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ORIGINAL PAPER

Alien palm invasion leads to selective biotic filtering of resident plant communities towards competitive functional traits

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Abstract Biological invasions drive biodiversity loss and ecosystem change on tropical islands. However, we know little about the implications of species losses on the functional structure of both resident and novel communities. Herein, we examined the potential effect of a non-native palm species, *Pinanga coronata,* on the taxonomic and functional assemblages of understory plant species in a Fijian rainforest. We predicted that competition from this invasive species would lead to trait convergence according to the competitive hierarchy hypothesis. Using a trait-based approach, we sampled plant communities in 280 plots across a gradient of *P. coronata* densities. We measured five functional traits, including height and leaf traits related to nutrient acquisition. We found that an increase in *P. coronata* density is strongly correlated with a decrease in taxonomic diversity (i.e., about − 50% for species richness and − 33% for Shannon diversity index) and a decrease in functional richness. Community-weighted mean values of traits of resident species (i.e., excluding *P. coronata*) converged toward competitive strategies such as higher leaf nitrogen content (LNC), lower carbon-to-nitrogen (C:N) ratios and leaf dry matter content (LDMC), a pattern that is significantly non-random for LDMC and C:N. This study demonstrates that *P. coronata* might act as a strong biotic filter responsible for species loss and functional changes. Our findings suggest that in response to increasing competition with this invasive plant, resident and novel plant communities shift toward less diverse and more competitive assemblages. Nevertheless, the intensity of this filtering is habitat dependent (e.g. less filtering effect under mahogany trees). Lastly, changes in resource acquisition strategies (mainly nutrient-based) in particular in low nutrient status of rainforest soils, could lead to long-term impacts on tree regeneration, in turn causing large-scale changes in ecosystem properties.

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Introduction

Tropical oceanic islands harbor many invasive alien plants (IAP) when compared to mainland areas (Russell et al. 2017; van Kleunen et al. 2015). In particular, Pacific islands are known to be highly vulnerable to biological invasions (Denslow et al. 2009; Kueffer et al. 2010; Keppel et al. 2014; Mueller-Dombois 2006). There exists a large body of work regarding invasive plant species on Pacific islands (e.g., Baruch et al. 1999; Daehler et al. 2004; Penuelas et al. 2010; Westerband et al. 2021). However, the rapid spread of IAP still requires great attention, especially in South Pacific islands (Meyer 2014). There, IAP-induced changes to ecosystems tend to readily manifest, given that the native biota is disharmonic, the functional redundancy is low, and food webs are simple. Recorded impacts on the biodiversity of Pacific island rainforests (e.g., by Dyer et al. 2018; Minden et al. 2010a) include the replacement of native understory species and the interruption of life cycles of foundation species (Boehmer et al. 2013; Keppel et al. 2014; Minden et al. 2010b; Mueller-Dombois and Boehmer 2013). Another notable impact of IAP is the alteration of habitat (e.g., a change in biogeochemical soil properties and microclimate) and ecosystem functioning (e.g., nutrient cycling and productivity) brought about as a consequence of species replacement and diversity loss (Pyšek et al. 2012, 2020; Vilà et al. 2011).

Plant functional traits are defined as any morphological, physiological, or phenological features measurable in individual plants that potentially affect their fitness (Violle et al. 2007) or their environment (Lavorel and Garnier 2002). Trait-based ecology has rapidly grown over the last decades and now offers a mechanistic means of predicting consequences of environmental changes upon plant communities (Violle et al. 2007; Adler et al. 2014). A large body of literature shows how plant traits relate to or influence ecological functions. Therefore, these traits have been used to estimate and understand the diversity of ecological and functional strategies of co-existing species (Burton et al. 2020). For example, species loss or extinction from a community may have scant consequences on functional diversity in the case of a high redundancy between species. Alternatively, it may lead to functional diversity erosion in the case of high functional complementarity between species (Cadotte et al. 2011; Hejda et al. 2017). Therefore, a loss of functional diversity may be observed regardless of taxonomic diversity variation, demonstrating the importance of considering the functional aspects of biodiversity (Tecco et al. 2010). Furthermore, community-weighted mean (CWM, i.e., the average trait value of all species) of the traits of species within a community may help reveal how the functional structure of native communities is altered by invasion (Pavoine et al. 2017), while also giving an insight into the consequences of invasion for ecological processes and ecosystem functions (Grime 1998; Muscarella and Uriarte 2016). Previous studies comparing native and invasive plants have revealed that the latter tend to have fast resource acquisition strategies according to the leaf economics spectrum described by Wright et al. (2004). More precisely, IAP have higher trait values for height, specific leaf area (SLA), and leaf nitrogen content (LNC) and lower trait values for leaf dry matter content (LDMC; Montesinos 2022) than most native plants. These traits make invasive species particularly competitive. Conversely, native species in invaded communities often display more conservative strategies (Jakobs et al. 2004; Liao et al. 2008; Van Kleunen et al. 2010).

Many hypotheses consider competition a major mechanism that determines the success of an invasion (Cleland et al. 2011; Vilà and Weiner 2004). A strongly competitive IAP can act as a biotic filter influencing native species. According to the limiting similarity theory (Abrams 1983; MacArthur and Levins 1967), competition from IAP can limit or even exclude native species that share similar traits. In turn, IAP competition is expected to have little or no impact on native species with dissimilar traits (Gallien and Carboni 2017; MacDougall et al. 2009). According to this hypothesis, through competitive interactions, an IAP can potentially lead to trait divergence in the resident community (i.e., overdispersion). This mechanism promotes the coexistence of different strategies and may limit the reduction in functional richness of the resident community following an invasion (Fried et al. 2019; Hejda et al. 2017). Alternatively, the competitive hierarchy hypothesis in the context of plant invasion, stipulates that the spread of a highly competitive invasive plant will exclude less competitive species while native species with a similar or a higher fitness will coexist with the invader (Fried et al. 2019; Hejda et al. 2017). As a consequence, IAP can diminish both species richness and functional richness (Díaz and Cabido 2001; Ebeling et al. 2018) as well as trait convergence (Sodhi et al. 2019). However, such changes in native assembly rules and native coexistence (trait convergence/divergence) as a consequence of an invasion, are generally, under-studied (however, see Sodhi et al. 2019). Instead, most studies on functional traits focus only on differences in traits between native communities and exotic species (e.g., Leffler et al. 2014). Ultimately, invasive species, through trait convergence/divergence and indirect effects (i.e., changes in abiotic properties), might induce character/trait displacement and thus act as evolutionary forces that shape plant communities (Beans et al. 2014). Studying the functional changes in native communities following an invasion may allow us to make inferences both about the mechanisms underpinning species losses and the consequences for ecosystem functioning and evolution. A functional approach is also particularly helpful in ecological restoration projects of invaded sites, either for selecting plant species mixtures with desired properties or function, and for influencing both plant and invertebrate species assemblages (e.g. Ostertag et al. 2015, 2020 in Hawaiian forests).

In Fiji, approximately 390 invasive alien species have been identified (Lenz et al. 2022). Among these, the non-native ivory cane palm *Pinanga coronata* (Blume ex Mart.) Blume (Arecaceae family) has considerable potential to fundamentally change the structure and diversity of the archipelago's rainforests (Dyer et al. 2018, 2019; Forey et al. 2021; Keppel and Watling 2011). In forest habitats, *P. coronata* has a strong advantage over understory species in competing for light due to its taller stature and architectural adaptation to shaded conditions (Kimura and Simbolon 2002). Consequently, it can potentially eliminate some understory species, leaving only mature preexisting canopies of dominant trees in place. Additionally, like most invasive palm trees (Fehr et al. 2020), *P. coronata* has the capacity to produce and disperse fruits and to spread clonally (Kimura and Simbolon 2002). Introduced to the country as an ornamental in the 1970s, the palm's invasive potential was first observed in the early 1990s (Watling and Chape 1993). By 2011, it had already been reported that the species formed a monodominant understory within the Colo-i-Suva Rainforest Reserve, which is north of Suva, Fiji's largest city. It was, at that time, deemed "the biggest threat to the native biodiversity of rainforests in Fiji" (Keppel and Watling 2011, p. 44). In recent years, it has been observed that *P. coronata* is preventing the establishment of native tree ferns (Dyer et al. 2018). However, no detailed ecological research has been carried out so far, and little is known about the ecological impacts of *P. coronata* on native plant communities. As a consequence, no invasion management actions have been initiated. Thus *P. coronata* in Fiji represents both a perfect practical case to study the functional consequences of invasion-induced species losses and an urgent conservation problem.

To understand and highlight the taxonomic effect of *P. coronata* on Fiji's forests together with the functional consequences, we compared understory plant communities along a gradient of *P. coronata* densities, from uninvaded plots to monostands of *P. coronata*. Given the highly competitive nature of this invasive plant and its relatively recent invasion of native plant communities, we expect to observe evidence supporting the competitive hierarchy hypothesis. Firstly, we predict that both the taxonomic and functional diversity of invaded plant communities will decrease along the gradient of increasing *P. coronata* density. Secondly, we predict that invaded plant communities will turn into more competitive plant assemblages (with high SLA, LNC, and height; and low LDMC and C:N) in response to increasing *P. coronata* density and competition in a closed forest habitat in comparison to non-invaded communities. In other words, we expect that the invasion by *P. coronata* will induce community trait convergence rather than expected at random (null models), in turn leading to possible important changes in ecosystem functioning.

Methodology

Study area

The Republic of Fiji is an archipelago consisting of 330 islands and approximately 500 islets and lies within a 570,000 km^2 area on the South Pacific Ocean

(Clark and Anderson 2009). This study was conducted in Colo-i-Suva (CIS) Forest Park, a government-protected reserve of Fiji's largest island, Viti Levu, and located approximately 12 km north of Suva, the capital city, in the southeastern area of the island. The Park has an altitudinal range of 120–240 m above sea level, while the climate is described as tropical wet to super-wet (Keppel et al. 2005; Richards 1996). According to the Fiji Meteorological Service (2006), the windward coasts of the main islands (i.e., those in the southeast) receive approximately 3,000 mm of rainfall annually—a figure that increases with altitude to produce an approximate average annual rainfall of ca. 4,000 mm in the study area (Watling 2005). The mean annual temperature, which is 24 °C, varies by only 2 °C between February and July—the warmest and coolest months, respectively (Kay 1986).

The CIS forest park was established in 1952, having being originally a lowland tropical rainforest, which was logged in the 1940s and 1950s (Paine 1991). In 1960, this reserve was inter-planted with South American mahogany (*Swietenia macrophylla*), an introduced tree used for timber production, which meant that there was clearing of the native rainforest in order to facilitate the establishment of the plantation (Tuiwawa 1998). The native and dominant trees mixed with mahogany are *Garcinia myrtiflora, Garcinia myrtiflora, Psychotria amoeba, Cryptocarya constricta* and *Haplolobus floribundus.* CIS is now classed as an old growth mahogany plantation given that it has not been logged since its establishment (Tuiwawa and Keppel 2012).

Sampling design

Within the 5 km^2 Colo-i-Suva Rainforest Park, starting in the northeast and moving in a southwesterly direction, 280 plots of 5 m × 3 m area were regularly distributed along a gradient to investigate the extent to which they had been invaded. This revealed a gradient of *P. coronata* density at the community level, which ranged from 0 individuals per 15 m^2 to 49 individuals per 15 m^2. Plots were purposely selected close to each other in order to minimize climatic variations while retaining a range of *P. coronata* density. The 15 m^2 plot areas facilitated correlations between *P. coronata* and understory plant species abundance, with a well-adapted sampling of understory species of tropical forest (Sutherland 2006).

For each plot, *P. coronata* density was measured by recording the number individuals, producing values that were strongly correlated with *P. coronata* relative cover within the plots ($r = 0.7$, p-value < 0.001). Thus, the population of *P. coronata* was recorded for each plot as a proxy for the extent of invasion (Appendix 1). Of the 280 plots examined, 61 did not contain any *P. coronata* individuals.

Vegetation sampling and measurements

The density (i.e., the number of individuals) of each herb and shrub understory species (i.e. plants less than 5 m in height including tree saplings) was recorded in each 15 m^2 plot in order to obtain plant relative abundance. A total of 120 vascular plant species were identified (Appendix 2). Of the 120 species recorded, nine were exotics (Appendix 2). We cannot rule out that some of these species could have already influenced the resident plant communities, but due to their low density and frequencies, these species are not currently considered to be threats. It should be noted that throughout this study we use the term "resident community" instead of "native community" due to the presence of these other exotic species in the native understory community. Additionally, the presence of mahogany (an exotic tree) was monitored within the 15m^2 plot. Several studies highlighted that such exotic trees could influence native plant diversity (Richardson et al 2015; Brundu et al. 2020). Regarding mahogany, it is unclear whether this exotic species can invade adjacent habitats and displace local plant species (Norghauer et al. 2011). We overall found mahogany within only 91 plots (33%) out of the 280 investigated.

For trait measurements, it is recommended to select the most abundant species that collectively make up 80% of cumulative standing biomass (Garnier et al. 2004; Pérez-Harguindeguy et al. 2003). Such a concentration of standing biomass is a good representation of the studied plant community and provides sufficient information to scale-up the values of traits to the plant community level (Cornelissen et al. 2003). Thus, for functional characterization, we sampled the 31 most abundant species across all plots (all belonging to shrubs or short-stature tree species). When the contribution of *P. coronata* (i.e., the invasive species) in every plot was excluded, we reached a threshold of 81.6 ± 14.2% (mean ± standard deviation) of cumulative relative abundance per plot. When the abundance of *P. coronata* in each plot was included, we reached a threshold of 92.9 ± 8.4%. The list of the 31 most abundant plant species used for the functional approach is provided in Appendix 3. In addition, in order to have a more comprehensive estimation of plant biomass and, subsequently, plant functions per plot (Garnier et al. 2004), plant density was converted to plant volume as follows: Volume (m^3) = max height (m) x line intercept cover (m) x width (m). For shrub and short-stature tree species, such an allometric model of volume provides an accurate prediction of aboveground biomass (Flade et al. 2020). For each species, the volume was measured on 20 randomly distributed individuals over the entire gradient. Lastly, the total volume of each species within a plot was calculated by multiplying the volume by the population density.

Five functional plant traits (Table 1) of the 31 selected species were directly measured for individuals collected in the field. Plant height (in cm) was measured for five different individuals of each species. After that, eight mature leaf samples of five individuals per species were collected. An exception was made for particularly large leaves—those that were greater in size than A3 paper. In such cases, only one sample per species was collected. Leaves were placed in a plastic container and transported to the laboratory in cool boxes. We rehydrated the fresh leaves overnight before leaf measurements (Cornelissen et al. 2003). Fresh leaves of each sample were weighed, photocopied for further analysis, and dried before grinding. LDMC was obtained by dividing the oven-dry mass of a leaf by its fresh mass ($mg.g^{-1}$). For SLA ($mm^2.mg^{-1}$), leaf areas were calculated by analyzing photocopied leaves using WinFOLIA™ software (Regent Instruments Inc., Canada). SLA was calculated by dividing the area of one side of a fresh leaf by its oven-dry mass, producing a value expressed in $cm^2.g^{-1}$. Using ground samples (n = 3 per species), leaf nitrogen (LNC) and carbon content values were calculated, from which C:N ratios were computed using a ThermoFisher Flash Analyzer 2000 in Ecodiv Laboratory (Université de Rouen, France). Both LNC ($mg.g^{-1}$) and leaf CN ratio (C:N) were used for functional analyses.

Data analyses

The indices of taxonomic diversity (species richness, Shannon diversity, and evenness) for each plot were calculated using the vegan package of R software (Aylward 2016) for the entire data set (120 species). Taxonomic indices were also calculated on the reduced data set (31 species) and we found similar patterns (data not shown). Then, indices of functional diversity were obtained using the reduced data set concentrating on the 31 most abundant species. Functional diversity was assessed using three complementary indices: functional richness (FRic), functional evenness (FEve), and the Rao quadratic entropy index (RaoQ) for functional dispersion. FRic relates to the amount of niche space occupied by each species within a community, totaling to a measure of the cumulative functional space occupied in the community (Villéger et al. 2008). Functional evenness (FEve) relates to the way in which the biomass of a community is distributed in a niche/functional space, which in turn appertains to the effective utilization of the available resources (Villéger et al. 2008). Lastly, RaoQ was used to calculate the mean

Table 1 Synthesis of traits and functions recorded for plant species in the Colo-i-Suva Forest Park

Trait	Abbreviation	Units	Correlation to plant strategy/function.[a]
Specific leaf area	SLA	$mm^2\ mg^{-1}$	Positively correlated with photosynthetic rate, relative growth rate (RGR), and leaf nitrogen content
Leaf dry matter content	LDMC	$mg\ g^{-1}$	Positively correlated with leaf lifespan, and negatively correlated with relative growth rate (RGR)
Height	H	cm	Positively correlated with competitive vigor, reproductive size, potential lifespan, fecundity, and resilience
Leaf nitrogen content	LNC	%	Photosynthetic rate, positively correlated with RGR
Leaf carbon nitrogen ratio	C:N	N/A	Nutrient acquisition, decomposition and soil fertility, negatively correlated with RGR

[a] Pérez-Harguindeguy et al. (2003)

distance of all individual pairs based on their functional traits, thus representing a measure of functional dispersion (Botta-Dukát, 2005). These indices were calculated using the dbFD function in FD package of R (Laliberté and Legendre 2010). *Pinanga coronata* density (number of individuals) was used to assess the gradient of the species invasion. To test our first hypothesis (i.e., that *P. coronata* could lead to both taxonomic and functional loss in native communities), we used linear regression to examine the relationships between the measured diversity indices and the gradient of *P. coronata* invasion. Finally, to account for the possible influence of the exotic tree mahogany in the plots, we performed linear separate regression for the whole set of plots and both subsets with and without mahogany.

The CWM of each trait per plot was calculated using functcomp function in the FD package for all plots, and for plots with or without mahogany. CWMs of trait correspond to the mean value of a trait across species (i.e., community) weighted by species abundance (Garnier et al. 2004; Violle et al. 2007). Trait CWMs are used to determine properties and processes within ecosystems. For example, a high CWM for LNC is likely to lead to high soil N input and fast decomposition rates (Reich 2014). These CWM trait values were calculated at the plant scale both for resident communities (i.e., without including the functional contribution of *P. coronata*) and for novel communities (i.e., with the functional contribution of *P. coronata*). In other words, analyses without *P. coronata* do not refer to plots that truly did not contain *P. coronata*, but just to the way in which we analyzed the data a posteriori.

To test our second hypothesis and link community trait variation to the gradient of *P. coronata* density, each CWM trait was regressed on the *P. coronata* gradient. Because p-values in these regressions can be biased by non-independence among the sampling points arising from the application of a species' mean trait value to each plot (Zelený 2018), we used the fourth-corner approach (Brown et al. 2014). It has been argued that this method is superior to conventional methods of trait CWM correlation and species niche centroid correlation in testing for trait–environment correlations (Peres-Neto et al. 2017). To get an overview of the overall functional strategies in communities along the invasion gradient, we performed a Principal Components Analysis (PCA) of the CWM of traits.

Lastly, we assessed non-random trait-convergence and trait-divergence assembly patterns on resident communities (i.e., without *P. coronata*) using null models as proposed by the "TCAP/TDAP" method of Pillar et al. (2009). According to Pillar et al. (2009), a trait-convergence assembly pattern (TCAP) can be observed when communities contain species with similar traits and when trait variation is related to an ecological (e.g., invasion) gradient beyond random expectations, suggesting that gradient is involved in filtering species within communities based on their traits. Based on the work by Pillar et al. (2009), we assessed TCAP by matrix correlation ρ(TE) between the trait CWMs (T) and the invasion gradient (E) and compared it to random expectations by permutation against a null model. Conversely, a trait-divergence assembly pattern (TDAP) can be identified when the turnover in community traits is also related to the gradient, but communities along the gradient increasingly contain species that do not share similar traits. Here, to quantify invasion-related TDAP as suggested by Pillar et al. (2009), we correlated communities weighted by their trait similarities (X) with the invasion gradient (correlation ρ(XE), which may indicate either TCAP or TDAP), and partialled out the TCAP component (partial correlation ρ(XE.T)). The observed correlation ρ(XE) for TDAP/TCAP and the partial correlation ρ(XE.T) for TDAP were also tested by permutation against null models (see Pillar et al. (2009) for details). Additionally, an iterative process (10,000 permutations) was employed to identify the optimal trait combinations that maximized convergence, divergence, or both (see Pillar and Sosinski 2003). All analyses relative to TCAP and TDAP were performed using the 'SYNCSA' software (Debastiani and Pillar 2012).

Results

Effect of *P. coronata* on taxonomic and functional diversity

All indices of taxonomic diversity are strongly correlated with the gradient of density of *P. coronata* (Fig. 1). Although the variability was high, species richness ($r = -0.53$, $p < 0.001$) and Shannon diversity index ($r = -0.38$, $p < 0.001$) significantly decreased with increasing *P. coronata* density. The species richness and Shannon diversity indices showed an average loss of 50% and 33%, respectively along the gradient of *P. coronata* (i.e., from uninvaded communities to communities containing the greatest abundance of *P. coronata*). Conversely, Shannon evenness slightly increased along the gradient of *P. coronata* density ($r = 0.14$, $p < 0.05$).

The increasing presence of *P. coronata* led to a 50% decrease in the overall functional richness ($-\ r = 0.23$, $p < 0.001$) and RaoQ ($r = -\ 0.07$, $p < 0.001$). There was no notable change in functional evenness ($r = 0.10$, $p = 0.11$) along the gradient. Note that these functional measures include the functional contribution of *P. coronata* in communities.

When analyzing plots with or without mahogany, *P. coronata* density was still negatively correlated with taxonomic and functional richness (Fig. 1). These correlations became non-significant for evenness (Fig. 2).

Effect of *P. coronata* on functional traits of resident plant communities

When *P. coronata* was excluded (i.e. by excluding the contribution of *P. coronata* from the data set), the gradient of invasion significantly influenced four CWM traits of resident species. LNC ($r = 0.14$, $p < 0.001$) and SLA ($r = 0.19$) increased significantly—up to + 17% on average—along the gradient of *P. coronata* density. Conversely, LDMC ($r = -\ 0.14$, $p < 0.05$) and C:N ($r = -\ 0.26$, $p < 0.001$) decreased by, on average, 8% and 22%, respectively, between uninvaded communities and communities facing the greatest abundance of *P. coronata* invasion (Fig. 2). Plant heights did not change significantly along the gradient ($p = 0.056$). When analyzing plots with or without mahogany, the correlation between *P. coronata* and CWM traits was only significant in plots without mahogany (Fig. 2).

The *P. coronata* density gradient induced patterns of trait convergence (TCAP, ρ(TE)) and overall changes in species similarity within communities (TCAP/TDAP, ρ(XE)) of the full set of traits. The maximum convergence pattern was obtained in a subset of traits containing only LDMC and C:N ($\varrho(\mathrm{TE}) = 0.33$, $p < 0.01$). This same subset of traits also maximized the combined effect of convergence and divergence ($\varrho(\mathrm{XE}) = 0.32$, $p < 0.01$; Table 2), thus suggesting that traits diverged at the beginning of the gradient and then converged at the end of the gradient (Fig. 2).

The first three principal components of the PCA performed on CWM traits (without *P. coronata* contribution) accounted for 45%, 28%, and 15% of the variance, respectively. Axis 1 of the PCA (Fig. 3) represents a relative gradient of nutrient acquisition from conservative strategies in the negative part (high C:N and LDMC values) to more acquisitive species (high LNC) in the positive part. The second axis of this PCA is, in comparison, linked to a strategy to optimize light, with species either characterized as having a high SLA or being particularly tall. Thus, communities in less invaded plots (negative area of axis 1) tend to be characterized by more conservative strategies (nutrient and light acquisition) than those in invaded plots.

Table 2 Trait subsets with maximum congruence for TCAP, TDAP, or both (TCAP/TDAP) for the 30 investigated plant species along the gradient of *P. coronata* invasion

	TCAP (= convergence)		TDAP (= divergence)		TDAP/TCAP (= divergence & convergence)	
	ρ(TE)	*p*	ρ(XE.T)	*p*	ρ(XE)	*p*
All traits:						
LDMC, SLA, C:N, LNC & H	0.28	0.017	0.18	0.763	0.30	0.009
Subset of optimized traits:						
LDMC & C:N	**0.33**	0.001	0.15	0.942	**0.32**	0.005
SLA & C:N	0.28	0.010	**0.23**	0.153	0.26	0.040

Abbreviations and a description of the five functional traits (LDMC, SLA, C:N, LNC, & H) are defined in Table 1

The best correlation (ρ) for each pattern is highlighted in bold. These significant values were obtained using two subsets of traits within all combinations of traits, producing p-values < 0.01

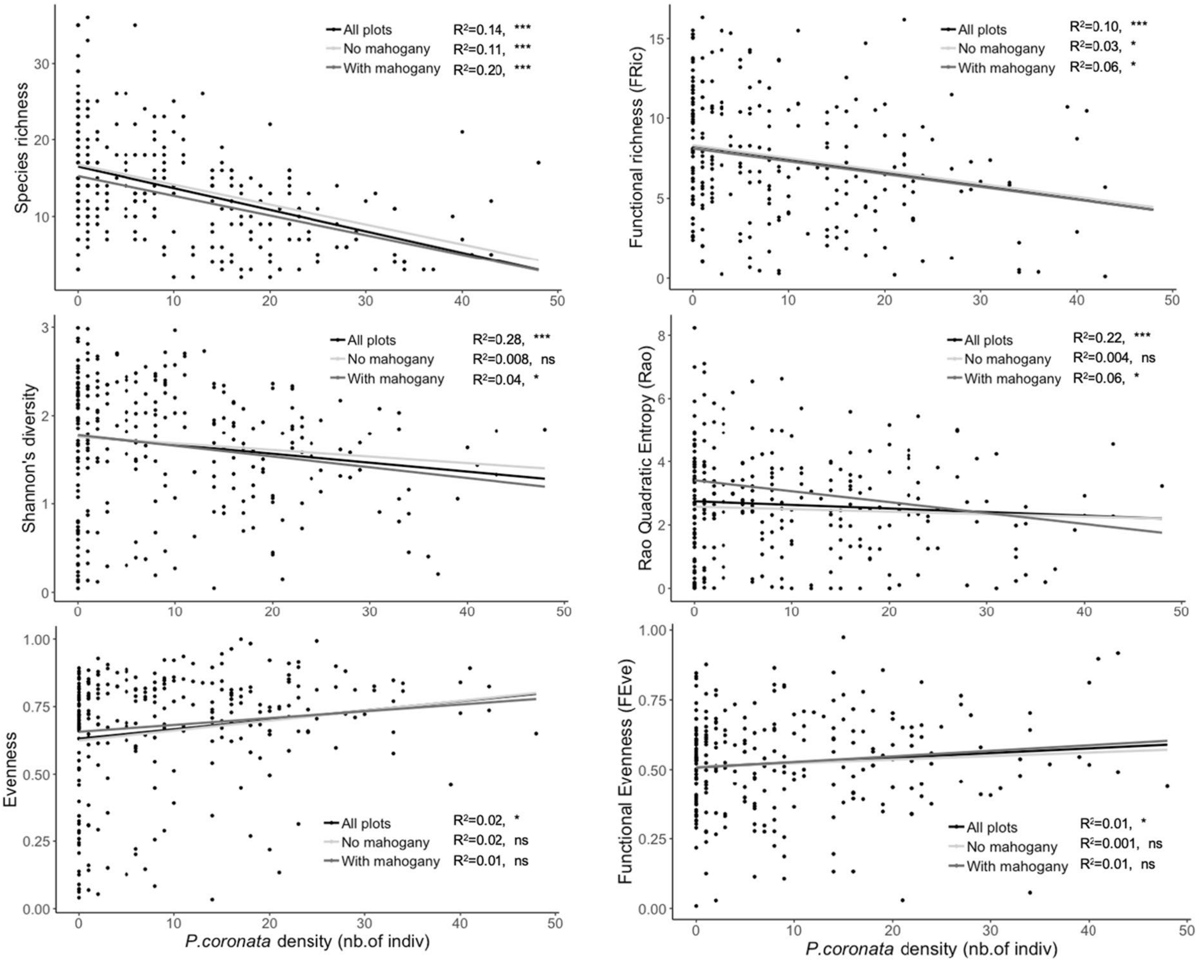

Fig. 1 Variation of taxonomic (left column) and functional biodiversity (right column) of plant communities along the gradient of *P. coronata* densities. Three regression lines are given: "all plots" (black regression) and two subsets "no mahogany" and "with mahogany" canopy (grey regressions). Taxonomic indices were calculated on the entire data set (120 species) and functional indices on the dominant 31 species. Regarding taxonomic data, the same patterns were observed when using the sub-set of 31 species (data not shown). Each point represents a plot. The total number of plots for taxonomic indices was N = 280. For functional indices N = 249. The difference of the number of N values between taxonomic and functional data was due to a lack of available values in plots with less than three species, which prevents the computation of functional diversity. R^2 is the coefficient of determination and asterisks indicate significance levels of the linear regression line: $***P < 0.001$; $**P < 0.01$; $*P < 0.05$, ns = not significant

Functional characteristics of novel communities (including *P. coronata*)

When including *P. coronata* in the calculation of functional traits, it was revealed that all CWM traits in highly invaded plots converge to those of *P. coronata* (Fig. 4). This is a result of the strong contribution of *P. coronata* to the novel plant communities. In plots where there are at least 10 individuals present, *P. coronata* accounts for more than 40% of the relative abundance of the novel community (Appendix 4). Thus, along the gradient of *P. coronata,* communities converge through higher SLA ($SLA_{P.\ coronata} = 16.7$ $mm^2.mg^{-1}$), LDMC ($LDMC_{P.\ coronata} = 356$ mg. g^1), C:N ($C{:}N_{P.\ coronata} = 29.5$), and height ($H_{P.\ coronata} = 280$ cm) and have a lower LNC ($LNC_{P.\ coronata} = 1.38\%$) when compared with less invaded plots (Fig. 4). It can be noted that LNC for plots without mahogany, and SLA and LDMC for

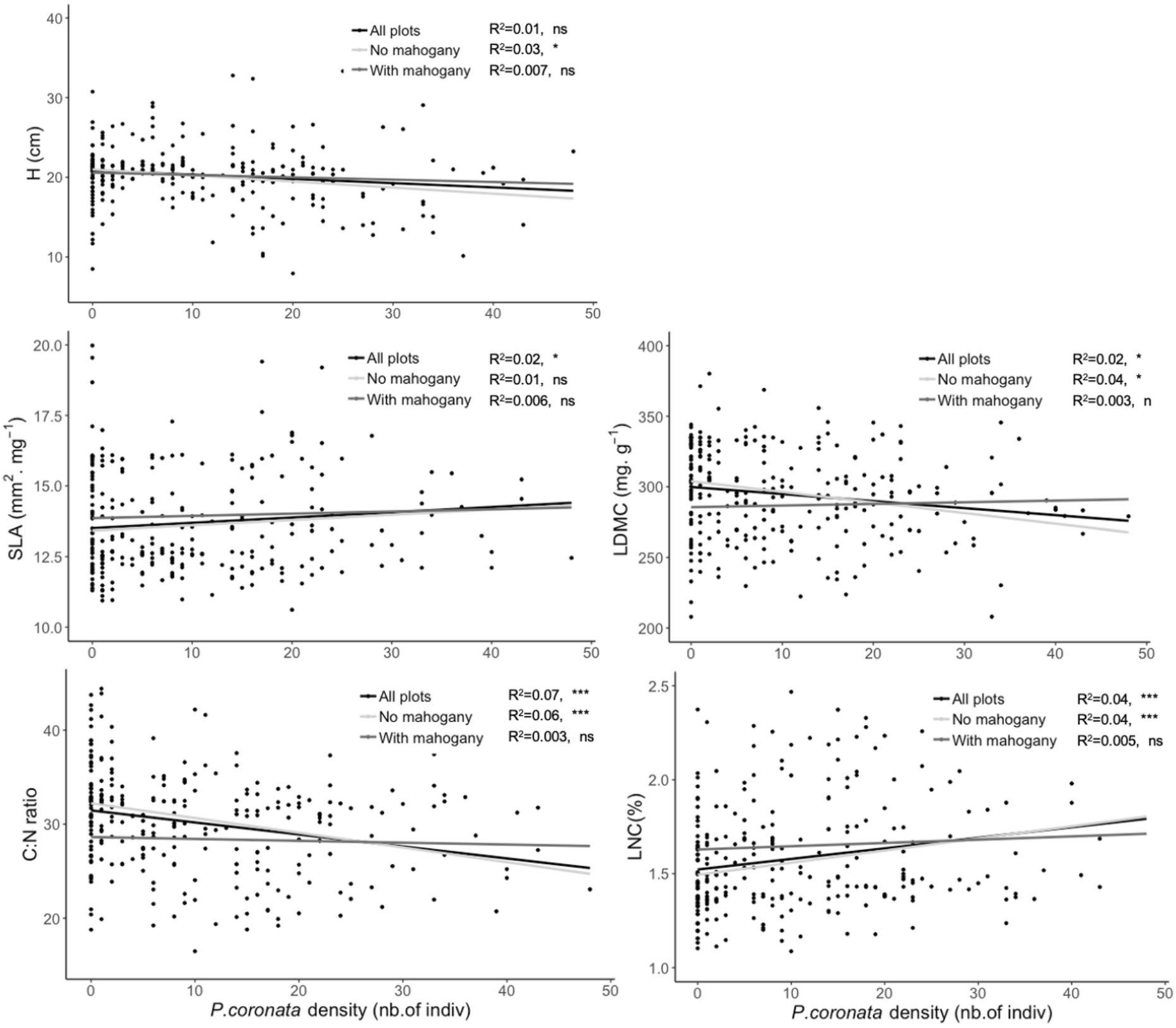

Fig. 2 Changes in CWM traits of resident plant communities (i.e., without *P. coronata* contribution) along the gradient of *P. coronata* densities for the five functional traits. Three regression lines are given: "all plots" (black regression) and two subsets "no mahogany" and "with mahogany" canopy (grey regressions). Invaded communities comprise 30 sampled dominant species, with *P. coronata* traits excluded from analyses. Each point represents a plot using N = 280. R^2 is the coefficient of determination and asterisks indicate significance levels of the linear regression line: ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$, ns = not significant

plots with mahogany were not significantly correlated with the gradient of *P. coronata* density (Fig. 4).

Discussion

Effect of P. coronata on taxonomic and functional diversity of resident plant species

Plant invasions can have harmful impacts on native vegetation, primarily by reducing species richness, diversity, and evenness, thus emphasizing the strong correlation between the dominance of invasive plants

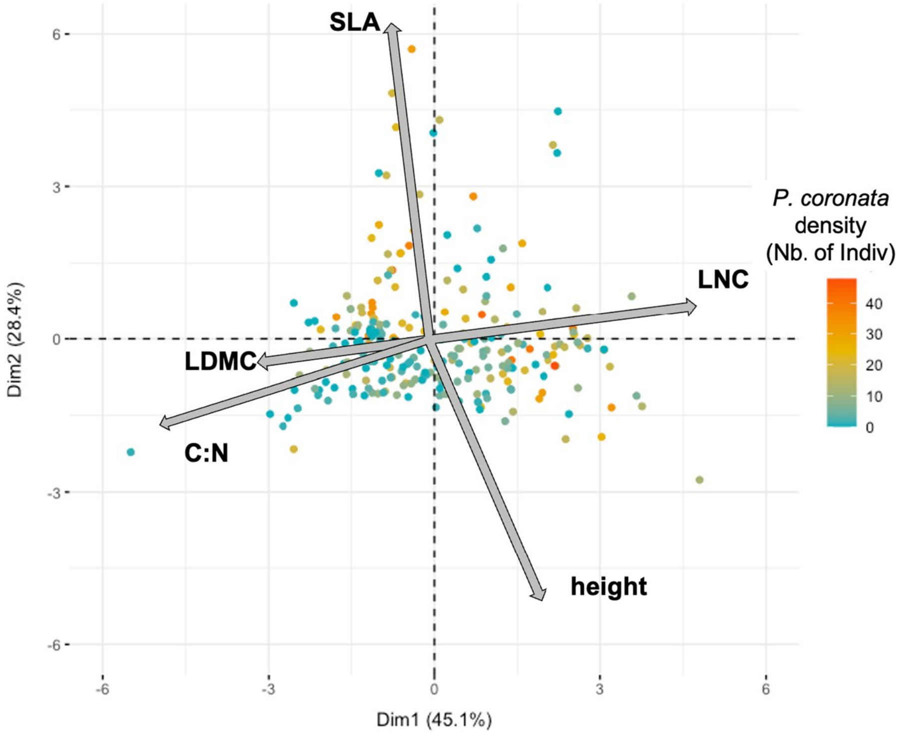

Fig. 3 Multivariate analyses (PCA from axis 1–2) without the contribution of *P. coronata*, showing the effect of *P. coronata* on functional traits in resident plant communities using five plant functional traits. SLA = specific leaf area. LDMC = leaf dry matter content. LNC = leaf nitrogen content. H = height. C:N = leaf CN ratio

and the decline of native plants (Didham et al. 2005; Hulme et al. 2008). This case study in a Fijian rainforest supports this idea by demonstrating that plant species richness and diversity are strongly and negatively correlated with the abundance of *P. coronata*, an invasive palm tree. In this CIS forest park, the exotic mahogany trees that were planted before the introduction of *P. coronata* could also be a potential confounding factor. Indeed, according to the 'Invasional meltdown hypothesis', the presence of invasive species in an ecosystem facilitates the invasion of other non-native species (Simberloff and Von Holle 1999). Nevertheless, our study does not provide evidence of invasional meltdown. Indeed, the majority of plots (two-thirds) were without mahogany canopy suggesting that mahogany did not directly facilitated *P. coronata*. Secondly, negative relationships observed between *P. coronata* and plant diversity were maintained independently on the presence or not of mahogany, with a tendency to have weaker correlations under mahogany canopy.

Thus, *P. coronata* might be a notable threat to Fiji´s unique assemblage of flora, particularly considering that approximately 50% of the country's land area is covered by tropical lowland rainforest (Mueller-Dombois and Fosberg 1998)—an ecosystem within which *P. coronata* clearly thrives. Biodiversity in these forests is extremely high, containing over 99% of the national endemic flora and fauna (Keppel et al. 2010; Olson et al. 2010). This rainforest ecosystem is among the most diverse in the Pacific, being classed as species-rich because 1,350 of the 1,769 different native vascular species are found within the forest environment (Mueller-Dombois and Fosberg 1998). Ecological studies on Fiji are scarce and, although the country has 390 recorded invasive alien species, this is the first study to quantify the potential effect of an invasive alien plant on the flora of Fiji.

Studies conducted by Daehler and Baker (2006) and Meyer et al. (2008) showed that although *P. coronata* displayed signs of becoming invasive in Hawaii and Tahiti, the species was not, at that time, viewed as a threat. However, later studies conducted by Parker and Parsons (2012) categorized the species as an invasive species in Hawaii. In Fiji, this study has presented ample evidence that *P. coronata* is a highly invasive species, forming populations with density and overall cover that are significantly greater than those of native species.

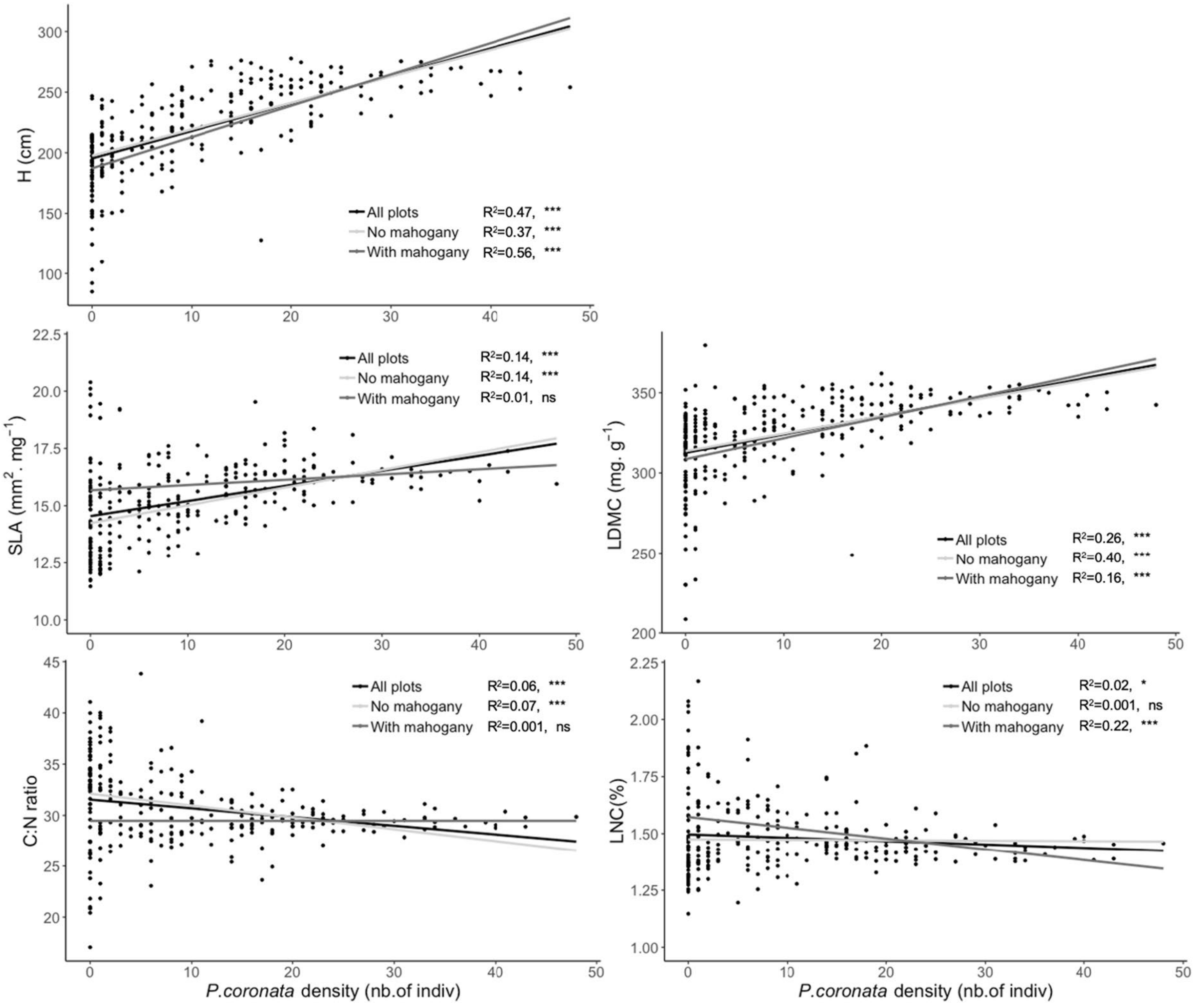

Fig. 4 Changes in community-weighted mean (CWM) traits of novel plant communities (i.e. with *P. coronata* contribution) along the gradient of *P. coronata* densities for the five functional traits. Three regression lines are given: “all plots” (black regression) and two subsets “no mahogany” and “with mahogany” canopy (grey regressions). Novel communities comprise a total of 31 sampled dominant species. N = 280. R^2 is the coefficient of determination and asterisks indicate significance levels of the linear regression line: $***P < 0.001$; $**P < 0.01$; $*P < 0.05$, ns = not significant

In addition to changing species composition and reducing plant diversity, fast-growing invasive species may also affect the functional diversity of vegetation (Michelan et al. 2010). The increasing abundance of *P. coronata* also led to a decline in FRic, suggesting that this invasive plant may cause a loss of functions or the original combination of traits found in understory resident species. Conversely to other functional indices, FRic measures the total functional range covered by a community and thus has the advantage of conveying information beyond species richness (Legras et al. 2018). Our results thus indicate that a *P. coronata* invasion is linked not only to a decrease in species richness but also to a decrease in the breadth of ecological strategies in rainforest communities.

Pinanga coronata ‘s effect on plant traits and strategies of resident communities

This study demonstrated that dominant resident species in invaded plots (i.e., communities without a *P. coronata* functional contribution) tend to have a high SLA and LNC and a low LDMC and C:N. This change in CWM traits was mainly driven by species that persisted along the gradient as opposed to the arrival of new dominant native species into the communities. Such a combination of leaf traits characterizes species that are adapted to competition and/or to disturbance. Thus, in the case of the invasion by *P. coronata*, traits of resident plants are filtered to form competitive understory communities in order to cope with competition from *P. coronata* for light and/or nutrients. Additionally, using the "TCAP/TDAP" method (Pillar et al. 2009), we were able to show that these patterns are beyond random expectations and that the gradient of *P. coronata* density led to greater trait convergence of resident species than would be expected by chance, most notably for LDMC and C:N. This trait convergence of plant communities (tested against null models) is supposedly due to the extent of habitat selection and not the consequence of a decrease in plant richness (Pilar et al. 2009). Such convergence suggests that the density of *P. coronata* can acts as a strong selective biotic filter that could reduce the diversity of trait values towards more competitive strategies, a feature also demonstrated by other invasive species (Sodhi et al. 2019). These results support the competitive hierarchy hypothesis.

In community assembly rules, convergence is usually explained by abiotic factors (see, for example, Bernard-Verdier et al. 2012). In a complementary experiment performed in the same mature forests in Fiji, we found that soil moisture and photosynthetically active radiation (i.e., light)—two important determinants for plant growth—were not influenced by *P. coronata* density along the gradient of invasion (Gopaul, pers. comm). Subsequently, we suggest that *P. coronata* outcompetes species by dominating the space and/or through higher soil nutrient uptake or storage, as opposed to water and/or light competition. Although not directly investigated in our study, the trait convergence observed when *P. coronata* is abundant may result from biotic interactions, such as competition. Alternatively, it is possible that *P. coronata* acts as an ecosystem engineer by changing ecosystem functioning and affecting other trophic levels which, in turn, filters plants in the ecosystem. For example, Forey et al. (2021), in the same forest, demonstrated that *P. coronata* led to a change in soil fauna communities (i.e., Collembola) and suggested a decrease in plant–soil interactions under *P. coronata* invasion.

Lastly we found, that the intensity of *P. coronata* filtering seemed to be modulated by the presence or absence of mahogany. Indeed, when considering only plots under mahogany, no CWM traits changes were observed suggesting that the canopy of mahogany might contribute to mitigate the effect of *P. coronata.* Further abiotic measurements (e.g. soil fertility, pH, water and light availability) are necessary to understand and hierarchize the different filters that act on resident understory communities.

Functional properties of novel plant communities

This study indicated that *P. coronata* influences the novel plant communities' functional assemblages, and as a result, the remaining species within the understory plant community tend to have traits that are related to fast resource acquisition. Indeed, when including *P. coronata* in the assessment of functional assemblage, it was found that the considerable dominance of this invasive plant results in CWMs of traits converging towards those of the invasive plant. When compared with the traits of resident species, *P. coronata* tends to have a more conservative strategy (higher LDMC and lower LNC) for nutrients but a more competitive strategy for light (high SLA) (Albert et al. 2010). Funk (2013), in a meta-analysis, demonstrated that invasive species in low-nutrient systems tend to have a higher SLA than native species, but this does not always translate into a shorter leaf lifespan than natives. Thus, it is likely that the apparent competition for nutrients between *P. coronata* and resident species is rather due to a greater ability to conserve nutrients (high biomass and long lifespan of palm leaves) rather than a faster nutrient uptake and plant growth. Additionally, *P. coronata* have a better competitive strategy for light than do resident species (Kimura and Simbolon 2002), and this allows the invasive to dominate the other species under a canopy of trees. Similar results were found by Pattison et al. (1998) in the understory of Hawaiian rainforests, where it was demonstrated that relative photosynthetic growth rates of invasive species growing in the sun and in a partial shade were significantly higher than those for native species.

The traits of invaders depend on the characteristics of the invaded habitats (Funk 2013), thus making it difficult to identify a suite of general traits explaining invasiveness. Nevertheless, according to the "try harder" hypothesis (Dainese and Bragazza 2012; Tecco et al. 2010), IAP should differ from resident species through traits that allow them to better deal with local conditions when compared with the resident species. More precisely, Funk and Vitousek (2007) suggested that, in low-resource environments, IAP tend to have more conservative functional traits (i.e., have long-lived, thick, tough leaves with high concentrations of defense compounds and a low nutrient content) than resident species. Conversely, in resource-rich environments, IAP should show more acquisitive characteristics – such as possessing thin, soft, and nutrient-rich leaves with a high SLA and short lifespan (Tecco et al. 2010) – than resident species. In this study, the nutrient conservation strategy of *P. coronata* is in agreement with studies that investigate plant growth strategies in tropical rainforest with low-nutrient soils (e.g., Bakker et al. 2010) and, in particular, the very low soil phosphorus concentrations limiting microbial processes (Camenzind et al. 2018).

The plant community composition subsequent to *P. coronata* introduction, with traits or rather markers of a fast resource acquisition strategy, can be detrimental to ecosystem resources as it will require more nutrients for growth and maintenance. This change in species dominance brought about by the presence of the invasive *P. coronata* is inducing a considerable change in the Fijian rainforest, thus inflicting wholesale changes in the structure and functioning of the ecosystem (Denslow 2007). In turn, these changes may have serious consequences for a number of important variables, including trophic structure, the nutrient content of the soil, decomposition, rare species, ecosystem services, and the overall productivity and diversity of the invaded habitat (Denslow 2007).

Conclusion

This study has highlighted the potentially negative effect that an invasive alien palm species (*P. coronata*) could have on the resident plant community and, indeed, on the overall ecosystem of the Colo-i-Suva Forest Park. Firstly, we demonstrated that the invasion of *P. coronata* was strongly correlated with a reduction in species richness and diversity but also with a drecrease of the functional diversity of resident plant communities. Secondly, using a functional approach and null models, we revealed that an invasion by *P. coronata* induced trait community convergence towards a fast resource acquisition strategy according to the competitive hierarchy hypothesis. Such functional changes of plant communities into competitive plant assemblages could notably alter the resilience of an ecosystem and its functioning. Additionally, it should be borne in mind that this study concerns a single invasive plant species, but interactions with other invasive species (i.e., a "cocktail" effect) are highly probable in insular ecosystems, and this might hamper our understanding of functional invasion consequences (Bruno et al. 2005; Johnson et al. 2009). Lastly, our study, like most *in-situ* invasive species studies, is correlative and we are aware that correlations are not causations and observed effects may be caused by unmeasured or confounding variables (Warren et al. 2017). Such observations should be confirmed by experimental studies.

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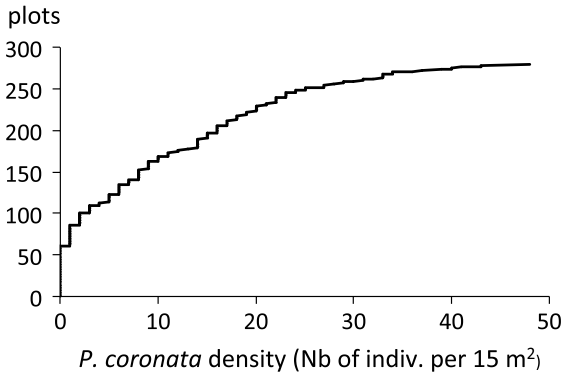
Data availability The datasets generated during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have not disclosed any competing interests.

Appendix 1

Cumulative ranked abundance curves of *P. coronata* density in the 280 plots ($15 m^2$) used for this study.



Appendix 2

List of the 120 species recorded in the 280 plots. Information based on the Global Plants Database operated by JSTOR. https://plants.jstor.org/

Species name	Family	Native/Exotic	Species name	Family	Native/Exotic
Acanthephippium vitiensis	ORCHIDACEAE	Native	*Gymnostoma vitiense*	CASUARINACEAE	Native
Agathis vitiensis	ARAUCARIACEAE	Native	*Haplolobus floribundus*	BURSERACEAE	Native
Aglaia elegans	MELIACEAE	Native	*Heliconia psittacorum*	HELICONIACEAE	Exotic
Aglaia sp.	MELIACEAE	Native	*Heritiera ornithocephala*	STERCULIACEAE	Native
Aglaia vitiensis	MELIACEAE	Native	*Hernandia olivacea*	HERNANDIACEAE	Native
Alstonia pacifica	APOCYNACEAE	Native	*Homalium vitiense*	FLACOURTIACEAE	Native
Alstonia vitiensis	APOCYNACEAE	Native	*Ixora pelagica*	RUBIACEAE	Native
Amaroria soulameiodes	SIMAROUBACEAE	Native	*Kingiodendron platycarpum*	FABACEAE	Native
Anacolosa lutea	OLACACEAE	Native	*Koelreuteria elegans*	SAPINDACEAE	Native
Ardisia crispa	MYRSINACEAE	Exotic	*Macaranga graeffeana*	EUPHORBIACEAE	Native
Astronidium confertiflorum	MELASTOMATACEAE	Native	*Macaranga harveyana*	EUPHORBIACEAE	Native
Atuna racemosa	CHRYSOBALANACEAE	Native	*Macaranga magna*	EUPHORBIACEAE	Native
Baccaurea seemannii	EUPHORBIACEAE	Native	*Maesa insularis*	MYRSINACEAE	Native
Balaka microcarpa	ARECACEAE	Native	*Maesopsis eminii*	RHAMNACEAE	Exotic

Species name	Family	Native/Exotic	Species name	Family	Native/Exotic
Barringtonia edulis	LECYTHIDACEAE	Native	*Medusanthera vitiensis*	ICACINACEAE	Native
Barringtonia seaturae	LECYTHIDACEAE	Native	*Melicope cucullata*	RUTACEAE	Native
Buchanania attenuata	ANACARDIACEAE	Native	*Melochia degeneriana*	STERCULIACEAE	Native
Calophyllum cerasiferum	CLUSIACEAE	Native	*Metroxylon vitiense*	ARECACEAE	Native
Calophyllum vitiense	CLUSIACEAE	Native	*Myristica castaneifolia*	MYRISTICACEAE	Native
Canarium harveyi	BURSERACEAE]	Native	*Myristica chartacea*	MYRISTICACEAE	Native
Cliderma hirta	MELASTOMATACEAE	Exotic	*Myristica gillespieana*	MYRISTICACEAE	Native
Cerbera manghas	APOCYNACEAE	Native	*Myristica grandifolia*	MYRISTICACEAE	Native
Citronella vitiensis	ICACINACEAE	Native	*Neuburgia corynocarpa*	LOGANIACEAE	Native
Cordyline fruticosa	ASPARAGACEAE	Native	*Pagiantha thurstonii*	APOCYNACEAE	Native
Cordyline terminalis	ASPARAGACEAE	Native	*Palaquium horneii*	SAPOTACEAE	Native
Crossostylis seemann ii	RHIZOPHORACEAE	Native	*Palaquium porphyreum*	SAPOTACEAE	Native
Cryptocarya constricta	LAURACEAE	Native	*Palaquium vitilevuense*	SAPOTACEAE	Native
Cyathocalyx insularis	ANNONACEAE	Native	*Pandanus tectorius*	PANDANACEAE	Native
Cynometra insularis	FABACEAE	Native	*Parinari insularum*	CHRYSOBALANACEAE	Native
Decaspermum vitiense	MYRTACEAE	Native	*Pinanga coronata*	ARECACEAE	Exotic
Dillenia biflora	DILLENIACEAE	Native	*Pittosporum arborescens*	PITTOSPORACEAE	Native
Dolicholobium latifolium	RUBIACEAE	Native	*Pittosporum pickeringii*	PITTOSPORACEAE	Native
Dysoxylum lenticellare	MELIACEAE	Native	*Planchonella garberi*	SAPOTACEAE	Native
Dysoxylum quercifolium	MELIACEAE	Native	*Podocarpus neriifolius*	PODOCARPACEAE	Native
Dysoxylum richii	MELIACEA	Native	*Polyscias multijuga*	ARALIACEAE	Native
Elaeocarpus kambi	ELAEOCARPACEAE	Native	*Pommetia pinnata*	SAPINDACEAE	Native
Emmenosperma micropetalum	RHAMNACEAE	Native	*Psychotria amoena*	RUBIACEAE	Native
Endiandra elaeocarpa	LAURACEAE	Native	*Psychotria cf. archboldiana*	RUBIACEAE]	Native
Endiandra gillespiei	LAURACEAE	Native	*Psidium guajava*	MYRTACEAE	Exotic
Endospermum macrophyllum	EUPHORBIACEAE	Native	*Samanea saman*	FABACEAE	Exotic

Species name	Family	Native/Exotic	Species name	Family	Native/Exotic
Ervatamia obtusiuscula	APOCYNACEAE	Native	*Schefflera seemanniana*	ARALIACEAE	Native
Ficus barclayana	MORACEAE	Native	*Scirpodendron ghaeri*	CYPERACEAE	Native
Ficus fulvo-pilosa	MORACEAE	Native	*Semecarpus vitiensis*	ANACARDIACEAE	Native
Ficus pritchardii	MORACEAE	Native	*Storckiella vitiensis*	LEGUMINOSAE	Native
Ficus theophrastoides	MORACEAE	Native	*Swietenia marcophylla*	MELIACEAE	Exotic
Ficus vitiensis	MORACEAE	Native	*Symplocos leptophylla*	SYMPLOCACEAE	Native
Garcinia myrtifolia	CLUSIACEAE	Native	*Syzygium cornynocarpum*	MYRTACEAE	Native
Garcinia pseudoguttifera	CLUSIACEAE	Native	*Syzygium curvistylum*	MYRTACEAE	Native
Garcinia sessilis	CLUSIACEAE	Native	*Syzygium malaccense*	MYRTACEAE	Native
Gardenia storckii	RUBIACEAE	Native	*Syzygium sp.*	MYRTACEAE	Native
Geissois superba	CUNONIACEAE	Native	*Syzygium spp.*	MYRTACEAE	Native
Geniostoma macrophyllum	LOGANIACEAE	Native	*Tapeinosperma ligulifolium*	MYRSINACEAE	Native
Geniostoma rupestre	LOGANIACEAE	Native	*Tapeinosperma megaphyllum*	MYRSINACEAE	Native
Gironniera celtidifolia	ULMACEAE	Exotic	*Terminalia pterocarpa*	COMBRETACEAE	Native
Glochidion seemannii	PHYLLANTHACEAE	Native	*Timonius affinis*	RUBIACEAE	Native
Glochidion vitiense	EUPHORBIACEAE	Native	*Turrillia vitiensis*	PROTEACEAE	Native
Gmelina vitiensis	LAMIACEAE	Native	*Vavaea amicorum*	MELIACEAE	Native
Gnetum gnemon	GNETACEAE	Native	*Vavaea harveyi*	MELIACEAE	Native
Gonystylus punctatus	GONYSTYLACEAE	Native	*Veitchia joannis*	ARECACEAE	Native
Guioa chrysea	SAPINDACEAE	Native	*Xylopia pacifica*	ANNONACEAE	Native

Appendix 3

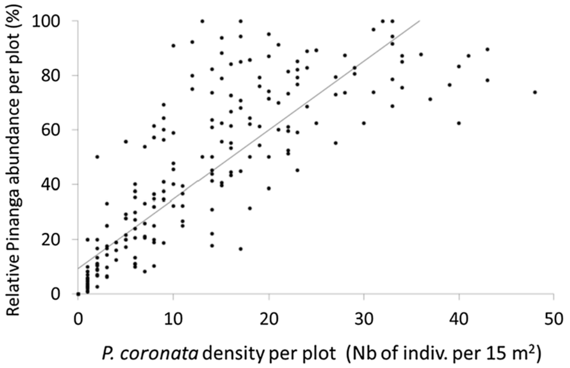
Trait values of the 5 functional traits measured on the 31 selected dominant plant species in Colo-i-Suva Park (Fiji). Abbreviations and description of the five functional traits (LDMC, SLA, C:N, LNC & Height) are defined in Table 1.

Plant species	SLA $mm^2.g^{-1}$	LDMC $mg.g^{-1}$	N %	C/N	Height cm
Aglaia elegans	12.9	316.4	2.023	21.44	140.4
Aglaia vitiensis	11.76	317.5	1.739	27.66	158
Amaroria soulameiodes	13.74	221.9	2.22	19.39	413.8
Anacolosa lutea	13.11	268.5	2.467	16.48	180.2
Astronidium confertiflorum	11.84	237.7	1.075	31.08	183.6
Atuna racemosa	16.11	335.1	1.367	32.53	215
Barringtonia edulis	21.07	206.3	1.526	27.77	92.6
Citronella vitiensis	13.31	235.1	0.902	49.05	162.4

Plant species	SLA mm^2.g^{-1}	LDMC mg.g^{-1}	N %	C/N	Height cm
Clidema hirta	23.67	345.5	1.671	24.76	79.3
Crossostylis seemannii	10.95	236.9	1.11	34.6	219.4
Cryptocarya constricta	11.52	420.5	1.363	32.83	270.2
Cynometra insularis	10.61	478.4	1.389	31.81	233.6
Dysoxylum quercifolium	14.9	295	1.271	37.32	153.2
Endiandra elaeocarpa	9.46	416.4	1.301	35.7	170.4
Garcinia myrtiflora	9.15	386.3	0.739	63.28	158
Garcinia sessilis	14	234.3	1.502	28.13	262.6
Glochidion seemannii	17.62	307.2	1.584	25.06	101.4
Glochidion vitiensis	14.35	282.3	1.435	29.86	94.5
Gnetum gnemon	12.15	293.7	2.372	18.78	217.4
Haplolobus floribundus	13.44	357.5	1.345	33.83	229.2
Heliconia psittacorum	20.37	207.7	2.035	20.38	85
Myristica castaneifolia	11.14	327.6	1.342	35.41	177.2
Myristica gillespieana	11.72	286.7	1.579	30.45	158.4
Palaquium horneii	10.3	345.1	1.02	45.84	198.4
Pinanga coronata	16.72	356.2	1.384	29.56	280
Psychotria amoena	12.06	205.3	1.852	22.21	295.4
Swietenia marcophylla	29.6	263.4	1.486	29.43	134.8
Syzygium cornynocarpum	15.09	297.1	1.098	40.55	150.4
Syzygium curvistylum	8.79	366.9	0.701	65.03	184.2
Vavaea amicorum	12.08	277.9	0.943	43.63	223
Xylopia pacifica	14.29	331.4	1.461	29.73	138.8

Appendix 4

Relationship between the relative abundance and density of *P. coronata* for each plot.



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