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1 **Assessment of the key evolutionary traits that prevent extinctions in human-**
2 **altered habitats using a spatially explicit individual-based model**

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ABSTRACT

21 Identifying key evolutionary strategies that support population persistence remains a
22 challenging task for biodiversity conservation. Here we assess if animal adaptations to
23 cope with low densities (i.e. that facilitate mate-findings or promote spatial aggregation
24 of individuals) can allow species to persist in human-altered habitats. A spatially
25 explicit and individual-based model was developed to assess if, and under what
26 circumstances, such adaptations maintain population viability. The model was
27 parameterised with data from the movement and demography of the spur-thighed
28 tortoise (*Testudo graeca*) and simulated scenarios with differences in adult
29 survivorships, initial population sizes and habitat alterations. Habitat alterations reduced
30 population viability, and extinction rates were dependent on population characteristics
31 and mate-finding distance. In contrast, philopatry around the birthplace did not prevent
32 extinctions. Our results highlight the importance of considering specific spatial traits of
33 species when assessing their vulnerability to human habitat alterations.

34

35 **KEYWORDS:** Allee effect; habitat fragmentation; habitat loss; low-movement species;
36 philopatry, spatial traits

37 **HIGHLIGHTS**

38 We developed STEPLAND, a spatially explicit IBM to assess population viability

39 We investigated if some spatial traits allow persistence in human-altered habitats

40 Mate-finding efficiency was essential for the viability of low density populations

41 We evidenced the importance of spatial traits when assessing species' vulnerability

42

43

1. INTRODUCTION

With more than half the Earth's land surface currently altered by human activities (Barnosky et al., 2012), habitat loss and fragmentation has been identified as one of the main drivers of biodiversity loss (Brooks et al. 2002). Therefore, assessing and predicting how species cope with habitat alterations are relevant challenges (Sala 2000). When assessing the vulnerability of animal species to habitat alterations, the consideration of the spatial component inherent to animal movement is crucial (Fahrig, 2007; Villard & Metzger, 2014; Niebuhr et al., 2015). Habitat alterations have been identified to cause animal mobility loss worldwide (Tucker et al., 2018), and loss of mobility can directly affect population persistence, but also ecosystem processes, such as predator-prey interactions, nutrient cycling and disease transmission (Tucker et al., 2018).

The interaction between movement ability and the landscape structure determines the response of organisms to the various landscape elements, which is known as species' functional connectivity (Tischendorf & Fahrig, 2000; Schooley & Wiens, 2003). According to this concept, connectivity is highly dependent on the organisms, population characteristics and landscapes being studied (Auffret et al. 2015). Therefore, human habitat alterations can critically reduce functional connectivity, which is especially detrimental for low-density populations of species with low movement capacity that are prone to Allee effects (e.g., lower population densities lead to fewer mating opportunities and diminished reproductive fitness) (Philip 1957; Wosniack et al. 2014). However, some of these species may have developed specific traits that allow them to persist in a low-density context if they evolved under such circumstances. Gascoigne et al. (2009) hypothesised that adaptations to mitigate mate-finding failures could also help to buffer the effects of human-altered habitats on population viability. These authors identified two evolutionary routes for this: (i) evolution of mechanisms such as calls, pheromones and hermaphroditism that make mate-finding at low density more efficient or less necessary; (ii) mechanisms that lead to the permanent or periodic aggregation of individuals and, therefore, weaken the strength of mate-finding Allee effects (e.g., reproductive aggregations). When populations are reduced by habitat alternations, Gascoigne et al. (2009) predicted that the species with adaptations of type (i) would be less likely to suffer from mate-finding Allee effects than species with adaptations of type (ii) because they had already adapted to cope with low density.

77 To find out if, and under which circumstances, these mechanisms can allow
78 populations to cope with human-altered habitats, it is necessary to embed them into a
79 demographic context (e.g., considering mortality, growth, and reproduction) and to
80 study the emerging spatial population dynamics. Correlated random walk models
81 (Kareiva & Shigesada, 1983) are powerful tools that reproduce the inherent stochasticity
82 of animal movements and behaviour (Kramer-Schadt et al. 2004, Börger et al. 2008,
83 Anadón et al. 2012). These mechanistic models simulate random walk trajectories that
84 emulate complex movement or behavioural processes, such as habitat selection or the
85 maintenance of home ranges (e.g., Moorcroft & Barnett, 2008). Individual-based
86 models are particularly suitable to study and predict the dynamics of complex systems,
87 which emerge from decision-making individuals that differ and interact locally
88 (DeAngelis & Grimm, 2014). Hence integrating correlated random walk models into
89 individual-based models that consider demographic processes should allow us to assess
90 if and under which circumstances the mechanisms proposed by Gascoigne et al. (2009)
91 allow maintenance of population viability in human-altered habitats (Kramer-Schadt et
92 al. 2005).

93 This study assessed the hypothesis that biological traits developed to deal with
94 low densities could allow animal populations to cope with the negative effects of
95 human-altered habitats. Two traits were tested as being representative of the two
96 evolutionary routes identified by Gascoigne et al. (2009): for the first route we used
97 “mate-finding efficiency”, modelled as the maximum distances among individuals that
98 allows for detection of conspecifics and subsequent mating, and for the second route we
99 used “philopatry”, modelled as the tendency of individuals to stay close to their
100 birthplaces (keeping home ranges) that potentially avoids movement into low density
101 areas.

102 To test our hypotheses we developed STEPLAND, an individual-based
103 simulation model that integrates the spatially explicit movement of individuals with the
104 demographic processes of mortality, aging and recruitment. This model was
105 parameterised with extensive bibliographic and field data of the spur-thighed tortoise
106 (*Testudo graeca*). This species is ideally suited to address our overall objective because
107 it is threatened by habitat fragmentation and loss (IUCN 2016), and low population
108 densities and low movement capacity make it prone to mate-finding Allee effects. Thus,
109 understanding the mechanisms that may allow *T. graeca* to deal with low densities in

110 human-altered habitats is a key for management of this species, and parameterization
 111 with field data is essential for this. For example, movement patterns and home ranges
 112 proved to be very different among individuals of *T. graeca* that inhabited natural and
 113 human-altered habitats (Anadón et al. 2012). As the effects of mate-finding efficiency
 114 and philopatry on population viability are likely to be context-dependent and be
 115 strongly affected by low-density conditions, they were tested herein for different
 116 landscapes, population densities and demographic conditions (i.e., adult survival).
 117 STEPLAND was applied to 12 simulation scenarios that arose from combining three
 118 initial population sizes, two adult survival rates and two distinct (natural and altered)
 119 landscapes (Table 1; Fig. 1). These scenarios well represent the range of real conditions
 120 of low density populations of the selected study system. For each scenario, the
 121 sensitivity of the extinction rates of *T. graeca* populations over 200 years was tested in
 122 relation to changes in the tested biological traits.

123

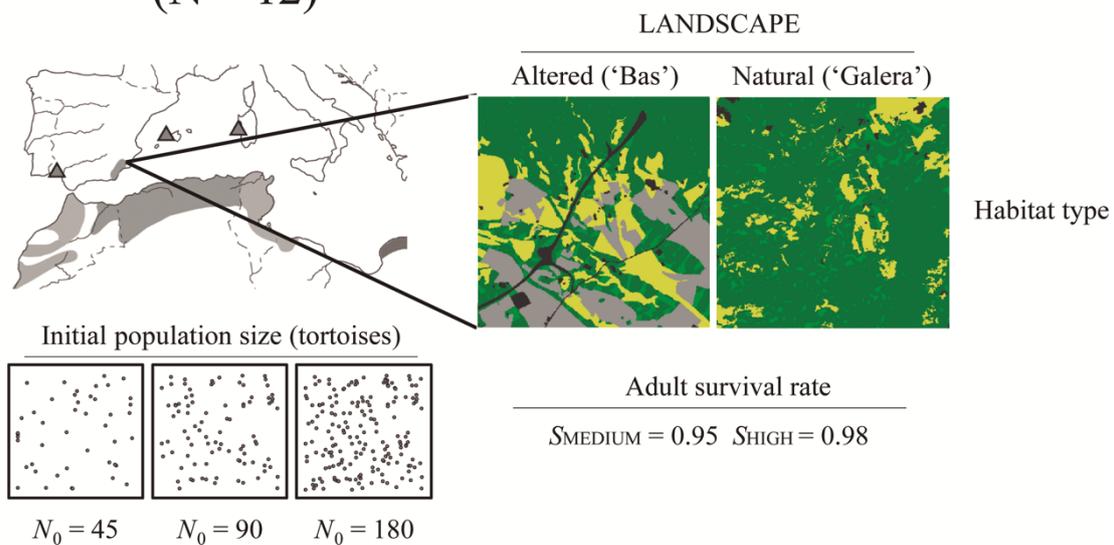
124 **Table 1.** The simulation scenarios and variation in the spatial traits considered in the simulations. To
 125 generate simulation scenarios, we combined the values of the initial population size, adult survival rates
 126 and landscape type, which resulted in 12 scenarios. To test the impact of the mate-finding efficiency and
 127 natal philopatry on population viability, we individually varied the values of parameters DIST in SITE for
 128 each scenario. The values of these parameters, which were maintained across simulations (“standard
 129 parameterisation”), are shown in bold. Table C1 in Appendix C describes the model’s full
 130 parameterisation.

Tested condition or spatial trait	Model variable	Values	Description	Justification/Reference
Scenarios				
Population size	N_0	45/90/180	Initial number of tortoises representing very low to medium densities.	Anadón et al., (2009)
Adult survival rate	S	0.95/0.98	Annual survival rates of adults	Sanz-Aguilar et al. (2011) Rodríguez-Caro et al. (2013)
Habitat	LANDSCAPE	Natural/ Human-	Landscapes of 3 km × 3 km that represent the natural	Real landscapes from SE

quality		altered	(Galera) and human-altered conditions (Bas)	Spain
Species traits				
Mate-finding efficiency	DIST	100/ 300/ 500 /700	Threshold of the maximal distance between females and males that allows mating (in metres).	The standard value matches the sum of the mean maximal annual displacement distances reported for males and females (Anadón et al. 2012)
Natal philopatry	SITE	YES /NO	Natal philopatry is simulated by maintaining the location of the focal-point attractor of tortoises for their lifetimes (“YES”). Alternatively, lack of such behaviour is simulated by reassigning this location to the last position reached each year (“NO”)	The standard value represents strong site-fidelity as found by Sanz-Aguilar et al. (2011)

131

Simulation scenarios (N = 12)



132

133 **Figure 1.** The simulation scenarios. Twelve plausible *T. graeca* populations were generated by
 134 combining two (natural and human-altered) landscapes from SE Spain, three initial population sizes (N_0)

135 that represent low-density populations, and two adult survival rates (S_a). The grey areas on the map on the
136 left show the approximate Western Mediterranean distribution range of *T. graeca* (triangles represent
137 small populations). The two considered landscapes are located north of the species' distribution range in
138 SE Spain.

139

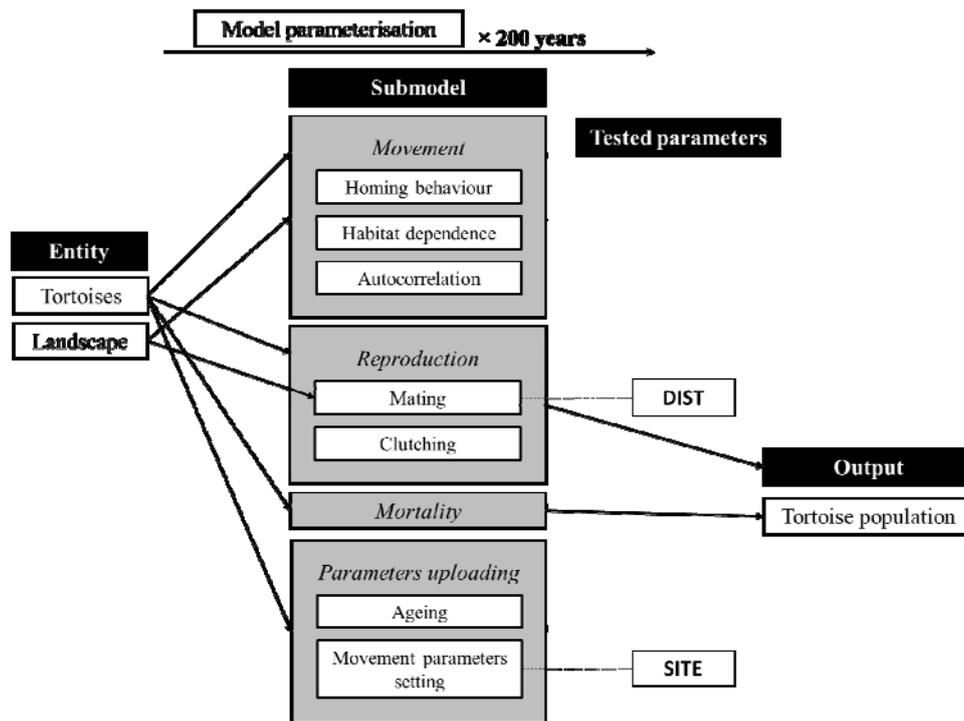
140 **2. METHODS**

141 **2.1 STEPLAND: a spatially individual-based model that integrates animal** 142 **movement and demography**

143 The spatially explicit individual-based model STEPLAND was implemented in Python
144 2.7 and integrated demographic processes (i.e., mortality, aging and recruitment) with a
145 detailed model of animal movement. The purpose of our study is to investigate the
146 response of population viability to changes in biological traits, population
147 characteristics and/or habitat landscapes. The model description follows the Overview,
148 Design concepts and Details protocol (ODD) proposed by Grimm et al. (2006, 2010).
149 Figure 2 presents a general model overview and its description is summarised in the
150 following paragraphs. A full ODD version is presented in Appendix A. STEPLAND
151 was parameterised with extensive data on the spur-thighed tortoise's (*Testudo graeca*)
152 movement and demography. However, after suitable re-parameterization it can also be
153 applied to other study systems with similar movement profiles (species with movement
154 adjustable to correlated walk trajectories).

155

156



157

158 **Figure 2. The main processes implemented into STEPLAND.** Each simulation started with an initial
 159 population that inhabited a given landscape and was governed by a specific model parameterisation. The
 160 model output comprised the generated tortoise populations after T years (here $T=200$). After parameter
 161 uploading, tortoises were subjected to the three basic demographic processes: movement, reproduction
 162 and mortality. Landscape characteristics influenced tortoise movements, while spatial constraints
 163 impacted reproduction (i.e.,: long distances between individuals, or barriers between males and females
 164 hinder mating). The effects of the selected parameters on population dynamics were assessed by a
 165 sensitivity analysis. See Table 1 and Fig. 1 for a description of the parameters and the simulation
 166 scenarios, respectively.

167

168 2.2 Studied species

169 The spur-thighed tortoise *Testudo graeca* is a medium-sized tortoise whose main
 170 Western European population is found in SE Spain (Fig. 1). This species inhabits
 171 mainly semiarid shrublands and traditional agricultural landscapes, and is heavily
 172 threatened by habitat loss and fragmentation (IUCN 2016). *T. graeca* individuals are
 173 non-territorial with overlapping home ranges that range from 1 to 5 ha in SE Spain
 174 (Anadón et al. 2006). They mature at the age of 8-10 years and use to live as long as 30-
 175 40 years (Díaz-Paniagua et al. 2001; Rodríguez-Caro et al. 2019). *T. graeca* females can
 176 store sperm for prolonged times after mating, a biological trait that allows clutches to be

177 fertilised for prolonged time periods after mating (Roques et al. 2004). Clutch sizes vary
178 mostly between 1 and 7 (the authors, unpublished data).

179 The spur-thighed tortoise is ideally suited to study the interaction between
180 habitat alteration and individual movement behaviour on population dynamics. Firstly,
181 radiotracking data, together with long-term capture-recapture studies, suggest that
182 individuals show a low-dispersal capacity and high site fidelity (Sanz-Aguilar et al.
183 2011, Anadón et al. 2012). These features make low-density populations especially
184 vulnerable to human habitat alterations (Sanz-Aguilar et al. 2011). Secondly, the basic
185 demographic aspects of *T. graeca* populations have been well studied (e.g., Díaz-
186 Paniagua et al. 2001, Sanz-Aguilar et al. 2011, Rodríguez-Caro et al. 2013, 2019).
187 Additionally, an individual-based model that simulates the movement behaviour of
188 adult *T. graeca* males and females in natural and human-altered landscapes has already
189 been parameterised and implemented (Anadón et al. 2012). STEPLAND extends this
190 movement model towards a dynamic population model by adding the demographic
191 processes of mortality, aging and recruitment.

192

193 **2.3 Model use and parameterisation**

194 *Entities, attributes and spatial scales.* STEPLAND contains two types of
195 entities: landscape and individuals (tortoises in this study). The 3 km × 3 km landscape
196 (Fig. 1) was composed of a grid of 10 m × 10 m cells. Each grid cell was characterised
197 by its position (x and y coordinates), and also by its assignment to a habitat category. In
198 this study, the four habitat categories used by Anadón et al. (2012) were considered:
199 intensive land use, traditional agriculture land, flat natural areas and natural areas on
200 slope, and an additional non-permeable infrastructure category. Landscapes were
201 enclosed by a non-permeable border that resulted in isolated populations.

202 The attributes of individuals were: sex, age, their locations over time and the
203 coordinates of their focal point attractor to represent philopatry (i.e., individual's
204 tendency to maintain a stable home range around the focal point). Each individual
205 obtains a movement parameterisation from a pool of parameterisations that were
206 compatible with observed radiotracking data (following Anadón et al. 2012; see
207 Appendix A for further movement parameterisation information).

208 *Input, initialisation and output.* The model inputs included the initial population,
209 the landscape and model parameterisation (Fig. 2). In this study, the initial number of
210 individuals for the different age classes followed a stable age distribution predicted by
211 an age-stage structured deterministic matrix population model (Caswell 2001) with the
212 demographic parameters used in STEPLAND. The R package POPBIO (Stubben and
213 Milligan 2007, R Core Team 2014; Appendix B) was used to derive the stable age
214 distribution that fitted age distributions observed in field (Rodríguez-Caro et al, 2019).
215 The individuals in the initial population were randomly distributed across the
216 landscapes and their initial locations were the same in all the simulation scenarios that
217 started with the same density. To avoid biases due to the excessive aggregation or
218 disaggregation of individuals we checked mean minimum Euclidean distances between
219 females and males in tentative initial populations before selecting suitable initial
220 populations (see section “Input, initialisation and output” in Appendix A for further
221 information). Model parameterisations were based on Anadón et al. (2012), empirical
222 data and a literature review (see Table C1 in Appendix C). The data output comprised
223 the surviving individuals of the population present at the end of the simulation.

224 *Temporal scales, process overview and scheduling.* Each time step represented
225 one day. In this study, simulations were run for 200 years. The model consisted of
226 submodels for movement, reproduction, mortality and aging happened at the end of the
227 year (Fig. 2). The scheduling of the different processes was adapted to the biology of
228 the species. Tortoise movement occurred on a daily basis, but followed a seasonal
229 activity pattern with no movement in winter and little movement in summer (i.e.,
230 hibernation and aestivation periods), but peak movement during the mating season
231 (April to May) (Fig. A4 in Appendix A).

232 I) *Movement submodel:* STEPLAND incorporates the movement model and
233 movement parameterisations of Anadón et al. (2012) based on the analysis of
234 radiotracking data using inverse and individual-based modelling approaches.
235 These authors found that tortoises showed high site fidelity in natural
236 landscapes, and only slight variability in their movement patterns. However,
237 movement behaviour varied strongly among individuals in altered landscapes. A
238 wide range of movement patterns was found particularly for females, which
239 ranged from strong homing behaviour to unbounded movements. For males,
240 Anadón et al. (2012) determined 129 and 51 different parameterisations of nine

241 parameters governing individual movement that were compatible with the
242 empirical movement data in natural and altered landscapes, respectively. For
243 females, there were 155 and 5,282 parameterisations of the nine parameters,
244 respectively (see Appendix A for further details). To reflect the individual
245 variability observed in the movement patterns, we randomly assigned one of
246 these movement parameterisations to a tortoise at birth (corresponding to its sex
247 and landscape type).

248 Individual movement consisted in a sequence of steps to the
249 neighboured $10\text{ m} \times 10\text{ m}$ cells (Fig. 3A). The stochastic rules that determined
250 the number of these “cell-to-cell” steps were governed by the two probability
251 distributions, PMOV and DMOV, which were directly taken from the detailed
252 radiotracking data (that divided the active period of 1 day into four 2- to 3-hour
253 periods). Firstly, on a given day, the probability of moving during a given 2-3
254 hour period was given by the corresponding probability of PMOV, and
255 depended on the month and sex of the tortoise in accordance with its activity,
256 hibernation and aestivation periods (Fig. A4 in Appendix A). Secondly, if the
257 PMOV trial indicated movement, DMOV decided how many cell-to-cell steps
258 the individual actually moved during this period (Fig. A4 in Appendix A). While
259 PMOV and DMOV governed the number of cell-to-cell steps in which an
260 individual moved, the actual movement decisions for the cell-to-cell step were
261 stochastic, but depended on three sets of weights that described autocorrelation
262 in movement, habitat use and homing behaviour towards a focal point attractor.
263 The three normalised weights were multiplied to calculate the final probability
264 of a cell being selected (Fig. 3B). See Appendix A for a complete description of
265 the movement submodel.

266

267 II) *Demographic submodel*: demography in STEPLAND included ageing,
268 reproduction and mortality. Reproduction included the three processes: mating,
269 sperm storage and clutching (Fig. 2).

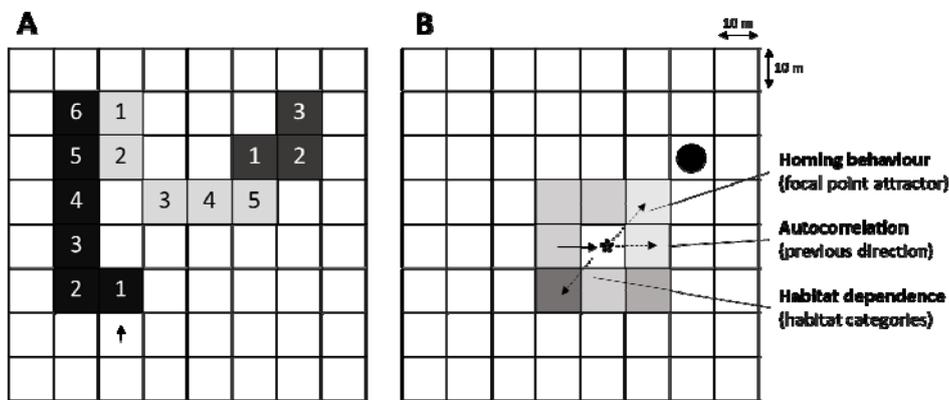
270 Mating occurred once during the spring. The STEPLAND model
271 assumed that mature females and males mated during this period if: (i) the
272 distance between female and male was shorter than the value of the parameter

273 DIST and (ii) females and males were not separated by barriers such as main
 274 roads, dense human infrastructures or intensive agriculture.

275 Sperm-storage and multiple paternity, which are specific traits of spur-
 276 thighed tortoises (Roques et al. 2004), were modelled as a temporal dissociation
 277 between mating events and clutching. Some studies have indicated that sperm
 278 can be viable in female oviducts for as long as 3-4 years (e.g., Cutuli et al.
 279 2013). Therefore, it was assumed that females could reproduce up to 3 years
 280 after their last mating. Adult females are able to lay up to three clutches a year as
 281 observed in real populations (Díaz-Paniagua et al. 1996, 1997; unpublished
 282 data).

283 Mortality was a single stochastic event at the end of each simulated year.
 284 Annual survival rates varied among age classes, including eggs, immature
 285 individuals, subadults and adults. Finally, surviving individuals aged one year.
 286 Appendix C provides the parameters values and an extended description of the
 287 criteria followed to select them.

288



289

290 **Figure 3.** The movement submodel. (A) Movement of a simulated tortoise on a given day: starting from
 291 the arrow, the tortoise moves during three of the four active periods (represented by different colours),
 292 with six, five and three cell-to-cell steps each (movement directions are represented by numbers). (B)
 293 Stochastic movement decision for one step: dependent on three sets of weights that described
 294 autocorrelation in movement, habitat use and homing behaviour towards to a focal point attractor. The
 295 three normalised weights (broken arrows) were multiplied to calculate the final probability of a
 296 neighbouring cell being selected. The asterisk indicates the individual's current position. The black dot
 297 represents the focal point attractor governing homing behaviour. The continuous arrow represents the
 298 previous movement. The cell colours indicate different habitat categories. See Appendix A for a complete
 299 description of the movement submodel.
 300

301

302 **2.4 Experimental design**

303 *Simulation scenarios.* Twelve simulation scenarios (Table 1, Fig. 1) were assembled
304 that resulted from combining three initial population sizes, two annual adult survival
305 rates and two distinct landscapes. Simulations started with 45, 90 and 180 tortoises (N_0),
306 which covered very low to medium population densities, as found in natural *T. graeca*
307 populations in SE Spain (0.05, 0.1 and 0.2 tortoises/ha; Anadón et al., 2009). As the
308 growth rate of long-living species is very sensitive to the annual survival rates (S) of
309 adults, independent simulations were conducted for two S values that represented high
310 and medium survival for *T. graeca* populations (Sanz-Aguilar et al. 2011, Rodríguez-
311 Caro et al. 2013; $S_{\text{LOW}} = 0.95$ and $S_{\text{HIGH}} = 0.98$; Table C1 in Appendix C). The
312 combinations of demographic parameters resulted in theoretical growth rates of $\lambda_{\text{LOW}} =$
313 1.008 (for S_{LOW}) and $\lambda_{\text{HIGH}} = 1.02$ (for S_{HIGH}) (see Table C1 in Appendix C). These
314 theoretical growth rates were calculated with the R package POPBIO, and represent
315 theoretical population growth (i.e., without effects of demographic or environmental
316 stochasticity or spatial Allee effects; Appendix B). However, in the populations
317 simulated with our spatially explicit individual-based model, spatial constraints could
318 impede the reproduction of some females in fragmented landscapes (see below) and
319 result, together with demographic stochasticity, in lower growth rates, or even in
320 population extinctions.

321 To represent natural and human-altered landscapes (the LANDSCAPE variable
322 in the subsequent analyses), two typical 3 km \times 3 km landscapes from SE Spain that
323 currently host *T. graeca* populations were used (Fig. 1). These two landscapes were also
324 used to parameterise the movement submodel for individual tortoises (Anadón et al.
325 2012). The “Galera” landscape represented the natural landscapes with very low cover
326 of intensive land uses and non-permeable infrastructures (1%), whereas the “Bas”
327 landscape represented altered landscapes with a much higher proportion of intensive
328 land uses or non-permeable infrastructures (26%). As the “Galera” landscape lacked
329 internal barriers, we assumed the population to be potentially panmictic (i.e., in theory,
330 all individuals can breed if located close enough to one another). In contrast, and as
331 mentioned above, we assumed that intensive land uses (i.e., intensive crops) and non-
332 permeable infrastructures (i.e., a highway) imposed barriers for reproduction (Fig. 1).

333 Note that the movement of tortoises across barriers was not totally impeded, but became
334 little likely because movement in human-altered landscapes was influenced by habitat
335 type (Fig. 3B; Fig. A7 in Appendix A). Anadón et al. (2012) determined individual
336 movement parameterisations separately for males and females, and also for natural and
337 the altered landscapes (see Appendix A for further movement parameterisation
338 information). Therefore, for the Galera simulations, the movement parameterisations of
339 individuals were randomly selected from the pool of natural landscape
340 parameterisations, and for the Bas simulations from the pool of altered landscape
341 parameterisations.

342 *Simulation experiments.* For all 12 scenarios, we assessed the effects of mate-
343 finding efficiency and philopatry on population viability (Fig.1 and Table 1). To test the
344 influence of mate searching efficiency, the parameter DIST was varied over a wide
345 range of values (100 m, 300 m, 500 m and 700 m). Note that the mean maximal
346 displacement distances observed during one-year period in the radiotracked *T. graeca*
347 males and females were 189-275 m and 148-271 m, respectively, as reported by Anadón
348 et al. (2012). In the standard simulations, tortoises' birthplaces were maintained as a
349 focal point attractor for their whole lifetime to represent philopatry (SITE = Yes). To
350 simulate lack of philopatry, the standard parameterisation was used (with DIST = 500),
351 but the focal point attractor was reassigned to the individual's last position at the end of
352 each year (SITE = No) (Table 1). This resulted in "wandering" behaviour.

353 **2.5 Data analysis**

354 The total number of independent model simulations was 4,608 (12 simulation scenarios
355 \times 5 parameterisations of spatial traits \times 64 replicates; Table 1). Scripts developed in R
356 (R Core Team 2014) and Python 2.7 processed model outputs to calculate extinction
357 rates. Multivariate binomial GLM models were used to assess the sensitivity of each
358 evaluated parameter for population extinction. The variables related to the scenarios
359 were treated as factors (N_0 , S , LANDSCAPE), while model parameters were treated as
360 numerical (DIST) or factor (SITE) variables. The selection of the best model for the
361 parameterisations that represented the variations in each trait was based on Akaike's
362 information criterion (AIC; Burnham and Anderson 2004) using a stepwise backward
363 algorithm. Model structures with $\Delta\text{AIC} < 2$ were assumed to receive similar support

364 (Hastie and Pregiborn 1992). *Post hoc* analyses (ANOVA function) served to calculate
 365 the explained deviance of each parameter to the selected model.

366 3. RESULTS

367 3.1 Effects of landscape type and population characteristics on population 368 viability

369 In the first set of simulation experiments, the standard model parameterisation (Table 1)
 370 was used to test the influence of the 12 scenarios on population viability. The results
 371 showed that variation in population and landscape characteristics in the scenarios
 372 affected the population dynamics of *Testudo graeca* (Table 2). The extinction rates
 373 (EX) over a 200-year time horizon differed strongly among the simulation scenarios.
 374 Lower initial density increased the extinction risk (mean EX = 0.37 for $N_0 = 45$, mean
 375 EX = 0.08 for $N_0 = 90$, and mean EX = 0 for $N_0 = 180$). Landscape type also influenced
 376 population viability as the extinction rate was higher in the altered landscape (mean EX
 377 = 0.18) than in the natural one (mean EX = 0.11). Finally, as expected, the lower adult
 378 survival (0.95 vs. 0.98) strongly enhanced the extinction rate (mean EX = 0.29 for S_{LOW} ,
 379 and mean EX = 0.01 for S_{HIGH}).

380 **Table 2.** Extinction rates (i.e., proportion of the 64 replicate simulations that became extinct) of the *T.*
 381 *graeca* populations over 200 years. Simulations were replicated 64 times using standard parameterisation
 382 based on both empirical data and a literature review (see Table C1 in Appendix C). The simulation
 383 scenarios combined different initial population sizes (N_0), adult survival rates ($S_{\text{LOW}} = 0.95$; $S_{\text{HIGH}} = 0.98$)
 384 and habitat quality (natural and human-altered landscapes). Note that the deterministic growth rate,
 385 estimated from the demographic parameters, yielded $\lambda_{\text{LOW}} = 1.008$ (for S_{LOW}) and $\lambda_{\text{HIGH}} = 1.02$ (for
 386 S_{HIGH}). Population extinction can arise from spatial constraints and demographic stochasticity, especially
 387 for those scenarios with $N_0 = 45$ and S_{LOW} .

388

	Very low density ($N_0 = 45$ tortoises)		Low density ($N_0 = 90$ tortoises)		Medium density ($N_0 = 180$ tortoises)	
Landscape	S_{LOW}	S_{HIGH}	S_{LOW}	S_{HIGH}	S_{LOW}	S_{HIGH}
Natural	0.66	0.02	0.02	0	0	0
Altered	0.77	0.02	0.30	0	0	0

389

390 3.2 Effect of mate-finding efficiency on population viability

391 Mate-finding efficiency, represented by the maximal distance DIST between males and
 392 females where mating occurred (within the 100-700 m range), strongly influenced the

393 population dynamics and extinction probability of *T. graeca*. For low adult survival
 394 (S_{LOW}), all populations went extinct for the lowest mate searching efficiency (i.e., DIST
 395 = 100 m), and most of them for the low mate searching efficiency (i.e., DIST = 300 m;
 396 Fig. 4). However, for DIST = 700 m, all simulations were viable for high adult survival
 397 (S_{HIGH}), and also for the majority of simulations run with S_{LOW} . Only the low density
 398 simulations that started with $N_0 = 45$ individuals showed a moderate percentage of
 399 extinctions for DIST = 700 (Fig. 4). Finally, intermediate DIST values (i.e., DIST = 300
 400 m for S_{HIGH} and DIST = 500 m for S_{LOW}) produced a wide range of population
 401 dynamics (Fig. 4). In these cases, extinction rates for S_{LOW} were related with landscape
 402 type and the initial population size; but for S_{HIGH} the mainly driver of variation was the
 403 initial population size (Fig. 4). Table D1 in Appendix D shows the extinction rates of
 404 the simulations.

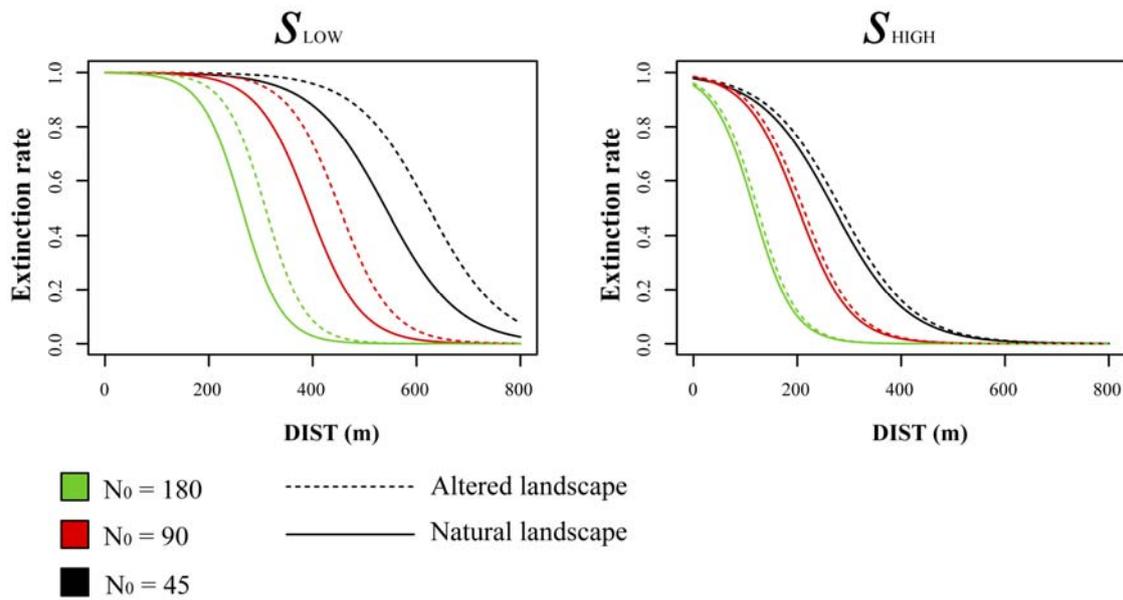
405 Multivariate binomial GLM models, used to assess the sensitivity of population
 406 extinction to the four variables DIST, S , N_0 , and LANDSCAPE, quantitatively revealed
 407 the relevance of the mate-finding efficiency for population viability. Most of the
 408 variation was explained by the DIST parameter (i.e. DIST explained 54.28% of the
 409 deviance, while the total deviance explained by the model was 65.23%; Table 3).

410

411 **Table 3.** The GLM results that describe the sensitivity of the three tested spatial traits for population
 412 extinction over 200 years. Parameters govern processes in relation to movement and behaviour (mate-
 413 finding efficiency and natal philopatry). The best model only includes those variables or interactions with
 414 $\Delta AIC < 2$. See Table 1 for the description of the parameters and variables.

Spatial trait	Parameter	Variables included in the GLM model	$\Delta\%$ of explained deviance
Mate-finding efficiency	DIST	DIST	54.28
		S	6.25
		N_0	4.51
		LANDSCAPE	0.19
		Total model	65.23
Natal philopatry	SITE	S	30.78
		N_0	25.44
		LANDSCAPE	0.92
		Total model	57.14

415



417

418 **Figure 4.** Extinction rates predicted by GLMs in dependence of DIST, for different survival rates (S), and
 419 initial population densities (N_0). This parameter imposes a maximal distance threshold between females
 420 and males to allow mating (in metres). The simulation scenarios included two different adult survival
 421 rates ($S_{LOW} = 0.95$; $S_{HIGH} = 0.98$), habitat types and the initial population sizes. See Table 1 and Table C1
 422 in Appendix C for further model parameterisation information.

423

424 3.3 Sensitivity of philopatry

425 In our simulations, the maintenance, or not, of stable home ranges around tortoises'
 426 birthplaces had no effect on the extinction rates of the *T. graeca* populations (Table 3).
 427 The SITE parameter, which governs the maintenance of the stable home range of
 428 tortoises among years and emulates philopatry, displayed only weak explanatory power.
 429 Table D1 in Appendix D shows the extinction rates.

430

431 4. DISCUSSION

432 The evolutionary history of species may result in traits that allow them to cope with
 433 human-altered habitats. For example, Gascoigne et al. (2009) hypothesised that
 434 evolutionary adaptations to persist under low-density conditions could allow species
 435 also to deal with human-altered habitats. This study employed an individual-based
 436 simulation model to assess the effects of such traits, mate-finding efficiency and

437 philopatry, on the viability of a low-movement species within a range of contexts given
438 by variations in initial population size, natural vs. human-altered landscapes and adult
439 survival.

440 Our results showed that increasing mate-finding efficiency had a high potential
441 to avoid population extinctions if initial population sizes are low, whereas philopatry
442 had no effect. The typical human-altered landscape negatively affected the viability of
443 *Testudo graeca* populations compared to the natural landscape, but this depended on
444 population characteristics (the initial population size and survival rates of adults).
445 Landscape type did not affected viability in the scenarios with high adult survival rates
446 (resulting in 2% maximal possible population growth), but extinction rate was
447 especially sensitive to the landscape type in the scenarios with lower adult survival rates
448 (0.8% maximal population growth) and a low and very low initial density of tortoises
449 (Table 2). These results agree with those of Pearson et al. (2014) who, in the broader
450 climate change context, found that species' vulnerability depends on a mixture of spatial
451 and demographic factors. These authors also identified population size and population
452 growth among the most important demographic predictors.

453

454 **4.1 Role of spatial traits in mitigating mate-finding Allee effects**

455 The consideration of species traits in ecological modelling allows from the study of the
456 population dynamics of one or several species (e.g. discrete traits distribution models
457 reproducing predator-prey dynamics; Tirok & Gaedke, 2010), to the description of the
458 temporal dynamics of a community (e.g. biomass produced by phytoplankton
459 considering distribution-based aggregate models under different selection regimes;
460 Klauschies et al. 2018). To produce robust predictions under global change scenarios,
461 recent studies claim the necessity to consider relevant species traits when projecting
462 species range distributions (Regos et al. 2019) or species vulnerability (Pearson et al.
463 2014). In this work, two adaptations with the potential to increase mating encounters in
464 human-altered habitats were assessed: mate-finding efficiency and philopatry to the
465 birth site. The population dynamics of spur-thighed tortoises was especially sensitive to
466 the mate-finding efficiency, but not to philopatry. These results confirmed the
467 expectations of Gascoigne et al. (2009), who predicted that the adaptations which

468 evolved to function well at low densities would have a very high potential to increase
469 the resilience of populations that declined in human-altered habitats.

470 *Mate-finding efficiency.* The maximum distance of male and female individuals
471 to be allowed for mating encounters, simulated by the DIST parameter in STEPLAND,
472 turned out to be a key factor for population dynamics and extinction. Despite being a
473 simplification of a complex biological process, our results agree well with our
474 knowledge on *T. graeca*. In our model simulations, a reduction in extinction risk
475 occurred for the DIST values of 300 m and 500 m, distances that match the sum of the
476 mean maximal annual displacement distances reported for *T. graeca* males and females
477 (189-275 m and 148-271 m, respectively; Anadón et al. 2012). Clearly unrealistically
478 high parameter values (e.g. > 500 m) would lead to a further reduction in the extinction
479 risk of small populations because they counteract the Allee effect. How conspecific
480 attraction underlies mating search strategies remains largely unknown (Galeotti et al.
481 2007), but our results support the notion that such a biological mechanism is key for
482 maintaining the viability of low-density populations (Reed and Dobson 1993, Berec and
483 Boukal 2004). Some evolutionary strategies, like pheromones, song or calls, prevent
484 mate-finding failures; alternatively, hermaphroditism or the ability to maintain pair
485 bonds, can reduce the frequency with which mate-finding needs to occur (Gascoigne et
486 al. 2009). Mate-finding is driven in tortoises by the production, detection and
487 recognition of sex pheromones (Norris and López, 2011). However, when considering
488 their limited dispersal capabilities, we hypothesise that female sperm-storage may also
489 play a major role in supporting population viability under low-density conditions
490 (Roques et al. 2004; Gascoigne et al. 2009). This evolutionary strategy has a high
491 potential for mitigating the effects of human-altered habitats in limiting the availability
492 of potential mates. However, further simulation experiments should elucidate the trade-
493 offs for the evolutionary potential that an increase in the use of this trait may cause (like
494 endogamy from using the sperm of a few parents over years).

495 *Philopatry.* The tendency to return to the birthplace is a mechanism that allows
496 individuals to obtain breeding sites of higher quality and in closer proximity of other
497 individuals, than settling at random locations. However, because trade-offs may arise in
498 relation to inbreeding, settling patterns have proved to be variable among individuals,
499 depending on the quality among breeding sites and on individuals' characteristics (e.g.,
500 age and sex; Schjørring, 2001). Hence, philopatry acts as a plastic biological trait with

501 variable relevance for population persistence depending on the context. In our
502 simulation experiments, the stable home ranges that remained during the lifetimes of
503 tortoises around their birthplace did not affect the population dynamics compared to the
504 home ranges that could shift every year (by displacements of the focal point attractors to
505 the last location in the year). Stable home ranges may offer tortoises high quality
506 feeding patches, refuge areas and places for laying eggs (e.g., Kaddour et al. 2006;
507 Anadón et al. 2012; Lecq et al. 2014), and may prevent tortoises from wandering into
508 low-density areas where mating encounters are rare. The fact that our simulation
509 experiments did not show effects of natal philopatry could be caused by the moderate
510 annual displacements of home ranges, which did not cause populations to drift apart in
511 the 3x3 km simulated landscapes. However, omission of homing behaviour resulted in
512 immediate population extinction when simulating colonisation processes at a larger
513 geographic scale (10x10 km landscapes) (results not shown). Indeed, philopatry has
514 proved be relevant for other chelonians (*Caretta caretta*) to prevent Allee effects during
515 range expansions (Stiebens et al., 2013).

516

517 **4.2 Is *T. graeca* able to counterbalance Allee effects in human-altered** 518 **landscapes?**

519 Habitat alterations generally reduce the quantity of high-quality habitats and enhance
520 border effects. Animal movement patterns in fragmented landscapes may play an
521 important role in mitigating the detrimental effects of human habitat alterations, and in
522 maintaining populations' functional connectivity (Mimet et al. 2013, Niebuhr et al.
523 2015). The present study was carried out under low-density conditions, far away from
524 the carrying capacity possible in our two landscapes, and the same demographic
525 parameters were assumed for the tortoises that inhabited both human-altered and natural
526 landscapes (except for movement parameterisations). Therefore, the differences in
527 population dynamics between the corresponding scenarios in the natural and altered
528 landscapes could only arise from the spatial mechanisms linked to mate-finding Allee
529 effects (i.e., lower mating encounter rates due to barriers). Our simulation experiments
530 suggested that the human-altered landscape increased the extinction risk of *T. graeca*
531 compared to the natural landscape by generating Allee effects in low-density
532 populations (i.e., isolation between sexes). As exemplified for *T. graeca*, some

533 populations that inhabited human-altered mosaic landscapes could disappear within
534 some decades (Alharbi and Petrovskii 2016). The fact that these tortoises are currently
535 present in highly disturbed areas is probably a result of their longevity and not due to
536 population viability (Henle et al. 2004).

537

538 **5. CONCLUSIONS**

539 Habitat changes have been identified among the main drivers of biodiversity loss
540 (Brooks et al. 2002). Therefore, assessing and predicting how species face human
541 habitat alterations are relevant challenges (Sala 2000). Our study exemplifies that
542 considering the spatial component inherent to animal movement (spatial traits) is
543 relevant when assessing animals' vulnerability to human-altered habitats. We
544 demonstrate that integrating individual-based correlated random walk models and
545 demographic population models allows for the identification of the key biological traits
546 governing populations' viability. As suggested by Gascoigne et al. (2009), we found
547 that increasing mate-finding efficiency has a higher potential to avoid population
548 extinctions in human-altered habitats than adaptations that lead to the aggregation of
549 individuals. This information points to vulnerability of species that base their
550 reproductive strategies on philopatric behaviours. Moreover, our modelling approach
551 could inform managing strategies of endangered species to, for example, assess and
552 increase the permeability of linear barriers that may cause isolation between sexes.
553 Further research is needed to explore the consequences of landscape changes not just for
554 population demography, but also for the evolutionary potential. Impacts on population
555 connectivity reduce gene flow on a landscape scale and promote local endogamy
556 (Méndez et al. 2014). Similarly, evolutionary strategies such as sperm-storage, that
557 facilitate reproduction when mate encounters are scarce, may help to support
558 populations persistence but also promote local endogamy. Then, the study of trade-offs
559 derived of the maintenance of reproduction in altered habitats turns out a relevant task
560 for individual-based models that consider specific traits of species in their spatial
561 context.

562 **6. SOFTWARE AVAILABILITY**

563 Model name: STEPLAND.

564 Developed by: Eva Graciá (egracia@umh.es), Ángel Luis García-García
565 (angelluis78@gmail.com).

566 Year available: 2019.

567 Availability: The full code of STEPLAND, its parameterisation and the main results
568 files are available at [XXX](#).

569 Cost: Free and open source.

570 Language: Python.

571

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585

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Appendix A. Overview, Design concepts, and Details protocol of the individual-based model used in this study

STEPLAND: a spatially explicit individual-based model to assess population viability

Purpose

The main objective of STEPLAND is to investigate the effects of biological traits, population characteristics (e.g., adult survival) and the habitat landscape, on population viability over a timespan of some hundreds of years. The model was implemented into Python 2.7 and its code will be available in [XX](#) repository.

Entities, attributes and spatial scales

STEPLAND comprises two different entities: landscapes and individuals. In this study we focus on individuals of the tortoise species *Testudo graeca*, and landscapes comprise an area of 3 km × 3 km composed of a 10 m × 10 m grid of cells (although other areas and grids are also possible). Each cell is characterised by its position (x and y coordinates) and its habitat category:

H1: intensive land use

H2: traditional agriculture land

H3: natural flat areas

H4: natural areas on slopes

H5: non-permeable infrastructures

These categories were taken from a previous study that investigated the effects of habitat loss and fragmentation on tortoise movements (Anadón et al. 2012). Landscapes are enclosed by a non-permeable border and host closed and isolated populations (Fig. A1).

Tortoises are characterised by the following attributes: gender, age, time for stored sperm caducity, their actual location and their past locations. Additionally, the

nine parameters AU1, AU2, dHB, rHB, H1W, H2W, H3W, H4W and H5W govern their movement and the location of their focal-point attractor. Except for H5W, these parameters were taken from the movement analysis of Anadón et al. (2012). See the description of the movement process for further information.

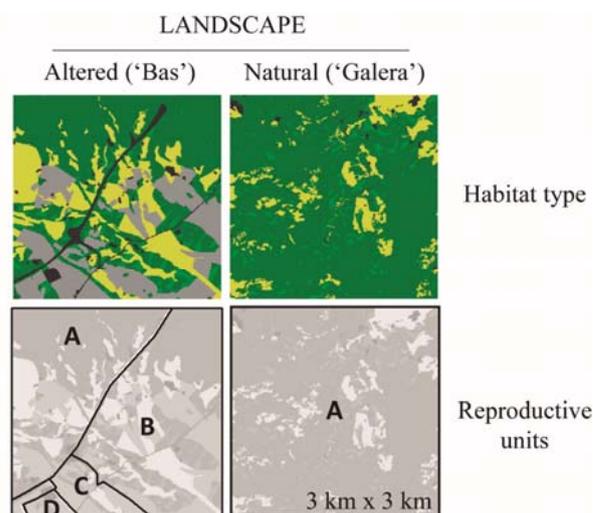


Figure A1. Landscapes used in STEPLAND. Habitat categories include: non-permeable infrastructures (black), intensive land use (grey), traditional agriculture lands (yellow), natural flat areas (light green) and natural areas on slopes (dark green). Grey landscapes show the barrier effects of landscape features for the mating submodel. The natural landscape lacks internal barriers, but roads and intensive agriculture divide the human-altered landscape.

Input, initialisation and output

Inputs include the landscape, the initial population and model parameterisation; they are all included in a SQL database that is directly read by the model. Initially, $N_0 = 45, 90$ and 180 tortoises are randomly distributed within the landscape, which represents the medium and low densities that are typically found in the natural species populations in SE Spain (Anadón et al. 2009). Note that the initial populations (individuals and their locations) were the same in all the simulation scenarios that started with the same N_0 . To avoid biases caused by extreme spacing of the initial locations of individuals, we tested 15 different sets of locations and selected for our study a set with medium mean minimum Euclidean distances between females and males (Table A1). Each parameterisation was then simulated 64 times in a given landscape using the same initial population.

Table A1. Test for biases in extinction probabilities after 200 years due to individuals' initial locations. We tested 15 sets of locations (5 per initial density) in the natural landscape with a standard parameterisation (Appendix C). Extinction rates were more variable for $N_0=45$ sets. For our study, three sets of locations with mean minimum Euclidean distances between males and females close to the obtained means from the tested simulations were selected.

Initial density	Mean extinction probability \pm SD	Mean min. fem-male distance \pm SD (m) in the tested sets of the initial locations	Mean min. fem-male distance \pm SD in the selected set of initial locations
$N_0=45$	0.51 \pm 0.18	673.5 \pm 303.4	627.5 \pm 174.35
$N_0=90$	0.06 \pm 0.07	422.5 \pm 142.2	417.4 \pm 150.62
$N_0=180$	0 \pm 0	295.9 \pm 38.8	338.6 \pm 169.19

The different age classes of the initial population follow a stable age distribution predicted by an age-stage structured deterministic matrix population model (Caswell, 2001) that was derived using the POPBIO package in the R software (Stubben & Milligan, 2007; R Core Team, 2014; R scripts are shown in Appendix B). The demographic parameters of the matrix model are the same as the demographic parameters of the simulation model, but the growth rate predicted by the deterministic matrix model does not consider demographic stochasticity and mate-finding Allee effects (Appendix B). The complete model parameterisation is shown in Appendix C.

Data output consists of CSV files that comprise the surviving tortoises of the population and their attributes (location in the landscape, gender and age) for every 10 years during the simulated years. Own scripts, developed in R (R Core Team 2016) and Python 2.7, allow these massive outputs to be processed. For operational reasons, the simulation stops if the total number of tortoises in the landscape exceeds 4,500.

Temporal scales, process overview and scheduling

In STEPLAND, each time step represents 1 day, while outputs are summarised for 10-year periods. All simulations were run for 200 years (corresponding to approximately eight tortoise generations).

Tortoises are subject to the basic processes movement, reproduction, mortality and aging. They can move up to 4 times a day according to their attributes and

movement parameters, the time of the year and the habitat category of surrounding cells (as modelled and parameterised by Anadón et al. 2012). Adult females can reproduce up to 3 times/year, as evidenced by own data and previous studies that have addressed the reproduction of this species (Díaz-Paniagua et al. 1996, 1997). In our model, the nutritional status of tortoises does not affect reproduction. However, spatial effects may hinder mating, including a too large distances between females and their nearest adult males, or presence of non-permeable barriers between them. Annual mortality rates are implemented through a single event of mortality at the end of the year. The age of surviving tortoises is then updated, and their movement attributes may also be updated (i.e., in some scenarios the last location of the year may be used as their focal point attractor; see movement submodel for further information). Figure A2 provides a general overview of the model and the following paragraphs describe the main processes in more detail.

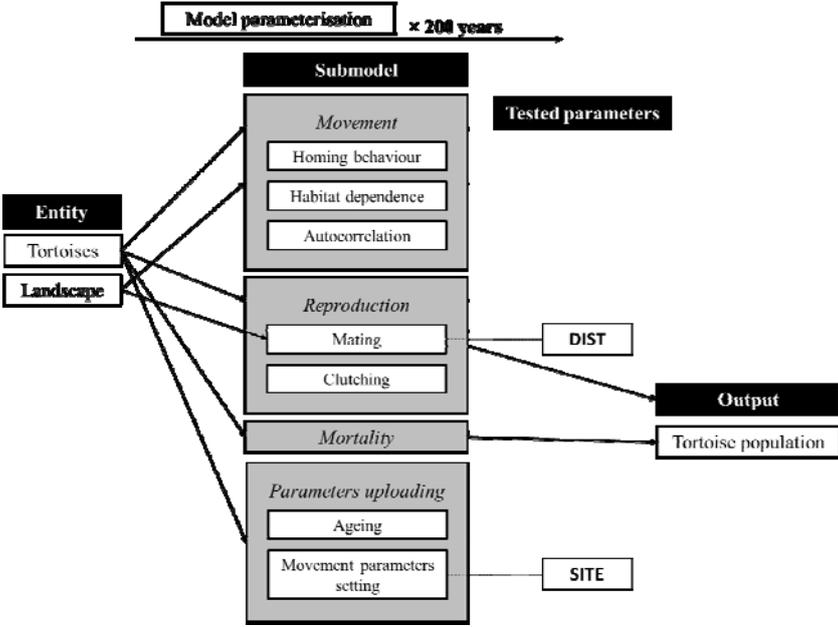


Figure A2. Main processes implemented in STEPLAND. Inputs are the landscape and the initial tortoise population. During the simulation, the individuals are subject to the basic processes: movement, reproduction, mortality and aging; and may be subject to parameter updates (e.g., variations in the location of their focal point attractor). In this study, we simulated population dynamics for 200 years and evaluated the sensitivity of extinction rates to variations in the SITE and DIST parameters.

Movement

STEPLAND includes the movement model developed and parameterised by Anadón et al. (2012). They used individual-based modelling and pattern-oriented modelling to parameterise the movement model based on radio-tracking data. One main result of Anadón et al. (2012) is that land-use intensification in SE Spain had a strong impact on spur-thighed tortoises' movement and behaviour. While tortoises showed high site fidelity and slight individual variability in natural landscapes, movement and behaviour varied strongly among individuals in human-altered landscapes. Particularly for females, a wide range of movement patterns was found, which ranged from strong home behaviour to unbounded movements. Anadón et al. (2012) determined a total of 5,627 individual parameterisations of annual movements that were compatible with the radio-tracking data (Table A2). Females in human-altered landscapes formed the largest set of individual movement parameterisations (Table A3).

Table A2. Subset as an example of the parameterisations assigned to individuals for their movements as determined by Anadón et al. (2012). In our simulations, these parameterisations were randomly assigned to the initial individuals and to the newborns (depending on sex and landscape type).

Sex and habitat type	AU1	AU2	dHB	rHB	Habitat-dependent weights for cells				
					H1W	H2W	H3W	H4W	H5W
male_natural	0.05	0.7	50	25	0.1	5	5	8	0
male_natural	0.05	0.65	75	3	0.1	20	11	3	0
male_natural	0.75	0.75	25	10	0.1	15	2	13	0
female_natural	0.1	0.25	50	7	0.1	11	17	10	0
female_natural	0.05	0.3	50	10	0.1	5	2	7	0
female_natural	0.15	0.9	25	10	0.1	17	5	13	0
male_altered	0.7	0.85	75	3	0.1	5	8	18	0
male_altered	0.65	0.65	100	10	0.1	5	15	6	0
male_altered	0.25	0.5	75	3	0.1	4	13	10	0
female_altered	0.55	0.85	175	60	0.1	9	12	2	0
female_altered	0.25	0.65	10000	30	0.1	8	16	1	0
female_altered	0.25	0.85	500	4	0.1	15	10	3	0

AU1: autocorrelation between consecutive movement steps; AU2: autocorrelation between cell steps; dHB: distance threshold below which no homing behaviour occurs; rHB: temporal delay (in days) of homing behaviour as dHB was exceeded; H1W: weight for cells with intensive land use; H2W: weight for cells with traditional agriculture; H3W: natural flat areas; H4W: natural areas on slopes; H5W: non-permeable infrastructures.

Table A2. Number of individual parameterisations for the movement process, as determined by Anadón et al. (2012).

	Natural landscape	Human-altered landscape
Males	139	51
Females	155	5,282

Tortoises older than the age threshold given by the parameter `age_first_mov`, can change their location up to 4 times/day (i.e., four movement steps; Fig. A3). The active period of one day is divided into four 2- to 3-hour periods, and each of these periods a random trial is made with the PMOV parameter being the probability of moving during a period. PMOV is dependent of the month and tortoise gender, for example, tortoises are inactive during their hibernation and aestivation periods (Fig. A4a). If the PMOV trial indicated movement, DMOV is the discrete probability of moving s cell steps in each movement step (“cell-to-cell movements”; Fig. A3). DMOV varies between adult males and females (Fig. A4b). It was also assumed that subadults have a reduced movement capability than adults. To implement this, the number of cell-to-cell steps in DMOV was assumed to increase gradually with age until the reproductive age:

$$DMOV_{\text{subadult}} = \text{round}(DMOV_{\text{adult}} \times (\text{subadult's age}) / (\text{reproductive age})) \quad (1)$$

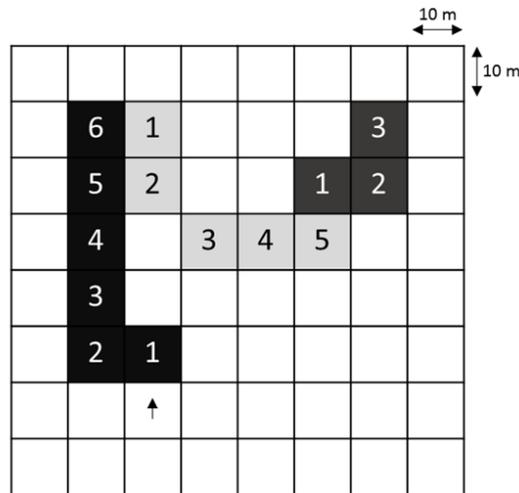


Figure A3. Example of the simulated movement of a tortoise during a given day. Starting from the arrow, the tortoise takes three movement steps during the day (represented by different colours), with six, five and three cell-to-cell steps each (movement directions are represented by numbers).

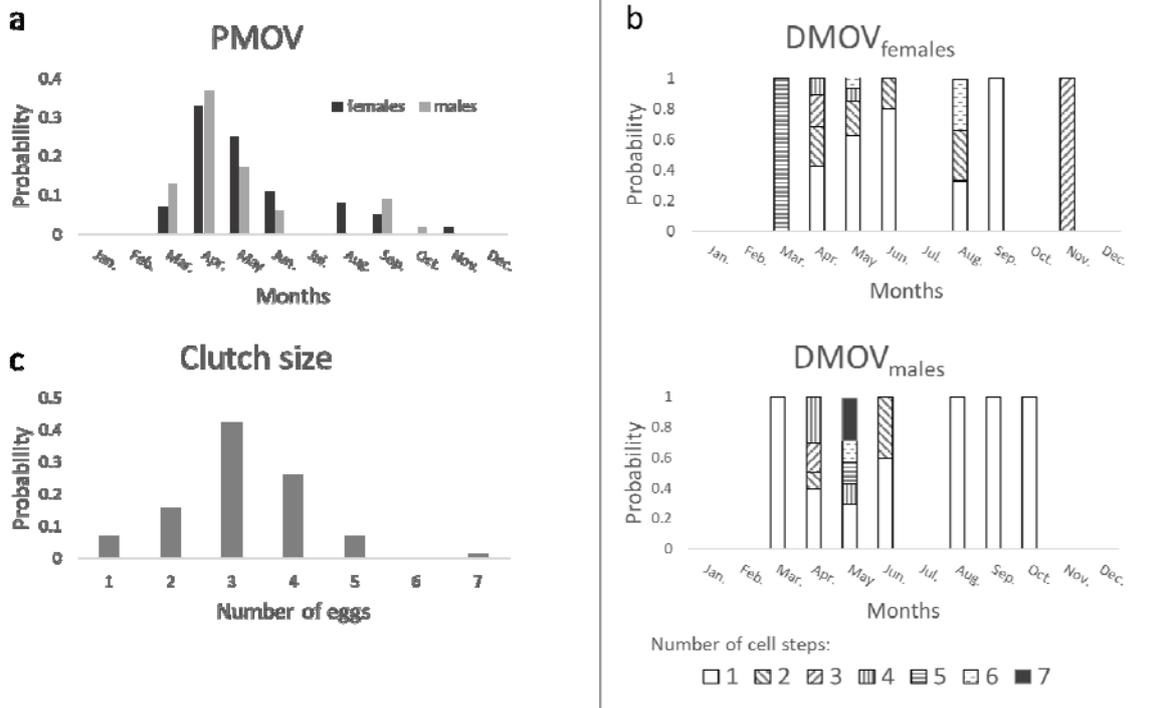


Figure A4. Discrete probability distributions of the parameters PMOV (a); DMOV of females and males (b) and clutch_size (c).

In each cell-to-cell movement step, three submodels interact in the selection of one of the eight neighbouring cells surrounding the tortoise by determining their associated weights, which are then multiplied to calculate its final probability to be occupied:

- i) *Autocorrelation*: describes the tendency of keeping the previous direction. The eight cells surrounding the present location are numbered from $i = 1, \dots, 8$, where the index $i = 1$ indicates the cell-by-cell step following exactly the previous direction. Then $i = 2, \dots, 8$ are numbered clockwise. The weights d_i of the neighbouring cells with indices $i = 1, \dots, 5$ (movement to the right) are calculated as:

$$d_i = \max[0, (1.5 + (0.5 - i) \times AU) / (1.5 - 0.5 \times AU)] \quad (2)$$

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attractor has a probability of $b_j = 1$ of being occupied, while the remaining seven cells have probability of $b_i = 0$. In intermediate situations in which $dHB < D < 2dHB$, the bias of b_j increases from 1/8 proportionally with distance D up to $2*dHB$ with the formula:

$$b_j = (D-dHB)/(dHB) \text{ and } b_i = (1 - b_j)/7 \text{ for } i \neq j \quad (3)$$

In order to enhance the model's biological realism, a temporal delay was considered so that homing behaviour came into force only after exceeding the distance threshold dHB from the focal point. This allows tortoises to temporarily leave their most regularly used areas to meet specific needs, such as egg-laying in females or mate-searching in males (Díaz-Paniagua et al. 1995, Pérez et al. 2002). The rHB parameter is the temporal delay (in days) of homing behaviour as dHB was exceeded (R , in days) (Fig. A6).

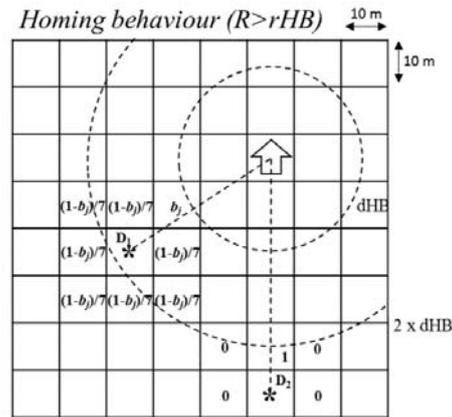


Figure A6. Schematic representation of the homing behaviour submodel. Asterisks indicate the location of tortoises, with distances D_1 and D_2 to the focal point attractor. NB: $dHB < D_1 < 2dHB$ and $D_2 > 2dHB$.

STEPLAND allows to leave the focal point attractors of the tortoises during their entire lifespan in the same location (representing philopatry; parameter SITE = Yes); or can, alternatively, be reassigned to the individuals' last position at the end of each year (allowing individuals 'wandering; parameter SITE = No) (Table 1; Appendix C).

- iii) *Habitat dependence*: in relation to habitat quality, the eight neighbouring cells receive habitat-dependent weights to be occupied through parameters H1W (intensive land use), H2W (traditional agriculture), H3W (natural flat areas), H4W (natural areas on slopes) and H5W (non-permeable infrastructures). The weights of the eight cells are subsequently normalised to add up to 1 (Fig. A7).

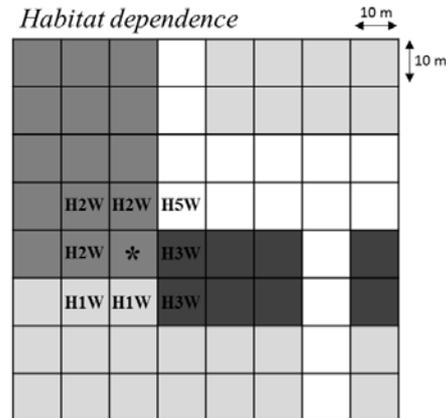


Figure A7. Schematic representation of the habitat dependence submodel. Cell colours represent habitat categories.

Reproduction

Only adult individuals (aged ≥ 7 years for males and ≥ 10 years for females) reproduce (Rodriguez-Caro et al. 2013). Sperm storage, a vital trait of spur-thighed tortoises (Roques et al. 2004), was modelled as a temporal dissociation between mating and clutching.

- iv) *Mating*: once a year at the beginning of spring, mature females localise mature males in their surroundings (both with ages over `female_repro_age` and `male_repro_age` in Appendix C). Given the spatial constraints to find mates, mating was assumed to occur only if the Euclidean distance between the female and the closest male was (at the time scheduled for mating) below a minimal distance given by the DIST parameter. Moreover, mating occurred only if there was no barrier between males and females (e.g. main roads or dense human infrastructures) (Fig. A1). Sperm can be viable in the oviducts of females of the

species *T. graeca* for as long as 3-4 years (Cutuli et al. 2013). Therefore, we modelled sperm-caducity in a simple way: females that mated can be, for the same probability, reproductive for the following 3 years (represented by the sperm_cad parameter). If females find mates, then the stored sperm-caducity timer is reset to zero; otherwise, 1 is added to the sperm-caducity timer. Females do not reproduce if their sperm-caducity timer reaches 3 and if they do not find a male during the next breeding season.

- v) *Clutching*: the repro_female parameter is the probability that females with available sperm will be gravid when clutching can take place in spring (Díaz-Paniagua et al. 1996, 1997; unpublished data). The number of eggs that gravid females lay is determined from the discrete probability distribution clutch_size (Fig. A4c). Clutch viability is later simulated by applying mortality rates for each egg (Díaz-Paniagua et al. 1997, Díaz-Paniagua et al. 2006; see the next paragraph and Appendix C for further details regarding model parameterisation).

Mortality

A single mortality event occurs at the end of each simulated year. Annual survival rates vary among age classes, including eggs (S_0), immature individuals ($S_{\text{immatures}}$; aged 1-3), subadults ($S_{\text{subadults}}$; aged 4-6), and adults (S_{adults} ; aged ≥ 7) (Díaz-Paniagua et al. 2001, 2002, Sanz-Aguilar et al. 2011). Eggs are identified as individuals whose age equals 0, while age cuttings apply (subadult_age, female_adult_age and male_adult_age) for the transition among the remaining classes (Table C1 in Appendix C1). The individuals (and their attributes) that died disappear from the population.

Parameters uploading

- vi) *Ageing*: the age of each living individual is increased at the end of the year by one.
- vii) *Temporal changes in movement characteristics*: in our model, the individuals may maintain the same focal point attractor for their whole lifetime (which emulates philopatry around birthplaces) or they may change it annually to their last location in every year (which allows wandering of individuals). At the beginning of the simulation, the parameterisations of the tortoises related with

movement (i.e., the parameter set AU1, AU2, dHB, rHB, H1W, H2W, H3W, H4W and H5W) are randomly assigned to the newborns from parameterisations determined in Anadon et al. (2012), according to the sex of the individual and landscape. The movement parameterisation is maintained for the whole life of the tortoise, thus simulating “individual personalities” (Golubović et al. 2014, 2017; see Appendix C for further details regarding model parameterisation).

Design concepts

Basic principles: the model assumes that: i) tortoises maintain age-class transitions and survival rates in human-altered landscapes; ii) habitat loss and fragmentation cause changes in their movement and behaviour (as reported by Anadón et al. 2012); iii) non-permeable barriers hinder tortoise mating.

Emergence: simulations may result in different population dynamics due to variations in tortoises’ reproductive success.

Adaptation: tortoises face fragmentation by modifying their movement decisions. They avoid intensive land uses and non-permeable infrastructures.

Objective: tortoises do not have any particular objective implemented into simulations but, as previously mentioned, they modify their movement decisions according to habitat characteristics.

Sensing: tortoises are able to detect habitat loss and fragmentation in landscapes of $3 \text{ km} \times 3 \text{ km}$ (i.e., natural vs. human-altered landscapes). They also recognise their surrounding habitat in $30 \text{ m} \times 30 \text{ m}$ (the eight adjacent grid cells).

Interaction: tortoises are able to mate if they are separated by a distance shorter than that given by the DIST parameter and if there are no geographical barriers between them.

Learning: tortoises do not change their behaviour according to their experience.

Prediction: tortoises do not have the capacity to predict future conditions.

Stochasticity: tortoises’ initial location, and assigning movement parameters to them, are purely stochastic processes. The remaining “reproduction”, “movement”,

“mortality” processes become semi-stochastic by implementing discrete probability distributions.

Collectives: there are no defined collectives in the model.

Observation: output serves to calculate the number of living individuals of a given population at a given time and, consequently, population viability over time.

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