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## Modeling long-distance seed dispersal of the invasive tree *Spathodea campanulata* in the Society Islands

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1 Modeling long-distance seed dispersal of the invasive tree *Spathodea*

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18

19 Open Research statement:

20 Digital Elevation Models [topographic data] of the surveyed islands were downloaded from

21 <https://www.data.gouv.fr/fr/datasets/modeles-numeriques-de-terrain-mnt-des-iles-de-la->

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22 polynesie-francaise/ by searching for the islands of Bora Bora, Huahine, Maiao, Maupiti,  
23 Mehetia, Moorea, Raiatea, and Tahiti. Data (Larrue et al., 2023) are available in Dryad at  
24 <https://doi.org/doi:10.5061/dryad.s4mw6m9b5>.

25 Keywords: atmospheric transport model, barrier effect, biological invasion, tropical oceanic  
26 islands

27

## 28 **Abstract**

29 Long-distance dispersal is a key factor explaining the success of invasive alien species,  
30 particularly across oceanic islands. However, it is often not feasible to reliably measure long-  
31 distance seed dispersal over many kilometres in the field. Here, we used a 3-D kinematic  
32 trajectory model (Computing Atmospheric Trajectory tool (CAT)) initiated from regional  
33 wind field data to assess the potential for long-distance seed dispersal (LDD) of a wind-  
34 dispersed invasive tree, *Spathodea campanulata* (African tulip tree) across the Society Islands  
35 (French Polynesia, South Pacific Ocean) following its initial planting and spread on the island  
36 of Tahiti. The main objective of our study was to determine whether *S. campanulata* can be  
37 expected to spread naturally among islands. Atmospheric dynamics, seed terminal velocity,  
38 precipitation and temperature of air masses were considered to assess the potential for LDD  
39 between oceanic islands, with the island of Tahiti serving as the island source for multiple,  
40 geographically distant invasions. Aerial trajectories of modeled *S. campanulata* seeds  
41 indicated that wind-dispersed seeds originating from trees on the island of Tahiti could reach  
42 most of the Society Islands and disperse as far as 1,364 km. This result suggests that  
43 *Spathodea* can be expected to spread naturally among the Society Islands. When rainfall  
44 events were modelled as causal agents of seed settlement, fewer seeds reached distant islands,  
45 but more seeds settled on the closest island (20 km away). Including effects of island  
46 topography (“barrier effects”) also resulted in more seeds settling on the closest island and

47 fewer seeds reaching the most distant islands. Overall, our findings suggest that recent  
48 atmospheric models can provide valuable insights into LDD and invasion patterns of wind  
49 dispersed invasive species.

50

## 51 INTRODUCTION

52 Due to their small land area, geographic isolation, and high level of endemism, the remote  
53 oceanic islands of the Pacific Ocean are particularly susceptible to biological invasions  
54 (Keppel et al., 2014; Larrue, 2013; Loope & Mueller-Dombois, 1989; Meyer, 2004; Russell et  
55 al., 2017). The distribution of alien species on the Society Islands has been well documented  
56 (e.g., Fosberg, 1992; Fourdrigniez et al., 2014; Meyer, 2004, 2014; Meyer & Florence, 1996;  
57 Pouteau et al., 2015), but our knowledge about long-distance seed dispersal of invasive plants  
58 between neighbouring islands is still very limited, although it is crucial for understanding  
59 plant invasions and the potential for a 'bridgehead effect' (Ricciardi, 2017; Trakhtenbrot et  
60 al., 2005). A bridgehead effect is said to occur when one population of an invasive species  
61 serves as the source of origin for many geographically distant populations of that invasive  
62 species (Lombaert et al., 2010), but assessing the possibility of a bridgehead effect requires  
63 identifying sources of geographically distant invasive populations and their pathways of  
64 movement.

65 The invasiveness of introduced plants in new geographic areas may be related to long-  
66 distance seed dispersal, and some invasive plants have natural modes of seed dispersal that  
67 potentially allow them to be dispersed over long distances (e.g., Egawa, 2017; Higgins &  
68 Richardson, 1999; Soons & Bullock, 2008). What constitutes a long-distance seed dispersal  
69 event from a source population may depend on the context of the study, and no consensus  
70 definition exists for what distance qualifies as long-distance dispersal (Jordano, 2017). Some  
71 researchers consider a seed dispersal event to be of long-distance if it is over 80-100 m

72 (Bullock & Clarke, 2000; Cain et al., 2000; Tackenberg, 2003) or several kilometers (Jordano,  
73 2007) up to thousands of kilometers (Muñoz et al., 2004). Two approaches are generally used  
74 to define long-distance dispersal: it can be based (1) on the probability distribution of  
75 dispersal distances for the species under study, corresponding to the farthest distances reached  
76 by a small proportion of all dispersed seeds, or (2) being greater than a fixed distance (Nathan  
77 et al., 2008).

78 Field measurements of the seed dispersal trajectories and distances are generally feasible only  
79 within the vicinity of a source tree (e.g., using seed traps), while projections of long-distance  
80 seed dispersal are needed over the scale of several kilometres to predict plant invasion  
81 patterns (Kuparinen et al., 2007), since long-distance seed dispersal and initial establishment  
82 may promote secondary establishment in other remote geographic areas, thus increasing  
83 global rates of invasions (Bertelsmeier et al., 2018; Garnas et al., 2016).

84 For wind-dispersed seeds, it is well known that wind velocity is an important determinant of  
85 seed dispersal distance (Cousens et al., 2008). Wind dispersal distance is also related to seed  
86 traits such as seed mass, shape and terminal velocity, as well as plant life form (e.g.,  
87 Einzmann & Zotz, 2017; Green & Johnson, 1989, 1995; Pasquill & Smith, 1983; Tackenberg,  
88 2003; Tamme et al., 2014, Zotz et al., 2016).

89 Models that consider a combination of plant height, seed traits and horizontal wind speed may  
90 be most useful to estimate the potential long-distance dispersal and invasion range for wind-  
91 dispersed plants (Thomson et al., 2011). However, recent studies showed that the maximum  
92 dispersal distances predicted by models based on key plant traits (e.g., growth form, dispersal  
93 syndrome, seed terminal velocity) were underestimated compared to those measured under  
94 field conditions (Egawa, 2017; Herrmann et al., 2016). Simulations indicate that expected  
95 dispersal distances increase with decreasing terminal velocity, and this change in dispersal  
96 distance is particularly dramatic between terminal velocities of  $0.4 \text{ m s}^{-1}$  and  $0.2 \text{ m s}^{-1}$

97 (Kuparinen et al., 2007); this range of terminal velocity is associated with a transition towards  
98 greater influence of atmospheric disturbances on particle dispersal and reduced influence of  
99 gravity. These discrepancies between modelled dispersal distances based on plant traits and  
100 actual field dispersal distances, may highlight the importance of including wind behaviours  
101 (i.e., vertical, horizontal and swirling wind) together with wind-speed data when predicting  
102 dispersal distances. Thus, for plants with wind-dispersed seeds, models assessing the potential  
103 for airborne seed dispersal across long-distances based on atmospheric mechanisms affecting  
104 particle movement are needed, even though they cannot be directly verified with field  
105 observations (Kuparinen et al., 2007).

106 Atmospheric models have been used to predict the long-distance dispersal of various  
107 organisms, including weeds or invasive species. For example, the Hybrid Single-Particle  
108 Lagrangian Integrated Trajectory model (HYSPLIT) of the National Oceanic and  
109 Atmospheric Administration (NOAA), which was first created to observe the atmospheric  
110 dispersal of pollution (Draxler & Rolph, 2003) has been used to predict wind dispersal of  
111 some invasive insects, such as the cotton boll weevil in Texas (Kim et al., 2010), and to  
112 confirm the passive long-distance dispersal of insects vectoring pathogens in Australia  
113 (Eagles et al., 2013) and invasive Hymenoptera in France (Lander et al., 2014). The model  
114 used in these studies was based on a digital elevation model and meteorological data at  
115 relatively low spatial resolution and did not incorporate the dispersing organism's terminal  
116 velocity during aerial transport. These limitations are likely to affect model predictions of an  
117 invader's atmospheric dispersion (Egawa, 2017, Liu et al., 2018).

118

119 In this paper, we examine the wind seed dispersal potential of an invasive alien tree across  
120 Pacific Islands by using a recent atmospheric model. This model considers trees at different  
121 elevations above sea level, the terminal velocity of the seed, and climatic conditions that seeds

122 may experience during their flight. Specifically, we focus on assessing the potential for long-  
123 distance seed dispersal of the alien invasive evergreen tree *Spathodea campanulata* P. Beauv.,  
124 1865 [Bignoniaceae] in the Society Islands (French Polynesia, South Pacific Ocean).  
125 *S. campanulata* was first introduced to the island of Tahiti as a garden ornamental tree in 1932  
126 and has since spread into natural environments across Tahiti, mainly through wind dispersal  
127 (Meyer, 1998). This invasive tree has also been reported on five other high volcanic islands of  
128 the Society archipelago: Bora Bora, Huahine, Moorea, Raiatea, and Tahaa (Fosberg, 1981;  
129 Fourdrigniez et al., 2014). It is not known whether *S. campanulata* reached these remote  
130 islands by means of human transportation or wind dispersal from the island of Tahiti. A  
131 previous study using a simple model with terminal velocity and typical trade wind speeds  
132 suggested long-distance seed dispersal of 42 km (Larrue et al. 2020). However, because this  
133 projection did not consider patterns of wind variation or advection, the natural dispersal  
134 distance of *S. campanulata* could have been dramatically underestimated.

135 We hypothesize that the wind dispersed seeds of the alien invasive tree *S. campanulata* can  
136 travel long distances naturally from the island source of Tahiti to other remote Society Islands,  
137 and thus the Tahiti population serves as a source for invading populations discovered in other  
138 geographically isolated islands. We also examined the potential for a “barrier effect” (i.e.,  
139 interception of seeds by island topography during aerial transport from Tahiti) that may be  
140 caused by combined effects of island elevation and spatial geography.

141

## 142 MATERIAL AND METHODS

### 143 *Study species*

144 Commonly called African tulip tree, *S. campanulata* (here after *Spathodea*) is a large tropical  
145 tree native to the wide Equatorial region of Africa (Smith, 1985). *Spathodea* trees introduced  
146 in the Pacific Islands originated from West Africa (Sutton et al., 2017). In 1998, *Spathodea*

147 was designated to be a species threatening native biodiversity by the Government of French  
148 Polynesia (decree 244 CM of the 12 February). Since that date, the planting and transportation  
149 of *Spathodea* have been forbidden in the Society Islands, as well as in every island of French  
150 Polynesia. This invasive tree is mainly propagated by wind-dispersed seeds contained in pods  
151 produced near the top of the canopy; each pod contains about 500 papery winged seeds  
152 (Fosberg et al., 1993; Staples et al., 2000). Generally, species with seed structures that  
153 promote wind dispersal, such as pappi, have low terminal velocities leading to potential for  
154 long dispersal distances (Cousens et al., 2008).

155

#### 156 *Atmospheric transport model*

157 The Computing Atmospheric Trajectory tool (CAT) model is a 3-D kinematic trajectory  
158 model using initialization wind fields from the ECMWF ERA-5 Reanalysis (Baray et al.,  
159 2020). A cluster of starting forward trajectory points is defined by the user. The advection of  
160 air masses between two grid points is estimated by the CAT model by using time and space  
161 interpolation of ECMWF ERA-5 wind fields, including the integration of topography at a  
162 resolution of around 10 km (Bezdek & Sebera, 2013). The ECMWF ERA-5 Reanalysis  
163 includes updates to the physical model, core dynamics and 4D-Var data assimilation  
164 (Hersbach et al., 2018; Hoffmann et al., 2019). Hoffmann et al., (2019) have quantified the  
165 differences between transport simulations using the recent ERA5 ECMWF reanalysis and the  
166 previous ERA-Interim reanalysis, showing an improvement of ECMWF's new-generation  
167 reanalysis on Lagrangian transport simulations. In the framework of the present study,  
168 forward trajectories were calculated with a modified version of CAT by including the  
169 *Spathodea* seed terminal velocity and atmospheric vertical wind to simulate the uplift and  
170 falling of the seeds during aerial transport. The falling terminal velocity of *Spathodea* seeds  
171 ranges from 0.241-0.642 m s<sup>-1</sup> with SD 0.069 and a mean terminal velocity of 0.378 m s<sup>-1</sup>



172 (n=250 seeds dropped at 3.65 m elevation in a closed environment, i.e., under windless  
173 conditions; Larrue et al., 2020). This terminal velocity is in the range associated with an  
174 important influence of atmospheric disturbances on long-distance dispersal (Kuparinen et al.,  
175 2007).

176

### 177 *Targeted islands*

178 The Society Islands is one of the five archipelagos forming the territory of French Polynesia  
179 in the South Pacific Ocean, lying between 7°–28°S and 134°–155°W. This archipelago  
180 consists of 14 tropical oceanic islands including five coral atolls (Manuae, Maupihaa, Motu  
181 One, Tetiaroa, Tupai), and nine high volcanic islands, namely Bora Bora, Huahine, Maiao,  
182 Maupiti, Mehetia, Moorea, Raiatea, Tahaa, and Tahiti (Fig. 1). The oceanic tropical climate of  
183 the Society Islands is dominated by a cooler season (May to October) with lower rainfall, an  
184 average monthly temperature of 25.1°C, and a warm wet season (November to April) with  
185 high rainfall, and average monthly temperature of 26.7°C (Laurent et al., 2004). The region is  
186 characterized by the persistence of southeastern trade winds blowing between 0.036 km h<sup>-1</sup>  
187 and 40.6 km h<sup>-1</sup> (Laurent et al., 2004), with a mean annual wind-speed at ca. 23 km h<sup>-1</sup>.  
188 With an island area of 1,045 km<sup>2</sup> and a summit at 2,241 m above sea level (asl), Tahiti is the  
189 largest and highest island of the Society Islands (Brousse, 1993). The main island of Tahiti is  
190 also a stepping-stone island for native plants in the Society Islands (Larrue, 2014) and in the  
191 Tuamotu archipelago of French Polynesia (Larrue et al., 2015). The earliest and now densest  
192 population of *Spathodea* is found on Tahiti, ranging from sea level up to 1,200 m elevation,  
193 with some scattered adults up to 1,415 m asl (Meyer, 2004).

194 The seven targeted Society Islands included the closest island and the most remote island  
195 from Tahiti, and included islands with and without an observed population of *Spathodea*. One

196 of the Society Island's nine high islands (Tahaa) was excluded from modeling because of its  
197 proximity to another island already included in the model (Table 1).

198 <Figure 1 near here>

199 <Table 1 near here>

200

201 *Source island of Tahiti*

202 A field area of 143 km<sup>2</sup> (11×13 km) was delineated on the island source of Tahiti by using  
203 Google Earth Pro Software. The field area (17.58-17.68°S; 149.48-149.60°W) was chosen  
204 according to densest population of *Spathodea* on Tahiti, including mature *Spathodea* near sea  
205 level and mature *Spathodea* on steep precipices at high elevation (Larrue and Meyer, pers.  
206 obs.). The field area ranged from 5 m to 1,200 m elevation. Geographic coordinates of the  
207 field area were imported into the atmospheric trajectory model as the starting domain for  
208 long-distance dispersal simulations. Long-distance dispersal from the field area was modeled  
209 using climate data for 4 months from September to December 2019. This time window  
210 corresponds to the fruiting season of *Spathodea* and potential release of wind dispersed seeds  
211 from the population on Tahiti (Larrue et al., 2020).

212

213 *Long-distance seed dispersal*

214 For the purposes of this study, a potential long-distance seed dispersal event (LDD)  
215 corresponds to the distance between the island source of Tahiti and the nearest Society Island,  
216 namely the island of Moorea 20 km away (Table 1). We also recorded the longest wind seed  
217 dispersal distance (km) observed in each simulation, even if the associated seed trajectory  
218 settled in the ocean.

219

220 *Long-distance transport estimation*

221 Atmospheric parameters used to calculate the forward trajectories were extracted from the  
222 ECMWF ERA-5 meteorological reanalysis data (Hersbach et al., 2018) with a grid resolution  
223 of  $0.25^\circ$  in latitude and longitude, comprising 20 vertical atmospheric levels between 1,000  
224 hPa (sea level) and 300 hPa (around 9 km altitude), and a temporal resolution of 3 hours.  
225 Simulation was done inside a large domain stretching from  $5^\circ$  to  $30^\circ$  South and  $120^\circ$  to  $160^\circ$   
226 West, encompassing the Society Islands and the surrounding ocean.  
227 Clusters of 138 seed release points were regularly distributed in the 143 km<sup>2</sup> field area of  
228 Tahiti. The starting altitude of the 138 points ranged from 30 m to 1,225 m, corresponding to  
229 the altitude of the topography plus 25 meters to consider the average height of mature trees in  
230 this region. From each release point, starting seed trajectories were calculated every 3 hours  
231 from 1 September 2019 0h UT to 31 December 2019 21h UT with: 138 (number of clusters in  
232 the field area)  $\times$  8 (number of starting seed trajectories per day and cluster)  $\times$  122 days  
233 (duration of analysis). Thus, a total of 134,688 starting seed trajectories were simulated from  
234 Tahiti.  
235 Every seed trajectory was then monitored inside the large domain for 168 hours (7 days) with  
236 a temporal resolution of 15 minutes (time between two successive trajectory points). In order  
237 to check whether extreme temperatures were encountered by the seeds during aerial transport,  
238 atmospheric temperature was extracted from ECMWF ERA5 and interpolated on each  
239 trajectory point during transport. To assess potential LDD, we then examined the spatial  
240 distribution of seed trajectory endpoints, determined by the number of trajectory points  
241 reaching the ground (terrestrial area or oceanic surface) per square of  $0.1^\circ$  size across the  
242 Society Islands and in the surrounding ocean.  
243 For the purpose of tracking seed dispersal potential from Tahiti, the seven islands were  
244 modelled in seven surveyed island-zones of 400 km<sup>2</sup> (20 $\times$ 20 km). The size of the surveyed  
245 island-zone was chosen to enclose the largest island of the sample (namely Raiatea; Table 1).

246 Each island-zone of 400 km<sup>2</sup> included the real island area and topography, plus a part of the  
247 surrounding ocean (as a “buffer”) to also account for seeds settled in the vicinity of island  
248 (Table 1). Measurements are reported for the island-zone, in addition to the island alone,  
249 because our simulation was done during 4 months of one specific year, and atmospheric  
250 conditions may slightly differ from one year to another. Thus, we assessed seeds settling in  
251 the vicinity of an island as a general measure of feasibility of dispersal to specific islands.

252

### 253 *Impact of rainfall*

254 Additionally, the role of precipitation on LDD is unknown and rainfall could reduce the  
255 percentage of *Spathodea* seeds reaching an island-zone from Tahiti. Thus, we incorporated an  
256 estimate of the impact of rainfall on seed dispersal in each island-zone. Whenever a seed  
257 spatial and temporal trajectory point corresponded to a zone of precipitation (as extracted  
258 from ECMWF ERA5) it was assumed that the seed would drop to the ground (or to the ocean)  
259 at the point when the precipitation was encountered. Different effects of precipitation on seed  
260 drop were used, ranging from a weak influence of rain (the seed falls to the ground or ocean  
261 only when it encounters a zone of precipitation greater than 1.2 mm h<sup>-1</sup>, corresponding to the  
262 90<sup>th</sup> decile of precipitation values in the region and period of study) to a strong influence of  
263 rain (the seed falls to the ground or ocean when it encounters a zone of precipitation greater  
264 than 0.017 mm h<sup>-1</sup>, corresponding to the 10<sup>th</sup> decile of precipitation values).

265

### 266 *Barrier effect of islands*

267 A barrier effect of high volcanic islands could help wind-dispersed seeds colonize some  
268 islands, while also reducing the feasibility of seeds reaching some remote island-zones  
269 beyond a “barrier island”. To simulate the barrier effect, a Geographic Information System  
270 (ArcGIS Pro 2.8 software, Intersect 3D-line with surface tool) with a Digital Elevation Model

271 of the Society Islands (DEM 5 m resolution) was used to identify seed trajectories derived  
272 from CAT that would have been intercepted by the main “barrier island” of Moorea, which  
273 lies immediately downwind from Tahiti during the predominant trade winds, as well as  
274 trajectories that would have been intercepted from elevated areas of the other six islands.  
275 Here, note that the resolution of the DEM was higher than the resolution of ECMWF ERA 5  
276 data. Consequently, the local effects of the elevated land mass on wind currents along the  
277 slopes of islands were not included in the CAT simulation. Thus, when the seed trajectory met  
278 an elevated terrestrial island area, the seed was immediately settled at that location. These  
279 results constitute the realized LDD (Table 2).

280

#### 281 *Successful connectivity*

282 For the purposes of this study, we refer to arrival of a seed from Tahiti to another island as  
283 ‘successful connectivity’. In addition to qualitatively assessing the potential for successful  
284 connectivity, we quantified the strength of the connection between Tahiti and the other islands  
285 by considering the number of seeds settled on the terrestrial island area relative to the entire  
286 number of seed trajectories simulated.

287 Thus, the “strength of connectivity” ( $B$ ) was estimated as:

$$288 B = (N_{dp}/N_r) \times 1,000$$

289 where  $N_{dp}$  is the number of seeds deposited on each terrestrial island area and  $N_r$  the total  
290 number of simulated trajectories from Tahiti ( $n=134,688$ ). This fraction was multiplied by  
291 1,000 to allow reporting with fewer decimal places, expressing  $B$  per ‰ simulated seed  
292 trajectories.

293

294 Because we did not have direct field observations of *Spathodea* seeds aerially transported  
295 from the island of Tahiti to the terrestrial area of remote islands, it was not possible to directly

296 validate our model; however, dispersal potential from Tahiti to the seven target islands, as  
297 predicted by the model, was compared to the documented presence of *Spathodea* on the seven  
298 targeted islands.

299

## 300 RESULTS

### 301 *Long-distance seed dispersal*

302 The distribution of the total seeds settled inside the large domain showed that 56.7% of all  
303 seeds settled beyond the arbitrary LDD threshold of 20 km while 43.3% of seeds settled in the  
304 first 20 km (Fig. 2), thereby indicating the potential for seeds to settle across the entire island  
305 of Tahiti. The furthest seed trajectory settled on the oceanic surface at 10.4257° South and  
306 159.8966° West, indicating a dispersal distance of 1,364 km from Tahiti (Fig. 2). Most seed  
307 trajectories (69%) settled in the domain were found in the region surrounding Tahiti shown in  
308 Figure 3. Our simulation suggests that *Spathodea* seeds can reach most of the Society Islands  
309 from Tahiti. The maximum altitude among trajectories reaching an island-zone was 2,068 m  
310 (not shown), while lowest atmospheric temperature encountered during a trajectory reaching  
311 an island zone was 11.3°C (Appendix S1: Figure S1).

312 <Figure 2 near here>

313 <Figure 3 near here>

314

### 315 *Impact of rainfall*

316 When we accounted for rainfall's potential impact on seed dispersal, we found that including  
317 a precipitation threshold for seed settling generally resulted in fewer *Spathodea* seeds settling  
318 in an island-zone (Fig. 4). Conversely, the number of settled seeds on the island-zone of  
319 Moorea increased with assumptions of seed drop in response to precipitation, and any level of  
320 precipitation increased seed drop over Moorea (Fig. 4).

321 <Figure 4 near here>

322

### 323 *Barrier effect*

324 The barrier effect of the high volcanic island of Moorea was very important in reducing the  
325 number of seeds that reached the more remote islands (Table 2). Based on the CAT  
326 simulation (i.e., 134,688 trajectories) and the barrier effect, the percentage of total seed  
327 trajectories associated with settlement on the studied islands was 2.9%. The realized LDD  
328 ranged from 0% (Mehetia) to 90.3% (Moorea) of total island settlement (Table 2). Thus, the  
329 island of Moorea received most of the simulated seeds that settled on the studied islands  
330 (Table 2).

331 <Table 2 near here>

332

### 333 *Successful connectivity*

334 No simulated seed was found on the terrestrial area of Mehetia (Table 2), although some  
335 seeds were observed in the surrounding ocean (Fig. 5), but simulated seeds were observed on  
336 the terrestrial areas for the other surveyed islands. The simulation demonstrated the potential  
337 for successful connectivity because seeds originating from Tahiti arrived at six out of seven  
338 distant islands, potentially accounting for invasion of those islands. Most seeds settled on the  
339 windward coast of the islands (Fig. 5), i.e., the coast exposed to the dominant humid eastern  
340 trade winds.

341 The relative “strength of connectivity” with Tahiti was nonexistent for Mehetia (0 ‰), very  
342 low for Bora Bora, Maiao, and Maupiti (< 0.5 ‰); it was low for Huahine and Raiatea (<  
343 1.5 ‰) and high for the closest island of Moorea (> 25 ‰) (Fig. 6). As a validation,  
344 *Spathodea* trees were reported on the island of Bora Bora, Huahine, Moorea and Raiatea,  
345 while no *Spathodea* were reported on the island of Maiao, Maupiti and Mehetia (Table 1).

346

347 <Figure 5 near here>

348 <Figure 6 near here>

349

350 DISCUSSION AND CONCLUSION

351 *Long-distance seed dispersal*

352 According to our simulation, *Spathodea* seeds can be dispersed and advected by wind from  
353 the island of Tahiti to most of the Society Islands, even to the remote island of Maupiti (300  
354 km from Tahiti). *Spathodea* was expected to exhibit LDD based on its plant traits (growth  
355 form, plant height, seed terminal velocity; Tamme et al., 2014); however, our study, coupling  
356 trait information with an atmospheric model, suggests that *Spathodea* has a surprisingly long-  
357 distance dispersal potential (> 1,000 km). Coupling plant traits with an atmospheric model  
358 also allowed us to explore how a range of scenarios (e.g., response of airborne seeds to  
359 rainfall, temperatures experienced during dispersal) can be expected to influence the spread of  
360 invasive plants from a source population to new islands via natural processes.

361 Our simulation showed substantial variation in the quantity of deposited *Spathodea* seeds  
362 among islands. Seed deposition was affected by the geographic location of islands relative to  
363 the source population and the southeast dominant trade winds. For example, the island of  
364 Raiatea (198 km northwest from Tahiti) received 4.4% of all seeds that landed on islands  
365 across all iterations while the island of Mehetia (180 km east from Tahiti) had no deposited  
366 seeds. Thus, the quantity of deposited seeds on an island is not only related to the distance  
367 from Tahiti but also to the geographic location of the island and dominant direction of trade  
368 winds (included in the CAT model). Mehetia, which lies east of Tahiti, was the only island  
369 that was largely protected from seed dispersal by the tradewinds that blow east to west  
370 (Appendix S1: Figure S2).



371 Our results showed that the barrier effect of some high islands can be an important  
372 phenomenon decreasing the number of seeds reaching more remote islands from Tahiti. For  
373 example, realized LDD showed that the high island of Moorea (20 km northwest from Tahiti)  
374 received more than 3,600 seeds, representing 90% of the total *Spathodea* seeds settled within  
375 the islands.

376 Finally, our findings showed that precipitation may decrease the number of seeds reaching the  
377 remote island-zones from the island source of Tahiti, thus reducing the chance for wind  
378 dispersed seed to be settled on an island. Conversely, rainfall increased the number of  
379 *Spathodea* seeds that settled on the closest island-zone of Moorea, increasing the chance for  
380 seed to be deposited on this island. However, some simulated trajectories never encountered  
381 rainfall, so rainfall does not continuously limit dispersal.

382

### 383 *Successful connectivity*

384 Our simulations suggest that substantial numbers of *Spathodea* seeds can reach the remote  
385 islands of the Society Islands, supporting a possible connection from Tahiti. However, it is  
386 well known that “realized dispersal” depends also on successful germination and seedling  
387 establishment (Schupp, 1995). There is no doubt that successful germination depends on seed  
388 viability, which could potentially be decreased by very cold atmospheric temperatures during  
389 wind dispersal. Our simulations indicated that atmospheric temperature decreased to as low as  
390 around 11°C during *Spathodea* seed dispersal events. Since this temperature is not lethal for  
391 the embryo of seed, germination remains possible after LDD. Additionally, *Spathodea*  
392 seedlings and adult trees were observed in natural environments with extreme low  
393 temperature reaching less than 10°C (Larrue et al., 2016). Furthermore, our simulation  
394 indicated that most seeds settle on the east, humid side of the islands (windward coast), and

395 the high humidity at these sites is a preferred condition for seed germination of *Spathodea*  
396 (Larrue et al., 2020).

397 Regarding seedling establishment upon arrival, *Spathodea* seedlings are known to  
398 successfully establish in various environments including human-disturbed forests, abandoned  
399 agricultural land, as well as native forests on tropical oceanic islands (Anderson et al., 1992;  
400 Smith, 1985; Staples & Cowie, 2001). On the island of Cuba, it was reported that the greatest  
401 abundance of *Spathodea* saplings was recorded in areas of abandoned coffee plantations  
402 (Labrada & DiazMedina, 2009), supporting that shaded or semi-shaded conditions provide a  
403 suitable habitat for *Spathodea* seedling establishment and growth. *Spathodea* seedlings were  
404 reported growing in different light environments of Hawaiian Islands, with an estimated mean  
405 compensation point below  $10 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$  photosynthetically active radiation (PAR)  
406 and a positive net carbon gain at  $50 \mu\text{mol photons m}^{-2} \cdot \text{s}^{-1}$  PAR, allowing seedling  
407 establishment in the understory of island rainforests (Larrue et al., 2014). Thus, previous  
408 research suggests that seeds settling in a variety of environments, both natural and human-  
409 modified, will have a chance of germinating and establishing, although some environments,  
410 such as sandy beaches and zones with high salt exposure, are likely to be unsuitable for  
411 germination or seedling establishment.

412

#### 413 *Presence of Spathodea across the Society Islands*

414 The CAT simulation shows that *Spathodea* seeds can be transported from the main island of  
415 Tahiti to the islands of Bora Bora, Huahine, Moorea, and Raiatea. These results are consistent  
416 with the documented presence of *Spathodea* trees on these islands. On the other hand, our  
417 simulation also showed an expected connection that extends to the terrestrial island areas of  
418 Maupiti and Maiao, two islands where *Spathodea* has not yet been observed (Fourdrigniez et  
419 al., 2014). This could be explained by failure of *Spathodea* seedling establishment, as this

420 depends on environmental conditions at the drop points. Additionally, establishment may not  
421 yet have occurred for stochastic reasons. The low simulated seed counts being settled on the  
422 island of Maupiti and Maiao these islands are likely proportional to the probabilities of  
423 establishment (Lockwood et al., 2005), which were very low for these islands.

424 We limited our examination to natural wind dispersal of seeds, though *Spathodea* is a popular  
425 ornamental tree in many tropical islands worldwide, where it has been introduced  
426 intentionally. Its seeds also have the potential to be accidentally dispersed via inter-island  
427 movements of local people and tourists. However, we have no evidence for human  
428 introduction (intentional or accidental) in the Society Islands other than to Tahiti. Moreover,  
429 note that the observed distribution of *Spathodea* does not coincide well with areas that receive  
430 substantial air and tourist traffic, such as the North of the island of Huahine (Meyer and  
431 Fourdrigniez, 2019). Likewise, human movement appears unable to explain the isolated  
432 *Spathodea* trees recently observed in a more remote region in the South of Huahine (M.  
433 Fourdrigniez, pers. com). Thus, in the case of *Spathodea*, we feel that model of wind  
434 movement can provide additional insights that cannot be explained by human movements.

435

#### 436 *Strength of connectivity*

437 The percentage of seeds reaching every island area was estimated for a given fruiting season  
438 based on a CAT simulation with 134,688 seed trajectories. Although the entire number of  
439 available *Spathodea* seeds per season is unknown on Tahiti, this number is certainly greater  
440 than our simulation, as there are at least several thousand mature trees on Tahiti, each  
441 producing more than 50,000 seeds per season (Larrue, pers. obs). Our finding suggests that  
442 early detection surveys on Huahine, Maupiti and Maiao could be warranted to prevent  
443 *Spathodea* establishment on these islands, with survey priority given to Huahine and Maiao,  
444 as our simulation indicates that Mehetia is at much lower risk of colonization by wind-

445 dispersed seeds of *Spathodea*. Here, relative strength of connectivity (%) allows us to provide  
446 relative probabilities of invading each island by wind dispersal. Additionally, our results  
447 support a possible “bridgehead effect” with the island of Tahiti as the source of origin for  
448 geographically distant populations of *Spathodea*, but further study of alternative invasion  
449 pathways in this system is warranted.

450

451

452 Our results suggest that *Spathodea* seeds can be dispersed at very long distance, up to 1,364  
453 km, reaching most of the Society Islands from the main island source of Tahiti. Thus, a  
454 connection from Tahiti is possible, even if some stochastic precipitation events may decrease  
455 the number of seeds reaching the remote islands. Overall, our findings suggest that studies of  
456 LDD in wind-dispersed invasive species, using atmospheric models with other physical  
457 parameters such as topography and rainfall, can help anticipate island invasions and provide  
458 new insights into spatial patterns of invasion.

459

460

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470

471 Conflict of Interest statement

472 The authors declare no conflict of interest.

473

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669 Table 1. Geographic characteristics of the nine volcanic islands of the Society Islands (French  
670 Polynesia). Seven island-zones (square with cross) were monitored for long-distance seed  
671 dispersal by *Spathodea* seeds using a simulation with CAT. Note: The island of Tahaa was  
672 not selected due to the very short distance between it and Raiatea Island (~5 km).

673

High volcanic islands (n=9)	Highest elevation (m)	Area (km <sup>2</sup> )	Distance from Tahiti (km)	Human Population (date) <sup>1</sup>	Targeted island-zone
<b>Windward Islands</b>					
Maiao	154	8	100	335 (2012)	☒
Maupiti	380	13.5	300	1,234 (2012)	☒
Mehetia	435	2.3	180	0	☒
Moorea	1,207	142	20	17,718 (2017)	☒
Tahiti (island source of <i>Spathodea</i> seeds)	2,241	1,045	0	192,760 (2017)	
<b>Leeward Islands</b>					
Bora Bora	727	29	248	10,605 (2017)	☒
Huahine	669	74	170	6,313 (2012)	☒
Raiatea	1,017	175	198	12,245 (2012)	☒
Tahaa	590	88	220	5,234 (2017)	

674 <sup>1</sup> last available population census (Gauchenot & Breuilh, 2017)

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678 Table 2. Potential and realized LDD (n=134,688 simulations) in 400 km<sup>2</sup> island-zones  
 679 including the real island area and the surrounding ocean. For each island, we report the  
 680 number of settled *Spathodea* seeds on both the island area and surrounding ocean within the  
 681 island-zone. The actual presence of *Spathodea* trees on each island is also reported (Society  
 682 Islands, French Polynesia). Distribution of *Spathodea* refers to a qualitative index of  
 683 distribution across the island: (1) sparse, (2) moderate, or (3) widespread.

684

Targeted 400 km <sup>2</sup> island- zone (n=7)	Latitude South (decimal degree)	Longitude West (decimal degree)	Potential LDD: Seeds in island- zone (footprint with CAT)	Realized LDD: Seeds on the island area	Realized LDD: Seeds on the surrounding ocean	Observed <i>Spathodea</i> on island	Distribution of <i>Spathodea</i>
Bora Bora	16.502326	151.737270	1,385	11	478	yes	1
Huahine	16.775940	150.989556	1,205	170	647	yes <sup>(1)</sup>	1
Maiao	17.658880	150.631852	734	15	568	no	-
Maupiti	16.444534	152.257128	1,509	1	523	no	-
Mehetia	17.875085	148.067235	72	0	71	no	-
Moorea	17.534741	149.83005	1,170	3,657	492	yes	3
Raiatea	16.839993	151.445463	1,258	181	398	yes	2

685 <sup>(1)</sup> adult *Spathodea* was mentioned in the handwritten and unpublished notebook field of F.R.

686 Fosberg (1981) as “it is less common on Moorea and still less on Huahine” (available at the  
 687 Smithsonian Institution of Washington, Meyer, pers. Com) but it was not reported on the  
 688 island of Huahine by Fourdrigniez et al. (2014). Recently, some *Spathodea* were observed in  
 689 the South of the island (M. Fourdrigniez, pers. Com).

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691

692 **Figure captions**

693 Figure 1. Study area. Location of the Society Islands in the French Polynesia territory (Pacific  
694 Ocean)

695

696 Figure 2. Dispersal distance distribution of the wind dispersed *Spathodea* seeds settled inside  
697 the simulation domain from the island source of Tahiti modeled with CAT (Society Island,  
698 French Polynesia).

699

700 Figure 3. Spatial density of settled *Spathodea* seeds (spatial resolution  $0.1^\circ$   
701 latitude/longitude), focusing on the Society Islands region.  $400 \text{ km}^2$  island-zones are indicated  
702 by black squares with “X” in the middle. Island barrier effects and effects of rainfall were not  
703 considered.

704

705 Figure 4. Effect of assuming that differing levels of rainfall cause seed drop in *Spathodea* in  
706 the seven  $400 \text{ km}^2$  island-zones modeled with CAT (Society Island, French Polynesia). Q  
707 indicates the amount of rainfall expressed as the percentile of observed rainfall events.

708

709 Figure 5. Realized LDD of *Spathodea* seeds in the seven  $400 \text{ km}^2$  island-zones of the Society  
710 Islands (French Polynesia) showing the seeds settled on islands area (black circles;  $n=4,035$ ),  
711 and in the surrounding ocean (white circles;  $n=3,177$ ). Each circle is a seed deposited on the  
712 surface from CAT simulation. Black triangles refer to the highest elevation. Rain effects were  
713 not considered.

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715 Figure 6. Relative strength of connectivity (‰) from the main island source of Tahiti to the  
716 seven targeted islands of the Society Islands (French Polynesia). Rain effects were not  
717 considered.

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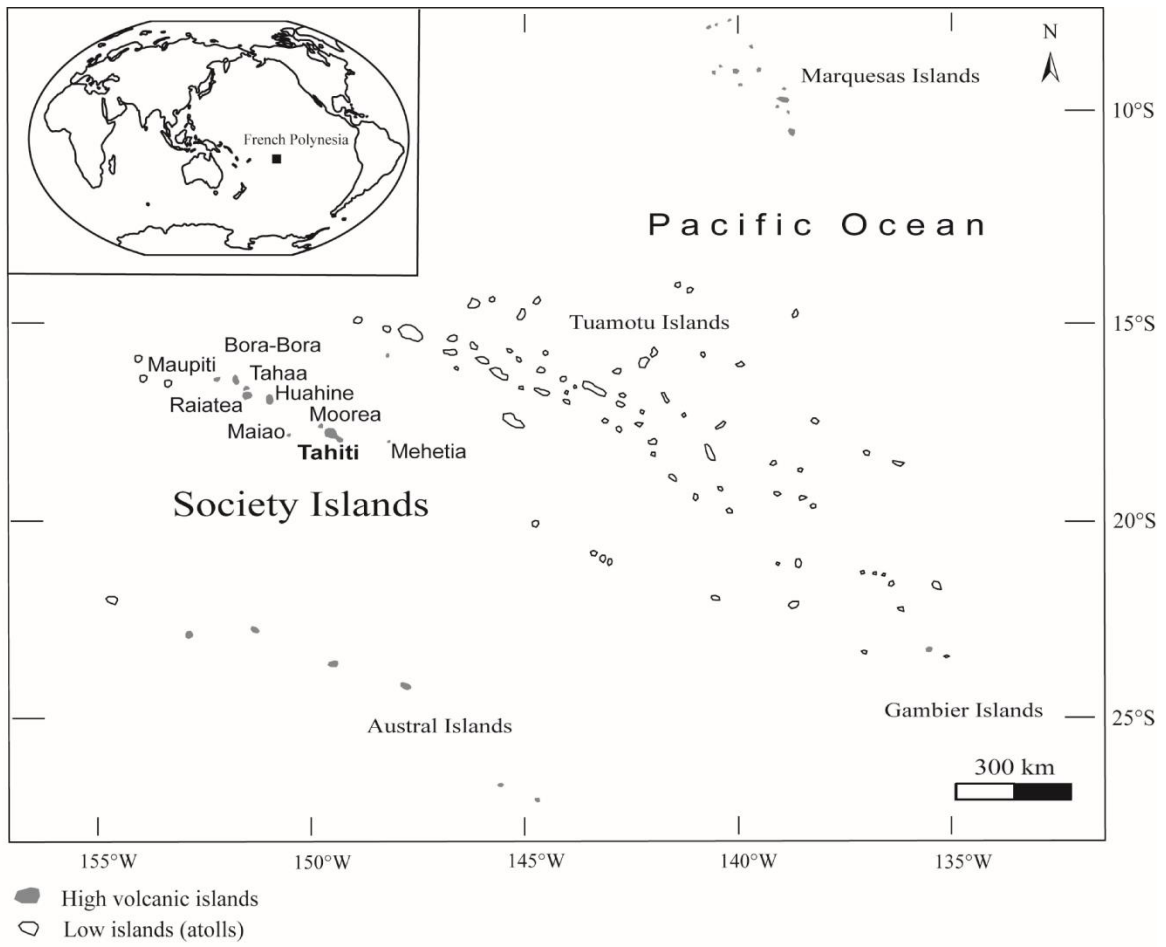
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742 Figure 1

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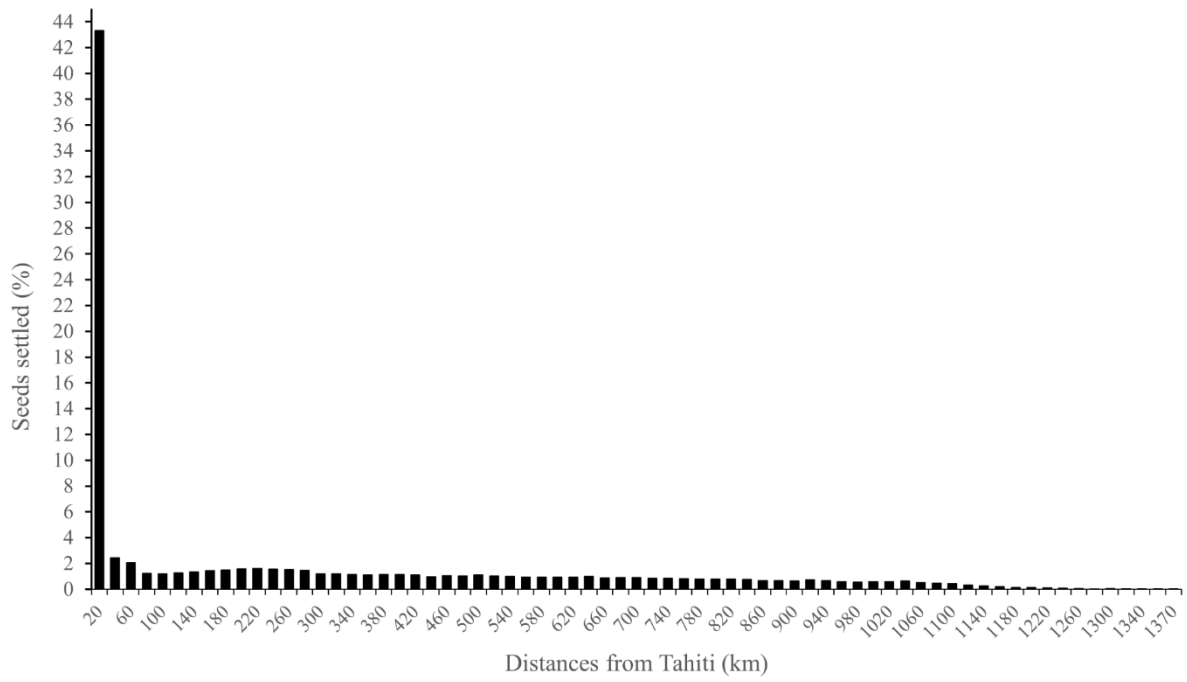
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756 Figure 2

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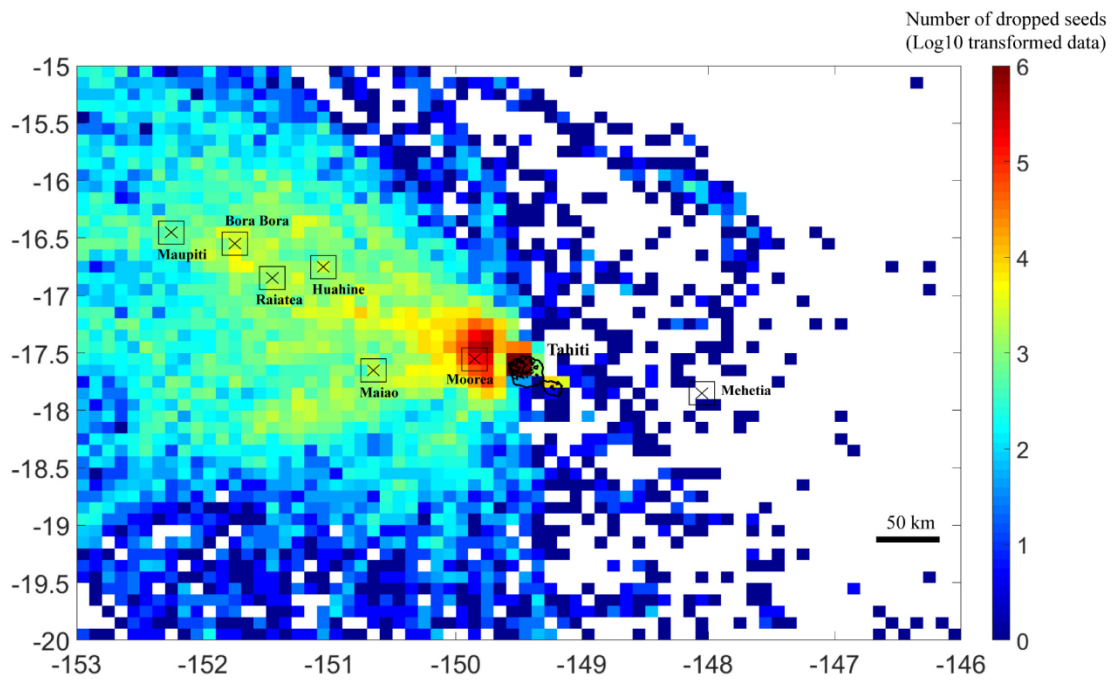
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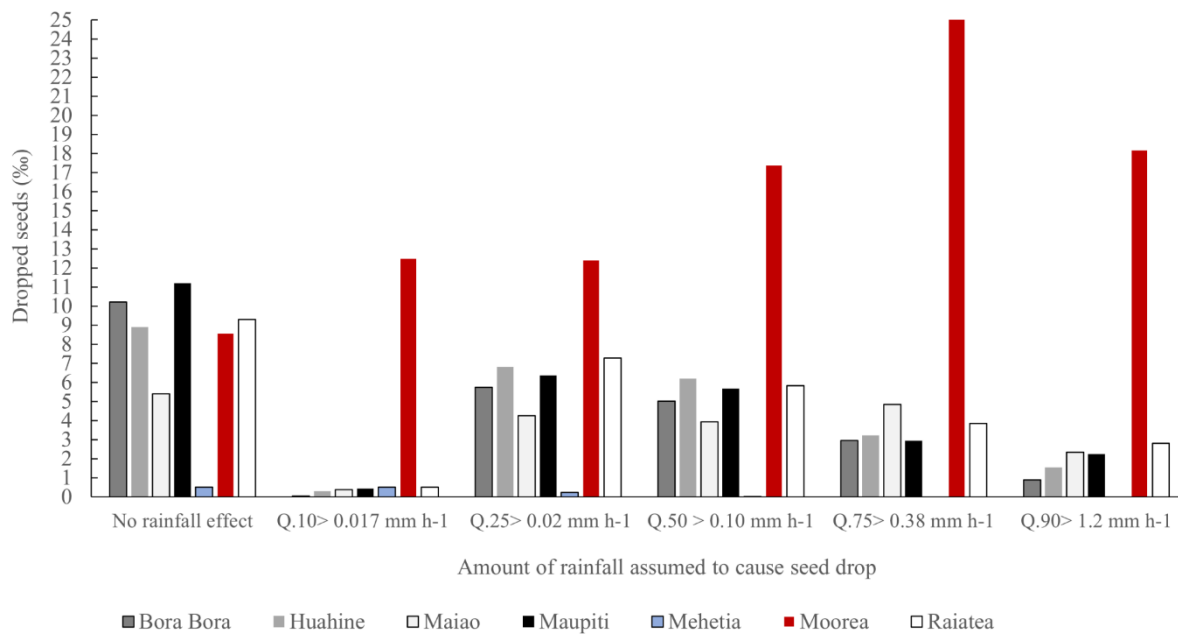
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787 Figure 4

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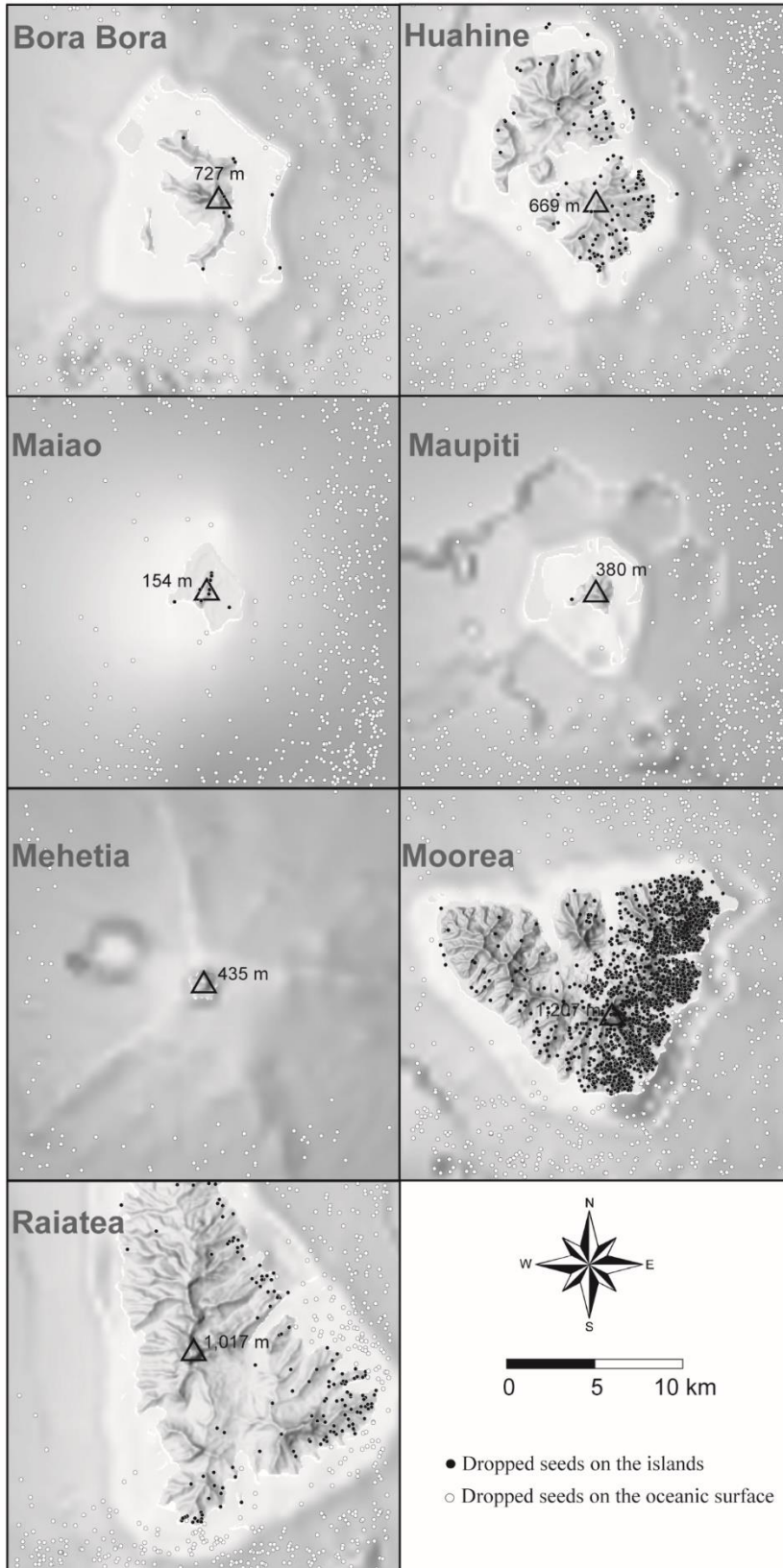
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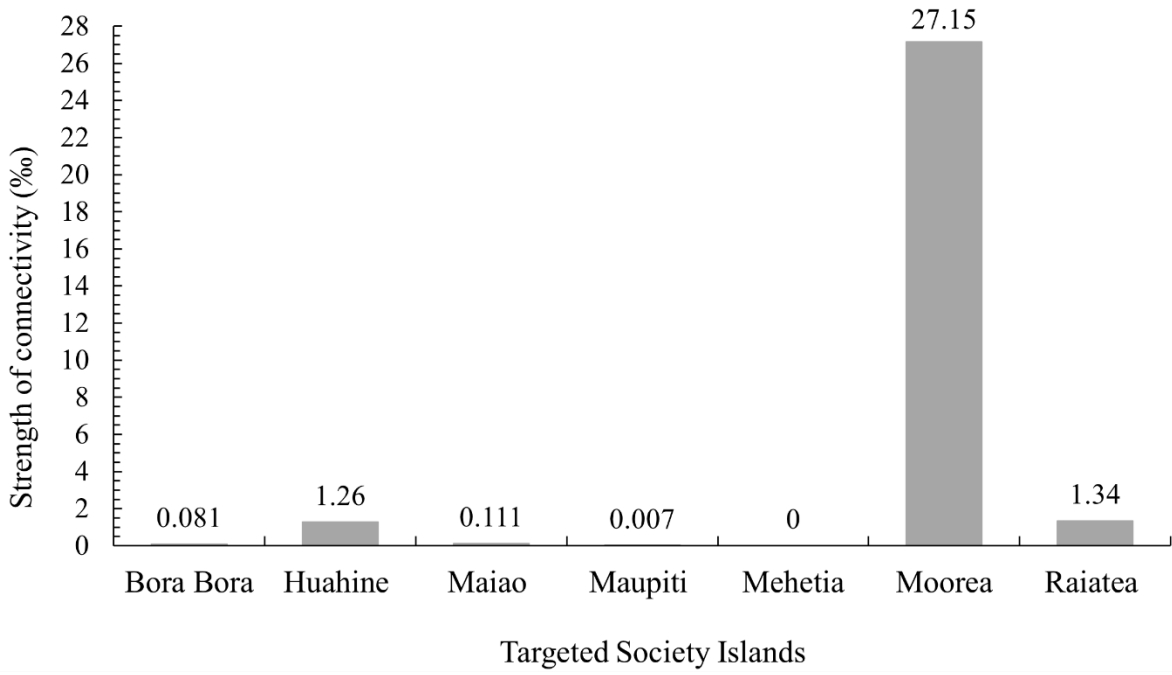


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803 Figure 5

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807 Figure 6

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