1 Quantifying the need and potential of assisted migration.

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26 **Abstract**

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28 Assisted migration is recognized as a possible method for species conservation under climate

29 change. Predicted decrease in range size and emergence of new suitable areas due to climate change

30 are the main reasons for considering assisted migration. The magnitude of such changes can be used

31 to guide decisions on the applicability of this conservation method. However, it has not been

32 formalized how predictions acquired, e.g., with the help of species distribution models or expert

33 assessments, should translate into recommendations or decisions. Climate change threat indices

34 concentrating on predicted loss of habitat are not directly applicable in this context as they do not

35 define whether a species has the potential to expand its range compared to the area that remains

36 suitable. Here we present a conceptual framework for identifying and quantifying situations in

37 which predictions indicate that a species could benefit from assisted migration. We translate

38 predicted changes in suitable area into separate metrics for migration need and migration potential

39 on the basis of the amount of lost, remnant, and new area. These metrics can be used as part of

40 decision-making frameworks in determining the most suitable conservation method for a specific

41 species. They also hold potential for coarser screening of multiple species to estimate the proportion

42 of species that could benefit from assisted migration within a given time frame and climate change

43 scenario. Furthermore, the approach can be used to highlight time frames during which assisted

44 migration or, alternatively, other conservation actions are the most beneficial for a certain species.

45

46 **Key words**: adaptive management, assisted colonization, climate change, ecological niche

47 modelling, managed relocation, translocation

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51   1. Introduction

52

53   Observed and potential effects of climate change on biodiversity are becoming evident (Dawson et

54   al. 2011, Brommer et al. 2012, Urban 2015). A concern that traditional conservation methods may

55   not be enough to safeguard species from decline has led to proposals of new proactive methods,

56   such as actively moving species to new areas in pace with the changing climate (Peters & Darling

57   1985; Hunter 2007, Schwartz et al. 2012). Although rarely implemented to date, this approach has

58   been extensively discussed. It has variously been called assisted migration, assisted colonization,

59   and managed relocation, among others, and also defined in different ways (Hällfors et al. 2014). In

60   the strict sense, however, it is a type of conservation translocation (*sensu* IUCN 2012) in which

61   species are moved from their indigenous range to areas where they would be predicted to move as

62   climate changes, were it not for anthropogenic dispersal barriers or lack of time (see Hällfors et al.

63   2014 for a thorough discussion); here we refer to the method in this sense and call it assisted

64   migration (AM). We use 'conservation' in the broad sense, i.e., include in it all actions aimed at

65   safeguarding biodiversity, both preserving approaches and conservation management.

66

67   To begin with, it should be noted that wide consensus on the acceptability of AM has not been

68   reached (Hewitt et al. 2011; Maier & Simberloff 2016; Siipi & Ahteensuu 2016). Nevertheless, AM

69   has already been conducted for the conifer *Torreya taxifolia* in the USA (Barlow & Martin 2004;

70   Marris 2009) and for two butterfly species in the UK (Willis 2009), and is being considered, e.g.,

71   for the butterfly *Euphydryas editha quino* (Marris 2009). Hence, it is important to develop best-

72   practice guidelines for the possible future implementation of the method even if their application, in

73   the end, may not turn into mainstream conservation practice. Indeed, several frameworks have been

74   presented for guiding decisions on whether and when a species needs AM, for risk evaluation, and

75   for planning the process if deemed feasible (Hoegh-Guldberg et al. 2008; Richardson et al. 2009;

76   McDonald-Madden et al. 2011; Perez et al. 2012; Schwartz & Martin, 2013).

77

78   Predictions of future changes in suitable areas have repeatedly been suggested as aids in evaluating

79   the need of AM (Chauvenet et al., 2012; Schwartz, 2012; Guisan et al., 2013; Gallagher et al 2014).

80   Such predictions can be derived at least through expert evaluation, mechanistic niche models, or

81   species distribution models (SDMs). All these approaches contain uncertainties and caveats, such as

82   biases in expert judgement, and assumptions on ecological equilibrium and local adaptation in niche

83   models. These have been extensively discussed in the literature (Heikkinen et al. 2006; Araújo &

84   Peterson, 2012; Martin et al. 2012). However, the prediction methodology is continuously

85   developing (Morin & Thuiller 2009; Martin et al. 2012, Braunisch et al. 2013) and holds clear

86   potential in this context as long as predictions are interpreted in the light of the limitations of the

87   applied methodology. Nevertheless, it has not been established how the information obtained from

88   predictions should be translated into decisions on whether or not to apply AM.

89

90   The absence of a recognized method for utilizing the information on range change predictions

91   means that managers wishing to evaluate the appropriateness of AM are left with a recommendation

92   on what tool to use but with no instructions on how to use it. This lack of guidance may result in

93   subjective decisions and thereby inconsistent policy, or even in a status quo where no decisions are

94   made, leading to a high risk of losing biodiversity in a rapidly changing world. A formal and

95   rigorous way of utilizing range change predictions for the specific purpose of AM evaluations and

96   decisions is therefore needed.

97

98   In evaluating species' vulnerability to and threat from climate change, formalizations of the use of

99   modelling outputs have been put forward (e.g., Thomas et al. 2011, Maggini et al. 2014). Although

100   the proposed frameworks may be suitable for evaluating general threat from climate change, being

101   vulnerable to climate change because of anticipated loss of distribution area does not necessarily

102   mean that AM would be a suitable conservation method for the species. Instead, a combination of

103   expected loss and gain of area is required for AM to be an appropriate response. A species that is

104   not losing suitable habitat does not need to migrate and a species that will not have new climatically

105   suitable area outside its current distribution area will not benefit from migration (with migration we

106   mean the processes of dispersal, colonization, and establishment, which in the case of AM are aided

107   by humans; Fig. 1). Hence, vulnerability assessments concentrating on species' sensitivity to

108   climate change (see, e.g., Pacifici et al. 2015 for a review) are not sufficient to inform decisions

109   regarding AM. Instead, both estimates on climate change exposure and on availability of new

110   suitable area for translocations are necessary when deciding on and planning AM.

111

112   On the basis of our conceptualization of when a species would benefit from AM (Fig. 1), we present

113   a straightforward method for converting predictions of changes in suitable area into metrics

114   describing AM benefit. These metrics can be utilized in decision-making frameworks to answer

115   those questions that concern range change. The predictions themselves can be constructed through a

116   variety of methods, including not only correlative SDMs but also mechanistic models and expert

117   evaluations, and be based on various data sources. Likely data include known species occurrences,

118   climate variables, dispersal abilities, habitat requirements, habitat availability, and biotic

119   interactions among species. The data needed for calculating the metrics we propose are readily

120   obtainable from the range change predictions, provided these are quantifiable into spatial units, such

121   as grid cells. The reliability of the results of predictions would largely depend on the degree of

122   expert knowledge, the quality of the data, and other assumptions made in the process of obtaining

123   the predictions. However, in this paper we do not attempt to test the usability of different prediction

124   methods for range changes nor how different input data or modelling assumptions affect the

125   predictions. Instead, the aim is to describe a process that can be used for supporting decisions in

126   conservation once sufficiently reliable predictions on changes in suitable area are available (see

127   Hällfors et al. 2016 for a real-life application of the method described here).

128

129

130   2. Methods

131

132   2.1. Derivation of the AM metrics

133

134   Assisted migration, i.e., human-mediated dispersal to and establishment in new areas, may be

135   applicable as a conservation method for species that meet the following criteria:

136

137   1. Migration need: Climate change, e.g.., changes in temperature and precipitation regimes, is

138   predicted to render (part of) the species' current distribution area unsuitable.

139   2. Migration potential: Climate change is predicted to bring about new suitable area for the

140   species.

141   3. Migration inability: The species either has poor intrinsic dispersal ability or faces

142   anthropogenic dispersal barriers.

143

144   Criteria 1 and 2 can be quantified using predictions of changes in climatic conditions and

145   corresponding changes in suitable area, in addition to information on current distribution and habitat

146   preferences. In this paper and in the simulations we present, we treat suitable and unsuitable area in

147   a binary fashion. However, the suitability of the area could also be weighted by the probability of

148   suitability, or by some metric of habitat quality or carrying capacity, resulting in a correspondingly

6

149   scaled measure of suitable area. For the purpose of introducing our method, however, we here use a

150   simple binary approach with either suitable or unsuitable cells.

151

152   The metrics presented here are defined under the assumption of complete dispersal inability within

153   the considered time frame. Although this may be the worst case scenario of Criterion 3 for most

154   species, we consider it a suitable starting point and assessment background. When the approach

155   presented here is applied, information on dispersal ability, if available, can be incorporated into the

156   development of range change predictions to obtain more realistic estimates.

157

158   The first metric is migration need, which we define as the relative need to compensate for the loss

159   of range caused by climate change. We quantify migration need at a given time t ($M_{Need,t}$) as the

160   proportion of a species' current distribution area that is projected to be lost due to climate change:

161

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

163

164    $A_{Original}$ is the size of the distribution area at the time (t = 0) selected as the initial point of the

165   assessment (e.g., current distribution; preferably observed and verified occurrences, but

166   alternatively modelled depending on species, method, and available data). $A_{Remnant,t}$ is the part of

167    $A_{Original}$ that remains climatically suitable at a time t in the future.

168

169    $M_{Need,t} = 0$ means that the entire current distribution area is covered by projected future suitable

170   area, i.e., $A_{Original} = A_{Remnant,t}$, which indicates no need for migration because of climate change

171   (other reasons, such as habitat destruction, may cause migration need, but in that case a possible

172   management intervention would be a conservation translocation other than AM; see definitions in

173   IUCN 2012 and Hällfors et al. 2014). The higher the value of $M_{Need,t}$, the more of the current

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

175   area remains climatically suitable.

176

177   The second component, migration potential ($M_{Potential,t}$), we define as the prospect of migration at

178   time t when new area becomes suitable with changes in climate. We model $M_{Potential,t}$ as the

179   proportion of new suitable area from the total suitable area at a certain point in time:

180

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

182

183   $A_{New,t}$ is the area that was previously unoccupied but is projected to become suitable due to climate

184   change according to the predictions. We scale $A_{New,t}$ by the prospective future suitable area ($A_{New,t} +$

185   $A_{Remnant,t}$), so that $M_{Potential,t}$ represents the potential for range expansion that a species has after the

186   loss of its original area, i.e., what its potential is in relation to what it has left (the prospect of

187   migration).

188

189   A small value of $M_{Potential,t}$ indicates that there is little possibility for range expansion under climate

190   change compared to what the species has left ($A_{Remnant,t}$). The species will therefore benefit only

191   marginally from migrating to the new area, as most of the available suitable area covers its original

192   distribution. Conversely, a high $M_{Potential,t}$ value indicates that the species could increase its range

193   considerably compared to what is left of $A_{Original}$ if it were able to disperse.

194

195   For species that have limited ability to disperse fast enough on their own, the need for and potential

196   of migration correspond to the need for and potential of AM. We therefore create a single metric

197   with the name $I_{AM,t}$ (AM index) composed of the geometric mean of its components $M_{Need,t}$ and

198   $M_{Potential,t}$:

199

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

201

202   We calculate the root of the product of $M_{Need,t}$ and $M_{Potential,t}$ to arrive at a constant rate of change of

203    $I_{AM,t}$ across low and high values of its components (when the components are in a constant ratio).

204   This makes the index more sensitive to changes when at least one of the components is low. These

205   properties facilitate comparison of the index across different species and climate change scenarios

206   and the detection of small changes in $M_{Need,t}$ and $M_{Potential,t}$. High values of $I_{AM,t}$ indicate that a

207   species has both the need of AM and the potential to benefit from it. Hence, on the basis of range

208   change evaluation, AM might be an appropriate approach in the conservation of this species.

209

210    $M_{Need,t}$, $M_{Potential,t}$ and $I_{AM,t}$ are all unitless metrics between zero and one. This facilitates their

211   interpretation, and comparison between different species, future time periods, and climate change

212   scenarios.

213

214   2.2. Simulations

215

216   We illustrate the behaviour of the metrics with simulated cases of possible changes in $A_{New,t}$ and

217    $A_{Remnant,t}$. The focus is on qualitatively different cases that are representative of possible changes in

218   suitable area of species, and on the response of $I_{AM,t}$ to these changes. Although real-life predictions

219   would normally include climate change projections into only a few future time windows or time

220   steps (e.g., the situation after three, five, and eight decades; see Hällfors et al. 2016) we use 50 time

221   steps to showcase in greater detail how the metrics change through time.

222

223 In simulation group 1, changes in $A_{New,t}$ and $A_{Remnant,t}$ are modelled as simple but qualitatively

224 differing functions. In accordance with criteria 1 and 2 above, we assume that climate change

225 decreases $A_{Remnant,t}$ and increases $A_{New,t}$ over time. We allow $A_{Remnant,t}$ and $A_{New,t}$ to change at

226 different rates, and present different combinations with changes being initially fast or slow. We also

227 consider a case of retrogression in $A_{New,t}$, where A_{New} first increases and later decreases, becoming

228 zero by the end of the simulation (signifying that no more A_{New} appears, which in real life could

229 happen when the climatically suitable area moves northwards until the edge of a continent is

230 reached, or up a mountain until the top is reached).

231

232 The temporal decrease in $A_{Remnant,t}$ (Fig. 2a) was modelled as $A_{Remnant,t} = 1 - (t/t_{max})^{\alpha}$, where t is the

233 time (arbitrary units) from current, t_{max} is the time at which the simulation ends, and α is a shape

234 parameter that defines whether the initial rate of change in $A_{Remnant,t}$ is faster ($\alpha > 1$) or slower ($0 < \alpha$

235 < 1) than linear. We used the values $\alpha = 2$ and $\alpha = 0.5$ for fast and slow initial change, respectively.

236 The temporal increase of $A_{New,t}$ (Fig. 2b) was modelled as $A_{New,t} = (t/t_{max})^{\alpha}$, with parameters as in

237 $A_{Remnant,t}$, except for the retrogression case that was modelled as $A_{New,t} = \max(0, -0.0005 \cdot t^2 +$

238 $0.04 \cdot t)$.

239

240 In simulation group 2, we mimic a possible progress of climate change by letting $A_{Remnant,t}$ and

241 $A_{New,t}$ change over time depending on different patterns of viable landscape (Fig. 3). The simulation

242 landscapes consist of 101×50 cell lattices, where the black and grey cells constitute the viable

243 landscape where different parts are, have been, or will become suitable (see caption of Fig. 3), while

244 the white cells remain non-viable throughout the simulations signifying habitat types that are

245 unsuitable regardless of the climatic conditions. Suitable climate at each time step is represented as

246 a square frame. It moves over the landscape, representing the change in climate, at a constant rate.

247 Depending on its location, the sliding frame will cover a different part of the simulated landscape

248 and therefore contain a different number of viable cells, which will be made up from Remnant and

249 New cells in different proportions. The direction of the movement represents the direction of

250 climate change, which in real-life is typically towards the poles or upwards along an elevational

251 gradient. The number of suitable landscape cells that fall within the square frame constitute the

252 climatically (and otherwise) suitable area for the species at each time step. We can now simulate

253 different scenarios of increase and decrease in $A_{New,t}$ and $A_{Remnant,t}$ by varying the pattern of viable

254 landscape cells.

255

256 We generated different patterns of viable landscape with a first order autoregressive process (AR1),

257 where the viability of a cell at the row i and column j of a landscape depends on the viability of its

258 four neighbouring cells at the previous iteration step. This is calculated as $X'_{i,j} = \varphi \cdot (X_{i-1,j} + X_{i+1,j} +$

259 $X_{i,j-1} + X_{i,j+1})/4 + \varepsilon_{i,j}$, where X is the initial spatial configuration with a normally distributed random

260 state ε (zero mean, unit variance), and φ is the autoregression coefficient (values $\varphi \leq 1$ are feasible).

261 Cells with $X'_{i,j} > 0$ are considered viable.

262

263 We used different values of φ to generate patterns of different spatial autocorrelation. The first case

264 (Fig. 3a, $\varphi = 0$) represents complete spatial randomness, where the probability of a cell being viable

265 is spatially independent (p = 0.5). This represents a landscape that is uniform at a large scale but

266 randomly patterned as viable or non-viable at a smaller scale. For instance, an insect specialised on

267 living on pine trees could see a large tract of uniform boreal forest like this. The case also serves as

268 a reference point for perhaps more common landscape patterns, where patches of suitable habitat

269 are interspersed in a matrix of non-suitable habitats. These kinds of patterns are positively

270 autocorrelated, i.e., a viable cell in our simulation landscape is more likely to have another viable

271 cell as an immediate neighbour than an unviable one.

272

11

273   We modelled such cases with increasing values of the autoregression coefficient that result in

274   intermediate (Fig. 3b, $\varphi = 0.900$) and high (Fig. 3c, $\varphi = 0.999$) spatial autocorrelation. The

275   increasing size of landscape patches allows large variation in climatically suitable area between

276   sampling intervals. Each value of φ was replicated 100 times to investigate the effect of a random

277   spatial pattern on $I_{AM,t}$ (Fig. 3d) and on the difference between $M_{Potential,t}$ and $M_{Need,t}$ (Fig. 3e) in

278   relation to $A_{Original}$. The state of the replicated systems was investigated at $t = 25$, which corresponds

279   to the climatic frame having moved half of its length from the original position and allows for the

280   highest variance in original, remnant, and new areas.

281

282   We measured the degree of autocorrelation in the simulated landscape patterns using global

283   Moran's I calculated with first degree neighbourhoods (Fortin and Dale 2005). The metric has been

284   used for quantifying the degree of habitat fragmentation (e.g., Gao and Li 2011) and it facilitates the

285   comparison of our simulated landscapes to patterns in nature. The value of global Moran's $I \approx 0$

286   represents complete spatial randomness in large samples, while $I = 1$ results from the landscape

287   being divided in two: a viable and an unviable half.

288

289   All computations were carried out using Matlab 8.5. (Release 2015a, The MathWorks Inc.). The

290   scripts for generating the simulations and figures 2, 3, and 4 are distributed as Supplementary Data

291   (Appendix A, B, and C).

292

293

294   2.3. Assisted migration threshold

295

296   There is no inherent threshold value of $I_{AM,t}$ that would indicate range-change-associated benefit of

297   AM for the species. Such thresholds could, however, be explored based on other widely applied

12

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% $\rightarrow$ score of 1, 4–7.5% $\rightarrow$ 2, >7.5% $\rightarrow$ 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

323 We next considered how the formation of $A_{New,t}$ affects $I_{AM,t}$. Following Thomas et al. (2011), we

324 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

325 = 0. The size of $A_{New,t}$ and the corresponding $M_{Potential,t}$ then become:

326

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

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

329

330 By substituting relevant factors in Eq. 3 with Eqs. 5 and 7, $I_{AM,t}$ becomes a function of p_{Gain} and

331 p_{Loss}, and the number of decades investigated. The time t is known from the point in time for which

332 the prediction was made, and we can present the threshold values for one decade (t = 1) as $I_{AM,1} =$

333 [0.1, 0.2, 0.27] in a parameter space of p_{Loss} and p_{Gain} (Fig. 4a). The loss rates are restricted to $0 \leq$

334 $p_{Loss} \leq 1$, because $A_{Original}$ cannot decrease by more than 100%, but no such restriction applies to the

335 rate of increase in area (i.e., $p_{Gain} \geq 0$). With increasing p_{Gain}, the corresponding value of p_{Loss}

336 approaches the threshold values $I_{AM,1} =$ [0.1, 0.2, 0.27]. With decreasing p_{Gain}, the corresponding

337 value of p_{Loss} approaches unity.

338

339

340 3. Results

341

342 As climate change causes progressive changes in $A_{New,t}$ and $A_{Remnant,t}$ for a species (simulation

343 group 1; Fig. 2a,b), the corresponding values of $M_{Need,t}$ and $M_{Potential,t}$ form trajectories in the

344 parameter space (Fig. 2d,e), where the value of the combined metric increases towards the top-right

345 corner (Fig. 2c). Depending on the rate of change in $A_{Remnant,t}$ and $A_{New,t}$, the relative magnitude of

346 $M_{Need,t}$ and $M_{Potential,t}$ can vary, and the trajectories move above or below the diagonal that divides

347 the parameter space.

348

349 When $A_{Remnant,t}$ decreases faster than $A_{New,t}$ increases, $M_{Need,t}$ is large relative to $M_{Potential,t}$, and

350 trajectories move below the diagonal (Fig. 2d). Slow reduction in $A_{Remnant,t}$ combined with fast

351 increase in $A_{New,t}$ results in large $M_{Potential,t}$ in relation to $M_{Need,t}$, and trajectories progress above the

352 diagonal (Fig. 2e). A fast decrease in $A_{Remnant,t}$ combined with equally fast increase in $A_{New,t}$ leads to

353 a trajectory that follows the diagonal (Fig. 2d). A slow decrease in $A_{Remnant,t}$ and slow increase in

354 $A_{New,t}$ leads to a similar trajectory, but $I_{AM,t}$ increases at a slower rate (Fig. 2e). $I_{AM,t}$ can also

355 decrease if $A_{Original,t}$ and $A_{New,t}$ do not change at an even rate. For example, if $A_{New,t}$ first increases

356 and then decreases, $I_{AM,t}$ similarly first increases and then decreases (Fig. 2e).

357

358 Under complete spatial randomness of viable and non-viable cells (simulation group 2; Fig. 3a),

359 $M_{Need,t}$ and $M_{Potential,t}$ increase at the same rate, owing to equally many new cells becoming suitable

360 at the leading edge (top) of the sliding sampling frame (i.e., the 'changing climate') as originally

361 suitable cells become unsuitable at the trailing edge (bottom) of the frame. At each advancing

362 simulation step, $A_{Remnant,t}$ therefore decreases by the same amount as $A_{New,t}$ increases, with slight

363 variation coming from the randomness in the distribution of viable cells. As a consequence, there is

364 little variation in $A_{original}$ and $I_{AM,t}$ between replicates of the pattern-generating process (Fig. 3d), and

365 M_{Need} and $M_{Potential}$ are nearly equal (Fig. 3e). This indicates that the trajectory of $I_{AM,t}$ would follow

366 the diagonal of the M_{Need} vs. $M_{Potential}$ parameter space (cf. Fig. 2c).

367

368 When the degree of spatial autocorrelation takes intermediate (Fig. 3b) or high (Fig. 3c) values,

369 $A_{original}$ and $I_{AM,t}$ vary more, and there is more variation in the relative magnitudes of $M_{Need,t}$ and

370 $M_{Potential,t}$ (Fig. 3e). If this was presented in the parameter space of $M_{Need,t}$ vs. $M_{Potential,t}$ (Fig. 2c), the

371 trajectory of $I_{AM,t}$ would in many cases be far from the diagonal and could also move from one side

372 of the diagonal to the other. Increasing spatial autocorrelation also brings about a negative

373 relationship between $A_{original}$ and $I_{AM,t}$ (Fig. 3d), and the value of $M_{Potential,t}$ decreases in relation to

374 $M_{Need,t}$ when $A_{original}$ increases (Fig. 3e). The first relationship shows that species already occupying

375 most of the viable cells in the landscape do not benefit from AM. The second relationship shows

376 that the decrease in $I_{AM,t}$ with increasing proportion of viable cells in $A_{original}$ results from a decrease

377 in $M_{Potential,t}$. The values of the autoregression coefficient φ used for simulating landscape patterns

378 resulted in large differences in degree of autocorrelation as measured by Moran's I. Complete

379 spatial randomness ($\varphi = 0$) led to Moran's $I = -0.0023 \pm 0.0066$ (mean $\pm$ SD), while the

380 autoregressive process with $\varphi = 0.9$ and $\varphi = 0.999$ corresponded to $I = 0.35 \pm 0.01$ and $I = 0.73 \pm$

381 0.03, respectively.

382

383 Our translation of Thomas et al.'s (2011) climate change threat scores into critical values of $I_{AM,t}$

384 can be interpreted so that, when $I_{AM,t}$ is calculated based on predictions extending one decade into

385 the future, a species with $0.1 < I_{AM,1} < 0.2$ is a possible candidate for AM, a species with $0.2 < I_{AM,1}$

386 < 0.27 is a probable candidate for AM and a species with $I_{AM,1} > 0.27$ is a strong candidate for AM

387 (Fig. 4a). For a prediction 100 years into the future (10 decades) the corresponding thresholds for

388 $I_{AM,10}$ are 0.31, 0.58, and 0.74 (Fig. 4b).

389

390

391 4. Discussion

392

393 The parameter space formed by all possible values of $M_{Need,t}$ and $M_{Potential,t}$ shows the nonlinear

394 relationship between $I_{AM,t}$ and its components (Fig. 2c). At the combined low $M_{Need,t}$ and low

395 $M_{Potential,t}$ (Fig. 2c: lower left corner of the parameter space), the low value of $I_{AM,t}$ indicates that a

396 species is neither losing its current range nor gaining new migration opportunities (Fig. 1a). This

397 could happen in reality, e.g., when a species has a wide distribution area to start with

398 (geographically or as regards climatic variation), or when it occurs in an area that is climatically

399 relatively stable even in the face of global change, such as refuge areas during Pleistocene climatic

400 oscillations. Alternatively, a species may be so strongly limited by other factors than climate that a

401 change in climate does not lead to a marked change in its distribution. Examples include some plant

402 species adapted to serpentine soils (Damschen et al. 2012).

403

404 When one of the components ($M_{Need,t}$ or $M_{Potential,t}$) is very small, $I_{AM,t}$ may not exceed the threshold

405 for the species to be considered a candidate for AM even if the other component is substantially

406 larger. This implies that AM is likely a poor conservation choice, since there is either little threat of

407 losing area or little new area available to translocate the species to. Therefore, a low $I_{AM,t}$ for a

408 certain species would support a decision of no intervention, if there is no threat of losing area, or the

409 application of actions other than AM in the conservation of the species, if there is loss of current

410 area but no emerging new area. If only $M_{Need,t}$ is high (Fig. 1b; Fig. 2c: lower right-hand part of

411 parameter space), the need for conservation is certainly more urgent than if only $M_{Potential,t}$ is high

412 (Fig. 1c; Fig. 2c: upper left-hand part), but AM is not an applicable method, as there would be no

413 suitable area to which the species could be assisted to migrate. Alternative conservation strategies

414 might then involve increased *in situ* management, *ex situ* conservation, or even conservation

415 introduction (IUCN 2012), i.e., translocating the species to any environmentally suitable area

416 outside of its indigenous range, where the species could not move on its own even with time, such

417 as another continent.

418

419 Only a species that gains new suitable area at the same time as it loses previously suitable area (Fig.

420 1d; Fig 2c: centre to upper right part of parameter space), but has difficulties in dispersing on its

421 own, is a clear candidate for AM. Changes in climatically suitable area of this kind are likely to

422 occur in settings lacking an elevational gradient and where an edge of a continent is not

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

424   2007).

425

426   Spatial autocorrelation increased variance in $A_{Original}$ of the modelled hypothetical species, and led

427   to variation in the value of $I_{AM,t}$ and the relative magnitude of its components (Fig. 3d,e). The

428   variance allows us to see the negative correlation between $A_{Original}$ and I_{AM}. When most of the viable

429   cells are within the original area, the result is a low $I_{AM,t}$ (Fig. 3d) and a relatively low $M_{Potential,t}$

430   (Fig. 3e). In the opposite case, where most of the viable cells in the landscape are outside the

431   original area (small $A_{Original}$), climate change will result in a high proportional loss of the original

432   area and a large proportional gain of new area in comparison to remnant area, which leads to a high

433   I_{AM} (Fig. 3d) and a relatively high $M_{Potential,t}$ (Fig. 3e). We can therefore expect a negative

434   relationship between $A_{Original}$ and $I_{AM,t}$ to arise from the spatial distribution of viable landscape cells.

435   This pattern emerged in a study where the method presented here was applied to real-world species

436   using range change predictions derived through SDMs (Hällfors et al. 2016). Based on the present

437   simulation results, the relationship between $A_{Original}$ and $I_{AM,t}$, or the relative magnitude of its

438   components should not automatically be attributed to biological processes or species characteristics

439   without additional evidence, as the relationship can simply result from landscape patterns.

440   Nevertheless, in real-life situations a large $I_{AM,t}$ for a species with a small $A_{Original}$ can also reflect an

441   ecologically relevant process for rare species: as climate change makes large parts of the original

442   area unsuitable, even if not much new area is gained, the proportional importance of the new area

443   increases, since remnant area is scarce. In such cases a high $I_{AM,t}$ value correctly reflects the need

444   and potential of AM, even though focal translocation areas may be limited.

445

446   Natural landscapes have values of Moran's I that correspond to our simulated landscapes. The

447   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 (φ = 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.

471   (2) Screening of large numbers of species to gain understanding about what proportion of a

472   regional biota might be in need of AM within a given time frame under a certain climate

473   change scenario.

474

475   In the first situation, the formalization can be used as part of decision-making frameworks (e.g.,

476   Perez et al. 2012; Schwartz & Martin 2013) to provide objective, quantitative answers to questions

477   concerning future decline and increase of suitable area. Here, its novelty comes from specifically

478   relating predictions in range change to the ecological usefulness of AM. The approach thus provides

479   instructions on how to apply previously identified tools, such as correlative species distribution

480   models and expert predictions of range change, in the context of decision-making concerning AM.

481   Obviously our method does not, however, represent a statement regarding how generally

482   recommendable AM of the species is.

483

484   An additional benefit of the AM index calculations is that they can provide guidelines on the

485   applicability and timing of application of other conservation methods too. If, for instance, $M_{Need,t}$

486   rapidly increases within the coming decades, while $M_{Potential,t}$ remains low, it may be advisable to

487   opt for designing and carrying through an *ex situ* conservation programme for the species. Since the

488   development of I_{AM} is non-linear, predictions further into the future may suggest that eventually

489   new climatically suitable area will appear, and then the *ex situ* population of the species could be

490   used for an introduction of the species into the newly emerged suitable area, should it be deemed

491   otherwise acceptable. This could be described as a delayed AM procedure, where the calculation of

492   I_{AM} and its components gave impetus to the intermediate *ex situ* conservation stage. Alternatively, if

493    $M_{Need,t}$ increases only gradually, while the increase in $M_{Potential,t}$ is delayed, more intensive *in situ*

494   management in the current distribution area may be the best option. This could help a population

495   stay viable until new climatically suitable area appears where the population can migrate (or be

496   assisted to migrate).

497

498   In the second situation, screening large numbers of species, formalized metrics make it possible to

499   calculate comparable percentages of species that could benefit from AM for different points in time,

500   e.g., after two, five, or eight decades. Here, the important aspect of our AM metrics is that their

501   values are likely to change non-linearly over time as climate change progresses in real-world

502   settings (see Hällfors et al. 2016). Hence they have the potential of highlighting time frames during

503   which specific conservation actions are the most beneficial, or even at all possible, for a certain

504   species. For instance, if the proportion of the biota needing AM increases considerably after five

505   decades, it is probably advisable to strive for avoiding that situation, e.g., through investing in

506   enhancing natural dispersal by increasing connectivity between habitat patches, since large-scale

507   AM is likely to be considerably challenging and costly, and may be challenged on other grounds too

508   (Maier & Simberloff 2016). Hence, the metrics introduced here can highlight resource need for

509   conservation under different climate change scenarios and help resource managers to plan ahead.

510   Moreover, scenarios like this can further emphasize the need to mitigate climate change, rather than

511   relying on adaptation to it.

512

513   The approach presented here can thus be used in a similar manner as the Red List Index (Butchard

514   et al. 2007). The Red List Index describes observed changes in species' threat status, and serves as

515   an evaluative and political tool for assessing conservation trends. However, our metrics concern

516   anticipating future challenges, rather than evaluating past changes. It is therefore important to

517   recognize the many uncertainties involved in methods for predicting change in suitable area

518   (Heikkinen et al. 2006; Martin et al. 2012). These include epistemic uncertainties regarding our

519   incomplete knowledge on the environmental requirements of species as well as uncertainty in

520 human decisions ranging from expert judgments to climate change mitigation. Although some of

521 this uncertainty can be handled or at least apprehended through ensemble modelling (Araújo and

522 New 2007; for application in the context of the method described here, see Hällfors et al. 2016), the

523 reliability of predictions will continue to depend on the quality and validity of the data and theory

524 used to develop them. However, because our metrics are based on explicit data and formalized

525 calculations, they have the advantage of being comparatively easy to update and re-evaluate as new

526 data and refined prediction methods become available.

527

533

534 **Glossary**

535 **Assisted migration** = safeguarding biological diversity through the translocation of representatives

536 of a species or population harmed by climate change to an area outside the indigenous range of that

537 unit where it would be predicted to move as climate changes, were it not for anthropogenic

538 dispersal barriers or lack of time (Hällfors et al. 2014).

539 **Migration** = the processes of dispersal, colonization, and establishment, which in the case of

540 assisted migration are aided by humans.

541 $A_{Original}$ = current distribution (observed or modelled depending on the species and available

542 occurrence data) of a species (measured in number of grid cells, km^2, or similar).

543 $A_{Remnant,t}$ = the part of $A_{Original}$ that remains suitable at a certain point of time in the future

544 (measured in number of grid cells, km^2, or similar).

545 $A_{New,t}$ = 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 $M_{Potential,t}$ = 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 $M_{Need,t}$ = 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 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/…

564

565

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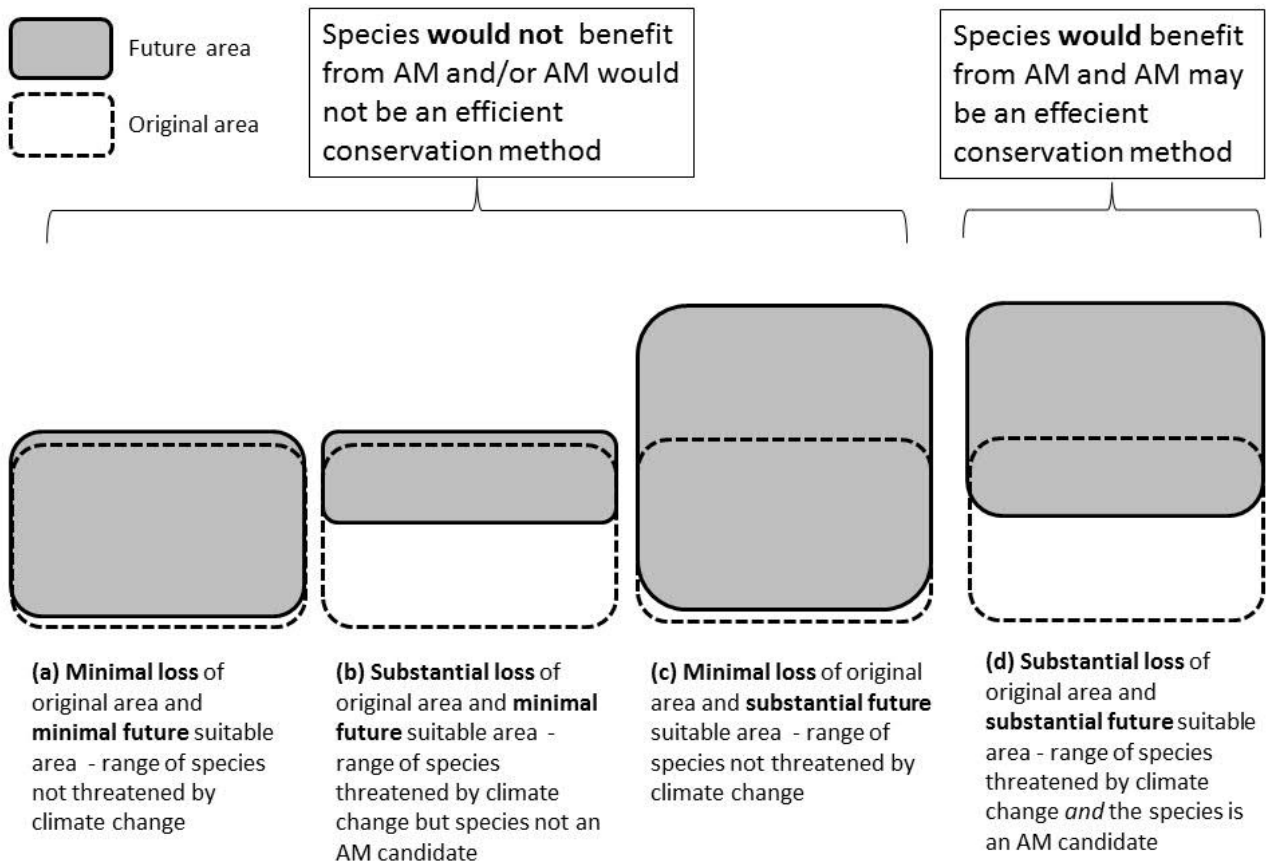
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Future area

Original area

Species **would not** benefit from AM and/or AM would not be an efficient conservation method

Species **would** benefit from AM and AM may be an effecient conservation method

(a) Minimal loss of original area and **minimal future** suitable area - range of species not threatened by climate change

(b) Substantial loss of original area and **minimal future** suitable area - range of species threatened by climate change but species not an AM candidate

(c) Minimal loss of original area and **substantial future** suitable area - range of species not threatened by climate change

(d) Substantial loss of original area and **substantial future** suitable area - range of species threatened by climate change *and* the species is an AM candidate

722

723

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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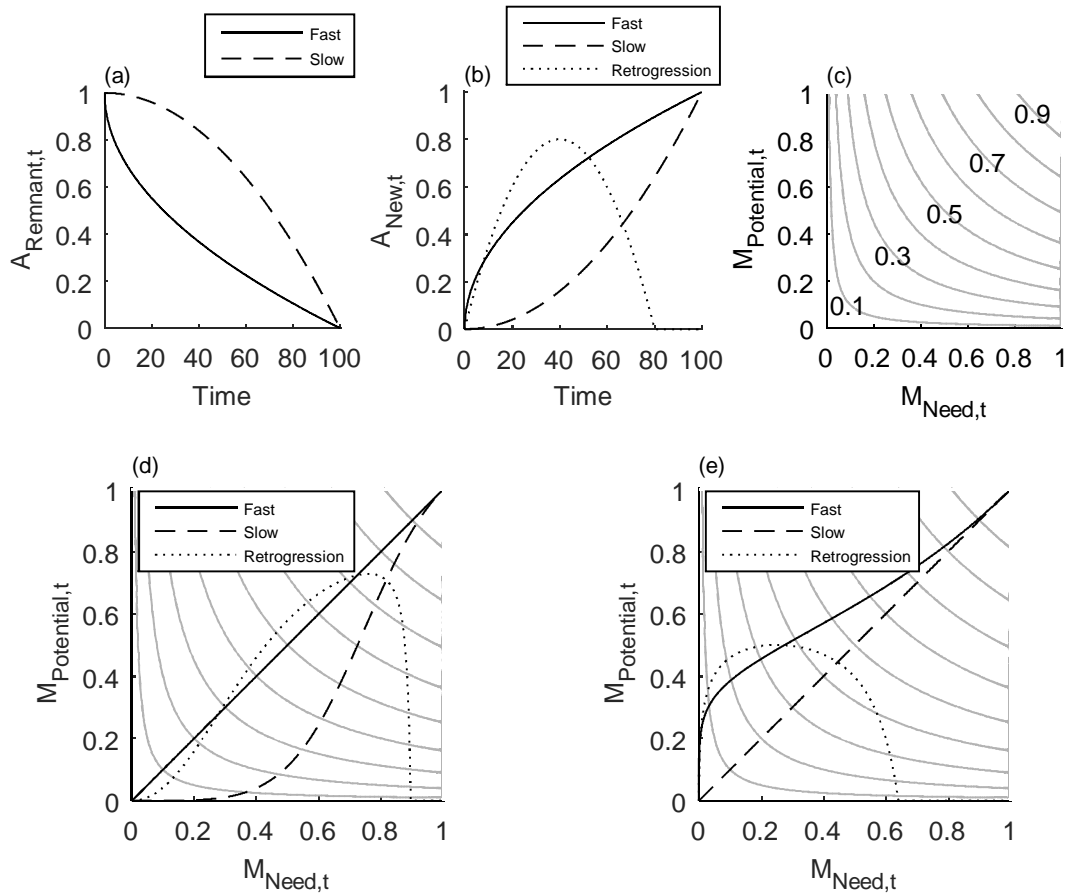
Fig. 2. Simulated development of remnant and new areas ($A_{Remnant}$ and A_{New}, respectively) and the corresponding $M_{Need,t}$, $M_{Potential,t}$, and $I_{AM,t}$. Scenarios for temporal development of (a) $A_{Remnant,t}$ and (b) $A_{New,t}$, under simulated climate change, and (c) a parameter space 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.
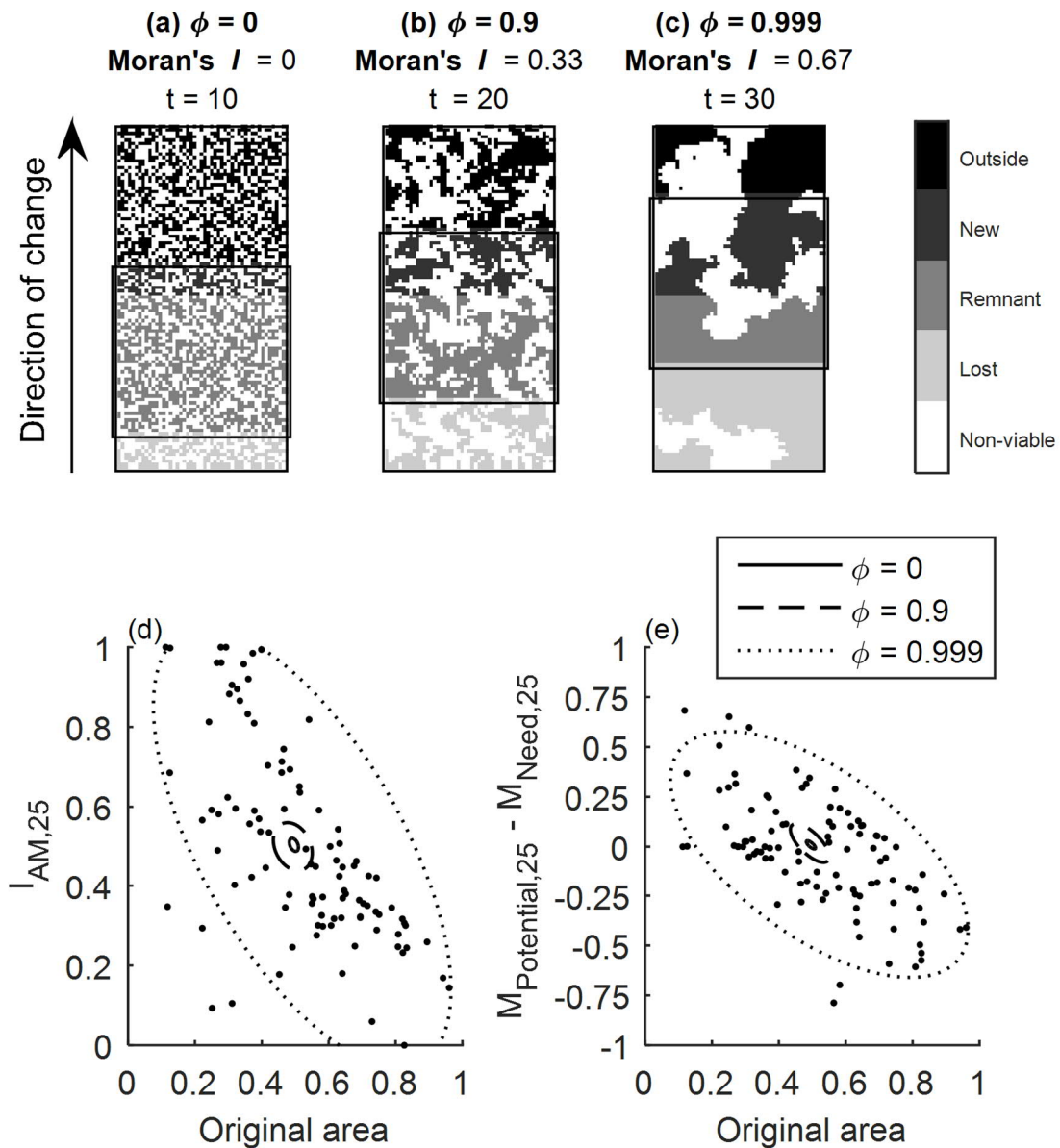
Fig. 3. (a-c) Examples of lansdcape patterns of viable (black and grey) and non-viable (white) cells simulated with different values of first order autoregression parameter phi and the corresponding measure of spatial autocorrelation as global Moran's I (first neighbours). The climatic suitability of cells is determined by a square frame representing the area of suitable climate. The frame moves over the landscape one cell row at the time in a bottom to top direction representing climate change, e.g., pole- or upward movement of mean temperature or other climatic variable(s). At the beginning 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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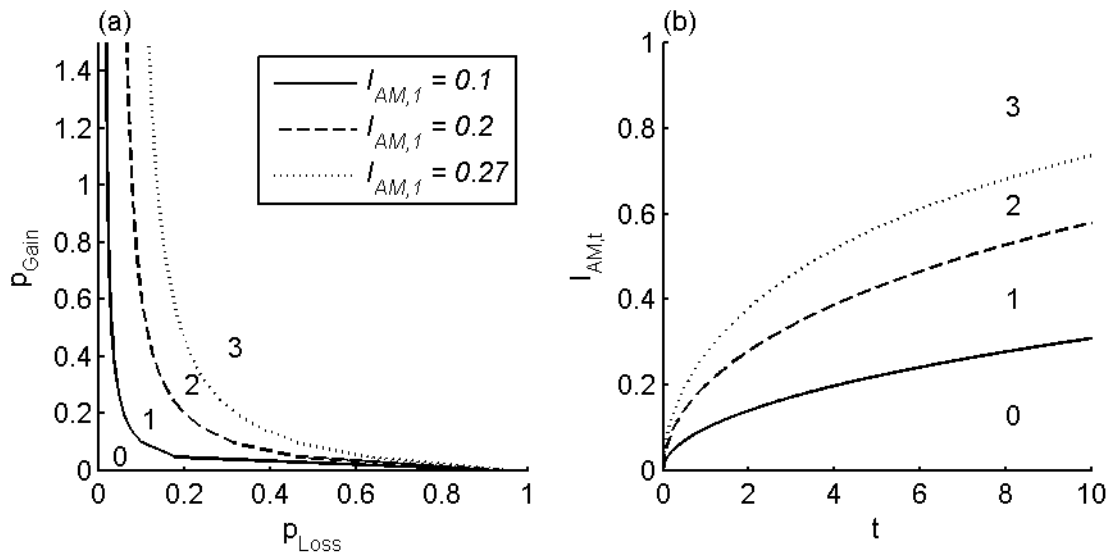
764

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