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

Sébastien Larrue, Jean-luc Baray, Julien Chadeyron, Jean-yves Meyer, Lucas Mazal, Curtis Daehler, Boris Fumanal

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

2 *campanulata* in the Society Islands.

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4 Sébastien Larrue^{(a)1}, Jean-Luc Baray^(b,c), Julien Chadeyron^(d), Jean-Yves Meyer^(e), Lucas

5 Mazal^(a), Curtis C. Daehler^(f), Boris Fumanal^(g)

6

7 ^(a) Université Clermont Auvergne, CNRS, GEOLAB – F-63000 Clermont-Ferrand, France

8 ^(b) Université Clermont Auvergne, CNRS, LaMP, UMR6105 – F-63000 Clermont-Ferrand,

9 France

10 ^(c) Université Clermont Auvergne, CNRS, OPGC, UAR833 – F-63000 Clermont-Ferrand,

11 France

12 ^(d) Université Clermont Auvergne, Department of Geography, F-63000 Clermont-Ferrand,

13 France

14 ^(e) Délégation à la Recherche, Government of French Polynesia, B.P. 20981, 98713 Papeete,

15 Tahiti, French Polynesia

16 ^(f) School of Life Sciences, University of Hawai'i at Mānoa, Honolulu, HI 96822, USA

17 ^(g) Université Clermont Auvergne, PIAF, UMR 547, F-63000 Clermont-Ferrand, France

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->

¹ Corresponding author: email; sebastien.larrue@uca.fr

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 m s^{-1} and 0.2 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⁻¹ with SD 0.069 and a mean terminal velocity of 0.378 m s⁻¹

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⁻¹
187 and 40.6 km h⁻¹ (Laurent et al., 2004), with a mean annual wind-speed at ca. 23 km h⁻¹.
188 With an island area of 1,045 km² 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 km² (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° 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° to 30° South and 120° to 160°
226 West, encompassing the Society Islands and the surrounding ocean.

227 Clusters of 138 seed release points were regularly distributed in the 143 km² 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° 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 km² (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 km² 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⁻¹, corresponding to the
262 90th 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⁻¹, corresponding to the 10th 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 ²)	Distance from Tahiti (km)	Human Population (date) ¹	Targeted island-zone
Windward Islands					
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)	
Leeward Islands					
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 ¹ last available population census (Gauchenot & Breuilh, 2017)

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678 Table 2. Potential and realized LDD (n=134,688 simulations) in 400 km² 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 ² 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 ⁽¹⁾	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 ⁽¹⁾ 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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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°
701 latitude/longitude), focusing on the Society Islands region. 400 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 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 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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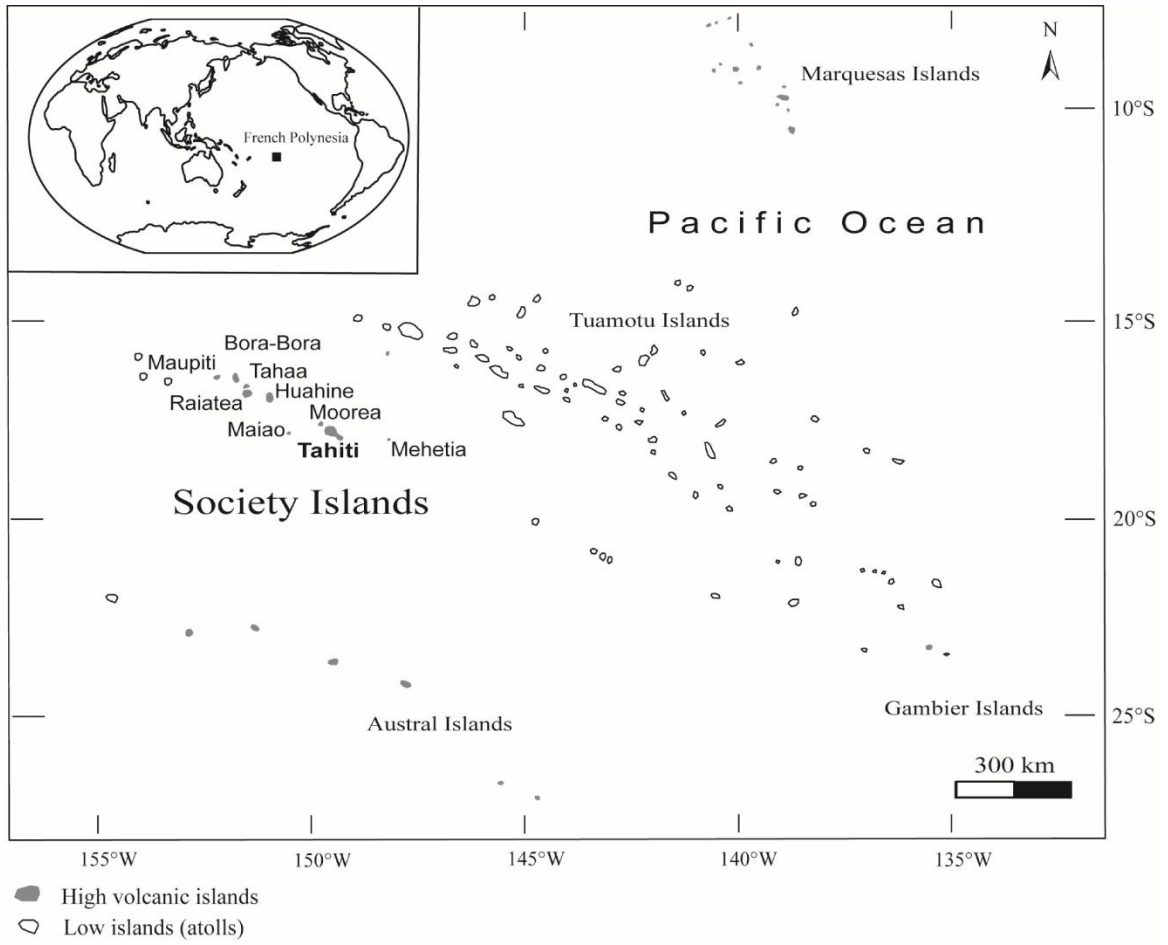
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742 Figure 1

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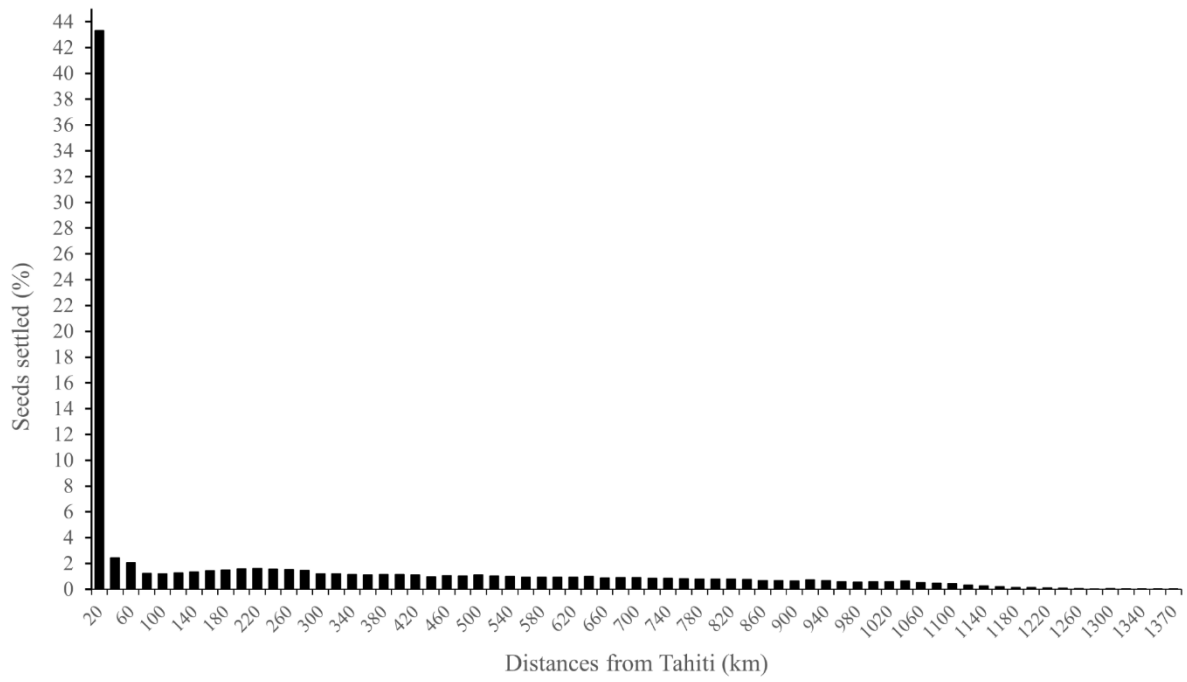
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756 Figure 2

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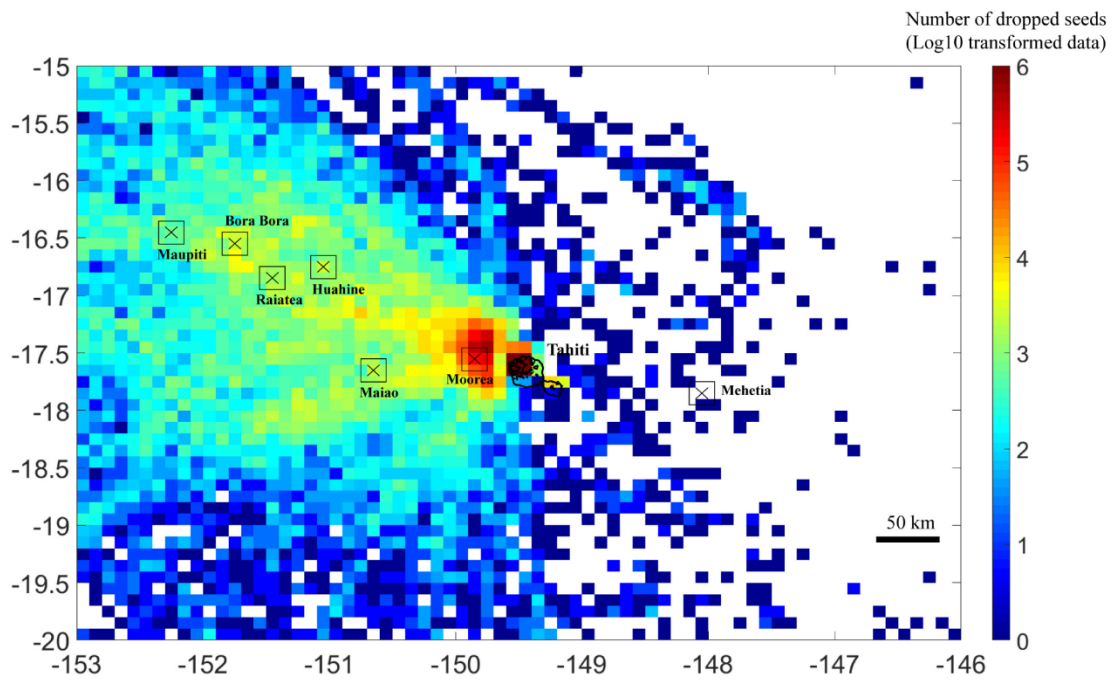
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772 Figure 3

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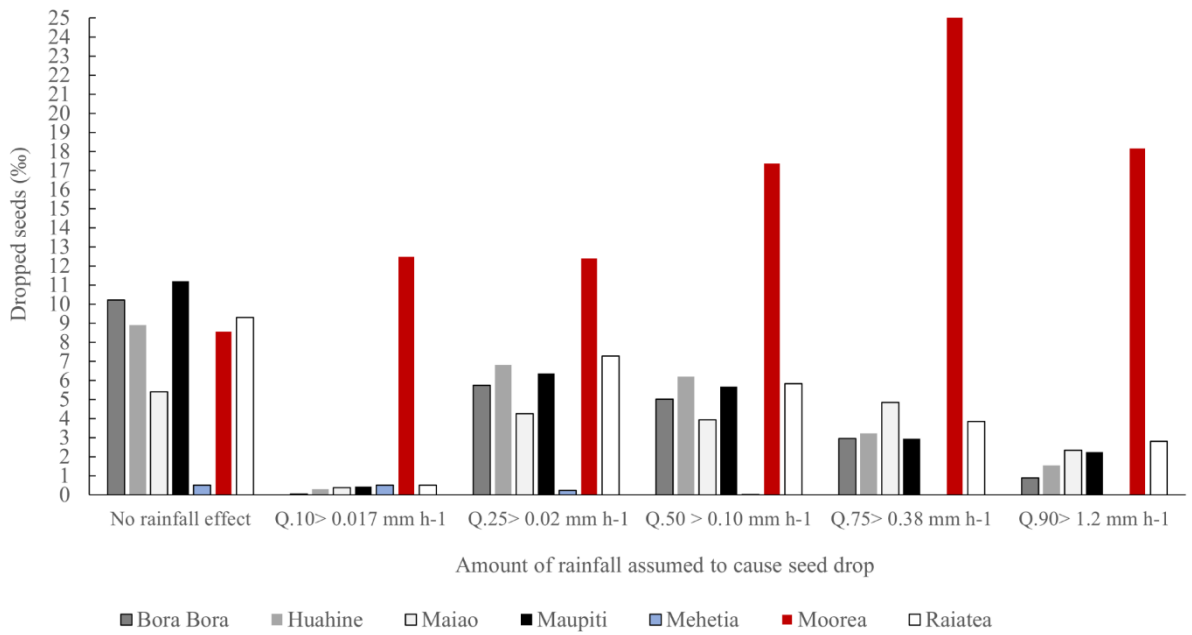
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787 Figure 4

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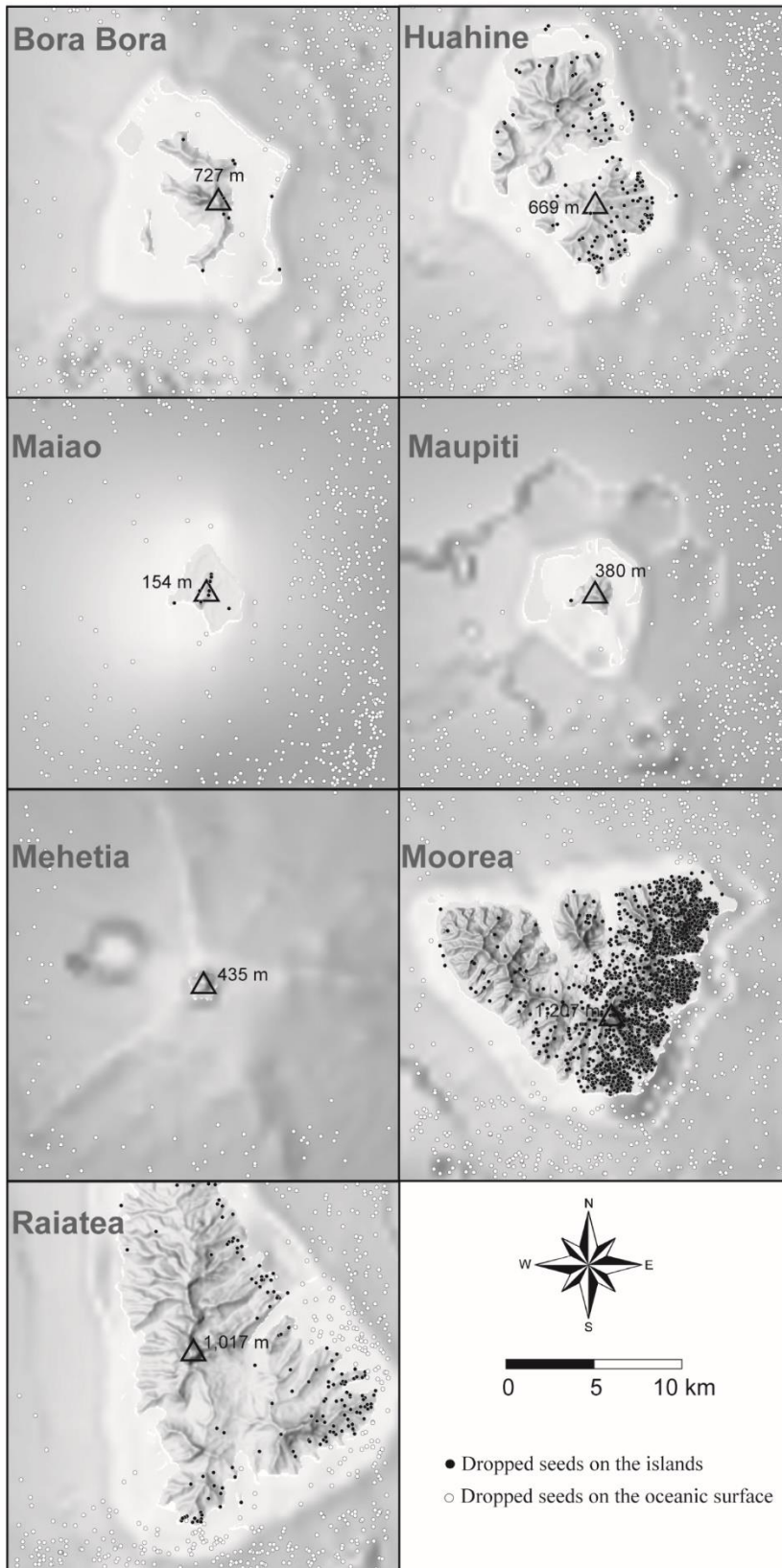
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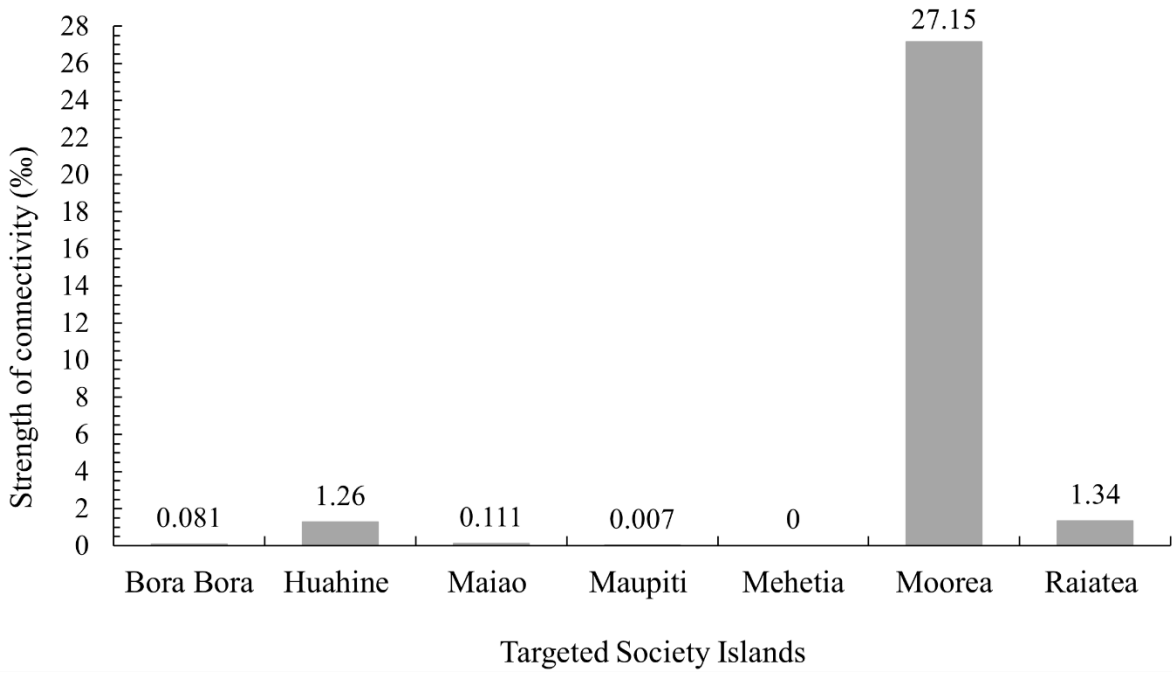


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803 Figure 5

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807 Figure 6

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