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

Peter J. Bellingham[a,*], Edmund V.J. Tanner[b], Patrick H. Martin[c], John R. Healey[d], Olivia R. Burge[a]

[a] Landcare Research, P.O. Box 69040, Lincoln 7640, New Zealand
[b] Department of Plant Sciences, University of Cambridge, Cambridge CB2 3EA, UK
[c] Department of Biological Sciences, University of Denver, Denver, CO 80208, USA
[d] School of Environment, Natural Resources and Geography, Bangor University, Deiniol Road, Bangor LL57 2UW, UK

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ABSTRACT

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

1. Introduction

Invasions of ecosystems by non-native plants often cause homogenization of communities and altered ecosystem functions and services (Ehrenfeld, 2010; Pyšek et al., 2012; van Wilgen et al., 2008). The consequences of these invasions for the diversity and richness of resident native plant communities, and the extent to which richer and more diverse communities are invadable, are contentious (Fridley et al., 2007). Tropical rain forests are very species-rich and most are not currently invaded by non-native plants (e.g. Fine, 2002), but there are increasing incidences of non-native tree invasions in tropical montane forests (Barbosa et al., 2017; Binggeli and Hamilton, 1993; Florens et al., 2016; Martin et al., 2004; Meyer, 1996). Plant invasions pose an emerging threat to these forests, compounding effects of deforestation and climate change (Martin and Bellingham, 2016), and forests on islands seem particularly susceptible (Denslow, 2003; Denslow and DeWalt, 2008; Kueffer et al., 2010; Pyšek et al., 2012).

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

The Greater Antilles of the Caribbean, including Jamaica, are

* Corresponding author.
E-mail address: bellinghamp@landcareresearch.co.nz (P.J. Bellingham).

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invaded by c. 500 non-native plant species (Rojas-Sandoval et al., 2017). They are also a global hotspot for endemism (Myers et al., 2000). In Jamaica's tropical montane rain forests, 41% of the tree flora is endemic (Tanner, 1986). We have conducted repeated measurements of tree species composition, growth and mortality in these forests over periods up to 40 years, which coincided with invasion by a non-native tree, *P. undulatum*. Longitudinal assessments like these, along with experimental studies, are needed to determine the relationships between plant invasions and native plant richness and diversity because correlational studies, based on point-in-time assessments, do not provide compelling evidence (Catford et al., 2012; Fridley et al., 2007).

Pittosporum undulatum is a tree native to eastern Australia that grows to 14 m height (Grubb et al., 2013). It is invasive in South Africa and on several islands including Lord Howe Island, St Helena, and Hawaii (Pasiecznik and Rojas-Sandoval, 2015) and it occupies about 30% of the forested area on the Azores (Silva et al., 2017). In Jamaica, it was intentionally introduced to the Cinchona Botanic Gardens on the southern slopes of the Blue Mountains in the late 19th century (Bellingham et al., 2005). By the 1970s, it had invaded nearby montane rain forests along the edges of trails (Grubb and Tanner, 1976). By the 1990s, *P. undulatum* was dominant in areas of secondary forest (McDonald and Healey, 2000; McDonald et al., 2003). By 2004, it had increasingly invaded longer-established natural forests (with canopies that range in height from 6 to 12 m and taller in gullies; Asprey and Robbins, 1953; Shreve, 1914), and occurred in 69% of forest plots, locally as canopy trees (Bellingham et al., 2005). Seedlings of *P. undulatum* in these forests grow to become mature canopy trees within 24 to 35 years after the creation of experimental canopy gaps (Chai et al., 2012). In this study, we evaluate whether the rapid increase in invasion observed in the 16 years after Hurricane Gilbert (1988) was sustained over the next decade. The forests have not been significantly disturbed by hurricanes since 1988 (Tanner et al., 2014) and a period without major disturbance, during which forest canopies reformed, might retard the rate of invasion (Murphy and Metcalfe, 2016). However, since *P. undulatum* is shade-tolerant (Gleadow et al., 1983; Chai et al., 2012), this need not be so (Martin et al., 2009). Our long-term data allowed us to evaluate how diversity and richness of native tree species have been affected by invasion at local and wider scales.

2. Methods

2.1. Study sites

The study sites are in upper montane rain forests in the western Blue Mountains of Jamaica (Fig. 1). A 40-year record of change derives from localised sites on and near the main ridge (18° 05′N; 76° 39′W, 1540–1620 m elevation; four sites, 'Col' 0.09 ha, 'Mor' 0.06 ha, 'Mull' 0.10 ha and 'Slope' 0.10 ha; Tanner, 1977), measured in 1974, 1984, 1989, 1991, 1994, 2004, 2009, and 2014. The 24-year record of change derives from 16 systematically placed, widespread 200 m^2 plots within c. 250 ha: six on the ridge crest, five on the northern slopes (windward to the prevailing trade winds), and five on the southern leeward slopes (18° 05′N; 76° 39–40′W, 1375–1920 m; Bellingham, 1991), measured in 1990, 1994, 2004, and 2014. Stem densities and tree species richness and diversity were measured (Table 1). In the localised sites and widespread plots, all stems ≥ 3 cm diameter at 1.3 m height (dbh) were identified to species, tagged with a unique number, their diameter recorded, and a band painted at the dbh datum. At each remeasurement, all stems were relocated and their new dbh recorded. Dead stems were recorded and stems that had grown to become ≥ 3 cm dbh at each remeasurement were identified to species, tagged, and painted. Across all measurements, there was a total of 3012 stems in the localised sites, including those that died and those newly recruited (on average 1802 live stems at each measurement) and 2682 stems across the widespread plots (on average 1876 live stems). Concentrations of total carbon (C), N, and phosphorus (P and Bray-extractable P) were determined from

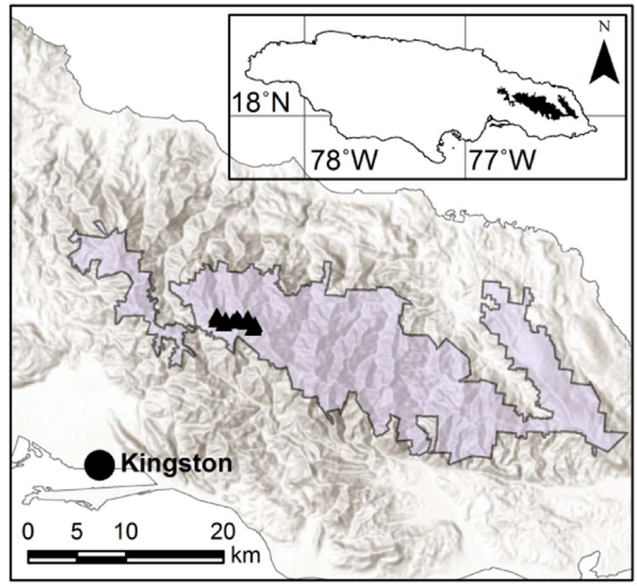

Fig. 1. Location of the study sites (inset shows location within Jamaica). Symbols denote locations of the widespread plots, and the boundary in both maps denotes the Blue and John Crow Mountains National Park.

soils collected in 2004 from each widespread plot (0–15 cm depth; Bellingham et al., 2005). Plot elevations were estimated from maps and GPS data.

The mean annual rainfall averages 2500–3000 mm, and the mean maximum monthly temperatures range from 18.5 to 20.5 °C and minima from 11 to 12 °C (Kapos and Tanner, 1985). Our study sites were affected strongly by Hurricane Gilbert on 12 September 1988 (Bellingham et al., 1995). No other hurricane eye passed within 50 km of the study sites during 37 years before Hurricane Gilbert, and none have since; those with tracks > 50 km away between 1988 and 2014 has not had strong effects (Tanner et al., 2014). Our study sites provide records of change in the forests for 14 years before and 26 years after Hurricane Gilbert in the localised sites, and a 24-year record (all post-Hurricane Gilbert) from the widespread plots.

2.2. Analysis

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