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1 **Endemic trees in a tropical biodiversity hotspot imperilled by an invasive tree**

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3

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11 Running head: Tree invasion reduces native tree diversity and richness.

12 Highlights:

- 13 • A non-native tree, *Pittosporum undulatum*, is invading Jamaican montane rain forests
- 14 • Its invasion accelerated after an intense hurricane in 1988 and has not slowed since
- 15 • Local-scale tree species richness and diversity declines the more it invades
- 16 • The percentage of stems of trees endemic to Jamaica declines the more it invades
- 17 • A programme of control and removal is needed now to prevent further declines

18

19

20 **Abstract**

21 Non-native plants invade some tropical forests but there are few long-term studies of these
22 invasions, and the consequences for plant richness and diversity are unclear. Repeated
23 measurements of permanent plots in tropical montane rain forests in the Blue and John Crow
24 Mountains National Park in Jamaica over 24 to 40 years coincided with invasion by a non-native tree,
25 *Pittosporum undulatum*. By 2014, *P. undulatum* comprised, on average, 11.9% of stems ≥ 3 cm
26 diameter and 10.4% of the basal area across 16 widespread plots within c. 250 ha of the forests.
27 Across these plots, the more *P. undulatum* increased in basal area over 24 years, the greater the
28 decline in local, plot-scale tree species richness, and the greater the reduction in the percentage of
29 stems of endemic tree species. Plot-scale tree diversity (Shannon and Fisher's alpha) also declined
30 the more *P. undulatum* basal area increased, but beta diversity across the plots was not reduced.
31 Declines in local-scale tree species diversity and richness as the invasion progresses is especially
32 concerning because Jamaica is a global biodiversity hotspot. Native birds disperse *P. undulatum*
33 seeds widely, and future hurricanes will probably further increase its invasion by reducing canopy
34 cover and therefore promoting growth rates of its established shade-tolerant seedlings. Remedial
35 action is needed now to identify forest communities with greatest endemism, and to protect them
36 through a continuing programme of control and removal of *P. undulatum*.

37 **Keywords:** biodiversity hotspot; Jamaica, *Pittosporum undulatum*; resilience; tree species richness;
38 tropical montane rain forest

39

40 **1. Introduction**

41 Invasions of ecosystems by non-native plants often cause homogenization of communities and
42 altered ecosystem functions and services (Ehrenfeld, 2010; Pyšek et al., 2012; van Wilgen et al.,
43 2008). The consequences of these invasions for the diversity and richness of resident native plant

44 communities, and the extent to which richer and more diverse communities are invadable, are
45 contentious (Fridley et al., 2007). Tropical rain forests are very species-rich and most are not
46 currently invaded by non-native plants (e.g. Fine, 2002), but there are increasing incidences of non-
47 native tree invasions in tropical montane forests (Barbosa et al., 2017; Binggeli and Hamilton, 1993;
48 Florens et al., 2016; Martin et al., 2004; Meyer, 1996). Plant invasions pose an emerging threat to
49 these forests, compounding effects of deforestation and climate change (Martin and Bellingham,
50 2016), and forests on islands seem particularly susceptible (Denslow, 2003; Denslow and DeWalt,
51 2008; Kueffer et al., 2010; Pyšek et al., 2012).

52 Tropical montane forests are limited by low light levels (because of fog and cloud cover) and low soil
53 nutrient concentrations (nitrogen, N, in particular) (Bruijnzeel et al., 2010; Dalling et al., 2016; Fahey
54 et al., 2016). Non-native plants that invade these ecosystems can be more efficient than native
55 species at using limiting resources (Funk and Vitousek, 2007). Many non-native tree species that
56 invade tropical montane forests have shade-tolerant seedlings that can grow rapidly if forest
57 canopies are disturbed (Funk, 2013; Martin et al., 2009). The rate of invasion of tropical montane
58 rain forests in Jamaica by a shade-tolerant tree, *Pittosporum undulatum* Vent. (Pittosporaceae),
59 increased sharply in the sixteen years after the forests were strongly affected by an intense
60 hurricane (Bellingham et al., 2005), supporting a view that disturbance can play a catalytic role in the
61 invasion of tropical forests (e.g. Dawson et al., 2015; Dillis et al., 2017; Murphy and Metcalfe, 2016).
62 It remains unclear how many invasions promoted by disturbances in tropical forests are transient
63 (Ackerman et al., 2017) or are widespread and persistent, especially if the plants are shade-tolerant
64 (Murphy and Metcalfe, 2016).

65 The Greater Antilles of the Caribbean, including Jamaica, are invaded by c. 500 non-native plant
66 species (Rojas-Sandoval et al., 2017). They are also a global hotspot for endemism (Myers et al.,
67 2000). In Jamaica's tropical montane rain forests, 41% of the tree flora is endemic (Tanner, 1986).
68 We have conducted repeated measurements of tree species composition, growth and mortality in

69 these forests over periods up to 40 years, which coincided with invasion by a non-native tree, *P.*
70 *undulatum*. Longitudinal assessments like these, along with experimental studies, are needed to
71 determine the relationships between plant invasions and native plant richness and diversity because
72 correlational studies, based on point-in-time assessments, do not provide compelling evidence
73 (Catford et al., 2012; Fridley et al., 2007).

74 *Pittosporum undulatum* is a tree native to eastern Australia that grows to 14 m height (Grubb et al.,
75 2013). It is invasive in South Africa and on several islands including Lord Howe Island, St Helena, and
76 Hawaii (Pasiiecznik and Rojas-Sandoval, 2015) and it occupies about 30% of the forested area on the
77 Azores (Silva et al., 2017). In Jamaica, it was intentionally introduced to the Cinchona Botanic
78 Gardens on the southern slopes of the Blue Mountains in the late 19th century (Bellingham et al.,
79 2005). By the 1970s, it had invaded nearby montane rain forests along the edges of trails (Grubb and
80 Tanner, 1976). By the 1990s, *P. undulatum* was dominant in areas of secondary forest (McDonald
81 and Healey, 2000; McDonald et al., 2003). By 2004, it had increasingly invaded longer-established
82 natural forests (with canopies that range in height from 6 to 12 m and taller in gullies; Asprey and
83 Robbins, 1953), and occurred in 69% of forest plots, locally as canopy trees (Bellingham et al., 2005).
84 Seedlings of *P. undulatum* in these forests grow to become mature canopy trees within 24 to 35
85 years after the creation of experimental canopy gaps (Chai et al., 2012). In this study, we evaluate
86 whether the rapid increase in invasion observed in the 16 years after Hurricane Gilbert (1988) was
87 sustained over the next decade. The forests have not been significantly disturbed by hurricanes since
88 1988 (Tanner et al., 2014) and a period without major disturbance, during which forest canopies
89 reformed, might retard the rate of invasion (Murphy and Metcalfe, 2016). However, since *P.*
90 *undulatum* is shade-tolerant (Gleadow et al., 1983; Chai et al., 2012), this need not be so (Martin et
91 al., 2009). Our long-term data allowed us to evaluate how diversity and richness of native tree
92 species have been affected by invasion at local and wider scales.

93

94 **2. Methods**

95 *2.1 Study sites*

96 The study sites are in upper montane rain forests in the western Blue Mountains of Jamaica (Fig. 1).
97 A 40-year record of change derives from localised sites on and near the main ridge (18° 05'N; 76°
98 39'W, 1540–1620 m elevation; four sites, 'Col' 0.09 ha, 'Mor' 0.06 ha, 'Mull' 0.10 ha and 'Slope' 0.10
99 ha; Tanner, 1977), measured in 1974, 1984, 1989, 1991, 1994, 2004, 2009, and 2014. The 24-year
100 record of change derives from 16 systematically placed, widespread 200 m² plots within c. 250 ha:
101 six on the ridge crest, five on the northern slopes (windward to the prevailing trade winds), and five
102 on the southern leeward slopes (18° 05'N; 76° 39–40'W, 1375–1920 m; Bellingham, 1991),
103 measured in 1990, 1994, 2004, and 2014. Stem densities and tree species richness and diversity
104 were measured (Table 1). In the localised sites and widespread plots, all stems ≥3 cm diameter at 1.3
105 m height (dbh) were identified to species, tagged with a unique number, their diameter recorded,
106 and a band painted at the dbh datum. At each remeasurement, all stems were relocated and their
107 new dbh recorded. Dead stems were recorded and stems that had grown to become ≥3 cm dbh at
108 each remeasurement were identified to species, tagged, and painted. Across all measurements,
109 there was a total of 3012 stems in the localised sites, including those that died and those newly
110 recruited (on average 1802 live stems at each measurement) and 2682 stems across the widespread
111 plots (on average 1876 live stems). Concentrations of total carbon (C), N, and phosphorus (P and
112 Bray-extractable P) were determined from soils collected in 2004 from each widespread plot (0–15
113 cm depth; Bellingham et al., 2005). Plot elevations were estimated from maps and GPS data.

114 The mean annual rainfall averages 2500–3000 mm, and the mean maximum monthly temperatures
115 range from 18.5 to 20.5 °C and minima from 11 to 12 °C (Kapos and Tanner, 1985). Our study sites
116 were affected strongly by Hurricane Gilbert on 12 September 1988 (Bellingham et al., 1995). No
117 other hurricane eye passed within 50 km of the study sites during 37 years before Hurricane Gilbert,
118 and none have since; those with tracks >50 km away between 1988 and 2014 have not had strong

119 effects (Tanner et al., 2014). Our study sites provide records of change in the forests for 14 years
120 before and 26 years after Hurricane Gilbert in the localised sites, and a 24-year record (all post-
121 Hurricane Gilbert) from the widespread plots.

122 *2.2 Analysis*

123 We determined whether tree and tree fern species were endemic (data from Adams (1972) and
124 Proctor (1985), both updated by <http://www.theplantlist.org/>; access date 16 February 2017). We
125 conducted rarefaction of stems in each plot based upon the fewest stems in a plot in a census
126 (Ecosim; Gotelli and Enstminger, 2006) before calculating, for each of the widespread plots in 1990
127 and 2014, species richness, Shannon H' and Fisher's alpha diversity (Magurran, 2003). We calculated
128 all ANOVAs and linear regressions in GenStat (14th edition). No data transformations were necessary
129 for ANOVAs to account for heteroskedasticity. To determine whether there were differences in beta
130 diversity across the widespread plots, we tested for differences using PERMDISP2 (implemented in
131 the R package *vegan* (function *betadisper*) in R version 3.3.2) based on stem densities and basal
132 areas of each tree species in each plot at each measurement between 1990 and 2014. We first
133 determined whether there were differences in the centroids in multivariate analyses (there were
134 none: $P > 0.99$ for both stem and basal area analyses, including all 16 plots in both 1990 and 2014).
135 We then evaluated whether the average distances of the 16 plots from the centroid differed among
136 years (F value), with a P value calculated by permuting distances among the groups of plots
137 (Anderson, 2006). We present an ordination of vegetation in the 16 widespread plots in 2014. Non-
138 metric multidimensional scaling with Jaccard distance was used to ordination the basal area data;
139 we overlay vectors of variables correlated with the ordination. We calculated correlation using the
140 *envfit* function from R package *vegan*.

141

142 **3. Results**

143 By 2014, *Pittosporum undulatum* occurred in 12 of the 16 widespread plots (75%), and comprised,
144 on average, 11.9% of stems and 10.4% of the basal area (Fig. 2), an increase of 3.2% and 4.7%
145 respectively since 2004, with both variables showing near-linear rates of increase from low levels of
146 invasion in 1990, soon after Hurricane Gilbert. The four localised sites studied since 1974 were much
147 less invaded in 2014; the Mull site was the most invaded (3.0% of the basal area, Fig. 2).

148 Across the widespread plots, the combined basal area of all species increased significantly by 9.7%
149 between 1990 and 2014, due nearly entirely to a 526% increase in *P. undulatum* basal area, since the
150 basal area of all other species (and the subset that are endemic) was unchanged (Table 1). In
151 contrast, the combined stem density of all species was unchanged between 1990 and 2014, but *P.*
152 *undulatum* stem densities increased by 500% while the stem densities of all other species declined
153 by 13.6% (Table 1). Endemic woody species richness per plot declined by 13.5% over the 24-year
154 period, and their stem densities by 17.6% (Table 1). Shannon H' and Fisher's alpha diversity of all
155 woody species per plot did not change significantly (Table 1).

156 Across the widespread plots, however, the greater the increase in the basal area of *P. undulatum*
157 over 24 years the greater the decline in local, plot-scale tree species diversity (Shannon H' and
158 Fisher's alpha) and richness, even after removing from the analysis an outlier highly-invaded plot
159 with substantially the greatest increase in *P. undulatum* basal area (Fig. 3a–c). The percentage of
160 stems of endemic tree species also declined over 24 years the more *P. undulatum* basal areas
161 increased (Fig. 3d), as did the number of endemic stems per plot ($r^2 = 0.35$, $P = 0.009$; data not
162 shown). Declines in tree species diversity (H' and Fisher's alpha), richness, and in the percentage of
163 endemic trees were most apparent where the basal area of *P. undulatum* increased $> 0.2 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$
164 over 24 years (Fig. 3). There were no differences, among any of these variables, in whether the
165 greatest declines occurred in plots on the northern or southern slopes or the ridge crest. Among
166 eight widespread plots not invaded in 1990 but invaded subsequently, there were no significant

167 relationships between the 2014 basal area of *P. undulatum* and the 1990 native tree species richness
168 or diversity (H' and Fisher's alpha; all $P > 0.11$).

169 There were no significant differences in beta diversity across the 16 widespread plots between 1990
170 and 2014, in terms of both basal area ($F = 0.0007$, $P = 0.98$) and stem density ($F = 0.220$, $P = 0.64$).

171 Among the 16 plots, tree species composition as expressed by basal area in 2014 was driven most
172 strongly by elevation, and also by soil C and N concentrations (Fig. 4). Centroids of plots on the
173 windward northern slopes did not differ significantly from those on the leeward southern slopes ($F =$
174 1.29 , $P = 0.13$; Fig. 4).

175 Annual increases in basal area of *P. undulatum* across the widespread plots were greater the lower
176 the soil N concentration (Fig. 5a) and the lower the soil C concentration (Fig. 5b). They were not
177 significantly related to soil P concentrations (both total P and Bray extractable P), soil pH, or to plot
178 elevation.

179

180 4. Discussion

181 Invasion by *Pittosporum undulatum* of Jamaican montane rain forests over c. 25 years increased at a
182 near-linear rate, with no sign of the rate slowing as forest canopies closed during recovery after
183 intense hurricane disturbance in 1988. By 2014, *P. undulatum* comprised, on average, c. 10% of the
184 stems and the basal area across the widespread plots. Its dominance is likely to continue to increase
185 because, in the most invaded of the widespread plots, *P. undulatum* comprised 72% of total stems
186 and 58% of the total basal area in 2014. There was no evidence, from the small sample of plots ($n =$
187 8) initially uninvaded but invaded subsequently, of any relationship between invasion success and
188 initial *in situ* native woody species richness. This contrasts with Puerto Rican forests, where the
189 greater the native tree species richness the less the likelihood of non-native plant invasion
190 (Ackerman et al., 2017). This could be because most invasive plants in Puerto Rico are non-persistent

191 “ruderal” species, whereas *P. undulatum* has attributes, notably shade-tolerance, that make it likely
192 to be a long-persistent invader of forests (Martin et al., 2009), irrespective of local tree species
193 richness (Fridley et al., 2007; Stohlgren et al., 2006).

194 Seeds of *P. undulatum* are bird-dispersed, like those of many non-native trees in tropical montane
195 forests (Binggeli and Hamilton, 1993; Huenneke and Vitousek, 1990; Meyer, 1996), and native
196 Jamaican birds are likely to have dispersed seeds throughout the forests, resulting in an advance
197 regeneration of established seedlings. Intense hurricanes are more likely as a result of climate
198 change (Knutson et al., 2010). Each time intense hurricanes occur, the canopy defoliation and
199 treefall gaps they cause will accelerate the growth of established *P. undulatum* seedlings to become
200 mature trees, as happened after Hurricane Gilbert, boosting invasion into forests where mature *P.*
201 *undulatum* trees are currently scarce (Bellingham et al., 2005; Murphy and Metcalfe, 2016). The
202 invasion by the non-native tree *Bischofia javanica* Blume (Phyllanthaceae) in subtropical forests on
203 Hahajima (Ogasawara Islands, Japan) has close parallels. Like *P. undulatum*, its seeds are bird-
204 dispersed and its seedlings are shade-tolerant (Yamashita et al., 2003), yet grow rapidly in response
205 to increased light (Yamashita et al., 2000). An intense typhoon in 1983 accelerated its rate of
206 invasion and it is now dominant in many areas (Fukasawa et al., 2009).

207 The decline in Jamaican native tree species diversity (H' and Fisher's alpha) and richness over 24
208 years up to 2014 the more *P. undulatum* gained in dominance provides more compelling evidence
209 than trends a decade earlier (Bellingham et al., 2005). These declines have parallels with the
210 consequences of invasions of non-native trees, especially *Psidium cattleianum* Afzel. ex Sabine
211 (Myrtaceae), in tropical forests in Mauritius. At one site in these forests, native trees species richness
212 (stems ≥ 1 cm dbh) declined over 21–27 years as the stem density of non-native trees increased
213 (Florens et al. 2017). Since stem radial growth rates of *P. undulatum* are 4–5 times greater than
214 native Jamaican tree species (Bellingham et al., 2005), *P. undulatum* probably reduced local-scale
215 species richness and diversity by niche pre-emption (Catford et al., 2012; Denslow, 2003),

216 exploitative competition (Catford et al., 2012; Malizia et al., 2017), or both. It may also exert
217 interference competition through potentially allelopathic effects (Gleadow and Ashton, 1981).
218 Although native species richness and diversity declined at a plot scale, there is no evidence so far
219 that the forests are becoming more homogeneous because of *P. undulatum* invasion, i.e. there was
220 no significant reduction in beta diversity. So far, the forests remain distinct along gradients of
221 elevation (Asprey and Robbins, 1953) and soil C and N concentrations (Tanner 1977).

222 Forests dominated by *P. undulatum* are widespread on the southern, leeward slopes of the western
223 Blue Mountains (McDonald et al., 2003) and along edges of the Port Royal Mountains further west.
224 Many of these forests developed through secondary succession on land cleared for coffee
225 plantations between 1790 and 1834 and later abandoned (Chai and Tanner, 2011), and, since then,
226 on abandoned small-scale cultivations (McDonald and Healey, 2000). A point-in-time assessment
227 conducted now might infer that *P. undulatum* has been dominant throughout succession but our
228 study shows this need not be so because native tree richness and diversity declined while *P.*
229 *undulatum* increased in dominance in these successional forests over 24 years.

230 Declining native tree species richness and diversity at a plot-scale as *P. undulatum* invades Jamaican
231 forests provides further evidence that island ecosystems are particularly susceptible to non-native
232 plant invasions (Pyšek et al., 2012). Since Jamaican montane forests are an international hotspot of
233 endemism (Myers et al., 2000), the decline in endemic tree species over 24 years at a plot scale is
234 especially concerning. Local declines of endemic species, as shown in Jamaica, represent the first
235 stage of invasion effects that could ultimately lead to their extinction (Downey and Richardson,
236 2016).

237 While our study focused on relationships between *P. undulatum* invasion and tree diversity, the
238 diversity of other native plants may also be affected. *Pittosporum undulatum* has a dense canopy
239 that reduces light intensity, which, in Australia, can suppress nearly all understorey plants (Gleadow
240 and Ashton, 1981). We lack data from Jamaica to determine whether understorey seedlings, as well

241 as understory herbs and ferns, in which there is also high endemism (Proctor, 1985), are similarly
242 suppressed. Epiphytes are prominent in Jamaican montane forests (Asprey and Robbins, 1953;
243 Grubb and Tanner, 1976), but nearly all the *P. undulatum* trees we measured, even large individuals,
244 lack trunk and branch epiphytes. Epiphytic bromeliads are common on many native tree species
245 (Grubb and Tanner, 1976) but are absent from *P. undulatum*. Growing dominance of forests by *P.*
246 *undulatum*, hence fewer epiphytic bromeliads, is in turn likely to affect other species; e.g.
247 bromeliads are key foraging sites for the endangered endemic Jamaican blackbird (*Nesopsar*
248 *nigerrimus* Osburn (Icteridae); Cruz, 1978), which has its greatest population densities in the Blue
249 Mountains (Varty, 1991). The negative effects of the *P. undulatum* invasion on forest epiphyte
250 abundance are also likely to affect other ecosystem functions. Trunk and canopy epiphytes, and the
251 arboreal soils that they support, play a prominent role in nutrient cycling and the hydrology of
252 montane forests (Gotsch et al., 2016; Ah-Peng et al., 2017). Studies are needed, comparing forests
253 highly invaded and uninvaded by *P. undulatum*, on the consequences for forest hydrology of the
254 reduction in arboreal soils and interception of stem flow by trunk epiphytes.

255 Hurricanes are a long-term selection pressure on Jamaican forests, yet the apparent resilience of the
256 montane forests' basal area after an intense hurricane in 1988 masks a significant shift in its
257 composition. Although the loss of overall forest basal area caused by the hurricane (Bellingham et
258 al., 1995) recovered over the next 26 years, it nearly entirely comprised *P. undulatum* (Table 1). It is
259 unclear whether this compositional shift altered other forest ecosystem properties. Tree growth in
260 tropical montane forests is limited not only by low light levels but also low soil nutrient
261 concentrations (Bruijnzeel et al., 2010; Dalling et al., 2016; Tanner et al., 1998). In montane rain
262 forests on Hawai'i, N limits tree growth, and the non-native invasive tree *Psidium cattleianum* has
263 greater N-use efficiency than the dominant native tree *Metrosideros polymorpha* Gaudich.
264 (Myrtaceae) (Funk and Vitousek, 2007). In Jamaican montane forests, its relationships with soil C and
265 N concentrations suggest that invasion by *P. undulatum* proceeded more rapidly in plots where their
266 concentrations were lowest. However, soil C and N were sampled in invaded and uninvaded plots

267 and it is unknown whether low soil N concentrations, especially in plots with rapid increases in *P.*
268 *undulatum*, resulted from depletion of soil N by this tree. Similarly, if rates of accumulation of soil
269 organic matter are low in invaded forests, then low soil C concentrations could be a consequence of
270 invasion. Moreover, forests with very high soil C concentrations do not restrict *P. undulatum*
271 invasion. Forests in Mor sites have 95% soil organic matter content and pH 3.6 in the top 10 cm
272 (Tanner, 1977), and have very low tree diversity because most native trees cannot establish in the
273 soils (Sugden et al., 1985). However, *P. undulatum* is now invading Mor sites (Fig. 2; Wardle et al.,
274 2015) and may cause changes to the soil that further accelerates its invasion through a positive
275 feedback process. Plant–soil feedbacks are well recognised as processes that accompany invasions
276 by non-native trees (Ehrenfeld, 2010; Vitousek and Walker, 1989; Wardle and Peltzer, 2017).
277 Increasing dominance of *P. undulatum* may have consequences for ecosystem services such as
278 nutrient cycling and soil formation if such feedbacks occur, and potentially for other services such as
279 water cycling, regulation of water flows, and erosion control. The resilience of forests dominated by
280 *P. undulatum* to natural disturbances, such as hurricanes and earthquakes, is unknown.

281 Conservation policy in Jamaica aims to prevent deforestation and to maintain the forest cover in
282 protected areas, including the Blue and John Crow Mountains National Park (Chai et al., 2009).
283 However, simply maintaining the area of forest cover will be insufficient to protect biodiversity
284 because there have been clear declines in its native tree diversity at a plot scale as a non-native tree
285 has invaded. Native birds disperse *P. undulatum* seeds to remote locations within the National Park
286 so it seems inevitable that the effects we have shown will become more widespread if the invasion
287 proceeds unchecked. An option could be to eliminate the large propagule pressure from forests
288 dominated by *P. undulatum* along the National Park’s southern borders, but the resulting
289 deforestation on steep, erosion-prone slopes could be disastrous for local farmers, because of
290 landslides and sedimentation (Barker and McGregor, 1988), and for ensuring water supplies
291 (including to the capital, Kingston). It would be prudent to embark now upon remedial action to
292 protect endemic Jamaican montane tree species, including identifying areas of forest communities

293 with greatest endemism and safeguarding these against invasion by a continuing programme of
294 physical removal of *P. undulatum* and its chemical control (currently drilling and injecting mature
295 trees with glyphosate during the dry season; Susan Otuokon, pers. comm.). The distinct crown
296 architecture of *P. undulatum* and the strong infra-red reflectance of its leaves mean that it can be
297 distinguished by remote sensing, which could identify areas invaded by adult trees for control
298 (Goodland and Healey, 1997), although extensive ground surveys are also needed to determine the
299 spatial extent and abundance of seedlings and saplings below native canopies that also require
300 control. In rain forests on Hawai'i, high-resolution airborne imaging spectroscopy determined
301 combinations of substrate type and elevation most susceptible to invasion by a non-native tree,
302 *Psidium cattleianum* (Barbosa et al., 2017). The same technology might be suitable for identifying
303 areas in which to focus control efforts and those most meriting protection against invasion by *P.*
304 *undulatum* in the topographically and geologically complex Blue Mountains. Biological control seems
305 a suitable option for *P. undulatum* because it is so widespread in the Blue Mountains and it has no
306 closely related Jamaican species. While there are no current options for the biological control of *P.*
307 *undulatum* (Pasiecznik and Rojas-Sandoval, 2015), this might be a focus for further research because
308 it is invasive in many countries.

309 The outstanding cultural and natural heritage of the Blue and John Crow Mountains National Park
310 resulted in its being declared a UNESCO World Heritage site in 2015. The Jamaican Government
311 administers the National Park, secures its boundaries, and manages tourism within it. The National
312 Park's managers may require international assistance to address the chronic degradation of the
313 forests caused by long-term invasion by *P. undulatum* and other non-native plants.

314

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329

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493 **Table 1.** Basal area and stem density (mean \pm SEM) across 16 widespread plots in tropical montane
 494 rain forests in Jamaica in 4 measurement years, with all woody species other than *Pittosporum*
 495 *undulatum* (all are native species except for *Cinchona officinalis* L. (Rubiaceae) in one plot), endemic
 496 woody species, *P. undulatum* alone, and all species combined, along with species richness per 200
 497 m² plot of woody species other than *P. undulatum*, and of endemic woody species, and Shannon H'
 498 and Fisher's alpha (the latter two computed after rarefaction based on the fewest stems per plot at
 499 any measurement); for significant differences (P <0.05) determined by repeat-measures ANOVA (F
 500 and P statistics tabulated), post-hoc differences were determined by paired t-tests (shared letters
 501 denote no significant differences between years, P >0.05).

	1990	1994	2004	2014	F	P
Basal area (m² ha⁻¹)						
Non- <i>P. undulatum</i>	49.24 \pm 3.97	49.17 \pm 4.05	48.91 \pm 4.30	49.36 \pm 4.75	0.02	0.906
Endemic woody species	15.45 \pm 2.55	15.17 \pm 2.49	15.10 \pm 2.44	15.85 \pm 2.58	0.43	0.560
<i>P. undulatum</i>	0.49 \pm 0.39 ^a	0.94 \pm 0.68 ^a	2.78 \pm 1.30 ^b	5.19 \pm 1.97 ^c	8.16	0.011
All species	49.72 \pm 3.98	50.11 \pm 4.06	51.69 \pm 4.12	54.55 \pm 4.26	6.91	0.009
	a	a	a	b		
Stems ha⁻¹ (\geq3 cm dbh)						
Non- <i>P. undulatum</i>	5669 \pm 549 ^a	5606 \pm 530 ^a	5266 \pm 527 ^a	4897 \pm 550 ^b	4.29	0.048
Endemic woody species	2278 \pm 302 ^a	2188 \pm 301 ^{ab}	1988 \pm 311 ^{bc}	1878 \pm 323 ^c	4.42	0.038
<i>P. undulatum</i>	144 \pm 118 ^a	322 \pm 225 ^a	681 \pm 348 ^b	863 \pm 425 ^c	5.05	0.038
All species	5813 \pm 588	5928 \pm 608	5947 \pm 629	5759 \pm 619	0.93	0.406
Non- <i>P. undulatum</i>	23.4 \pm 1.6	22.9 \pm 1.6	22.6 \pm 1.6	21.1 \pm 1.6	2.96	0.091
woody species richness per 200 m ²						

Endemic tree woody	11.1 ± 1.0^a	10.4 ± 1.0^b	10.2 ± 1.0^{ab}	9.6 ± 1.0^b	4.08	0.030
species richness per						
200 m ²						
Shannon H'	2.7 ± 0.1	2.7 ± 0.1	2.7 ± 0.1	2.6 ± 0.1	1.45	0.249
Fisher's alpha	10.0 ± 1.1	9.5 ± 0.9	9.5 ± 1.0	8.9 ± 0.9	1.53	0.238

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504

505 **Figure legends**

506 **Fig. 1.** Location of the study sites (inset shows location within Jamaica). Symbols denote locations of
507 the widespread plots, and the boundary in both maps denotes the Blue and John Crow Mountains
508 National Park.

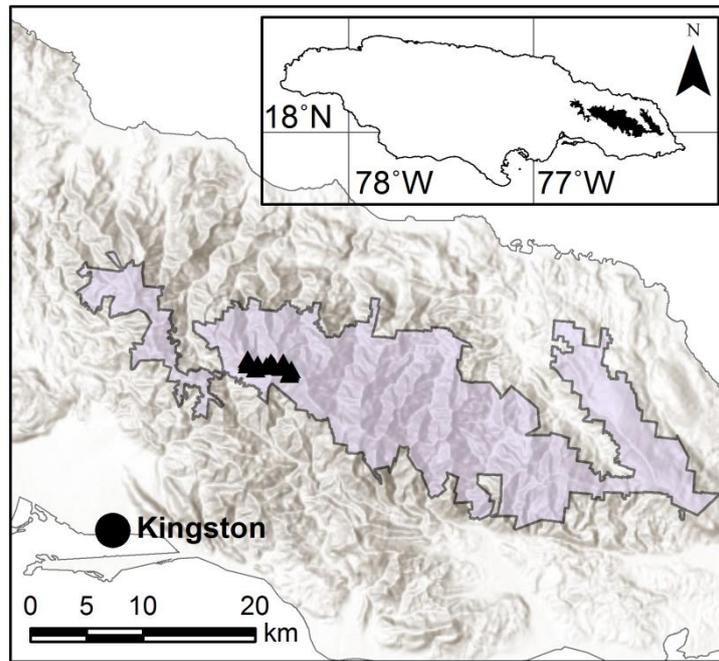
509 **Fig. 2.** The percentage of (A) basal area comprised by *Pittosporum undulatum* over 40 years in four
510 localised sites and (B) basal area and stems comprised by *P. undulatum* across 16 widespread plots
511 (mean + SEM) over 24 years in Jamaican montane rain forests; NB: Fig. 2a corrects an error in
512 Bellingham et al. (2005), where the percentage basal area in the Col site in the 2004 measurement
513 should have been higher than reported.

514 **Fig. 3.** Changes in tree diversity (A: Shannon H' ; B: Fisher's alpha), tree species richness (C), and
515 percentage endemic trees (D) per plot over 24 years (all calculated after rarefaction per plot on the
516 census with fewest stems) in relation to annual change in basal area of *Pittosporum undulatum*
517 across 16 widespread plots in Jamaican montane rain forests (regressions were calculated omitting
518 the bracketed datum with large leverage; black circles = plots on northern slopes, white circles =
519 ridge crest, triangles = southern slopes).

520 **Fig. 4.** Non-metric multidimensional scaling (NMDS) ordination of vegetation composition in
521 widespread plots, based on basal area in 2014. Filled symbols indicate plots invaded by *Pittosporum*
522 *undulatum*, unfilled symbols non-invaded plots on northern slopes, range crest, and southern slopes.
523 Arrows indicate significant correlations between elevation, soil nitrogen (N) and carbon (C)
524 concentrations with the ordinated vegetation.

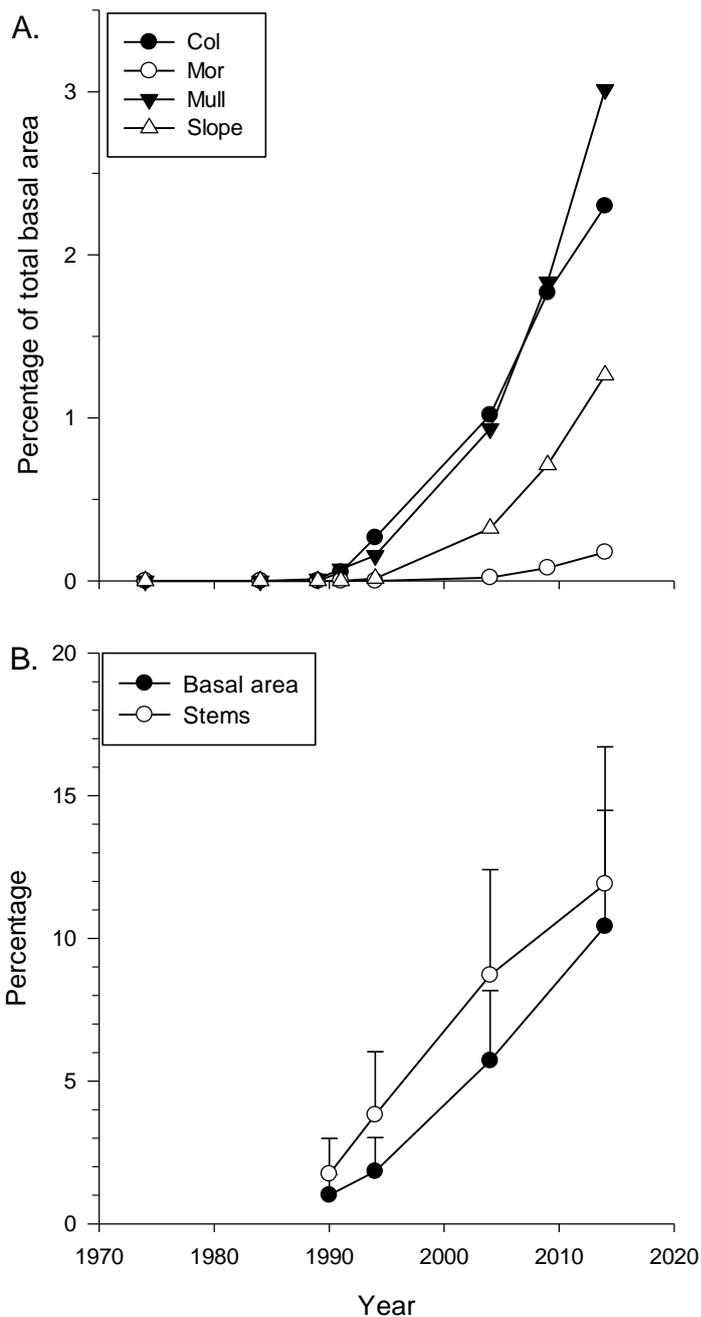
525 **Fig. 5.** A: total soil nitrogen (N) concentration (%) and B: total soil carbon (C) concentration (%) in
526 relation to annual change in basal area of *Pittosporum undulatum* across 16 widespread plots in
527 Jamaican montane rain forests (regressions were calculated omitting the bracketed datum with

528 large leverage; black circles = plots on northern slopes, white circles = ridge crest, triangles =
529 southern slopes).



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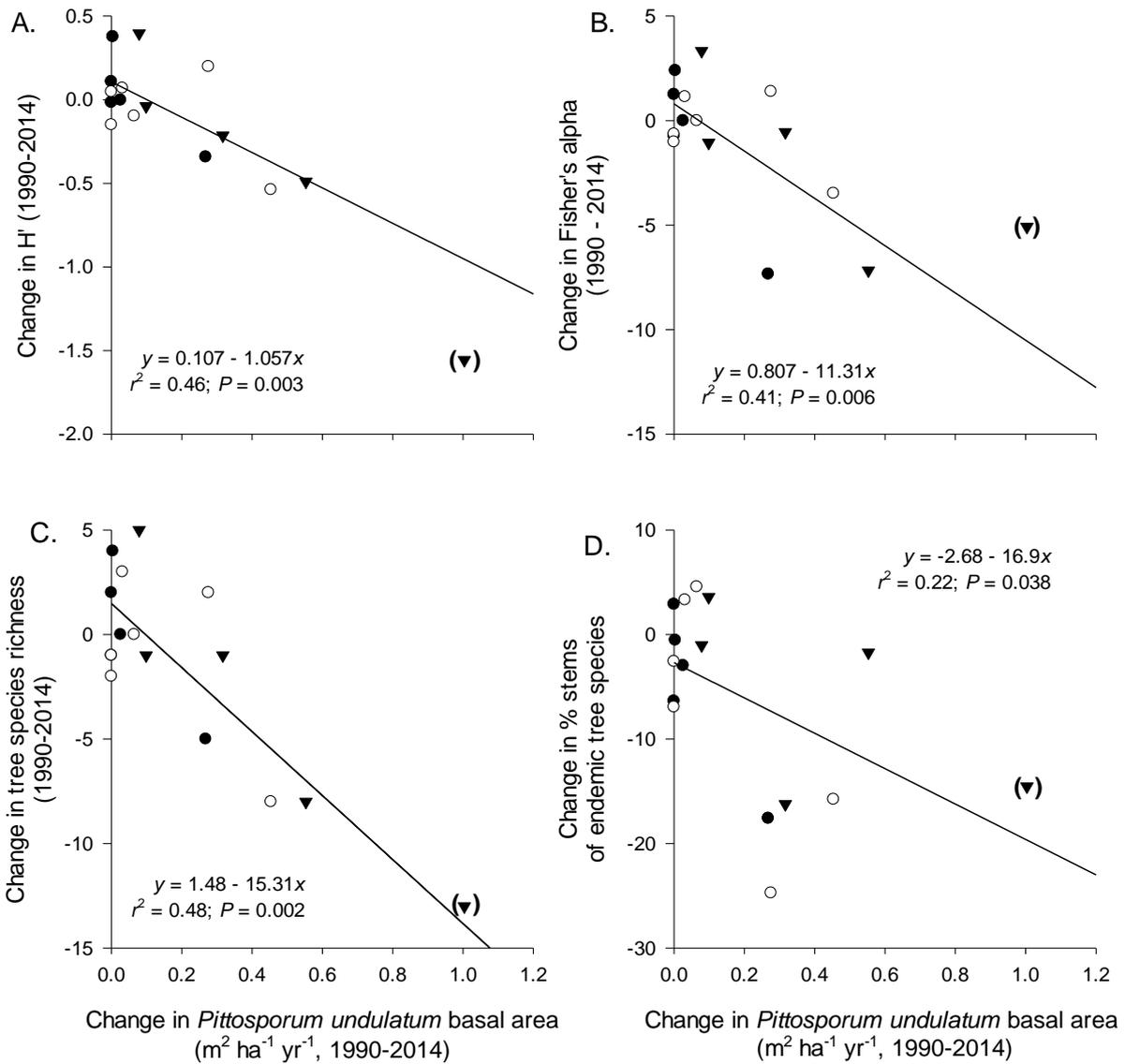
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532 the widespread plots, and the boundary in both maps denotes the Blue and John Crow Mountains
533 National Park.



534

535 **Fig. 2.** The percentage of (A) basal area comprised by *Pittosporum undulatum* over 40 years in four
 536 localised sites and (B) basal area and stems comprised by *P. undulatum* across 16 widespread plots
 537 (mean + SEM) over 24 years in Jamaican montane rain forests; NB: Fig. 2a corrects an error in
 538 Bellingham et al. (2005), where the percentage basal area in the Col site in the 2004 measurement
 539 should have been higher than reported.

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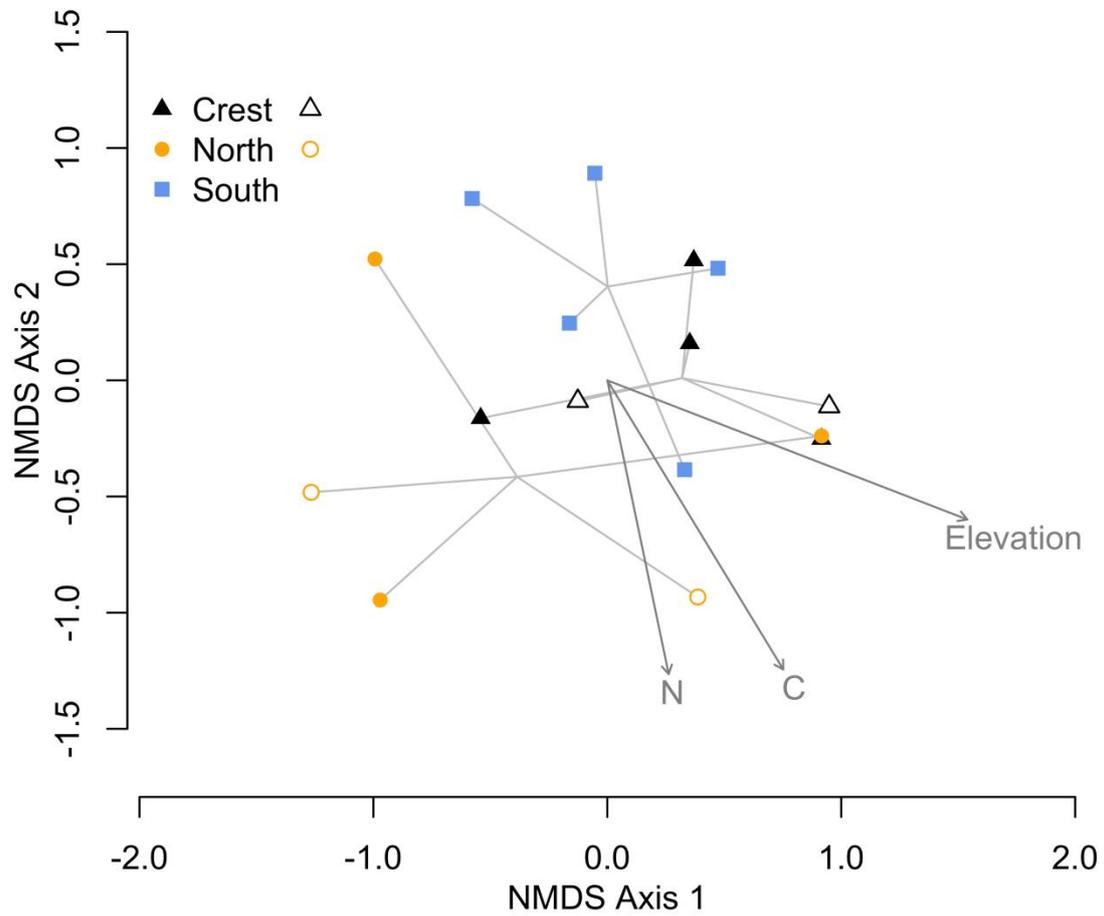


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543 **Fig. 3.** Changes in tree diversity (A: Shannon H' ; B: Fisher's alpha), tree species richness (C), and
 544 percentage endemic trees (D) per plot over 24 years (all calculated after rarefaction per plot on the
 545 census with fewest stems) in relation to annual change in basal area of *Pittosporum undulatum*
 546 across 16 widespread plots in Jamaican montane rain forests (regressions were calculated omitting
 547 the bracketed datum with large leverage; black circles = plots on northern slopes, white circles =
 548 ridge crest, triangles = southern slopes).

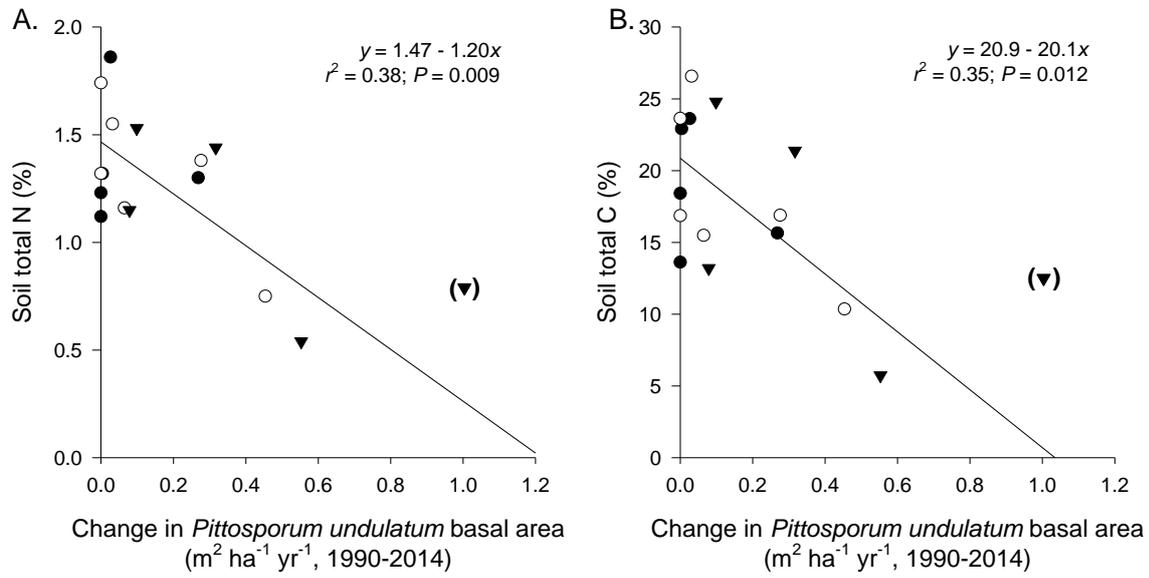
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551 **Fig. 4.** Non-metric multidimensional scaling (NMDS) ordination of composition in widespread plots,
 552 based on basal area in 2014. Filled symbols indicate plots invaded by *Pittosporum undulatum*,
 553 unfilled symbols non-invaded plots on northern slopes, range crest, and southern slopes. Arrows
 554 indicate significant correlations between elevation, soil nitrogen (N) and carbon (C) concentrations
 555 with the ordinated vegetation.

556



558 **Fig. 5.** A: total soil nitrogen (N) concentration (%) and B: total soil carbon (C) concentration (%) in
559 relation to annual change in basal area of *Pittosporum undulatum* across 16 widespread plots in
560 Jamaican montane rain forests (regressions were calculated omitting the bracketed datum with
561 large leverage; black circles = plots on northern slopes, white circles = ridge crest, triangles =
562 southern slopes).