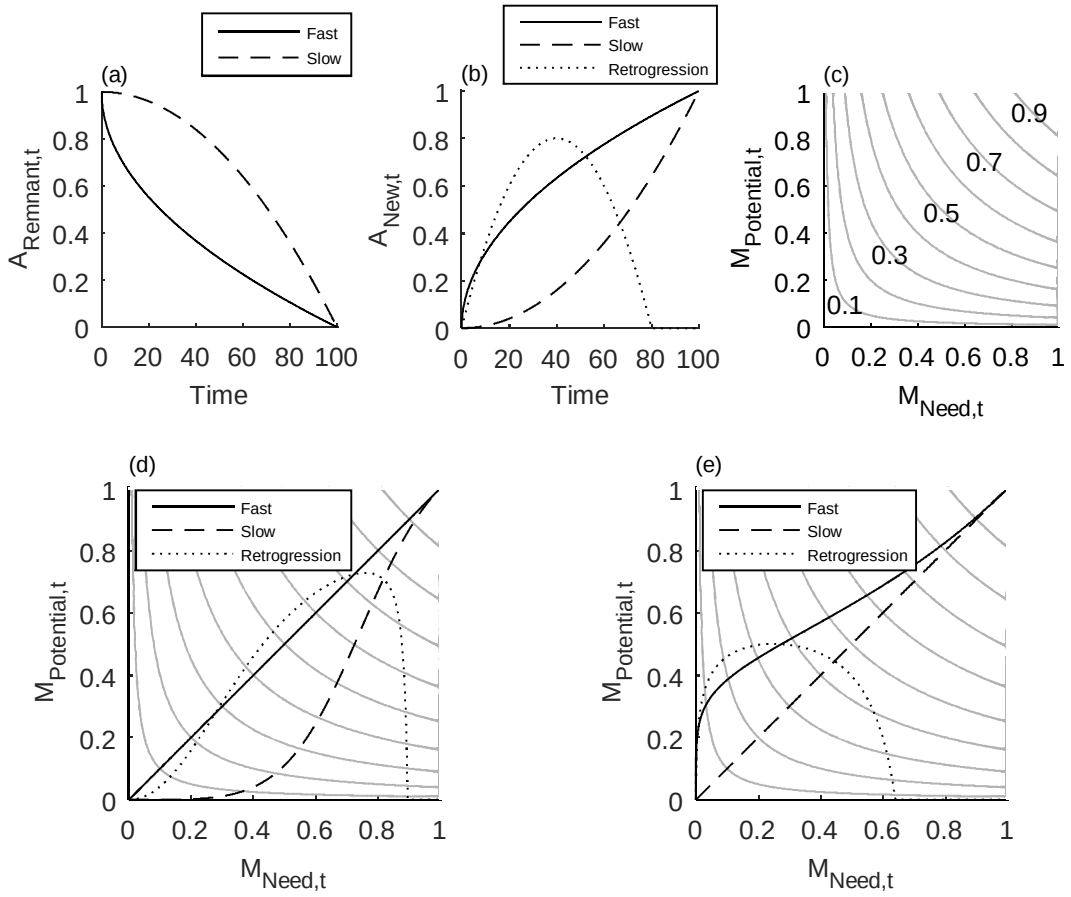
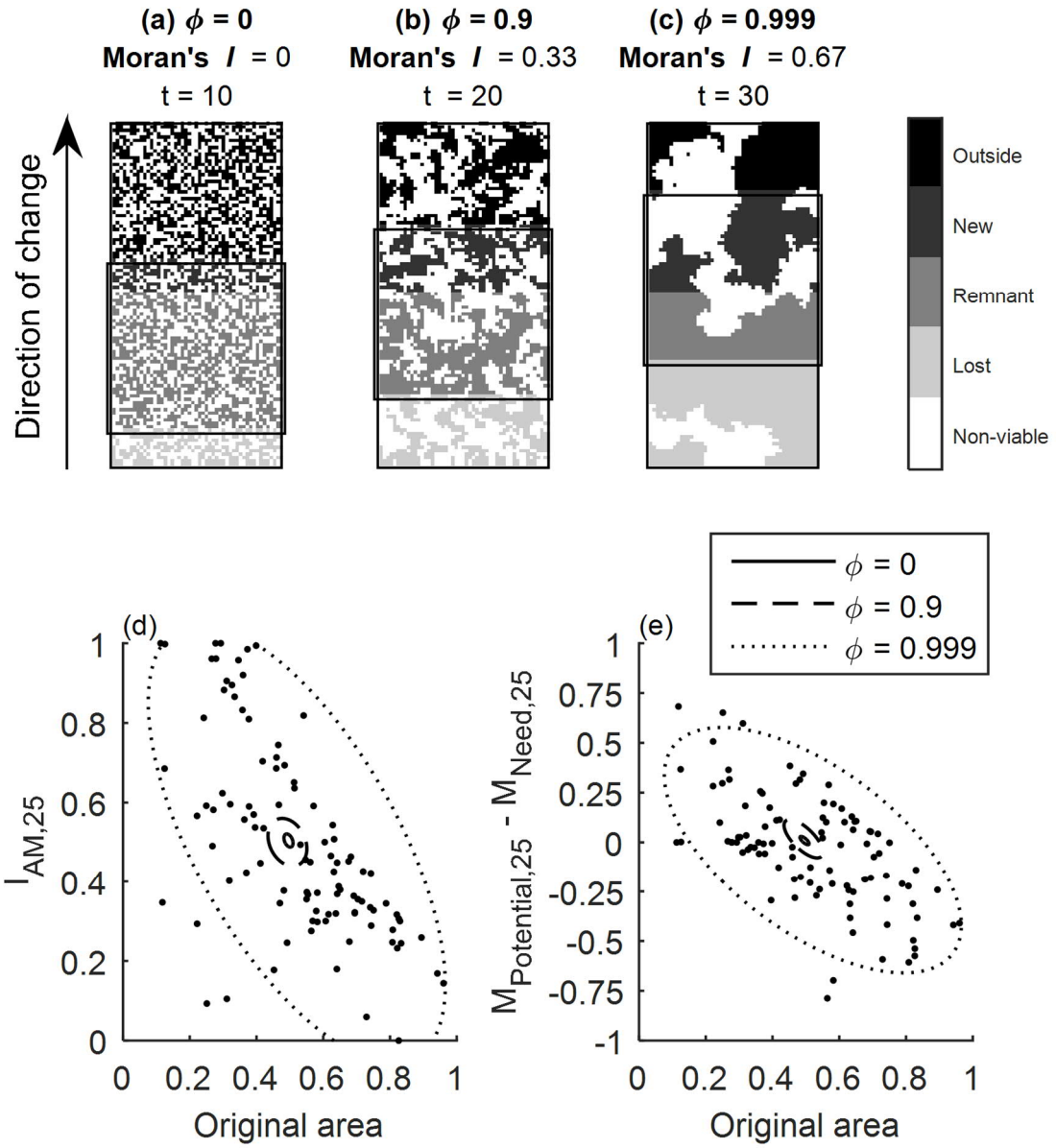


Fig. 2. Simulated development of remnant and new areas ($A_{Remnant}$ and A_{New}, respectively) and the corresponding $M_{Need,t}$, $M_{Potential,t}$, and $I_{AM,t}$. Scenarios for temporal development of (a) $A_{Remnant,t}$ and (b) $A_{New,t}$, under simulated climate change, and (c) a parameter space plot with the axes $M_{Need,t}$ and $M_{Potential,t}$ and the corresponding values of $I_{AM,t}$ (isoclines at 0.1 unit intervals). The lower panels show trajectories of $I_{AM,t}$ corresponding to the three scenarios of $A_{New,t}$ development shown in b, that are combined with $A_{Remnant,t}$ decreasing initially at a (d) fast, and (e) slow rate, as in panel a. $A_{Original} = 1$ in all cases.

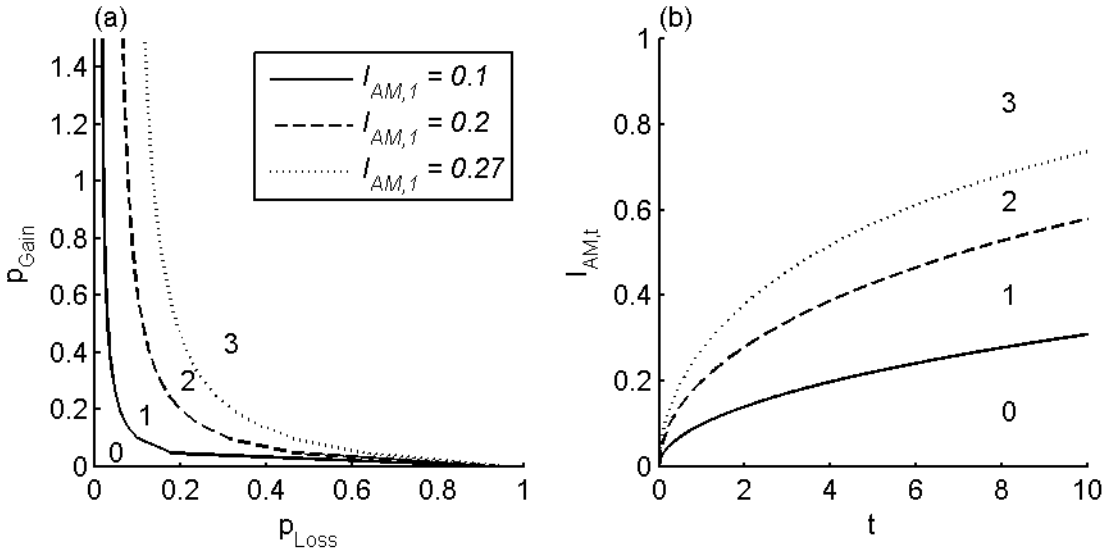


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745 Fig. 3. (a-c) Examples of lansdcape patterns of viable (black and grey) and non-viable (white) cells
746 simulated with different values of first order autoregression parameter phi and the corresponding
747 measure of spatial autocorrelation as global Moran's I (first neighbours). The climatic suitability of
748 cells is determined by a square frame representing the area of suitable climate. The frame moves
749 over the landscape one cell row at the time in a bottom to top direction representing climate change,
750 e.g., pole- or upward movement of mean temperature or other climatic variable(s). At the beginning
751 of the simulation, the climatic frame coincides with the original area ($A_{Original}$). As the climatic

752 frame moves over the landscape, some cells initially part of $A_{Original}$ become unsuitable (i.e., Lost),
753 while others remain suitable (Remnant). Cells that were not part of $A_{Original}$ but become suitable by
754 the movement of the climatic frame constitute the New area. The Outside cells represent the area
755 that has not yet become climatically suitable, but may in the future be part of the New area. The
756 panels (a-c) illustrate the location of the climatic frame at different time steps (t = 10, 20, 30 cells or
757 time steps upwards from the bottom). Panels d and e show $I_{AM,t}$ and the difference between $M_{Need,t}$
758 and $M_{Potential,t}$ at the time t = 25 in relation to the original area. The dots are replicates of the
759 landscapes simulated with $\varphi = 0.999$ and the dotted ellipse is a 95% confidence ellipse fitted to the
760 scatterplot. For clarity, the scatterplot of other values of φ are omitted and these cases are
761 represented only by their confidence ellipses.
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765 Fig. 4. a) AM index ($I_{AM,1}$) as a function of proportional loss of area p_{Loss} and gain of area p_{Gain} per
766 decade. The threshold values $I_{AM,1}$ = [0.1, 0.2, 0.27] correspond to 1, 4 and 7.5% reduction rates
767 evaluated over a single decade (t = 1). b) $I_{AM,t}$ thresholds for scores of 0-3 over 0-10 decades (t),
768 where the scores are: 0 = not a candidate for AM; 1 = possible candidate for AM; 2 = probable
769 candidate for AM; and 3 = strong candidate for AM.

770