

1 **Light converts endosymbiotic fungus to pathogen,**
2 **influencing seedling survival and host tree recruitment**

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4 Patricia Alvarez-Loayza^{*}, James F. White Jr.^{*}, Nathalie Gil[†], Jens-Christian Svenning[‡],
5 Henrik Balslev[‡], Thea Kristiansen[‡]

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7 ^{*}*Department of Plant Biology and Pathology, Rutgers University, New Brunswick, NJ*
8 *08901, USA*

9 [†]*Universidad Nacional San Antonio de Abad, Cusco, Peru*

10 [‡]*Department of Biological Sciences, University of Aarhus, DK-8000 Aarhus C,*
11 *Denmark*

12 **Endophytic fungi that asymptotically colonize plants¹ are**
13 **diverse and abundant in tropical ecosystems². These**
14 **organisms can be weakly pathogenic³ and/or mutualistic,**
15 **frequently enabling plants to adapt to extreme environments,**
16 **alter competitive abilities of host individuals and improve host**
17 **fitness under abiotic or biotic stresses^{4,5,6}. *Diplodia mutila* is**
18 **a symbiotic endophyte/plant pathogenic fungus infecting the**
19 **palm *Iriartea deltoidea*⁷, which dominates many wet lowland**
20 **Neotropical forests. The fungus is an asymptomatic**
21 **endophyte in mature plants, and disease and mortality are**
22 **expressed in some seedlings, while others remain disease**
23 **free. Here we show that seedlings bearing the endophyte**
24 **show enhanced resistance to insect herbivory. However, high**
25 **light availability triggers pathogenicity of the fungus, while**

26 **low light favors endosymbiotic development, constraining**
27 **recruitment of endophyte-infested seedlings to the shaded**
28 **understory by limiting survival of seedlings in direct light.**
29 **These results provide evidence that patterns of plant**
30 **abundance and the mechanisms maintaining tropical forest**
31 **biodiversity are the result of a more complex interplay**
32 **between abiotic and biotic environments than previously**
33 **thought.**

34 The palm *Iriartea deltoidea* is one of the most dominant tree species in wet
35 lowland and premontane tropical forests of western Amazonia⁸⁻¹⁰ and the Chocó- and
36 Central American region^{11,12}. In contrast to most large palms¹³, this species does not
37 depend on large forest gaps for recruitment¹⁴, perhaps related to its peculiar growth
38 strategy¹⁵. However, the inordinate success of *I. deltoidea* in wet New World tropical
39 forests remains an enigma and cannot be explained by morphological attributes such as
40 fruit size or height¹⁰. A partial explanation may be found in the fact that palms have
41 tougher leaves than dicots and thus are less susceptible to insect herbivory¹⁶. In this
42 study we investigate the influence of a common pathogen-endophytic fungus, *Diplodia*
43 *mutila*, on *I. deltoidea* survival and recruitment. *Diplodia mutila*¹⁷ may be both an
44 asymptomatic endophyte and a pathogen of *I. deltoidea*, causing mortality in young
45 seedlings after 5 to 16 days of infection and producing foliar spots in adult plants⁷ (Fig.
46 1A-D). In the pathogenic phase, *D. mutila* forms pycnidia, flask-shaped asexual
47 structures that exude masses of uni-cellular to bi-cellular, hyaline to brown conidia¹⁸
48 (Fig. 1E). In its endophytic phase the fungus exists only as mycelium within tissues of
49 the host's leaves, stems and seeds¹. *Diplodia mutila* and related species have been
50 reported as endophytes or latent pathogens for several plant species worldwide^{19,20}.
51 This fungus is frequently an asymptomatic endophyte in leaves of healthy juvenile and
52 mature plants, as well as fruits and seeds of *I. deltoidea*⁷.

53 It has been suggested that “a species’ abundance at local and large scales may be a
54 simple function of its ability to recruit in close proximity with conspecific adults”¹⁰.
55 *Iriartea deltoidea* seedlings and juveniles are relatively abundant in proximity to adult
56 trees. Demographic censuses of 518 *I. deltoidea* seedlings in 10 plots conducted in 150
57 days show that distribution of *D. mutila*, infected seedlings, was not consistent with the
58 Janzen and Connell model of plant infection^{21,22}. The proportion of plants affected by
59 *D. mutila* was similar near and far from *I. deltoidea* adult plants, $\sim 10\% \pm 0.05\%$, $P > 0.3$
60 (mean \pm SE). The proportion of seedlings affected by stem borers within the first 2.5 m
61 was significantly higher near *I. deltoidea* adult plants, $8\% \pm 0.01\%$ versus $3\% \pm 0.01\%$,
62 $P > 0.045$ *(mean \pm SE). However the proportion of surviving healthy seedlings (no
63 foliar diseases or insect attack) did not vary significantly with distance from adult
64 palms, $\sim 15\% \pm 0.05\%$, $P > 0.9$ (mean \pm SE).

65 We found evidence that *D. mutila* benefits its host plants by enhancing resistance
66 to herbivory by some insects. Field surveys in the 10 surveyed plots, showed that insect
67 herbivory (stem borers: order Coleoptera) decreased with increasing incidence of *D.*
68 *mutila* infection ($F_{1,10} = 18.49$, $P = 0.0026$, $r^2 = 0.69$). Plots with few *D. mutila*
69 infested *I. deltoidea* plants had higher incidence of stem borer mortality, whereas plots
70 with higher incidence of plants colonized by *D. mutila* had lower rates of stem borer-
71 induced mortality. Additional feeding experiments employing *I. deltoidea* fruits and
72 PDA media (Potato Dextrose Agar) colonized by *D. mutila* showed that adults of the
73 beetle *Coccotrypes* sp., and two unidentified species of larvae of the order Coleoptera
74 avoided consumption of fruits and PDA colonized by *D. mutila*. The resistance to
75 insect predators such as stem and seed borers conferred by *D. mutila* may allow *I.*
76 *deltoidea* to escape the generally high intraspecific density- and distance-dependent
77 mortality and recruit near adult trees^{23,24}.

78 This study found that *Diplodia mutila* is beneficial to the plant in understory
79 conditions but strongly reduces the capacity of *I. deltoidea* to recruit in high-light forest
80 gaps. Seedlings of *I. deltoidea* preferentially occur under shady conditions. Extensive
81 sampling at two sites in western Amazonia found out that approximately ~92% of *I.*
82 *deltoidea* seedlings were found in understory conditions. Additionally, the foliar
83 necrotic spot symptoms produced by *D. mutila* appeared more frequently in seedlings
84 and juveniles that grew in gaps or diffusely open canopy conditions. Plants with visible
85 symptoms caused by *D. mutila* received significantly higher illumination, 408.3 ± 17.3 ,
86 than plants with no visible symptoms, 208.2 ± 6.1 , $P < 0.0001$, t test, $n = 808$ (mean
87 $\mu\text{mol m}^{-2} \text{s}^{-1} \pm \text{SE}$). Disease development was faster and more lethal in seedlings with
88 two leaves or less when exposed to higher light conditions ($F_{1,22} = 55.4$, $P = 0.0001$,
89 $r^2 = 0.73$), (Fig. 2A). Ontogenic or age-related resistance may be responsible for
90 differences in disease expression between seedlings in different stages of development
91 ²⁵. An additional experiment showed that pathogenicity of *D. mutila* increased with
92 light availability. We inoculated 22 healthy 6-month old *I. deltoidea* seedlings (no
93 foliar spots or insect marks) with *D. mutila*, following inoculation procedures from
94 previous studies⁷. Foliar spots produced by *D. mutila* had a higher growth rate and
95 mortality was greater and faster at higher light availability ($F_{1,22} = 93.26$, $P = 0.0001$,
96 $R^2 = 0.816$) (Fig. 2B).

97 Using transplant experiments we demonstrated that increased light availability
98 switched the endosymbiotic phase of the fungus to its pathogenic phase. Diametric
99 growth rate of foliar spots produced by *D. mutila* was higher and faster in full sun
100 conditions, 19.5 ± 2.5 cm/day, than in reduced light, 10.0 ± 2.5 cm/day, and shaded
101 conditions 0.52 ± 2.5 cm/day, analysis of variance (ANOVA), $F_{3,30} = 12.62$, $P =$
102 0.0001 , (mean \pm SE) (Fig 3). *Diplodia mutila*-induced seedling mortality in plants
103 exposed to full sun was 80% after 10 days. Seedlings under shaded conditions had 10%
104 mortality and seedlings in the greenhouse had 40% mortality.

105 Laboratory assays showed that fungal growth (measured as diameter of mycelial
106 colonies or as density of mycelium comprising colony) was greater when a 12-hr
107 alternating light-dark cycle was provided than when periods of light were restricted to 3
108 hours. On Water Agar medium (WA) the average growth rate per day of the colony
109 mycelium for five days was higher under a 12-hour light cycle, 0.52 ± 0.03 , than under
110 a 3-hour light cycle, 0.38 ± 0.03 , $P > 0.004$, (mean growth rate (cm) per day \pm SE). On
111 Potato Dextrose Agar medium (PDA) the average growth rate per day of the colony
112 mycelium was faster and also higher under the longer light period, 1.25 ± 0.01 ,
113 compared to 1.11 ± 0.11 for the 3-hour photoperiod, $P > 0.018$, (mean growth rate (cm)
114 per day \pm SE) and the mycelium was notably denser with more aerial mycelium (Fig.
115 4A). We recorded greater melanization of mycelium in colonies exposed to the longer
116 light period. This was especially evident in colonies grown on PDA. Melanization of
117 mycelium has been linked to enhanced virulence in numerous plant and animal
118 pathogenic fungi²⁶. Colonies grown in PDA under the 12-hour light cycle had
119 significantly faster growth of the central melanized area, 0.71 ± 0.05 , than colonies
120 exposed to the 3-hour light treatment, 0.5 ± 0.05 , $P > 0.022$, (mean growth rate (cm) per
121 day \pm SE), (Fig. 4B, Fig. 4D). Similar significant results were obtained for colonies
122 growing in WA medium (Fig. 4B.)

123 Our field surveys and experiments demonstrate that *D. mutila* has a less
124 destructive effect on *I. deltoidea* seedlings growing under closed canopy conditions than
125 under gap conditions. Pathogenicity of the endophytic phase of this fungus is triggered
126 by increased light availability. Laboratory observations on the pathogen indicate that *D.*
127 *mutila* mycelial growth and melanin production increase with light exposure. We
128 suggest that higher light intensity could increase both the rate of development of this
129 fungus in plants as well as its virulence. It is apparent that *D. mutila*-colonized *I.*
130 *deltoidea* seedlings survive better under closed canopy conditions due to the effect of
131 light in triggering the pathogenic phase of the endophyte. When these plants become

132 older seedlings, the pathogen does not seem to affect plant performance even at high
133 light availability and, additionally, may confer other advantages to these plants, i.e.,
134 defensive mutualism²⁷. Endophytes in many plants have been shown to provide hosts
135 with increased herbivore and/or environmental stress resistance⁴⁻⁶. The case of *D.*
136 *mutila* demonstrates that the environment can drastically impact how an endosymbiotic
137 fungus affects fitness of its host. Thus, we ask: to what extent are microorganisms
138 really influencing tropical ecosystems? Most ecological research attempting to explain
139 plant distributions has concentrated on: 1) understanding how abiotic factors interact
140 with plants to maintain biodiversity and determine plant abundance in tropical rain
141 forests; or 2) examining how biotic factors such as morphological characters,
142 herbivores, pathogens or seed dispersers influence these mechanisms and patterns. This
143 case study of *I. deltoidea* shows that host plant characteristics such as age, light-
144 dependent pathogenicity and virulence of an endophyte-pathogen (i.e., *D. mutila*) and
145 endophyte-enhanced defense against insects, are intrinsically connected, influencing
146 patterns of seedling survival and potentially explaining species abundance on larger
147 scales.

148 **Methods**

149 **Demographic Censuses**

150 In northeastern Peru 28 we arbitrarily placed 102 transects (5 x 500 m, divided in
151 5 x 5 m subunits) located in mature primary tropical rain forest within 300 km of
152 Iquitos, Peru (excluding transects located in secondary forests, white sand soils, steep
153 topographical conditions and human disturbed forests). Sites in southeastern Peru were
154 located at Cocha Cashu, (CCBS)²⁹ and Los Amigos, (LABS)³⁰. Ten plots were
155 established in May 2007, in primary floodplain forest, with similar floristic composition
156 and topographic characteristics. Five of plots were located at CCBS and five at LABS.
157 Nine plots measured 900 m² and one plot at CCBS measured 2.25 ha. In each plot all *I.*

158 *deltoidea* plants were tagged with numbered plastic tags and mapped in an X - Y
159 coordinate system. The total number of plants located in the 10 plots was 1068: 63
160 fruiting adults, 518 seedlings and 487 were considered juveniles-adults (non-fruiting)
161 (SI). We measured height of the tallest photosynthetic leaf (cm) and number of leaves
162 and diameter of foliar spots caused by *D. mutila* (cm) for all seedlings. The amount of
163 disease was calculated by dividing the diameter of the foliar spot by the diameter of the
164 affected leaf and expressed as ‘% disease’. Disease development over a period of 150
165 days was calculated by subtracting the % disease in the initial estimate from the final
166 estimate.

167 **Distribution of seedlings affected by stem borers and *D. mutila***

168 Plants damaged and killed by epicotyl borers, such as caterpillars, beetle larvae or
169 crickets, were considered as “damaged by stem borers” (SI). Plants located in the
170 southeastern Peru plots were monitored for presence/absence of *D. mutila* and stem
171 borers, three times after initial establishment (7, 50 and 150 days). In each plot, the
172 minimum distances, from all seedlings to the nearest *I. deltoidea* fruiting plant were
173 computed using the coordinates of the labelled plant under consideration and the
174 coordinates of the nearest fruiting tree within the plot. We surveyed seedlings in 5
175 concentric 2.5 m annuli centred on a focal fruiting tree. The number of seedlings
176 affected by stem borers and *D. mutila* was tallied for each 2.5 m annulus and then
177 divided by the total number of plants located in the selected annulus to yield
178 proportions. One-way ANOVA was used to compare diseases and mortality
179 proportions among plots for each distance annulus (Tukey's HSD used to contrast
180 means). The proportion of plants affected by stem borers within the first 2.5 m was
181 significantly higher than proportions in the other 4 annuli, in the first census, after ~7
182 days, $8\% \pm 0.01\%$, $6\% \pm 0.01\%$, $4\% \pm 0.01\%$, $3\% \pm 0.01\%$, $3\% \pm 0.01\%$, ($F_{4,50} = 2.65$,
183 $P > 0.045^*$) and the second census, after ~50 days, $10\% \pm 0.01\%$, $4\% \pm 0.01\%$, $1\% \pm$

184 0.01%, $2\% \pm 0.01\%$, $0.7\% \pm 0.01\%$ ($F_{4,50} = 4.28$, $P > 0.0051^*$). Stem borer attack
185 decreased in the last census.

186 **Light availability measurement.**

187 In northeastern Peru light availability was measured using the canopy scope
188 methodology³¹. In southeastern Peru light availability was estimated above the tallest
189 photosynthetic leaf of each *I. deltoidea* seedling, using the average value of light
190 intensity over the leaf with a light meter (Environmental Concepts Plant Light Intensity
191 Meters, LIM2500, USA). The average value was obtained from three measurements
192 over each plant at 6 am, 12 pm and 5 pm for three consecutive days. The total number
193 of seedlings in the northeastern Peru transects was 660, 94% of seedlings were located
194 at understory conditions (canopy scope <5). The negative correlation between the
195 number of *I. deltoidea* seedlings and canopy openness in the 102 transects (Spearman r
196 = -0.117, $P < 0.05$) was estimated using, $n = 280$ 5-m \times 5-m subplots with at least one *I.*
197 *deltoidea* seedling. Statistical significance was assessed as a one-tailed test and
198 correcting for spatial autocorrelation using Dutilleul's approach for computing the
199 geographically effective degrees of freedom = 227³². The total number of seedlings in
200 the southeastern Peru plots was 518 seedlings (less than 25 cm), 91% seedlings were
201 located in dense understory ($\sim 55\text{-}120 \pm 15 \mu\text{mol m}^{-2} \text{s}^{-1}$).

202 ***Diplodia mutila*–mediated insect protection in *I. deltoidea*.**

203 On December 2007, ~ 370 *Coccotrypes* sp. beetles and larvae were extracted from
204 more than 100 fruits and seeds of *I. deltoidea*. In a Petri plate (60 x 15 mm, Fisher
205 Scientific Co. Canada) we placed two 1-cm² of PDA (Potato Dextrose Agar) and two 1-
206 cm² of PDA infested with *D. mutila*, covered with squares of non-acidic paper to
207 simulate dark conditions found inside seeds and fruits. PDA was replaced everyday for
208 the duration of the experiment to avoid contamination of non-infested PDA by *D.*
209 *mutila*. We set up 12 repetitions following this procedure. Six to ten beetles were

210 released in the each Petri plate and monitored daily for 8 to 12 days. Beetles
211 consistently preferred PDA (SI) and avoided *D. mutila* infested PDA, 4.8 ± 0.14 versus
212 1.4 ± 0.14 , (Repeated Measurement Analysis, Random Effect $F_{4, 456} = 160.13$, $P =$
213 0.0001^{**}). Similar results were also obtained when the experiment was performed
214 using *Coccotrypes* sp. adults and *I. deltoidea* fruits instead of PDA (SI).

215 **Transplant experiments**

216 We transplanted 30 *I. deltoidea* seedlings from one plot at Cocha Cashu where
217 adults, juveniles, seeds and fruits were colonized by *D. mutila*. Ten seedlings were
218 transplanted to shade conditions, $\sim 55 \pm 15 \mu\text{mol m}^{-2} \text{s}^{-1}$, 10 to a reduced light
219 environment in a greenhouse, $\sim 491 \pm 34 \mu\text{mol m}^{-2} \text{s}^{-1}$, and 10 to full sun exposure,
220 $\sim 1058 \pm 23 \mu\text{mol m}^{-2} \text{s}^{-1}$. All seedlings had 2 leaves and did not have any visible
221 disease symptoms produced by *D. mutila* or any other foliar spot. Light availability was
222 measured three times a day (6 am, 12 pm and 5 pm) for a period of 10 days and all
223 disease symptoms and insect damage were recorded and measured daily. The average
224 daily temperature in the understory and full sun conditions was $23^{\circ} \text{C} \pm 3$ and $26^{\circ} \text{C} \pm 5$
225 in the greenhouse.

226 **Laboratory Assays**

227 To assess the effect of light on the fungus, laboratory observations were made on
228 mycelial growth in Water Agar (WA) and Potato Dextrose Agar (PDA). Two
229 photoperiod treatments were employed for five days with six *D. mutila* samples per
230 treatment. The first treatment consisted of 12-hour cycle of darkness and 12-hour cycle
231 of white light (fluorescent, $100 \pm 10 \mu\text{mol m}^{-2} \text{s}^{-1}$), while the second consisted of 21-
232 hour cycle of darkness and 3-hour cycle of light for five days, (6 repetitions per
233 treatment, constant temperature for all treatments was 24°C).

234

235 **Supplementary Information** accompanies the paper on www.nature.com/nature.

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245 Correspondence to: Patricia Alvarez-Loayza. Correspondence and requests for materials should be
246 addressed to P. A-L. (E-mail:palvarez@eden.rutgers.edu).

247

248 **Figure 1** Foliar spots in *Iriartea deltoidea* caused by *Diplodia mutila*, at different
249 infection stages. **(A)** Leaf spot infection for a plant with 2 leaves and one spot
250 covering less than 20% of the leaf **(B)** A plant with two leaves and with a spot
251 covering ~40% of one leaf **(C)** A plant with two leaves and with the two foliar
252 spots covering 50% of both leaves **(D)** Foliar spots covering the entire plant
253 represented 100% of infection. These plants died after 15 to 31 days. **(E)**
254 *Diplodia mutila* pycnidia produced slowly maturing, non-striate, brown, 1-septate
255 conidia measuring 26-28 × 15-20 μm. Liquid conidial darkening and septation
256 was recorded to take place after discharge.

257 **Figure 2** Higher light intensities increased disease development produced by
258 *Diplodia mutila*. **(A)** For young seedlings with 2 leaves or less there was a

259 significant interaction between amount of infection (% of *D. mutila* foliar spots in
260 *Iriartea deltoidea* leaves) and light level ($F_{1,22} = 55.4$, $P = 0.0001^{**}$, $r^2 = 0.73$).

261 **(B)** The diametric growth rate of the foliar spots produced by *D. mutila* was
262 higher at higher light conditions ($F_{1,22} = 93.26$, $P = 0.0001^{**}$, $r^2 = 0.816$).

263

264 **Figure 3** Increased light availability switched the endosymbiotic phase of *D.*
265 *mutila* to its pathogenic phase. Young seedlings that were colonized with
266 endophytic *Diplodia mutila* showed faster growth rates of diameter of foliar
267 spots (cm) caused by the pathogenic phase of *D. mutila* at higher light
268 intensities ($\sim 1058 \pm 23 \mu\text{mol m}^{-2} \text{s}^{-1}$) than seedlings under shaded conditions
269 ($\sim 55 \pm 15 \mu\text{mol m}^{-2} \text{s}^{-1}$) ($n = 30$, t test, $P = 0.0001^{**}$). There were also
270 significant differences of foliar spot growth rates among plants growing in the
271 greenhouse ($\sim 491 \pm 34 \mu\text{mol m}^{-2} \text{s}^{-1}$) and plants growing under shaded
272 conditions ($n = 30$, t test, $P = 0.024^*$). Foliar spot growth rates among plants
273 growing in the greenhouse were lower than plants growing under high light
274 intensities ($n = 30$, t test, $P = 0.013^*$), (Tukey Kramer ANOVA, $F_{3,30} = 12.62$, P
275 $= 0.0001^{**}$).

276

277 **Figure 4 (A)** Mycelial radial growth of *Diplodia mutila* on Potato Dextrose Agar
278 (PDA) was faster under a 12-hour cycle than the 3-hour cycle $\sim 1.25 (\pm 0.03)$
279 cm/day vs. $1.11 (\pm 0.03)$ cm./day ($n = 12$, t test, $P > 0.018^*$). On Water Agar
280 (WA) the average radial growth rate per day of the colony mycelium was ~ 0.51
281 cm/day under a 12-hour light cycle; while under a 3-hour light cycle the average
282 growth rate of the colony mycelium was significantly lower, at ~ 0.41 cm/day
283 after 7 days ($n = 12$, t test, $P > 0.004^*$). **(B)** Colonies grown in PDA under the
284 12-hour light cycle had a more rapid melanization of the central area of the

285 colony (~0.71 cm/day) than colonies exposed to 3-hours of light (~0.5 cm/day)
286 (n =12, *t* test, *P* > 0.022*). Similar results were obtained for colonies growing in
287 WA (n =12, *t* test, *P* > 0.0258*). **(C)** Melanization of colonies of *D. mutila*
288 growing in PDA observed on 4 days (from left to right). Rate of melanization
289 was reduced in the 3-hour cycle treatment (above). Faster melanization was
290 observed in cultures maintained in a 12-hour light cycle (below).

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 292 1 Petrini, O., Taxonomy of endophytic fungi of aerial plant tissues in
 293 *Microbiology of the Phyllosphere*, edited by N. J. Fokkema & J. van den
 294 Heuve (Cambridge University Press, Cambridge, UK, 1986), pp. 175-187.
 295 2 Arnold, E., Maynard, Z., Gilbert, G., Coley, P.D., & Kursar, T.A., Are Tropical
 296 Fungal endophytes hyperdiverse? *Ecology Letters* 3, 267-274 (2000).
 297 3 Schulz, B. & Boyle, C., The endophytic continuum. *Mycological Research* 109,
 298 661–686 (2005).
 299 4 Arnold, A.E. *et al.*, Fungal endophytes limit pathogen damage in a tropical tree.
 300 *Proc. Natl. Acad. Sci.* 100, 15649-15654 (2003).
 301 5 Arnold, A.E. & Engelbrecht, B.M.J., Fungal endophytes nearly double minimum
 302 leaf conductance in seedlings of a tropical tree. *J. Trop. Ecol.* 23, 369-372
 303 (2007).
 304 6 Rodriguez, R.J., Redman, R.S., & Henson, J.M., The Role of Fungal Symbioses
 305 in the Adaptation of Plants to High Stress Environments. *Mitigation and*
 306 *Adaptation Strategies for Global Change* 9, 261-272 (2004).
 307 7 Álvarez-Loayza, P., White, J.F., Bergen, M., & Cadenas, C., *Diplodia mutila*
 308 causing seedling mortality of *Iriartea deltoidea* palm trees. *Plant Pathology* 57,
 309 382 (2008).
 310 8 Macía, M.J. & Svenning, J.-C., Oligarchic dominance in western Amazonian
 311 plant communities. *J. Trop. Ecol.* 21, 613-626 (2005).
 312 9 Valencia, R. *et al.*, Tree species distributions and local habitat variation in the
 313 Amazon: large forest plot in eastern Ecuador. *J. Ecology* 92 (214-229) (2004).
 314 10 Pitman, N.C.A. *et al.*, Dominance and Distribution of Tree Species in Upper
 315 Amazonian Terra Firme Forests. *Ecology* 82, 2101-2117 (2001).
 316 11 Clark, D.B., Palmer, M.W., & Clark, D.A., Edaphic factors and the landscape-
 317 scale distributions of tropical rain forest trees. *Ecology* 80, 2662-2675 (1999).
 318 12 Wattenberg, I. & Breckle, S.-W., Tree species diversity of a premontane rain
 319 forest in the Cordillera de Tilaran, Costa Rica. *Ecotropica* 1 (21-30) (1995).
 320 13 Svenning, J.-C., On the role of microenvironmental heterogeneity in the ecology
 321 and diversification of neotropical rain forest palms (Arecaceae). *Botanical*
 322 *Review* 67, 1-53 (2001).
 323 14 Svenning, J.C., Recruitment of Tall Arborescent Palms in the Yasuni National
 324 Park, Amazonian Ecuador: Are Large Treefall Gaps Important? *J. Trop.*
 325 *Ecol.* 15, 355-366 (1999).
 326 15 Terborgh, J. & Davenport, L., Endogenous and Exogenous Control of Leaf
 327 Morphology in *Iriartea deltoidea* (Palmae). *J. Trop. Ecol.* 17, 695-703 (2001).
 328 16 Grubb, P.J. *et al.*, Monocot leaves are eaten less than dicot leaves in tropical
 329 lowland rain forests: Correlations with toughness and leaf presentation. *Annals*
 330 *of Botany*, 11 (2008).
 331 17 Sutton, B.C., *The Coelomycetes*. (Commonwealth Mycological Institute, Kew,
 332 UK 1980).
 333 18 Crous, P.W. *et al.*, Phylogenetic lineages in the Botryosphaeriaceae. *Studies in*
 334 *Mycology* 55, 235–253 (2006).
 335 19 Damm, U., Crous, P.W., & Fourie, P.H., Botryosphaeriaceae as potential
 336 pathogens of *Prunus* species in South Africa, with descriptions of *Diplodia*
 337 *africana* and *Lasiodiplodia plurivora* sp. nov. *Mycologia* 99, 664-680 (2007).

- 338 20 Slippers, B. & Wingfield, M.J., Botryosphaeriaceae as endophytes and latent
 339 pathogens of woody plants: diversity, ecology and impact. *Fungal Biology*
 340 *Reviews* 21, 90-106 (2007).
- 341 21 Connell, J.H., On the role of natural enemies in preventing competitive
 342 exclusion in some marine animals and in rain forest trees in *Dynamics of*
 343 *numbers in populations*, edited by P.J. Den Boer & G.R. Gradwell (Centre for
 344 Agricultural Publication and Documentation. , Wageningen, Netherlands.,
 345 1971), pp. 298–312
- 346 22 Janzen, D., Herbivores and the Number of Tree Species in Tropical Forests. *Am.*
 347 *Nat.* 104, 501-529 (1970).
- 348 23 Peters, H., Neighbour-regulated mortality: the influence of positive and negative
 349 density dependence on tree populations in species-rich tropical forests. *Ecology*
 350 *Letters* 6, 757–765 (2003).
- 351 24 Queenborough, S.A., Burslem, D.F.R.P., Garwood, N.C., & Valencia, R.,
 352 Neighborhood and Community interactions determine the spatial pattern of
 353 tropical tree seedling survival. *Ecology* 88, 2248-2258 (2007).
- 354 25 Panter, S.N. & Jones, D.A., Age-related resistance to plant pathogens in
 355 *Advances in Botanical Research* (Academic Press, 2002), Vol. 38, pp. 251-280.
- 356 26 Langfeldera, K., Streibela, M., Jahn, B., Haase, G., & Brakhage, A.A.,
 357 Biosynthesis of fungal melanins and their importance for human pathogenic
 358 fungi. *Fungal Genetics and Biology* 38, 143-158 (2003).
- 359 27 Clay, K. & Holah, J., Fungal Endophyte Symbiosis and Plant Diversity in
 360 Successional Fields. *Science* 285, 1742-1744 (1999).
- 361 28 Normand, S., Vormisto, J., Svenning, J.-C., Grández, C., & Balslev, H.,
 362 Geographical and environmental controls of palm beta diversity in paleo-
 363 riverine terrace forests in Amazonian Peru. *Plant Ecology* 186, 161-176 (2006).
- 364 29 Terborgh, J., *Five New World primates: a study in comparative ecology*.
 365 (Princeton University Press, Princeton, 1983).
- 366 30 Pitman, N.C.A. An overview of the Los Amigos watershed, Madre de Dios,
 367 southeastern Peru. (ACCA, Puerto Maldonado, Peru, 2007).
- 368 31 Brown, N., Jennings, S., Wheeler, P., & Nabe-Nielsen, J., An improved method
 369 for the rapid assessment of forest understorey light environments. *Journal of*
 370 *Applied Ecology* 37, 1044-1053 (2000).
- 371 32 Rangel, T.F., Diniz-Filho, J.A.F., & Bini, L.M., Towards an integrated
 372 computational tool for spatial analysis in macroecology and biogeography.
 373 *Global Ecology and Biogeography* 15, 321-327 (2006).
- 374
 375













