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IESTR: a novel method to analyze Introduction Effects in Space and Time on species Range dynamics

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1 **TITLE PAGE**

2 **Title**

3 IESTR: a novel method to analyze Introduction Effects in Space and Time on species Range
4 dynamics.

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25

26

27 **IESTR: a novel method to analyze Introduction Effects in**
28 **Space and Time on species Range dynamics.**

29 **Abstract**

30 Rapidly shifting climates will lead to species range shifts over the next
31 century. Artificially introducing species in new locations to enhance species
32 migration, termed assisted migration (AM), has been suggested as one possible
33 strategy to avoid species extinction. While current methods are used to explore
34 future areas of introduction, we lack a method able to identify the best sets of
35 locations and timing for species introductions that maximizes AM outcomes.

36 We developed a novel method to explore the effects of species Introduction
37 Effects in Space and Time on species Range dynamics (IESTR). The method uses
38 transition matrices that combine spatial and temporal species suitability changes and
39 dispersal information. A metaheuristic algorithm is run to achieve an objective target
40 of range area optimizing introduction locations and times, while minimizing spatially
41 explicit cost surfaces. We apply the method to a virtual species to showcase the
42 potential of IESTR to explore range dynamics with artificial introductions. We assess
43 optimal AM strategies under climate change and with different land use cost
44 scenarios. We found a strong effect of early introductions enhancing species range
45 shifts, as well as differences in introduction sites and timing under different cost
46 scenarios.

47 IESTR is a fast and efficient technique for exploration of range shifts under
48 artificial introductions, tackling both the spatial and temporal dimensions. The
49 method has been developed in Cpp, available as an R package. Given the heated
50 debate around AM and introductions, our method provides a new tool to explore
51 strategies in spatial conservation planning in the Anthropocene.

52

53 **1 Introduction**

54

55 Climate is changing at a speed rarely reached in the history of terrestrial climatology
56 (Burke et al., 2018; Loarie et al., 2009). Evidence shows that past extinctions and the
57 degree of endemism are related to climate stability (Harrison & Noss, 2017; Song et
58 al., 2021), thus the fast-ongoing climate change will likely lead to an increase in
59 species vulnerability and contribute to the ongoing sixth mass extinction (Barnosky et
60 al., 2011; Cowie et al., 2022).

61

62 Under such a current fast climate change, the outcome for species has been
63 summarized as either resist new environmental conditions, adapt, move (i.e., change
64 its distribution) or go extinct (Berg et al., 2010; Corlett & Westcott, 2013; Duputié et
65 al., 2015). While some degree of adaptation and resistance is expected, evidence
66 shows that range shifts are a common response to past and current climatic changes.
67 Distribution shifts occur in many groups (Lenoir et al., 2020), such as butterflies
68 (Habel et al., 2021) and plants (Graae et al., 2018). The direction of species range
69 shifts has been hypothesized to counteract increasing temperatures by migrating
70 poleward and upwards (Lenoir & Svenning, 2015), but these could follow other
71 directions by tracking drivers other than temperature, such as water balance
72 (Dobrowski et al., 2013; Serra-Diaz, Franklin, Dillon, et al., 2016), being influenced
73 by human activities (Lenoir et al., 2020), and ultimately lead to several range shift
74 directions other than isotherms (VanDerWal et al., 2013; Wason & Dovciak, 2017).

75

76 Empirical and modeling studies suggest that the pace of climate change is faster than
77 species ability to migrate (Corlett & Westcott, 2013; Serra-Diaz et al., 2014). This is
78 especially true for terrestrial sessile organisms (Lenoir et al., 2020). Indeed, the slow
79 migration rates do not allow species to readily track climate changes, leading to a
80 disequilibrium between species distributions and climate (Svenning & Sandel, 2013),
81 and a potential range reduction that increases species extinction risk. That is, ranges
82 are reduced on the trailing edge but areas that become favorable at the leading edge
83 are unoccupied. To cope with species migration lags, conservation sciences and
84 natural resource managers may consider species translocations as one potential
85 strategy to maintain biodiversity.

86

87 Assisted migration (AM)– also termed assisted colonization, managed relocation,
88 assisted range expansion and species translocation (Hällfors et al., 2014)– refers to the
89 action of purposefully introducing a species to an area where it is not present, with the
90 objective of supporting species natural migration as a consequence of climate change
91 (Hayward, 2009; Heller & Zavaleta, 2009; Hewitt et al., 2017; Hoegh-Guldberg et al.,
92 2008; Richardson et al., 2009). AM could be an effective strategy to compensate for
93 the slow movement of some species in order to prevent their decline or extinction
94 (Hällfors et al., 2018; Peterson St-Laurent et al., 2018). Nevertheless, AM is still a
95 contentious conservation strategy (Aubin et al., 2011; Hunter, 2007; McLachlan et al.,

96 2007; Ricciardi & Simberloff, 2021; Vitt et al., 2010), as it could lead to a number of
97 undesired outcomes like disease transmission (Simler et al., 2019), unintended
98 establishment of invasive species (Mueller & Hellmann, 2008) or lack of local
99 adaptation (Tíscar et al., 2018). While there are unknowns on how to identify such
100 potential issues before an AM action is undertaken, part of the challenge in assessing
101 potential AM plans is to identify where and when it is more effective to perform AM
102 to reach a migration goal. Specifically, we lack methods able to identify what are the
103 time frames and locations where species would benefit the most from AM to track
104 climate change considering species characteristics, biological risks, economic costs,
105 and future climatic time-series.

106

107 Current tools allow modeling species distribution shifts using correlative approaches
108 and mapping suitable conditions at snapshot in time (Franklin, 2010a) – typically
109 using 20 to 30 year averages. Static climate change projections that produce a
110 snapshot under future conditions may provide future suitable areas of colonization.
111 However, such static projections do not inform how a given introduction or
112 colonization affects subsequent migration dynamically. Alternatively, there exist
113 mechanistic or dynamic distribution modeling which explicitly account for key
114 migration processes such as dispersal (Lehsten et al., 2019), evolution (Bocedi et al.,
115 2021; Bush et al., 2016), disturbances (Liang et al., 2018; Serra-Diaz et al., 2015), and
116 species interactions (Keyel et al., 2016). However, those models involve high level of
117 parametrization and/or require computationally intensive simulations of range shifts.
118 Such computationally demanding models preclude exploring spatial and temporal
119 introduction effects on species range dynamics. Indeed, it becomes unfeasible to
120 simulate species range shifts with mechanistic models by testing all – potentially
121 billions – combinations of species introductions in each spatial unit (cell, pixel) at
122 every time step of the simulation, with the goal of optimizing species range shift
123 outcomes.

124

125 To date, quantifications for the need of assisted migrations have used metrics derived
126 from species distribution models (Hällfors et al., 2016, 2017), but to our knowledge
127 no spatial conservation planning method has dealt with the issue of assisted migration
128 with efficiently allocate species assisted migration efforts in space and time. (Chu &
129 Beasley, 1998)(Chu & Beasley, 1998)

130

131 Here, we present a new method implemented through an R package that explores the
132 effects of introductions in space and time on species range shifts, and further
133 optimizes the allocation of introductions to obtain a probabilistic target on species
134 range size – typically a minimum range area that would preclude extinction. We call
135 this novel mathematical framework IESTR (Introduction Effects in Space-Time on
136 species Range dynamics). IESTR can determine, with a minimum of computation
137 load, the effect of establishing a population at a given location at a given time on
138 species range area. We use this framework to optimize AM choices in space and time,

139 by means of metaheuristic algorithms. The method has also been implemented in an R
140 package available on GitHub upon manuscript acceptance.

141

142 **2 Methods**

143 The method is divided into two phases: preprocessing and optimization (Fig. 1). First,
144 during the preprocessing stage we create the transition matrices which will be used in
145 the second phase, the optimization phase, where the choice of species introduction is
146 identified in space and time.

147 The study area is represented as a grid. The size of a cell may vary according to data
148 characteristics. We discretize the time period studied in a regular time step. Two key
149 dynamics are considered in the system: the dispersal of the species and the survival of
150 a species according to the conditions of a cell at a given time.

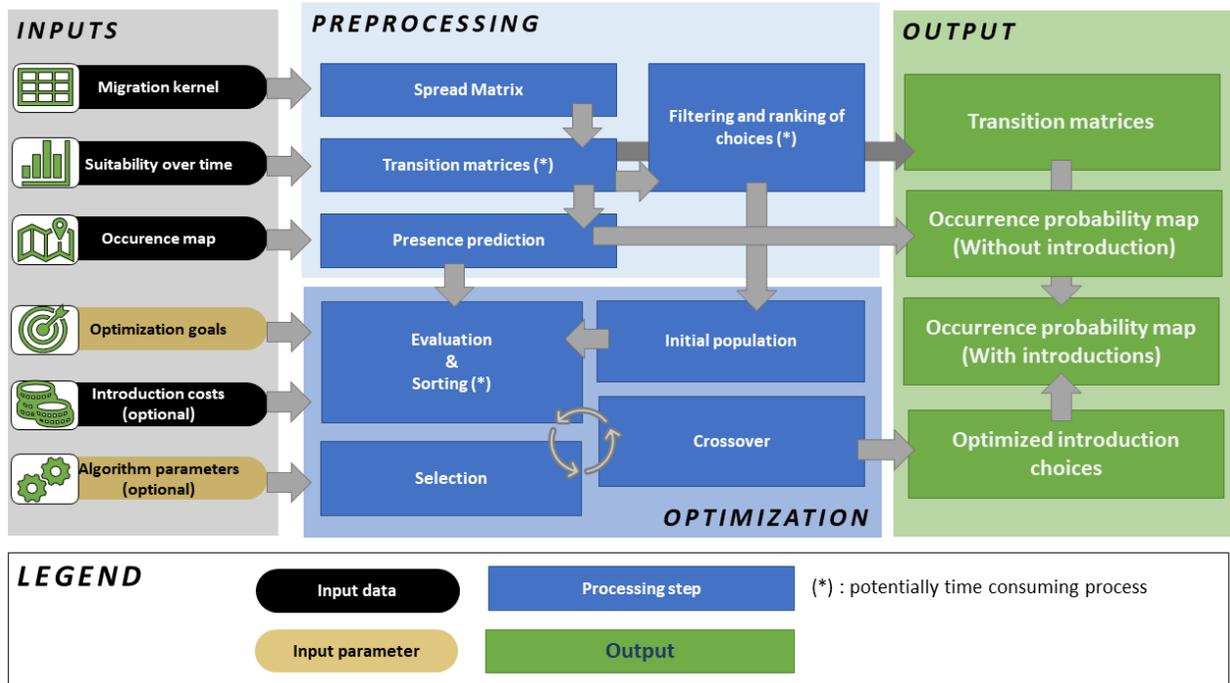
151 The algorithm needs at least three input data and optimization parameters. Additional
152 parameters can be added to the model to specify the behavior of the optimization
153 phase.

154 **2.1 Input data and parameters**

155 IESTR requires three types of input data and an optional input (Fig. 1, left box). The
156 first user-input required data is the *migration kernel*. For a given species and a given
157 grid map, the migration kernel corresponds to the chance that the species spread into
158 the neighboring cells during one step time. This migration kernel should be a function
159 cell size and the dispersal capacity of the species. The second required user-input are
160 the *suitability matrices over time*. For each discrete time t , we define a suitability
161 matrix as a grid with values between 0 and 1 corresponding to the survival chance of
162 the species in each cell of the map between time t and time $t + 1$. Suitability indices
163 may be derived from climatic condition and/or other factors such as land use, soil
164 properties or species interactions. Third, the algorithm needs the *occurrence map* of
165 the species at the initial time. This is a grid with value of 0 for the absence of the
166 species and 1 for the presence.

167 The algorithm needs the user to input the optimization goals of introduction (Fig 1,
168 left box). IESTR is currently designed to deal with two types of AM problems, both
169 mathematically corresponding to a constrained objective optimization function: (1)
170 minimizing cost while ensuring a fixed target range size or (2) maximizing the range
171 size with a limited budget. Mathematically, these constraints lead to a problem similar
172 to the *knapsack problem*: we want to assess a set of introduction choices in space and
173 time that optimizes an objective function (maximizing the species range size,
174 minimizing the cost) while verifying the constraints (limiting the budget, maintaining
175 the size of the area where the species is present).

176 Optional inputs can be added to control the optimization phase. The first optional
 177 input data is the *introduction cost matrix*. By default, the algorithm considers the cost
 178 of introduction to be the same for every cell, but they can be changed to account for
 179 spatial differences in costs. These costs may reflect in economic terms (financial costs
 180 involved in the introduction), management and land tenure (public/private,
 181 conservation area) or an ecological value (introduction risk for recipient ecosystems).
 182 Other optional inputs are the *parameters of the genetic algorithm*, that can drive the
 183 speed and the precision of the package. These parameters are calculated by default
 184 depending on the map size but can be adjusted (see code).



185
 186 *Figure 1: Scheme of the IESTR workflow. The workflow is divided into two main*
 187 *phases from inputs two outputs: (1) pre-processing of inputs (light blue box), and (2)*
 188 *optimization for introduction choices in space and time (dark blue box). Arrows detail*
 189 *inputs and outputs for each process.*

190
 191 **2.2 Preprocessing**

192
 193 **2.2.1 Step 1: Spread matrix**

194 The first part of the preprocessing builds the spread matrix. This matrix defines
 195 species accessibility in space over one-time step. It is here calculated using the
 196 migration kernel and it contains the probability of colonization site to site given
 197 optimal environmental conditions. If the user possesses more precise information

198 about species spread, he/she can directly calculate it instead of using a migration
 199 kernel. This can be useful if the dispersal potential isn't spatially uniform.

200

201 The migration kernel allows us to directly evaluate how the presence in one unique
 202 cell drives the probability of potential colonization in every other cell after one
 203 timestep. If a species is present in multiple cells initially, the probability of presence
 204 after one timestep in a cell is exactly the probability that at least one of the initial cells
 205 with presence colonizes the cell.

206 For ease of notation, we introduce the special addition operator, $\tilde{+}$, such as for a and b
 207 with values between 0 and 1 (Eq1):

$$208 \quad a\tilde{+}b = a + b - ab \#(Eq1)$$

209

210 Specifically, by summing the probabilities of two Bernoulli events with this operator,
 211 we obtain the probability of the union of the two events.

212

213 Let t be a time-step, i and j two sites of the map, N the number of sites, $M_{i,j}$ the
 214 probability that a presence in the site j leads to a presence in the site i at the next
 215 timestep, and X_j^t the probability of presence in the site j and at the time t of the
 216 species. Then the probability C_i^{t+1} that the site i is colonized by the species at the time
 217 $t+1$ is, with our notation (Eq2):

218

$$C_i^{t+1} = \sum_{j \in [1, N]}^{\sim} M_{i,j} X_j^t \#(Eq2)$$

219

220 This formula can be seen as a scalar product without linear properties. Let X and Y
 221 be two vectors of size N with values between 0 and 1. We define the operator between
 222 two vectors $\langle . | . \rangle$ as (Eq3), with the special sum described in (Eq1) :

$$\langle X | Y \rangle = \sum_{i \in [1, N]}^{\sim} X_i Y_i \#(Eq3)$$

223 As we defined an operator between two vectors of the same size, we can associate
 224 a matrix product with it. Let A and B be two matrices of a size $M \times N$ and $N \times L$
 225 respectively, with values between 0 and 1. Then we define the operator between two
 226 matrices $\tilde{*}$ as (Eq4):

$$A \tilde{*} B = \begin{pmatrix} \langle A_{1,\cdot} | B_{\cdot,1} \rangle & \cdots & \langle A_{1,\cdot} | B_{\cdot,L} \rangle \\ \vdots & \ddots & \vdots \\ \langle A_{M,\cdot} | B_{\cdot,1} \rangle & \cdots & \langle A_{M,\cdot} | B_{\cdot,L} \rangle \end{pmatrix} \#(Eq4)$$

227

228 With this notation, we can express the vector C^{t+1} with the spread matrix M and
 229 the vector of presence at the time t (Eq5):

$$C^{t+1} = \begin{pmatrix} C_1^{t+1} \\ \vdots \\ C_N^{t+1} \end{pmatrix} = \begin{pmatrix} \langle M_{1,\cdot} | X^t \rangle \\ \vdots \\ \langle M_{N,\cdot} | X^t \rangle \end{pmatrix} = M \approx X^t \#(\text{Eq5})$$

230

231 2.2.2 Step 2: Building the transition matrices

232 The transition matrices merge the information of the spread matrix (step 1) and the
 233 species suitability of each site over time (Fig. 1). Transition matrices thus allow to
 234 calculate the probability of presence in a future time step, while considering the
 235 initial distribution of the species.

236

237 Let s_i^t be the suitability value of the species in the site i , at time t . The probability of
 238 species occurrence in the site i at the time $t + I$, X_i^{t+1} , is calculated as the probability
 239 that the site is colonized at $t+I$ (C_i^{t+1}) multiplied by the probability of the species
 240 establishment and survival (suitability) s_i^t in this cell (Eq6):

$$X_i^{t+1} = s_i^t C_i^{t+1} \#(\text{Eq6})$$

241 By doing this for the whole vector X^{t+1} , we obtain a formulation for the transition
 242 matrix $T_{t \rightarrow t+1}$ that allows us to calculate presence probabilities from X^t to X^{t+1} (Eq7):

$$X^{t+1} = \begin{pmatrix} X_1^{t+1} \\ \vdots \\ X_N^{t+1} \end{pmatrix} = \begin{pmatrix} s_1^t \langle M_{1,\cdot} | X^t \rangle \\ \vdots \\ s_N^t \langle M_{N,\cdot} | X^t \rangle \end{pmatrix} = \begin{pmatrix} \langle s_1^t M_{1,\cdot} | X^t \rangle \\ \vdots \\ \langle s_N^t M_{N,\cdot} | X^t \rangle \end{pmatrix} = T_{t \rightarrow t+1} \approx X^t \#(\text{Eq7})$$

243 with : $T_{t \rightarrow t+1} = \begin{pmatrix} s_1^t M_{1,1} & \cdots & s_1^t M_{1,N} \\ \vdots & \ddots & \vdots \\ s_N^t M_{N,1} & \cdots & s_N^t M_{N,N} \end{pmatrix}$

244 The formula is recursive. Let t_1 and t_2 be two times such as $t_1 < t_2$, then we can
 245 obtain a formulation of X^{t_2} with X^{t_1} , by combining the different transition
 246 matrices we already have (Eq8) (Eq9):

$$X^{t_2} = T_{t_2-1 \rightarrow t_2} \tilde{*} X^{t_2-1} = T_{t_2-1 \rightarrow t_2} \tilde{*} (T_{t_2-2 \rightarrow t_2-1} \tilde{*} X^{t_2-2}) = T_{t_2-1 \rightarrow t_2} \left(\dots \tilde{*} (T_{t_1 \rightarrow t_1+1} \tilde{*} X^{t_1}) \right) \#(Eq8)$$

$$X^{t_2} = (T_{t_2-1 \rightarrow t_2} \tilde{*} (T_{t_2-1 \rightarrow t_2} \tilde{*} (\dots \tilde{*} T_{X^{t_1} \rightarrow X^{t_1+1}}) \dots)) \tilde{*} X^{t_1} = T_{X^{t_1} \rightarrow X^{t_2}} \tilde{*} X^{t_1} \#(Eq9)$$

$$\text{with : } T_{t_1 \rightarrow t_2} = (T_{X^{t_2-1} \rightarrow X^{t_2}} \tilde{*} (T_{X^{t_2-2} \rightarrow X^{t_2-1}} \tilde{*} (\dots \tilde{*} T_{X^{t_1} \rightarrow X^{t_1+1}}) \dots))$$

247 The calculation of $T_{t_1 \rightarrow t_2}$ in (Eq9) must be made in the right order for the equation
 248 to be true, as the $\tilde{*}$ operator is not associative. With this equation, we can calculate the
 249 probability of presence of the species at any point in time, knowing the probability of
 250 presence at a particular time in the past and these transition matrices.

251 To be able to evaluate and compare species introduction(s) effect, we set the last
 252 time-step of study, t_{max} , as a target time-step, and focus on all the transition matrix of
 253 the form $T_{\rightarrow t_{max}}$. These matrices allow calculating the effect of introduction(s) on the
 254 probability of the presence of a species in any cell, at any time. An introduction in a
 255 cell i and a time t leads to a probability of presence in each of the cells at the end equal
 256 to the vector $(T_{t \rightarrow t_{max}})_{\cdot, i}$

257 The effect of the multiple species presence can be summed up, as the probability of
 258 presence in a cell in the final system state is the probability that at least one of the
 259 present species (initially present or introduced) establishes in this cell. Let t_0 be the
 260 initial time, K the number of introductions, $[(i_1, t_1) \dots (i_K, t_K)]$ The different choices of
 261 introduction defined as pairs of a cell (i) and a time-steps (t). Then, the probability of
 262 presence in all the cells in the final state of the system is (Eq10):

$$X^{t_{max}} = T_{t_0 \rightarrow t_{max}} \tilde{*} X^{t_0} \tilde{\dagger} \sum_{k \in [1, K]} \tilde{*} (T_{t_k \rightarrow t_{max}})_{\cdot, i_k} \#(Eq10)$$

263 The construction of these transition matrices makes it possible to obtain the results
 264 of a simulation of the introduction of species over time by a direct calculation. A
 265 quantitative worked example of its use can be found in Appendix S1.

266 2.3 Optimization

267 We calculate the effect of introducing the species in different sites and times based on
 268 transition matrices and implement optimization algorithms to evaluate alternative
 269 introduction schemes.

270

271 **2.3.1 Optimization problem formulation**

272 The aim is to find the best set of introductions (site, time) to satisfy the constraint
 273 while optimizing the objective function. Two kinds of problems are currently
 274 implemented in IESTR: (1) the target range area (TRA) and (2) the best allocation of
 275 a budget (BAB). In TAR we optimize the minimum cost needed to maintain the
 276 species at a targeted range size, whereas in BAB we maximize species range area
 277 given a maximum budget.

278 To implement these optimizations, we need to define a choice evaluation function
 279 (CEF), that allows us to summarize the efficiency of a set introductions. This function
 280 takes as parameters a set of introductions choices, the probability of presence in each
 281 of the sites at the end of the period without introductions (e.g. suitability and
 282 dispersal), the transition matrices, and a precision factor α . The function returns the
 283 minimal number of sites colonized at the end of the period considering introduction
 284 choices, with a $\alpha\%$ certainty. The two problem formulations are currently expressed
 285 in Eq. 11 for the TRA problem, and Eq. 12 for the BAB problem, with VC being the
 286 set of viable choices of introductions to choose from:

$$\left\{ \begin{array}{l} \min_{A \subset VC} \sum_{(i,t) \in A} cost(i) \\ CEF \left(T_{t_0 \rightarrow t_{max}} \tilde{*} X^{t_0} \tilde{\dagger} \sum_{(i,t) \in A} (T_{t \rightarrow t_{max}})_{\cdot,i}, \alpha \right) \geq \text{minimal final range area} \end{array} \right. \quad \#(Eq11)$$

$$\left\{ \begin{array}{l} \max_{A \subset VC} CEF \left(T_{t_0 \rightarrow t_{max}} \tilde{*} X^{t_0} \tilde{\dagger} \sum_{(i,t) \in A} (T_{t \rightarrow t_{max}})_{\cdot,i}, \alpha \right) \\ \sum_{(i,t) \in A} cost(i) \leq \text{maximum total cost} \end{array} \right. \quad \#(Eq12)$$

287 In case the costs are not specified, the sum of costs becomes equivalent to the number
 288 of introductions.

289
 290 **2.3.2 Step 3: Pre-evaluation of introductions and occurrence probability predictions**
 291 **without introductions.**

292 We reduce all potential combinations of introductions in space and time to a
 293 smaller set by using two filters. The result of this pre-evaluation will lead us to assess
 294 the optimization only using this subset of *viable* solutions among the panel of all
 295 introduction sets.

296 The first filter assesses the effectiveness of the introduction at a site at a given time.
 297 Each cell and time of introduction (i,t) is assigned in the transition matrices a
 298 probability vector of presence at the end of the study period. Summing the values of

299 this vector gives the mean number of sites where the species will be present at the end
300 of the period by introducing the species at that site at the corresponding time (Eq13):

$$eval\left((T_{t \rightarrow t_{max}})_{\cdot,i}\right) = \sum_{j \in [1,N]} (T_{t \rightarrow t_{max}})_{j,i} \quad \#(Eq13)$$

301

302 A threshold parameter controls, for each potential choice of introduction, if this
303 choice offers a mean number of colonized sites by the end of the study period
304 sufficient. We have set a default value of 1 for this threshold, which is low enough not
305 to miss any low efficient sites that could be used for the solution. This threshold can
306 nevertheless be modified. In particular, many possibilities for a small number of
307 introductions could lead to a more drastic elimination of the inefficient sites, and
308 therefore a need to increase the threshold.

309 The second filter discards sub-optimal times of introduction. For a set of times of
310 introduction for a given site, the filter eliminates all the times that are giving lower
311 probabilities of presence at the end of the period for all sites, compared to the other
312 sites. In other words, if it's strictly better to introduce a species at a time compared to
313 another time, the second time will be discarded from potential solutions, as there
314 would be no reason to choose him over the other.

315

316 2.3.3 Genetic algorithm

317 We implemented a genetic algorithm to optimize the introductions in space and time
318 for a given goal (see input parameters) on set of *viable solutions* (see Pre-evaluation
319 section). A genetic algorithm is an evolutionary algorithm whose goal is to find the
320 most optimal solution to an optimization problem, potentially under constraints, with
321 a mechanism inspired by biological evolutionary phenomenon (Chu & Beasley,
322 1998). The objective here for the algorithm is to find the set of pairs of cells and time
323 solution to the problems (2.3.1). Details on the algorithm workflow and
324 parametrization are specified in Appendix S2.

325

326 2.4 A case study on assisted migration

327 IESTR aims to be a general method, which can be adapted to the size of the study
328 area. Input data changes with the scale of the problem and must be determined on a
329 case-by-case basis. We provide some guidance about products and scales that could
330 be used to build such applications with a special focus on tree species as programs of
331 assisted migration are already underway (Appendix S3). We decided to use a virtual
332 case study rather than a direct application. Unlike a real case study, where our results
333 would be idiosyncratic to the choice of species and the the study area environmental

334 structure, the virtual case study allows for better understanding of models' behavior
335 under different constraints.

336

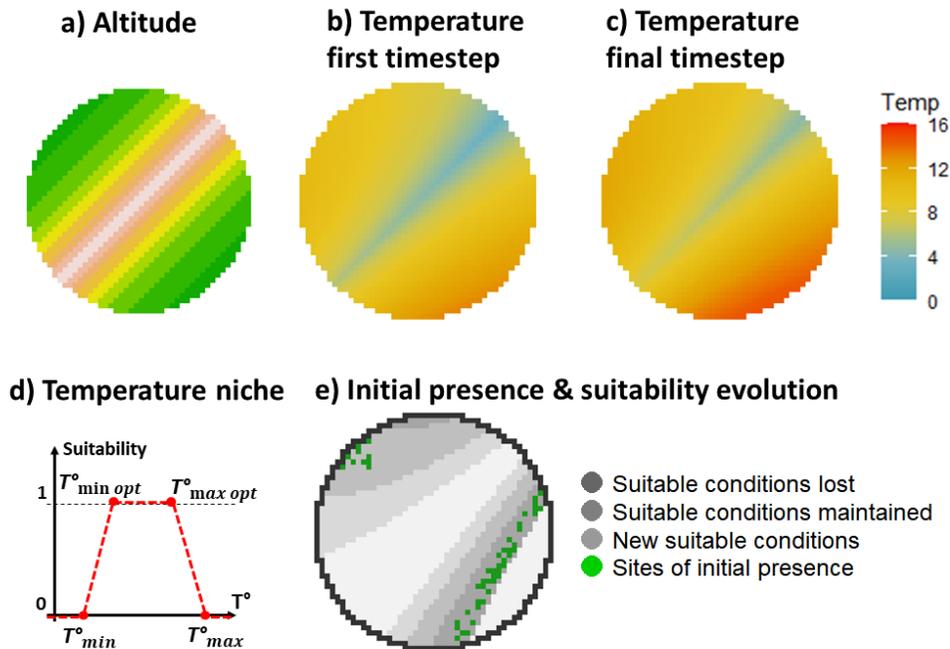
337 We applied IESTR to a case study of assisted migration of a plant species. The study
338 area consists of a simulated circular island characterized by a range of climate
339 conditions structured by a mountain range with a diagonal orientation (Fig 2a). The
340 surface of the island is represented by a 50-column by 50-row grid, each cell being a
341 potential site of presence/absence of the species. Climate change projections are
342 simulated as a shift in temperature conditions on the island of 1.5 C on average, but
343 with warming occurring at a faster rate in the high altitude of the island (Fig 2b & 2c).
344 The target species is initially present in 50 sites, situated in the margin of its
345 ecological niche (Fig. 2d), divided in two disjunct populations on the island (Fig. 2e).
346 Our objective is to identify potential assisted migration sites and time steps to
347 introduce the species in order to prevent species range reduction under climate change
348 from 2030 to 2060. That is, keeping the species range area to 50 sites (cells). To
349 simulate a simplified distribution area, we will only consider temperature for the
350 calculation of the suitability of the theoretical species. The temperature in a cell is
351 determined by three factors: altitude (it is colder at high altitudes), latitude (it is
352 warmer in the south than in the north) and elapsed time (it gets warmer everywhere).
353 The climate change simulation is divided into 30 time-steps, one for each year of the
354 period.

355 The equation used is the following, with *altitude*, *latitude* and *time* factors between
356 0 and 1, and with $T_{min,alt=0}$, $\Delta T_{latitude}$, $\Delta T_{altitude}$, $\Delta T_{climatechange}$ as external
357 factors:

$$Temperature = T_{min,alt=0} + \Delta T_{latitude} * latitude + \Delta T_{altitude} * altitude + \Delta T_{climatechange} * time \#(Eq1)$$

358 The species input parameters to the algorithm consists of a migration core matrix, a
359 set of matrices describing species suitability index over space and time, and a matrix
360 identifying the current species distribution. We set the migration kernel as a 3x3 matrix
361 with a value of 1 in the center representing the current presence of the species and 0.01
362 in all other cells. That is, a 0.01 probability of colonizing each year each of the eight
363 cells around the center cell. The suitability matrices are based on species climatic
364 suitability on the island along the time series analyzed. It is a temperature
365 T_{min} compatible with the survival of the species. The suitability is calculated from the
366 temperature as follows, with the ordered external variables $T_{min,opt}$, $T_{max,opt}$, T_{max} and
367 $T_{min,opt}$, where T_{max} and T_{min} represent species niche margins while $T_{min,opt}$ and
368 $T_{max,opt}$ limit the optimal part of the range where the survival rate is the highest (Fig.
369 2d).

370



371

372 *Figure 2. Topographic and climatic conditions of the simulation, and species*
 373 *suitability characteristics. The surface of the island is represented by a 50-column by*
 374 *50-row grid, each cell being a potential site of presence/absence of the species. (a)*
 375 *Virtual island with a Southwest-Northeast mountain range, (b) initial climate*
 376 *conditions with a decreasing temperature gradient both with altitude and toward NW*
 377 *direction and (c) final temperature conditions at the end of the simulation period (30*
 378 *time steps) showing a uniform temperature increase of 1.5 °C (d) Species niche*
 379 *parameters for the study species for temperature and (e) initial presence of the*
 380 *species at 50 sites (cells), and suitable area dynamics under simulated climatic*
 381 *change.*

382

383 We applied IESTR to three assisted migration situations: Experiment 1 – range
 384 dynamics without assisted migration operations (Experiment 1, Fig. 3); Experiment 2
 385 – with assisted migration using equal costs among all land (Fig. 4), and Experiment 3
 386 – using introduction costs decreasing with the altitude (Experiment 3, Fig. 5).
 387 Because the optimization stems from a pseudo-stochastic process, we evaluated part
 388 of the uncertainty of the algorithm by running 100 repetitions of the algorithm and
 389 comparing the stability of the results for Experiment 2 and 3. Experiment 1 does not
 390 optimize any introduction thus repetitions are not necessary.

391

392 **3 Results**

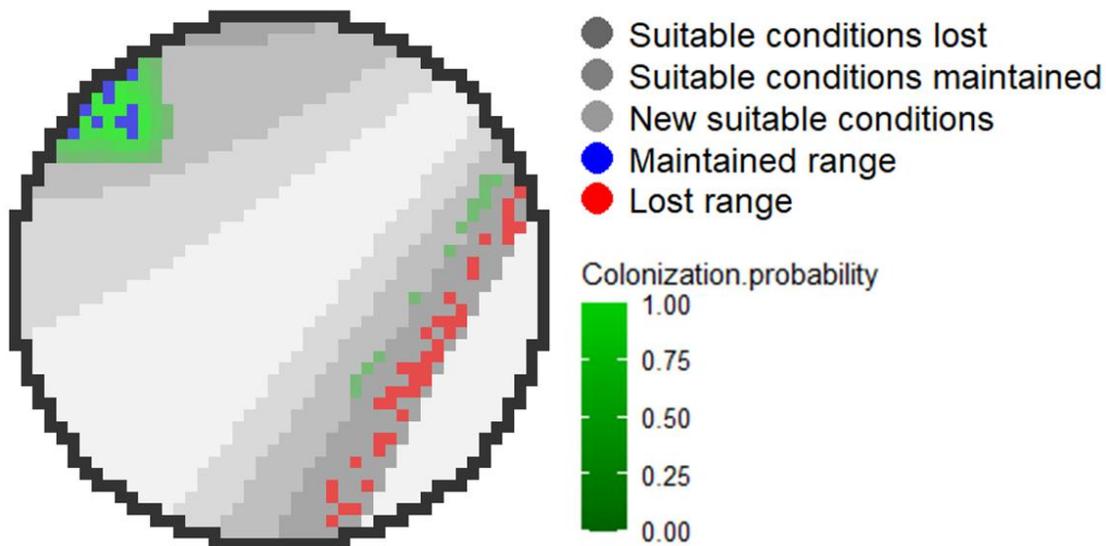
393

394 The algorithm run during 4'05'', with a use of 525 Mb memory on RAM on an
395 Intel(R) Core(TM) i7-10875H CPU @ 2.30GHz for each of the two cost scenarios.
396 Experiment 1, where no optimization is performed, was performed in 0'05''.

397

398 **3.1 Experiment 1: Presence predicted without introduction(s)**

399 Species disappeared where the climate becomes unfavorable – southern section of the
400 island – and colonize its new range, according to the shifts of the climate suitability
401 through time (Fig. 3). At the end of the period, the species is present in 18 sites: 10
402 initial sites (Fig. 3, blue cells) and at least 8 colonized sites (with a probability of
403 90%) (Fig. 3 in green cells), while it was present in 50 sites at the start. This first
404 output of the method thus shows species range change without introductions, and it is
405 calculated with the transition matrix $T_{t_0 \rightarrow t_{max}}$.



406
407 *Figure 3. Species distribution shifts obtained through IESTR algorithm after 30*
408 *timesteps of climate change. The output shows occurrences that maintained (blue) or*
409 *lost (red) as a result of shifts in climate suitability. The probability of species*
410 *colonization (green gradient) along the 30 years of climate change accounts for both*
411 *dispersal and climate (via species suitability) at each site. Species occurrence shifts*
412 *are overlaid on climate suitability shifts in gray.*

413

414

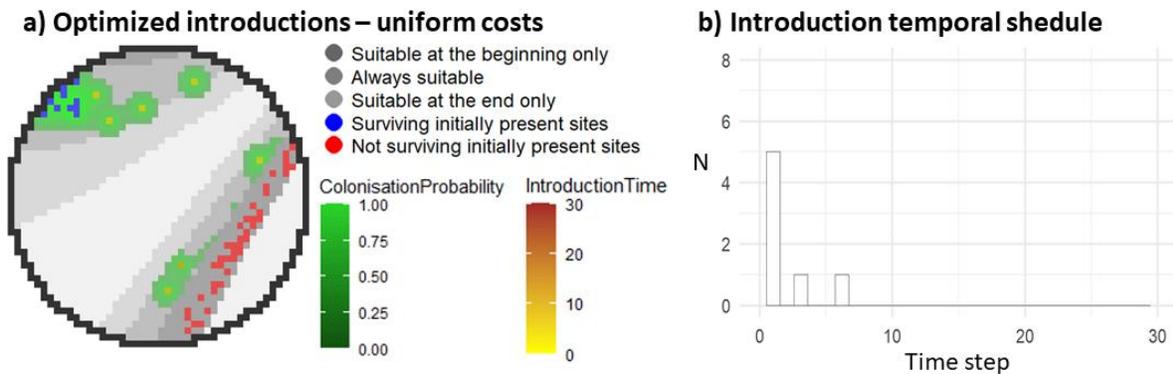
415 **3.2 Experiment 2: Introductions with uniform costs to maintain range area**

416 At the end of 30 years (time steps) of simulated climate change, the species survived
417 in 10 sites (Fig. 4a, blue points), and it was necessary to introduce it in 7 sites (yellow
418 to brown points) to maintain species range area to 50 sites. Not-assisted colonization
419 was estimated to occur in at least 33 sites with a 0.9 probability. Note that the
420 algorithm does not directly predict where colonization occurs. It identifies at the end
421 of the period what are the probabilities of presence in each cell.

422
423 Introductions are found in the north and south of the island, in areas with more
424 favorable suitability gradients (Fig. 2b-c).

425
426 The results of the model suggested that planting as early as possible is an optimal
427 solution to enhance species migration (Fig. 4b). Introductions in areas that become
428 unsuitable were never selected, nor introductions in areas that become suitable during
429 the studied period.

430



431 *Figure 4: Introduction scheme according to IESTR output in order to maintain the*
432 *initial range area of 50 cells: (a) Introduction sites in space and time and their effect*
433 *on the probability of presence of the species at the end of the period (30-time steps),*
434 *and (b) temporal distribution of introduction events, with N the number of*
435 *introductions at each time-step. The final range area comprises 10 initial sites, 7*
436 *introduced sites and at least 33 sites colonized via species dispersal (e.g. colonization*
437 *probability >0.90).*

438

439

440

441 **3.3 Experiment 3: Introduction with spatially heterogeneous costs to maintain**
442 **range area.**

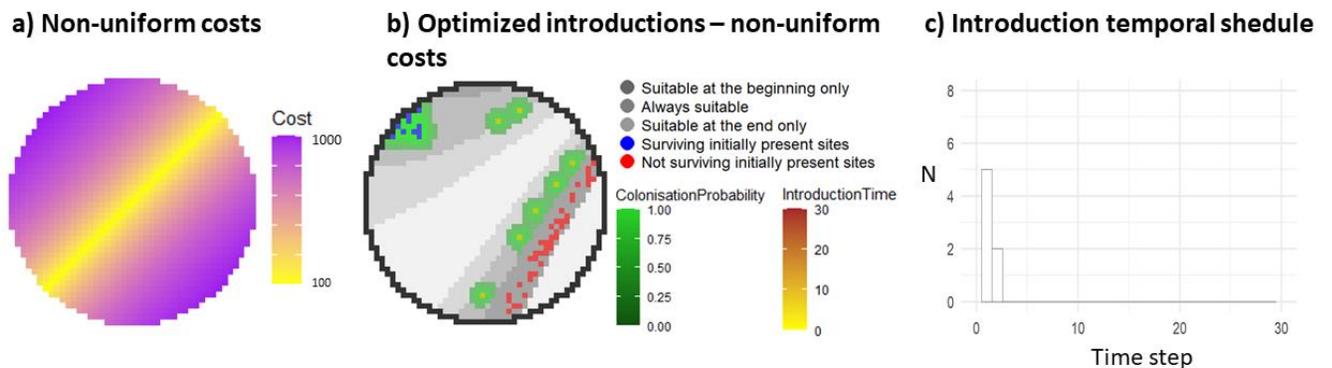
443

444 If costs surfaces are provided to the algorithm (Fig. 5a), the introduction choices
445 achieved by IESTR differed from those obtained with uniform cost (Experiment 2).

446 At the end of 30 years (time-steps) of simulated climate change, the species persisted
 447 in 10 sites (Fig. 5b, blue points) and was expected to colonize 18 sites without
 448 assisted migration (at probability >0.90, Fig. 5b). Thus, introductions in 7 sites were
 449 necessary to maintain species range area to 50 sites (Fig. 5b, yellow to brown points).
 450 This represents the same introduction number than in the case of uniform costs.

451
 452 Optimal introductions are located in the Southern section of the island (Fig. 5b),
 453 which is in stark contrast with the Northern introductions suggested in Experiment 2
 454 (Fig. 4b). For these sites, it should also be noted that the optimal introduction time is
 455 the same as in Experiment 2 (Fig. 4c).

456
 457 With a decreasing introduction cost with altitude, the algorithm seeks to minimize
 458 costs by favoring areas that have a lower cost concentrated on the north west.
 459



460
 461 *Figure 5. : Introduction scheme according to IESTR output in order to maintain the initial range*
 462 *area of 50 sites under non-uniform cost surfaces: (a) Cost map used for the case study, modeled*
 463 *as higher costs on lowlands and lower costs in the mountain tops (see Fig. 2), (b) Introduction*
 464 *sites in space and time and their effect on the probability of presence of the species at the end of*
 465 *the period, and (c) temporal distribution of introduction events. The final range area comprises*
 466 *10 initial sites, 7 introduced sites and at least 33 sites colonized via species dispersal*
 467 *(colonization probability >0.90).*

468
 469 **3.4 Output uncertainty**

470 Since the optimization algorithm is metaheuristic, it returns a single solution
 471 according to a stochastic algorithm. However, the algorithm may find different sets of
 472 introduction sites as solutions under multiple iterations with the same input
 473 parameters. We explored the uncertainty around AM costs using 100 iterations with
 474 the same inputs.

475

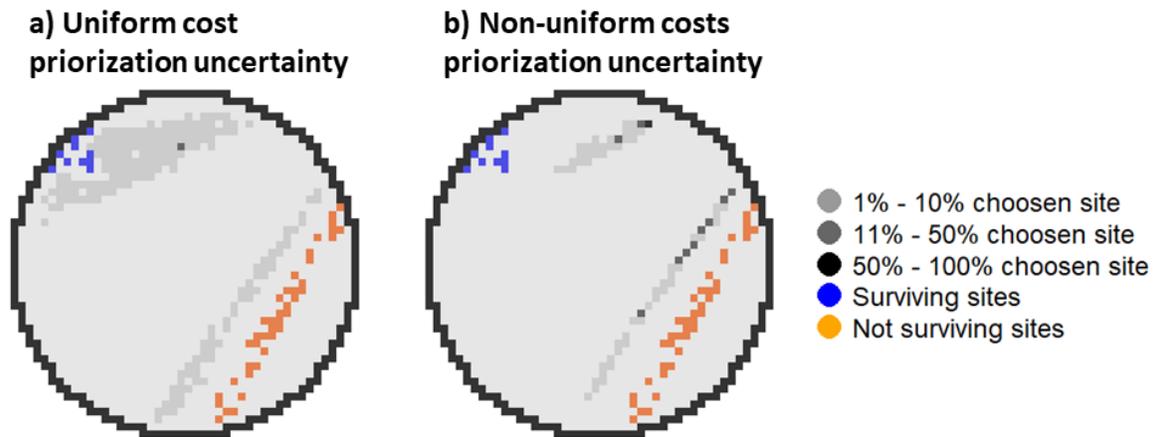
476 We observed that none of the sites were constitutively selected more than 50% of the
477 times for uniform costs, and only one more than 10% of the times (Fig. 6a grey cells).
478 For the non-uniform costs, 3 sites were selected more than 50% of the times and 10
479 were selected between 10% and 49% of the times (Fig. 6b, grey & black cells).

480

481 We observed an overall larger area of potential introduction sites under uniform than
482 non-uniform cost surfaces (Fig 6, light grey area), albeit with low selection rates (i.e.,
483 less than 1% of the iterations selecting the site).

484

485



486

487 *Figure 6: Uncertainty around introduction prioritization from 100 model repetitions.*
488 *Percentages show the rate at which each of the cells is selected as an introduction*
489 *site, in the (a) uniform costs scenario and (b) heterogeneous costs scenario.*

490

491

492 4 Discussion

493

494 The results of our case study showcase that IESTR can produce the desired outcome
495 of maintaining species range size, favoring range shifts and quantifying the
496 uncertainty around introductions in space and time. Specifically, we found that under
497 smooth climate gradients and theoretical conditions (uniform costs), the algorithm
498 suggests planting early in the simulation to enhance species range shifts. This is still
499 the case when simulations introduce costs that may counteract that effect. These
500 results suggest that as risks or costs vary in space, and as temporal variation increases
501 – typically the conditions expected in real case studies, e.g. extreme events— it will
502 become crucial to identify the precise time and space where to help species migrate in
503 the landscape.

504

505 Our results, however, show that there is uncertainty in our virtual species case study
506 (Fig. 6). We argue here that our designed case study represents a strong test as the

507 surfaces modelled for climate and costs are modelled as smooth gradients, making
508 introduction solutions harder to optimize. In more heterogenous landscapes (species
509 suitability and costs) optimization of introductions choices would be reduced,
510 lowering the variability in the IESTR outputs. That is likely to be the case in
511 mountain regions where there is a high spatial variability in climates and
512 microclimates (Davis et al., 2019; He et al., 2017). Likewise, in highly seasonal
513 ecosystems and areas affected by strong climatic perturbations (e.g. el Niño) may
514 produce highly temporal variation in colonization and extinctions (Davis et al., 2016;
515 Serra-Diaz, Franklin, Sweet, et al., 2016) that will likely reduce the introduction sets.
516 Finally, such reduction in the introduction choices may also be found in landscapes
517 where the spatial structure of costs is highly heterogenous with complex agro-forestry
518 mosaics and strong conservation policies where introductions may not be possible
519 (Fahrig, 2003; Laforge et al., 2022).

520

521 IESTR is based on data and assumptions that need to be carefully considered in each
522 case. Our model inherits the same key simplifications of the KISSmig model (Nobis
523 & Normand, 2014): the entire colonization process is described by the probability of
524 direct spread from a presence area, thus integrating the set of complex processes of
525 reproduction, dispersal and establishment into a single value over time. Indeed, our
526 dispersal kernel does not vary in space and time and does not reflect variation in
527 dispersal effort via reproduction (Ronce et al., 2000), or variation in dispersal vectors
528 such as wind or animals (González-Varo et al., 2021; Kling & Ackerly, 2021; Pires et
529 al., 2018). This information (albeit static) in IESTR is considered when adjusting the
530 migration kernel that, for instance, could be based on traits (Tamme et al., 2014).
531 Importantly, in our example, the dispersal kernel does not consider low probability of
532 long-distance dispersal. Long distance dispersal has been key in plants shifting their
533 distribution in past climatic changes (Nathan, 2006), and it is still important under
534 present conditions (Alsos et al., 2007; Baltzinger et al., 2019). We argue that in its
535 current version, IESTR is rather designed not rely on such low probability events to
536 guide (assisted) migration. Nevertheless, migration kernels could be modified to
537 reflect long-distance dispersal events.

538

539 Similarly, species fitness has been reduced to a single parameter which we modelled
540 via an ecological niche model or species distribution model. There is still a
541 contentious debate whether the outputs of such model reflect species biomass growth,
542 establishment, or population parameters (Serra-Diaz et al., 2013; Thuiller et al.,
543 2014). Our choice in this case study reflects the widely use metric of species
544 suitability as a metric of overall exposure to climate change (Dawson et al., 2011),
545 and is interpreted as population survival. However, other metrics could be used. For
546 instance, the population growth rate output from integral projection models (Merow,
547 Latimer, et al., 2014) represents an informative metric based on species demography.
548 Furthermore, it is possible to decompose the suitability values by life stage, by
549 aggregating different models thus better informing different aspects of vulnerability
550 between juveniles and adults (Serra-Diaz, Franklin, Sweet, et al., 2016). The choice

551 on how to build that fitness and survival metric will be dependent on the ecological
552 knowledge, data and models at hand for a given species.

553

554 The novel method implemented here draws from heuristic algorithms used in spatial
555 conservation planning such as Zonation (Lehtomäki & Moilanen, 2013), but it
556 incorporates spatio-temporal dynamics at high resolution. Therefore, we could further
557 our quantification for the need (or not) of species assisted migration beyond the
558 suitability outputs of species distribution models (Hällfors et al., 2016). Crucially, the
559 introduction of the time scale integrates the temporal stochasticity and the effects of
560 extreme events on spatial conservation planning. This is especially important given
561 the increase of disturbance and extreme events under climate change (Fischer et al.,
562 2021; Seidl et al., 2017) , as well as their effect on species tracking their niches (Early
563 & Sax, 2011; Liang et al., 2018, 2023; Serra-Diaz et al., 2015).

564

565 Borrowing from spatial conservation planning, we introduced the cost matrix
566 allowing to tackle with both biological processes and/or anthropogenic costs. We
567 observed a stark shift in introduction sites as well as the time of introduction (Fig. 4
568 vs Fig. 5). Such behavior is in line with spatial conservation prioritization algorithms,
569 where the design of different cost surfaces shifts the spatial allocation of conservation
570 areas (Jung et al., 2021; Moilanen et al., 2011). It is important to note, however, that
571 those costs may not necessarily reflect land use economic values, or AM
572 implementation costs, but could also reflect ecological values or a combined effect of
573 the two types. For instance, these could reflect the potential risk to the ecosystem
574 hosting a new species. A current limitation is that these costs are not dynamic through
575 time, although we expect land use type and intensity to change according to
576 socioeconomic pathways projected in the 21st century (Schrammeijer & Verburg,
577 2019). Such land use intensity shifts are observed in current conservation areas in
578 groups such as trees (Guo et al., 2022) where AM plans are being undertaken.

579

580 The optimization process of IESTR has been specifically designed to explore
581 different scenarios of species assisted migration. We provide some guidance about
582 products and scales that could be used to build such applications with a special focus
583 on tree species as programs of assisted migration are already underway (Appendix
584 S3). However, the outputs from the model could be used in other applications. For
585 instance, transition matrices can provide site-level information on the effects of
586 planting at a given site and time. Indeed, the use of transition matrix could inform
587 invasion biology. That is, the optimization process and its parameters could be
588 modified to identify sites that maximize the spread of an invasive, thus identifying
589 high risk invasion sites beyond the use of climate similarity or raw outputs of species
590 distribution models (Cardador et al., 2022; Redding et al., 2019). Another potential
591 application could be developed in paleoecology, to hindcast the most likely past
592 refugia from which species could have been spread to result in current species
593 distributions. These widely used applications were formerly used either through static
594 models, or through time-costly simulations.

595

596 The large effects of climate change on species redistributions require flexible
597 methods that aid decision-making. Given the importance and yet contentious debate
598 on introductions (either purposely or not), IESTR will help explore the risks and
599 potential schemes for assisted migration based on quantitative analysis. It will
600 provide insights into effects of species introduction based on data available for many
601 species and support new research perspectives on conservation ecology.

602

603

604

605

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861 **Data Accessibility Statement**

862 The R package is available through Github at <https://github.com/ArndCallebaut/IESTR>, and in
863 the supplementary material. The data of the case study are built with a script available in the
864 supplementary material.

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869 Appendices

870

871 Appendix S1: Example of transition matrix use

872 Let us consider a species and its presence and absence at four sites, A, B, C and D, on
873 two time-steps. The species is present at the initial time at site C. We want to quantify
874 the effect of a species introduction on the state of the system at the end of the two
875 time-steps, on each site and in each time step. On the first time-step, the species
876 suitability (understood as a proxy of survival) is 1 in sites A and C, and 0.5 in sites B
877 and D. These values are reversed for the second time step. Migration potential
878 between sites are also set (A↔B: 0.5; A↔C: 0.8; A↔D: 0; B↔C: 0.4; B↔D:0;
879 C↔D: 0.2). The transition matrix at each time step is represented in (Eq14) and
880 (Eq15):

881

$$T_{1 \rightarrow 2} = \begin{pmatrix} 0.5 & 0.25 & 0.4 & 0 \\ 0.5 & 1 & 0.4 & 0 \\ 0.4 & 0.2 & 0.5 & 0.1 \\ 0 & 0 & 0.2 & 1 \end{pmatrix} \#(Eq14)$$

882

$$T_{0 \rightarrow 2} = \begin{pmatrix} 0.68 & 0.45 & 0.65 & 0.08 \\ 0.74 & 0.68 & 0.71 & 0.08 \\ 0.4 & 0.42 & 0.67 & 0.15 \\ 0 & 0.08 & 0.28 & 0.52 \end{pmatrix} \#(Eq15)$$

883

884 Reading the third column of the matrix $T_{0 \rightarrow 2}$ (Eq15) allows us to calculate, for
885 example, that according to the model, since we know that the species is present at site
886 C, we have a 65% chance of the species being present in A, 71% in B, 68% in C and
887 28% in D. Then, if we want to artificially add the species to site B during the second
888 time step, we can calculate the chances of presence in each site at the end (Eq16):

889

$$\begin{pmatrix} 0.25 \\ 1 \\ 0.2 \\ 0 \end{pmatrix} \tilde{+} \begin{pmatrix} 0.65 \\ 0.71 \\ 0.67 \\ 0.28 \end{pmatrix} = \begin{pmatrix} 0.74 \\ 1 \\ 0.7 \\ 0.28 \end{pmatrix} \#(Eq16)$$

890

891 According to the model, we will have a 73% chance of the species being present in
892 A, 100% in B, 70% in C and 28% in D. This gives us exactly the chances of presence
893 in each site, depending on the choices made in terms of assisted migration.

894

895 Appendix S2: The Genetic Algorithm

896

897 In this section we will detail exactly how the genetic algorithm works. We proceed as
898 follows: Firstly, from all the possibilities of introduction at sites s and times t to plant, we
899 calculate the *eval* value (Eq. 13) to rank the sites. We then calculate, with $X_{i,t}$ as the vector of

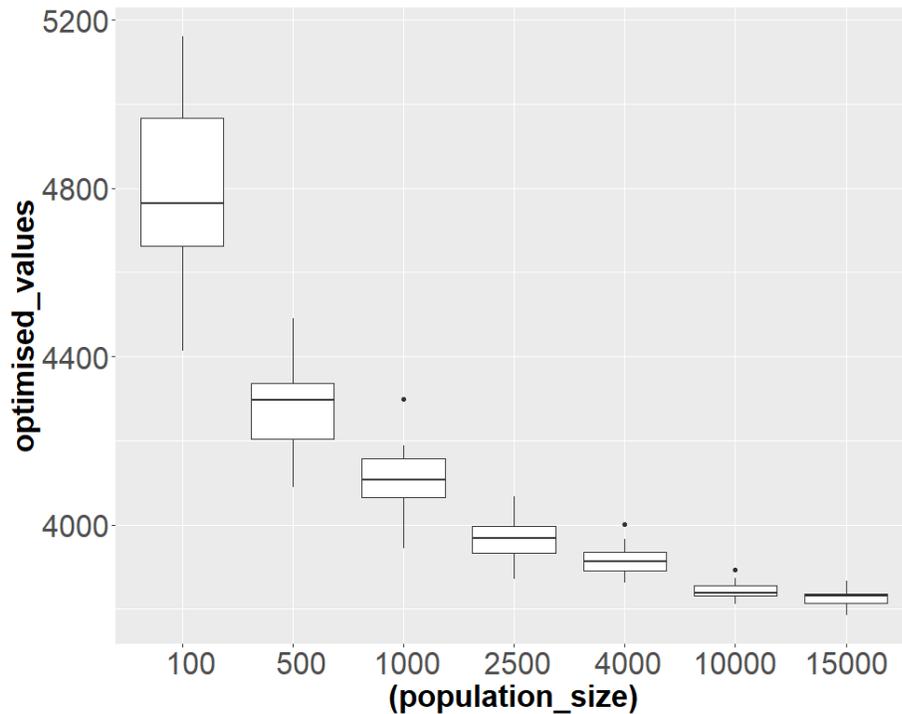
900 presences by the end of the period in each site due to the introduction of the species in site i
901 at time t ; for each site s and each time t , the weight W as :
902

$$W(s, t_0) = \frac{eval(X_{s,t_0})}{\sum_{t \in [0, t_{max}]} \sum_{i \in [1, N]} eval(X_{i,t})}$$

903
904 A set of pairs -sites s and time t - is called an individual. An individual corresponds to a
905 complete introduction schedule. A set of individuals is called a population. A population is
906 therefore a set of possible plans for the introduction of the species. A first parameter involved
907 in genetic algorithms is the size of the population used. Here we set the size of this initial
908 population at 10000 as a good balance between good results and a low calculation time, after
909 testing multiple population size (Fig. S2.1). Each individual initially contains a number of
910 pairs (s, t) equal to the number of sites required to meet the constraint. These pairs are chosen
911 randomly, according to a weight that has been calculated according to their *eval* value.

912 We subsequently check for each individual whether it meets the constraints of the problem. If
913 it does not meet the constraints, the algorithm tries to correct it by adding or removing a site.
914 If this still does not work, the individual is considered defective. If the individual checks the
915 constraints, then we check if it can gain or lose a site in order to improve the objective
916 function. The non-defective individuals are then sorted according to their value with the
917 objective function. Among the population, we will keep only a proportion of “best”
918 individuals (named “survivors” hereafter), that satisfies the objective function the most for
919 the next generation. Here we have used 10% as the proportion. The lower the proportion, the
920 faster the algorithm will tend towards the solution of the problem, but also the greater the
921 chance of missing an unexpected optimal solution.

922 The rest of the population is then replaced by “children” of the survivors. Each child
923 individual is constructed by randomly selecting two “survivor” individuals. Each of these two
924 individuals gives half of its introductions (s, t) to the “child” individual. For each “child”
925 individual, there is also a chance that one of the sites will be randomly changed from the new
926 set of available sites. We set this probability to 1% in our example, for each site. Finally, the
927 next population is made up of the best individuals of the previous generation, and
928 recombined elements from its best elements. The process is repeated for a number of
929 generations (default of 30). At some point, we get an individual who will be optimized.
930 Because the algorithm stems from a stochastic process, it is not guaranteed that the obtained
931 solution is absolutely optimal, but rather an approximate solution.



933

934

935 Figure S2.1: Number of introductions found by the IESTR model using the genetic
 936 algorithm with different population size, with a survivor rate of 10% and 30
 937 generations, under the map condition of the case study (Experiment 3).

938

939 **Appendix S3: Guidance on the application of IESTR to real case studies**

940

941

Scale of the study	Continental	Regional
Size of the cells	From 1km ² to 20 km ²	From 100m ² to 1km ²
Obtaining the map of presence of the species.	Presences derived from the Global Biodiversity Information Network or any other presence database. IUCN species ranges	Presences derived from the Global Biodiversity Information Network or any other presence database. IUCN species ranges
Example of how to calculate suitability over time	Species Distribution Models (Kearney & Porter, 2020), (Franklin, 2010b) ; (Merow, Dahlgren, et al., 2014)	With the use of climatic data prediction at a local scale, edaphic data and a niche model. We can consider more local specificities that can drive the dynamic of the species in or niche model.

How to calculate the migration kernel	If possible, find precise measurement of the potential speed of the species to set the migration Kernel. In most cases it is impossible, then use global values of speed of migration based on paleoecological studies.	Use dispersal kernels based on species traits and/or available published information.
Optimization goals examples	Find the minimum cost of an assisted migration plan in a given region, that must ensure that the species covers X% of the surface area of a species in danger of extinction in that region.	Find the minimum cost of an assisted migration plan to assist the migration of a species in the mountains to higher altitudes, with a minimal presence over Xkm ² , to prevent its extinction.

942 Table S3.1 Examples of products and goals to apply to IESTR to assisted migration
943 studies.

944