1 **Linking animal migration and ecosystem processes:**

2 **data-driven simulation of propagule dispersal by migratory herbivores**

3 **Marius Somveille[1,2]*, Diego Ellis-Soto[3,4]**

4 [1] Department of Biology, Colorado State University, Fort Collins, CO 80523 USA

5 [2] Centre for Biodiversity and Environment Research, Department of Genetics, Evolution and

6 Environment, University College London, London WC1E 6BT, UK

7 [3] Department of Ecology and Evolutionary Biology, Yale University, New Haven,

8 Connecticut, USA

9 [4] Center for Biodiversity and Global Change, Yale University, New Haven, CT, USA

10 * marius@somveille.com

11 **Authors' ORCID**

12 MS: 0000-0002-6868-5080

13 DES: 0000-0003-4766-021X

Abstract:

1. Animal migration is a key process underlying active subsidies and species dispersal over long distances, which affects the connectivity and functioning of ecosystems. Despite much research describing patterns of where animals migrate, we still lack a framework for quantifying and predicting how animal migration affects ecosystem processes.

2. In this study, we aim to integrate animal movement behavior and ecosystem functioning by developing a predictive modeling framework that can inform ecosystem management and conservation. Our framework models individual-level migration trajectories between populations' seasonal ranges as well as the resulting dispersal and fate of propagules carried by the migratory animals, and it can be calibrated using empirical data at every step of the modeling process.

3. As a case study, we applied our framework to model the spread of guava seeds, *Psidium guajava*, by a population of migratory Galapagos tortoises, *Chelonoidis porteri*, across Santa Cruz Island. Galapagos tortoises are large herbivores that transport seeds and nutrients across the island, while Guava is one of the most problematic invasive species in the Galapagos archipelago.

4. Our model is able to predict the pattern of spread of guava seeds alongside tortoises' downslope migration range, and it identified areas most likely to see germination success and establishment. Our results show that Galapagos tortoises' seed dispersal may particularly contribute to guava range expansion on Santa Cruz Island, due to both long gut retention time and tortoise's long-distance migration across vegetation zones. In particular, we predict that tortoises are dispersing a significant amount of guava seeds into the Galapagos National Park, which has important consequences for the native flora.

5. The flexibility and modularity of our framework allows for the integration of multiple data sources. It also allows for a wide range of applications to investigate how migratory

39   animals affect ecosystem processes, including propagule dispersal but also other

40   processes such as nutrient transport across ecosystems. Our framework is also a valuable

41   tool for predicting how animal-mediated propagule dispersal can be affected by

42   environmental change. These different applications can have important conservation

43   implications for the management of ecosystems that include migratory animals.

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45   **Key words:** seed dispersal, ecosystem process, animal migration, migratory connectivity,

46   Galapagos tortoises

1.0   Introduction

Ecosystems are connected through flows of energy and materials transported passively by the abiotic environment or actively through the transport of individuals, gametes or spores (Loreau *et al.* 2003). The movement of animals is a key process shaping active subsidies and dispersal of plants, which affects the functioning and connectivity of ecosystems (Côrtes & Uriarte 2013; Earl & Zollner 2017; Schmitz *et al.* 2018; Subalusky & Post 2018; Ellis-Soto *et al.* 2020). In particular, animal migration – the regular, directional movement of animals between specific destinations – involves billions of animals across the planet (Hu *et al.* 2016; Dokter *et al.* 2018) and provides important ecosystem services (Bauer & Hoye 2014). However, despite the ecological importance of the migration phenomenon and the research efforts to describe patterns of where animals migrate, we still lack a predictive framework that we can use to quantify how migratory animals impact ecosystem functioning.

One of the main ecosystem services provided by migratory animals is propagule dispersal, and particularly seeds (Bauer & Hoye 2014). More than half of all plant species are dispersed by animals (Aslan *et al.* 2013), and such animal-mediated seed dispersal influences plant species survival and range expansion into new environments (Nathan & Muller-Landau 2000; Kendrick *et al.* 2012; Travis *et al.* 2013). The movement ecology of seeds has thus been highlighted as a key knowledge gap to improve our understanding of plant distribution (Beckman *et al.* 2019). Quantifying and predicting the role of animals in seed dispersal is also particularly relevant given that the scale of animal movements is declining globally in response to human activities (Tucker *et al.* 2021), which has important implications for plant-animal interactions (Neuschulz *et al.* 2016). Animal migrations, in particular, are disappearing at alarming rates (Wilcove & Wikelski 2008) with unknown, but likely significant, consequences on ecosystem functioning. For instance, the loss of Pleistocene megafauna and their long

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71 ranging movements is thought to have significantly reduced seed dispersal across large spatial

72 scales (Malhi *et al.* 2016; Pires *et al.* 2018).

73   Dispersal kernels, which allow modeling how far seeds can be dispersed, have been

74 usually employed to understand dispersal of plant species (Nathan 2006; Nathan *et al.* 2012;

75 Bullock *et al.* 2017; Pires *et al.* 2018). For animal-mediated seed dispersal, however, it is

76 important to take into account intra-specific variation in the seed dispersal ability of animals

77 (Zwolak 2018). In addition, modeling seed dispersal must ideally be spatially-explicit in order

78 to account for the context dependency of where seeds are deposited and the probability of

79 successful germination and establishment (Nathan & Muller-Landau 2000). Developments in

80 tracking technologies allow quantification of the movement of animals at fine spatio-temporal

81 scales for long periods of time (Kays *et al.* 2015). This opens up opportunities to study animal

82 movement and understand its underlying environmental and internal drivers (Nathan *et al.*

83 2008; Hawkes *et al.* 2011; Jesmer *et al.* 2018). Recent years have seen an increase in studies

84 coupling GPS tracking of animals with ecosystem processes, especially seed dispersal

85 (Kleyheeg *et al.* 2017, 2019; Oleksy *et al.* 2017; van Toor *et al.* 2019). This approach provides

86 a spatially explicit, individual-based understanding of seed dispersal by migratory animals that

87 integrates animal movement, seeds dispersed and gut retention times. However, previous

88 studies have only modeled dispersal from a single location, which limits the potential

89 applications of such approach. In addition, these studies do not use empirical data explicitly to

90 model the fate of the dispersed seeds once released in the environment.

91   Here we propose a novel modeling framework that combines simulation and empirical

92 data from a variety of sources to model the spread of seeds by migratory herbivores. Our

93 framework allows to model individual-level migration trajectories between the seasonal

94 distributions of populations together with the resulting dispersal and fate of seeds carried by the

95 migratory animals, and it allows using empirical data to calibrate every steps of the modeling

96   process. This approach aims to quantitatively harmonize behavioral ecology and ecosystem

97   process and make quantitative predictions that could inform ecosystem management and

98   conservation. As a case study, we applied our framework to model the spread of guava seeds,

99   *Psidium guajava* (Linnaeus), by a population of migratory Galapagos tortoises, *Chelonoidis*

100 *porteri* (Rothschild) (IUCN critically endangered), across Santa Cruz Island. Galapagos

101 tortoises are the largest terrestrial ectotherms worldwide and are considered ecosystem

102 engineers through the transport of seeds and nutrients, as well as herbivory and trampling

103 (Gibbs *et al.* 2010; Blake *et al.* 2012; Ellis-Soto 2020), while Guava is one of the most

104 problematic invasive species in the Galapagos archipelago, having been introduced in the late

105 19th century (Walsh *et al.* 2008).

106   Santa Cruz Island contains the highest human population on the Galapagos. The island

107 harbors more introduced plant species that native species (Guézou *et al.* 2010), which threatens

108 endemic biodiversity. On Santa Cruz Island, presence of invasive guava has modified native

109 plant community and ecosystems, especially so in the humid highlands (Guézou *et al.* 2010),

110 and several ongoing eradication initiatives have so far proven unsuccessful (Gardener *et al.*

111 2010). Guava is heavily consumed by Galapagos tortoises (Blake *et al.* 2015), which perform

112 seasonal migrations across the elevational gradient of the island, and disperse guava seeds

113 throughout their range (Blake *et al.* 2012, 2013; Ellis-Soto *et al.* 2017). Most of the island's

114 surface is located within the Galapagos National Park (GNP) and surrounds heavily degraded

115 agricultural land where invasive species such as guava are widespread (Trueman *et al.* 2014;

116 Benitez-Capistros *et al.* 2019). The permeability of national park boundary to agricultural lands

117 means that animals like tortoises can regularly cross from the park into farm land, where they

118 consume introduced plants including fruits, before returning to the park (Benitez-Capistros *et*

119 *al.* 2018). Taking advantage of a long-term study on Galapagos tortoises (Blake *et al.* 2012,

120 2013, 2015; Yackulic *et al.* 2016; Benitez-Capistros *et al.* 2019, Sadeghayobi *et al.* 2011), we

121   use data on tortoise ecology, migratory behavior, seed dispersal ability, diet preference and gut

122   retention times in order to calibrate our modeling framework and simulate how tortoises spread

123   guava across Santa Cruz island. Specifically, we aim to (i) simulate realistic migration

124   trajectories for tortoises across the population's geographical range, (ii) model how guava seeds

125   are spread by migrating tortoises, and (iii) use empirical data to calibrate the model and validate

126   the seed dispersal predictions.

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128   **2.0   Material and Methods**

129   **2.1   Empirical data**

130   **2.1.1   Study site and habitat**

131   We obtained a landcover map for Santa Cruz Island, Galapagos, from (Rivas-Torres *et al.*

132   2018a) and shapefiles of the Galapagos National Park and agricultural land from the 2014

133   census conducted by the Ecuadorian Ministry of Agriculture (CGREG 2015). This allowed us

134   to estimate the proportion of different habitats where invasive guava is deposited through seed

135   dispersal by *C. porteri* as well as the ratio of seed deposition in national park and agricultural

136   land to better understand the context dependency of these events. To estimate available

137   resources for tortoises, we used the Normalized Difference Vegetation Index (NDVI), a remote-

138   sensing measure of greenness that correlates well with primary productivity, and which has

139   been shown to be an important drivers of tortoises annual migration (Blake *et al.* 2013; Yackulic

140   *et al.* 2016; Bastille-Rousseau *et al.* 2019). To estimate the spatial distribution of guava, we

141   made use of a recently published land cover classification of the Galapagos which provides the

142   distribution of guava patches at very high resolution in Santa Cruz Island (Laso *et al.* 2019).

143   To estimate whether guava seeds can germinate and become adult reproductive trees,

144   we made use of a species distribution model (SDM) for guava previously published (Ellis-Soto

145   *et al.* 2017). This model relates environmental predictors (i.e., temperature and precipitation

146   long term averages and seasonality commonly referred to as bioclimatic variables; (Hijmans *et*

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147   *al.* 2005)) to georeferenced guava locations and indicates how suitable a given location in Santa

148   Cruz is for this plant species. This model was then overlaid on adult guava trees on Santa Cruz

149   to understand at which suitability score guava plants can germinate, survive and establish under

150   current and future climatic conditions.

151   **2.1.2   Tortoise migratory movements**

152   We used tracking data of 9 tagged adult male Galapagos giant tortoises for which hourly

153   locations were recorded between 2013 and 2018 (attachment procedures and GPS sampling

154   regimes are described in Blake *et al.* 2013). To identify the starting and end locations of

155   individual downslope migrations between 2013 and 2018, we made use of the locator() function

156   from the graphics package in R on plots representing individual tortoise net square displacement

157   (Singh *et al.* 2016), which provided us with 16,464 GPS tortoise locations. We removed

158   empirical migratory tracks that were too sinuous as their characteristics generate convergence

159   issues for the model described below. We retained 19 downslope migration trajectories from 5

160   individuals (i.e. individuals were tracked for several years; Fig. S1), sampling each track to one

161   point per day (i.e., taking the first GPS point when multiple points where present for a single

162   day).

163   **2.1.3   Tortoise diet and gut retention**

164   Sampling of 222 tortoise dung piles revealed that guava is the most common dispersed plant

165   species by *C. porteri* with an average of 624 seeds per dung pile (Ellis-Soto *et al.* 2017). Feeding

166   trial experiments with pseudo seeds identified the gut retention time of *C. porteri* during the

167   period of downslope migration (μ = 7.5, σ = 2.16 in days, respectively) (Sadeghayobi *et al.*

168   2011), which applies to guava seeds. In addition, *ex situ* germination trials suggests that tortoise

169   ingestion and dung does not influence germination success of guava seeds neither positively

170   nor negatively (Blake *et al.* 2012).

171   **2.2   Modeling framework**

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2.2.1   Model overview

We simulated the migratory movement of tortoises from the highlands to the lowlands of Santa Cruz Island using a two-step modeling process: first, we simulated the migratory connectivity of the population (i.e. links between seasonally-occupied sites based on individual tortoises migratory movements), and second, we simulated the trajectory of migrating individuals (Fig. 1).

2.2.2   Simulating migratory connectivity

We simulated migratory connectivity between the seasonal distributions of tortoises, i.e., in the highlands and in the lowlands. To map areas seasonally utilized by tortoises, we calculated 95 percentile utilization distribution (UD) (Fieberg & Kochanny 2005) for each of the nine tortoises (see 2.1.2) using the adehabitatHR package (Calenge 2006). We then drew a geometric convex hull around these UD's to obtain a population-level highland and lowland range. Highland and lowland areas were converted into presences and absences on a grid of hexagons with equal area ($\sim$1.18 km^2) and shape covering Santa Cruz Island.

To simulate migratory connectivity between the seasonal distributions of tortoises, we used a model called the Optimal Redistribution Simulator (ORSIM), which was shown to capture well avian migratory connectivity patterns (Somveille *et al.* in review). This model is based on energy optimization, and captures two processes: minimizing energetic costs associated with relocating between seasonal grounds, and intra-specific competition for access to energy supply. ORSIM uses a solution to the Monge-Kantorovich transportation problem (Hitchcock 1941; Rachev 1984) from linear optimization, which can be formalized linear programming as follows.

Let $H = \left\{ \left(h_1, k_{h_1}\right), \ldots, \left(h_m, k_{h_m}\right)\right\}$ be the distribution of energy available during the season spent in the highland, where h_i is highland site i and k_{h_i} is the weight of this site, which corresponds to the energy available at this site; and $L = \left\{ \left(l_1, k_{l_1}\right), \ldots, \left(l_n, k_{l_n}\right)\right\}$ be the

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197 distribution of energy available during the season spent in the lowland, with n lowland sites,

198 where l_j is lowland site j and k_{l_j} is the weight of this site, which corresponds to its energy

199 supply. We want to find a total flow $F = [f_{ij}]$, with f_{ij} the flow of energy between h_i and l_j,

200 that minimizes the overall cost

201
$$C(H, L, F) = \sum_{i=1}^{m} \sum_{j=1}^{n} c_{ij} f_{ij}$$

202 where c_{ij} is the energetic cost associated with relocating between sites h_i and l_j. This function

203 is subject to the following constraints:

204
$$f_{ij} \geq 0 \qquad 1 \leq i \leq m, \quad 1 \leq j \leq n \tag{1}$$

205
$$\sum_{j=1}^{n} f_{ij} \leq k_{h_i} \qquad 1 \leq i \leq m \tag{2}$$

206
$$\sum_{i=1}^{m} f_{ij} \leq k_{l_j} \qquad 1 \leq j \leq n \tag{3}$$

207
$$\sum_{i=1}^{m} \sum_{j=1}^{n} f_{ij} = \min\left(\sum_{i=1}^{m} k_{h_i}, \sum_{j=1}^{n} k_{l_j}\right) \tag{4}$$

208 Constraint (1) allows energy to move from H to L and not vice versa. Constraint (2) limits the

209 amount of energy that can move away from the highland sites in H and reflects the energy

210 demand of departing individuals. Constraint (3) limits the lowland sites in L to receive no

211 more energy than their energy supply. Finally, constraint (4) specifies that the total amount of

212 energy must be equal to either the total energy demand of highland sites or the total energy

213 supply of lowland sites, whichever one is the smallest, thus forcing to move the maximum

214 amount of energy possible.

215 This modeling framework assumes that energy is transferred between highland and

216 lowland sites via migrating tortoises, which are energetically equivalent, i.e., they all have the

217 same energetic needs and cost function, and the same competitive ability. Energy availability

218 across the highland and lowland distributions of tortoises was estimated using NDVI values

219 (see 2.1.1). We rescaled these NDVI values so that a total of 1000 migrating individuals were

220   generated by the model. For a complete description of ORSIM including more details about the

221   underlying assumptions see Somveille *et al*. (in revision).

222   A solution to the transportation problem from linear optimization is implemented in the

223   Earth Mover's Distance (EMD) algorithm (Rubner *et al.* 2000), which uses the transportation-

224   simplex method (Hillier & Lieberman 1990). To simulate migratory connectivity, we used the

225   FastEMD algorithm (Pele & Werman 2008, 2009), which is implemented in the Python wrapper

226   PyEMD. No distance threshold was used when running FastEMD.

227

2.2.3   Simulating migration trajectories

229   We simulated the explicit migration trajectories of migrating tortoises between their starting

230   point in the highland and the respective destinations in the lowland that are generated by the

231   migratory connectivity model (2.2.2). To do so, we used the empirical Random Trajectory

232   Generator (eRTG; Technitis *et al.* 2015) in the R environment. This algorithm generates the

233   movement between two endpoints with a fixed number of steps, which retains the geometric

234   characteristics of real observed trajectories based on tracking data (see detailed description in

235   Kleyheeg et al. 2019 and van Toor et al. 2019). The eRTG is similar to a biased correlated

236   random walk and can be best described as a mean-reverting Ornstein-Uhlenbeck process

237   (Smouse *et al.* 2010). The algorithm uses empirical tracking data as a template, and takes

238   empirical distributions of the following characteristics of animal movement: step length,

239   turning angles, their autocorrelation at a lag of one step, and the covariance of step length and

240   turning angle. We estimated the distributions of these movement characteristics using the

241   empirical tracking data on tortoises' downslope migratory movement described above.

242   Using the eRTG, we simulated the movement trajectories of the 1000 migrating

243   tortoises generated by the model of migratory connectivity. For each simulated migrating

244   tortoise, we used the following procedure: we ran eRTG 10 times with the shortest empirical

245   track (i.e., with the least number of movement daily steps); if the model converged, we selected

246   the resulting simulated trajectory, but if the model did not converge at least once, we then ran

247   eRTG 10 times with the second shortest empirical track; and we continued for all 19 empirical

248   tracks until the model converged. All models (i.e., for each simulated individual) ultimately

249   converged.

2.2.4   Simulating seed dispersal

251   To simulate the spread of guava seeds by migrating tortoises, we combined the simulated

252   migration trajectories with an empirically informed simulator of tortoises' consumption and

253   excretion of guava seeds. In our model, tortoises are assumed to engage in migratory movement

254   once a day, although we also ran a sensitivity analysis in which tortoises move twice and four

255   times a day. During the rest of the day when they are not migrating, tortoises are assumed to

256   stay put, eat and produce excrements. When not migrating, if a tortoise is located where guava

257   is present, we assumed that it eats guava. In addition, each tortoise has a probability of excreting

258   guava seeds based on gut retention time and the results of previous feeding events, determined

259   as:

$$P_g = \sum_{d=1}^{d_{max}} R(d, F_d)$$

261   with P_g: probability of excreting guava seeds ; d: number of days since a feeding event; F_d:

262   results of foraging event at d (i.e. whether or not guava was eaten); R: gut retention time

263   distribution, which was estimated empirically as a truncated normal distribution with $\mu = 7.5$

264   and $\sigma = 2.16$ (Sadeghayobi et $al.$ 2011); and d_{max} indicates a threshold, which was set to 20

265   days, above which guava seeds were considered to be no longer present in the gut. For each of

266   the 20 days preceding the start of the simulation, a tortoise was set to have eaten guava given

267   probability = 0.21, which corresponds to the proportion of the highland distribution that is

268   covered by the spatial distribution of guava.

269   To determine whether guava is excreted when a tortoise in not migrating, we sampled a

270   value between 0 (no guava excreted) and 1 (guava excreted) based on P_g. Then, if guava is

271   excreted, the number of guava seeds excreted during the excretion event is determined by

272   randomly sampling an empirically-estimated truncated normal distribution with $\mu = 1443$ and

273      $\sigma = 2057$ (Ellis-Soto *et al.* 2017). Using this methodology, we modeled where and how many

274   guava seeds are excreted along the migratory trajectory of each simulated migrating tortoises,

275   which we call 'seed rain'. We then overlaid the seed rain on the projection of the SDM that

276   predict germination success (i.e. binary value of successful versus non-successful germination,

277   based on Ellis-Soto *et al.* 2017; see section 2.1.1) in order to determine whether seeds are likely

278   to germinate or not (i.e. seed fate).

279   **2.3   Model validation**

280   To validate the seed dispersal prediction of our model, we used information of collected dung

281   piles containing guava seeds from Ellis-Soto et al. (2017) and added a few others

282   opportunistically collected since them. We obtained a total of 101 dung piles containing guava

283   across an elevation gradient from 28m to 419m. To better understand the spatial context in

284   which tortoise-dispersed guava seeds are deposited across our study area, we associated dung

285   pile occurrences with landcover classes of Santa Cruz Island from (Rivas-Torres *et al.* 2018b).

286   We focused specifically on an area locally known as 'La Reserva' to the south and southwest

287   of the island, which is the core distribution area of *C. porteri* (Ellis-Soto et al. 2017). We

288   extracted landcover information at the location of the observed and simulated dung piles

289   containing guava. We inspected whether the frequency density of dung piles containing guava

290   seeds across elevation as well as the distribution of dung piles containing guava seeds across

291   habitats, in particular in agricultural areas versus the Galapagos National Park, were similar for

292   simulated versus observed dung piles.

293   **2.4   Seed fate**

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294   Besides landcover, we made use of a previously estimated species distribution model (SDM)

295   for guava as a proxy of seed fate for seeds deposited across a gradient of climatic suitability.

296   We used the thresholded guava SDM from Ellis-Soto et al. (2017) to identify suitable habitat

297   for establishment of guava (seed dispersal efficiency). Briefly, the threshold was chosen based

298   on the minimum climatic suitability in which an actual guava plant was observed during a

299   vegetation survey across Santa Cruz Island.

300   **3.0   Results**

301   **3.1   Simulated and observed seed dispersal by migratory tortoises**

302   Our data-driven modeling framework was able to simulate the downslope migration of adult

303   male Galapagos tortoises between highland and lowland seasonal grounds on Santa Cruz Island

304   (Fig. 2a). The vast majority of trajectories and the overall migration pattern of the population

305   simulated by the model appear realistic. The resulting dispersal of guava seeds by migrating

306   tortoises spreads from the highland distribution to the lowland distribution, decreasing in

307   intensity as tortoises arrive closer to the lowlands (Fig. 2b). This pattern matches well empirical

308   data of dung piles containing guava seeds that were not used to parameterize the model (Fig. 3,

309   Fig. S2). The occurrences of observed and simulated dung piles containing guava peak at ca.

310   180m and 150m in elevation respectively, with a decay towards lower (Galapagos National

311   Park areas) and higher (Agricultural and privately owned areas) elevations (Fig. 3a,c).

312   However, simulated guava seeds appear to be somewhat higher than observed at lower

313   elevations, c.a. 80m, and lower than observed at high elevation, c.a. 400m (Fig. 3a,c, Fig. S2).

314   Both observed and simulated dung piles containing guava seeds are outside the current

315   elevational range of guava in Santa Cruz Island, potentially facilitating the expansion of this

316   invasive species (Fig. 3). The sensitivity analysis of the number of times tortoises engage in

317   migratory movement per day indicates that simulation results match empirical data less well

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318   when modeled tortoises were migrating, eating and execrating more often, in particular because

319   it increases unrealistically the long-distance dispersal of guava seeds to the lowland (Fig. S3).

320   **3.2   Estimating seed fate using landcover and species distribution models**

321   By combining the guava seed rain simulated from our model (Fig. 2b) with landcover

322   categories, we provide a spatial and ecological context in which guava seeds were deposited.

323   Simulated guava seeds were deposited in five different landcover classes, with a pattern of

324   deposition in these different landcover classes that largely matches the one from empirical data

325   (Figs. 3b,d and S4). Guava seeds were deposited mostly in agricultural areas but also reached

326   the Galapagos National Park (Fig. 3b,d). Some discrepancies exist between simulation and

327   empirical data, notably that the model predicts guava seeds to be deposited substantially more

328   than suggested from empirical data in areas occupied by invasive species but less than empirical

329   data suggests in evergreen forests and shrubs (Fig. S4). In addition, when applying our threshold

330   guava SDM mask, we were able to create a spatially explicit prediction of successful seed

331   dispersal for *C. porteri,* simulating guava seeds with the potential to germinate and establish

332   under current climatic conditions (Fig. S5).

333

334   **4.0   Discussion**

335   In this study, we developed a novel modeling framework for simulating the dispersal and fate

336   of propagules carried by migratory animals. Our model couples empirical data on animal

337   behavior related to feeding and movement as well as data on the geographical distribution and

338   climatic/habitat suitability of the dispersed species. Our model is data-driven, spatially explicit,

339   and it accounts for intraspecific variation in animal migratory movements. It provides a

340   quantitative framework for predicting long-distance propagule dispersal events by animals,

341   which have rarely been quantitatively predicted despite their ecological importance (Nathan &

342   Muller-Landau 2000). In particular, our model is able to predict the magnitude and direction

343   under which a migratory animal population disperses plant species into novel habitats, and

344   quantify how the seasonal migration of herbivores may be a major seed dispersal vector and

345   expand the distribution range of invasive plant species.

346   We applied our modeling framework to guava seed dispersal by Galapagos tortoises (*C.*

347   *porteri*) on Santa Cruz Island, which is a data-rich system with relevance for conservation. Our

348   model has good predictive ability for the pattern of spread of guava seeds by migrating tortoises

349   (Fig. 3), and can therefore be used for making predictions beyond the individuals and areas

350   where data were collected. We predicted clusters of heavy seed dispersal alongside tortoises'

351   downslope migration range (Fig. 2) and identified areas most likely to see germination success

352   and establishment (Fig. S5). We found that Galapagos tortoises' seed dispersal may particularly

353   contribute to guava downslope range expansion on Santa Cruz Island, due to both long gut

354   retention time and tortoise's long-distance migration across vegetation zones. In particular, we

355   predict that tortoises are dispersing a significant amount of guava seeds into the Galapagos

356   National Park, which has important consequences for the native flora as guava is an invasive

357   species that has already altered natural ecosystems on the Galapagos (Wiggins & Porter 1971;

358   Weber 2003) and is threatening local and endemic plant species (de Lourdes Torres & Mena

359   2018). Our results also highlight that the frequency at which behavior (i.e. migratory

360   movements, eating, excreting) is repeated during the migration season has an important role to

361   play in predicting long-distance dispersal events (Fig. S3), thus highlighting an avenue for

362   further research.

363   Our framework is flexible and modular as it allows for increasing complexity and the

364   integration of multiple data sources (Fig. 1). For example, if the number of seeds excreted and

365   germination success are unknown for a study system, this information could be omitted and the

366   model could simply predict the location of seed dispersal events across space. More information

367   on population distribution and individual-level movement, which is increasing exponentially

368 thanks to advances in citizen science and tracking technology (Kays *et al.* 2020), could be used

369 to calibrate more accurately the animal migration module (i.e. model components UD, ORSIM

370 and eRTG; Fig. 1). In addition, besides using SDMs, other proxies for seed fate such as

371 additional landcover information or microclimate based on fine scale topography could be

372 employed (Leempoel *et al.* 2015; Maclean *et al.* 2019; van Toor *et al.* 2019). *In situ* germination

373 trials of seeds along environmental gradients would provide greatest insights in the seed

374 dispersal efficiency of a migratory animal species, which is relevant as plant mortality depends

375 on environmental conditions and is highest when plants are seedlings (Terborgh *et al.* 2014).

376 Future studies could also include plant demography in addition to the movement ecology of

377 seeds in order to fully model the contribution of animal-mediated seed dispersal to the range

378 expansion of an invasive species (Beckman *et al.* 2019).

379 A research avenue for which our modeling framework could provide an important

380 contribution is investigating the impact of environmental change on ecosystem processes. In

381 particular, change in climate and habitat quality might alter animal migration patterns and seeds

382 germination success, thus affecting animal-mediated seed dispersal. As it integrates models of

383 animal movement influenced by the distribution of resources (using NDVI here but other data

384 could be used) and seeds germination success based on climate suitability from species

385 distribution modeling (Ellis-Soto et al. 2017), our approach could be used to make future

386 predictions for where will seeds disperse and successfully establish under various scenarios of

387 environmental change. Thus, the predictive ability and flexibility of our framework makes it a

388 valuable tool for investigating seed dispersal under climate change, which cannot be easily

389 predicted using existing modeling approaches.

390 Our framework can be applied to a wide range of systems where ecosystem processes

391 are affected by migratory animal species. It would be interesting for example to investigate how

392 migratory populations living in different environmental settings would spread an invasive plant

393   in different ways, such as for example how different populations of tortoises spread guava on

394   different islands in the Galapagos. Such predictions would allow identifying which islands and

395   ecosystems are most at risk of invasion by guava and it would therefore inform where to focus

396   conservation efforts. In addition, our modeling framework could be used to investigate the

397   relative roles of different animal species, given their movement ability and patterns, in

398   spreading the seeds of an invasive plant throughout an ecosystem, which is a promising research

399   avenue with important consequences for conservation and ecosystem functioning. In the case

400   study presented here, giant tortoises are not the only animals capable of dispersing seeds across

401   Galapagos Islands. Galapagos mockingbirds (*Mimus parvulus*), Darwin finches (Geospiza spp.)

402   and introduced cattle, pigs and goats also consume guava, but they move shorter distances

403   (Buddenhagen & Jewell 2006) and cross less from agricultural areas in the highlands to the

404   national park in the lowlands when compared to tortoises. Humans in the Galapagos are also

405   potential long-distance dispersers of guava (Auffret *et al.* 2014). It would be informative to use

406   our model to quantify the relative contributions of these different vectors to the spread of guava.

407   Finally, our modeling framework could also be used to investigate ecosystem processes other

408   than seed dispersal. For example, it would be possible to apply it to quantitatively model how

409   migratory animals affect nutrient transport across ecosystems, which can be quantified either

410   through empirical measurements of excretion rate or metabolic measurements. These different

411   applications can improve our understanding on how animals connect ecosystems and

412   landscapes across spatiotemporal scales and have important conservation implications for the

413   management of ecosystems that include migratory animals.

414

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422   and providing permits.

423

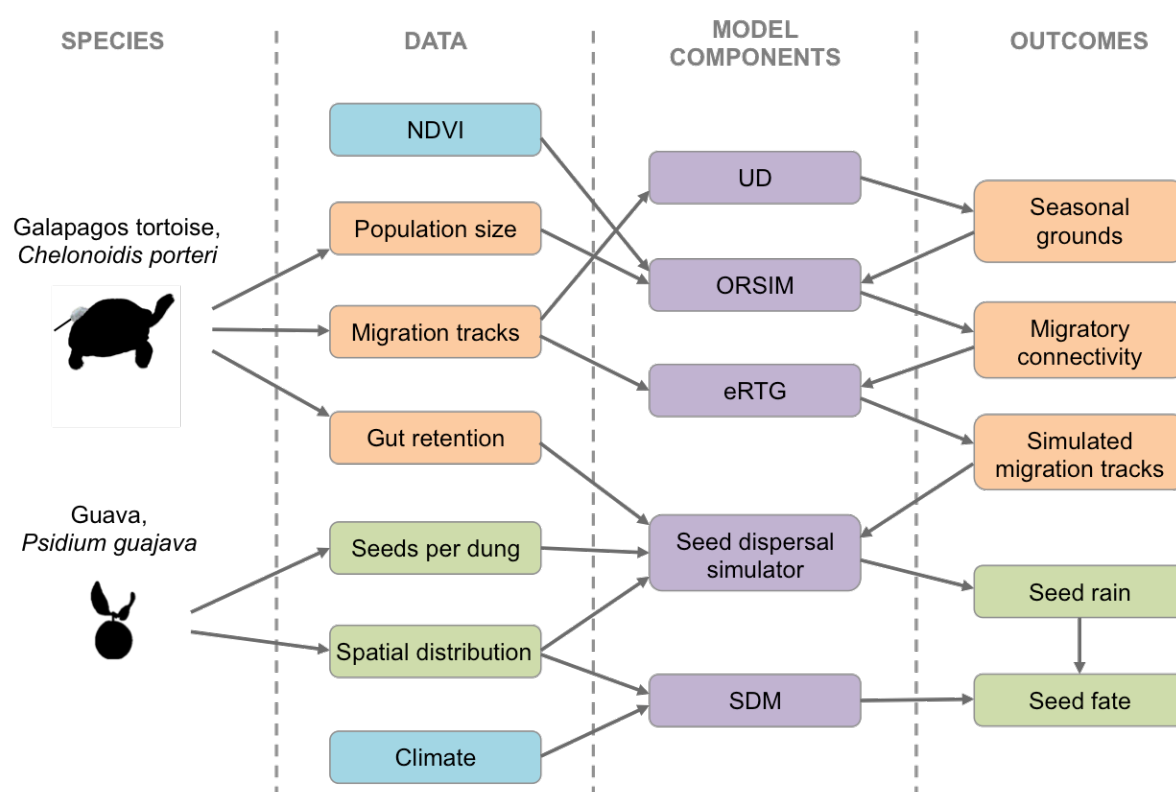424   **6.0   Figures**

425

426   **Figure 1. Workflow for data-driven simulation of seed dispersal by a migrating species.**

427   Orange boxes indicate data and simulation outcomes for migratory Galapagos tortoises; green

428   boxes indicate data and simulation outcomes for the invasive plant species guava; blue boxes

429   indicate environmental data; and purple boxes indicate model components (see Material and

430   Methods for details). NDVI: normalized difference vegetation index, a remote sensing

431   measure capturing primary productivity; UD: utilization distributions, computed from

432   empirical movement tracks; ORSIM: optimal redistribution simulator, which simulates

433   migratory connectivity; eRTG: empirical random trajectory generator, which generates a

19

434   movement between two end points that is calibrated by empirical migration tracks; SDM:

435   species distribution model, indicating guava germination success. Seed rain refers to the

436   spatial distribution of the density of seeds resulting from seed dispersal by migrating tortoises;

437   seed fate refers to the spatial distribution of the density of germinated seeds resulting from

438   seed dispersal by migrating tortoises.
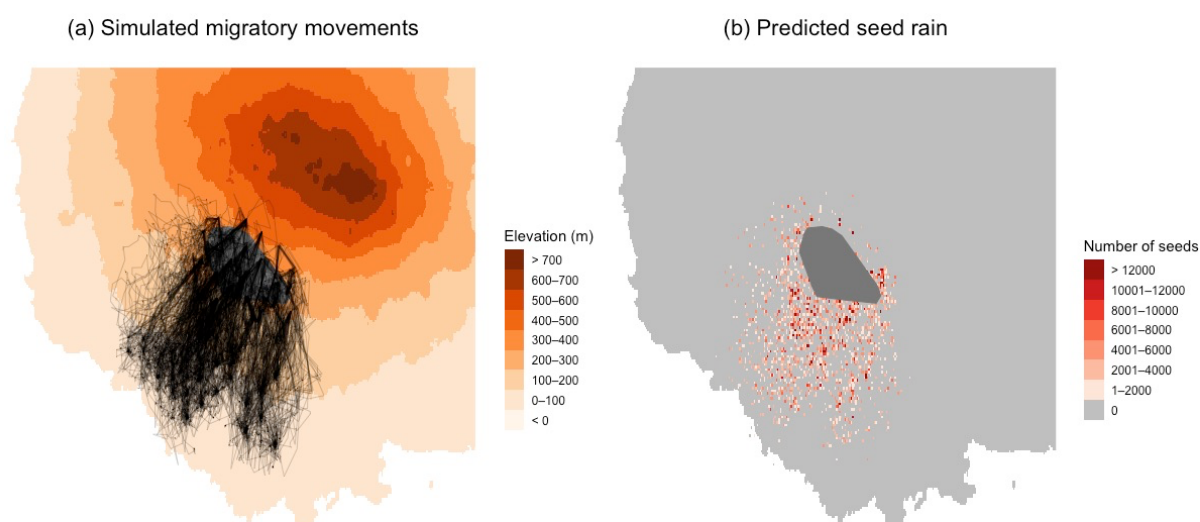
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441   **Figure 2. Simulated tortoise migrations and resulting guava seed rain.** (a) Simulated

442   migration trajectories of tortoises, from highland to lowland. Each black line indicates the

443   simulated migration of an individual. (b) Density of guava seeds dispersed by simulated

444   migrating tortoises, also called 'seed rain'. The highland seasonal distribution of the

445   population is represented by the grey polygon.
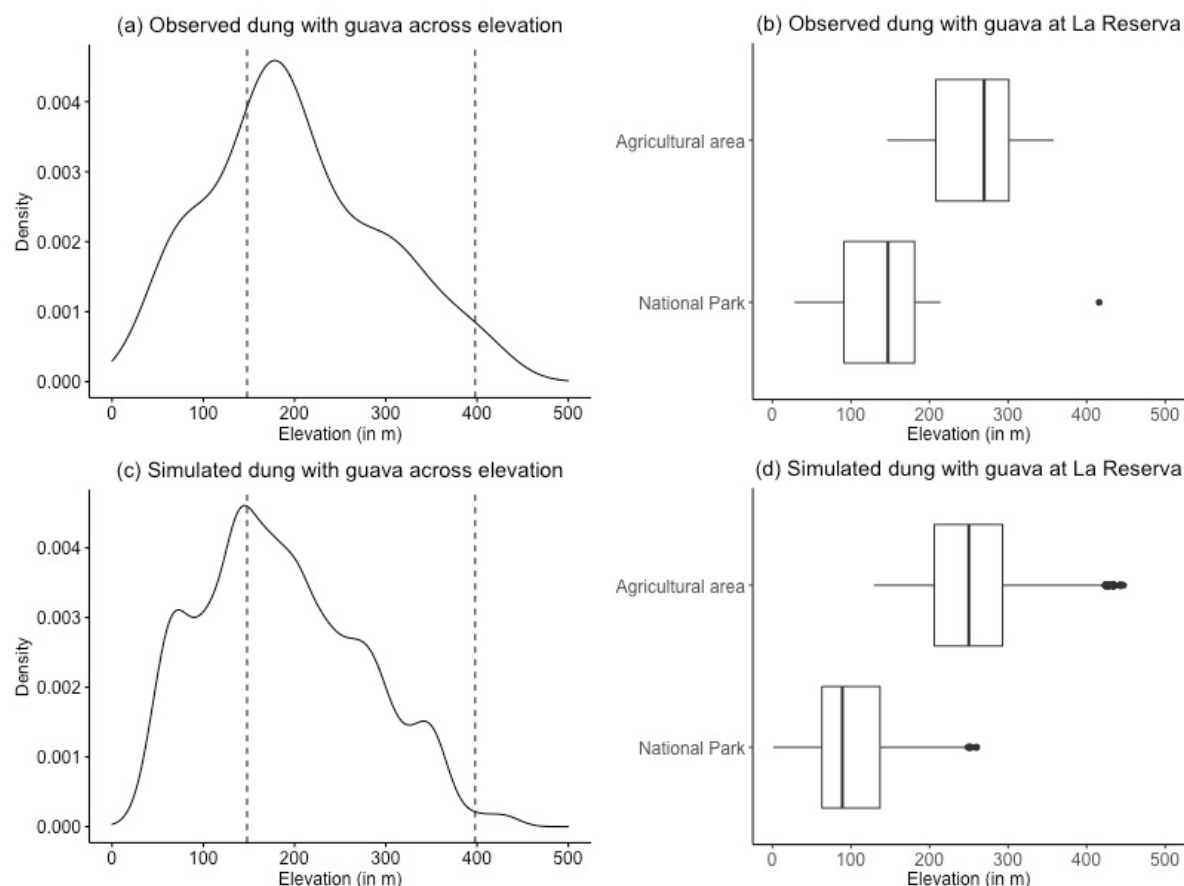
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Figure 3. Model simulation captures empirical dispersal of guava seeds by migrating tortoises. Distribution of observed and simulated tortoise dung piles with guava across the elevational gradient of Santa Cruz Island. Observed (a) and simulated (c) guava seed deposition (left panel density plots) and location in agricultural- and national park areas deposition (b, d, right panel boxplots) across the elevational gradient of site "La Reserva" in Santa Cruz, Galapagos.

7.0   Data Availability Statement

Land cover classification maps are available on the supplementary material of Rivas-Torres *et al.* (2018) and guava distribution in Santa Cruz Island is available on the supplementary material of Laso *et al.* (2019). Galápagos giant tortoise tracking data used in this study will be archived in a public Movebank data repository, should the manuscript be accepted, and the data DOI will be included at the end of the article. The computer code used for this study is available at https://github.com/msomveille/galapagos-tortoises.git.

21

8.0   References

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