

Vulnerability and resilience of rainforests to plant invasions in a tropical island of the South Pacific: a sixteen-year survey

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Research Article

Keywords: Disturbance, Endemic flora, Homogenization, Long-term monitoring

Posted Date: September 27th, 2024

DOI: <https://doi.org/10.21203/rs.3.rs-4980518/v1>

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Additional Declarations: No competing interests reported.

Version of Record: A version of this preprint was published at Biodiversity and Conservation on September 3rd, 2025. See the published version at <https://doi.org/10.1007/s10531-025-03143-5>.

Abstract

Island biodiversity is considered to be particularly vulnerable to biological invasions. However, the direct impacts of invasive alien plants on native and endemic flora are often difficult to assess. Indeed, invasion by woody species is a relatively slow process, and natural or anthropogenic disturbances that favor some plant invaders, also contribute to biodiversity loss, and might act as confounding factors. Hence, we conducted a long-term monitoring of rainforest composition and structure in the small tropical high volcanic island of Moorea (French Polynesia, South Pacific) over a 16-year (2006–2022) period without any major disturbance. All endemic, native and alien woody species with a stem ≥ 1 cm in diameter were identified and measured with a 4-year frequency in ten 20 m $\times$ 20 m plots. The variation of species richness, Shannon diversity, Pielou evenness and abundance over time was analyzed using linear mixed-effects models with identities of the plots as random factors. Results revealed an increase in the number of stems of alien plants (+ 50% in 16 years), especially the two most common invasive alien trees, *Miconia calvescens* (Melastomataceae) and *Spathodea campanulata* (Bignoniaceae). In contrast, we found a decrease in the richness (from 28 species to 19) and abundance (-20% of stems) of endemic and native species, especially in the higher-elevation plots. Three plots remained relatively stable in terms of plant invasions according to Shannon and Pielou indices, and some common native and endemic woody species persisted over time. Although a continuous decline of plant diversity, including species extirpation, was observed, our results also suggest a relative resilience of certain forest types and associated communities to plant invasions. Efforts to control invasive alien plants should therefore target the most vulnerable native habitats.

Introduction

Island terrestrial biodiversity is considered particularly vulnerable to global and local environmental changes, and particularly to biological invasions (Brockie et al. 1988; Loope and Mueller-Dombois 1989; Kueffer et al. 2010; Russell et al. 2017; Fernández-Palascios et al. 2021). However, the direct impacts of invasive alien plants on endemic and native flora are often difficult to assess, with little evidence that invasive alien plants have led to the extirpation (*i.e.*, population extinction) or global extinction of native plants (Sax and Gaines 2008; Jäger et al. 2009; Downey and Richardson 2016). One reason is probably that invasions by plants, especially by woody plants, are a relatively slow process. Another possible reason might be the difficulty to disentangle the direct impact of plant invaders from that of natural (e.g., cyclones, landslides) or anthropogenic (e.g., logging, intentional or accidental fires) disturbances that may also contribute to habitat changes and biodiversity losses (MacDougall and Turkington 2005). The important role of natural or human-caused disturbances have often been proposed to explain plant invasions in primary forests. Indeed, many invasive alien plants are fast-growing light-demanding, early successional pioneer species that require disturbances to invade closed-canopy forests (Hobbs and Huenneke 1992; Fine 2002). Therefore, continental tropical rainforests usually show some sort of resilience to plant invasions or lower “invasibility” (Cronk and Fuller 1995; Rejmanek et al. 2005) because of their higher native biota diversity and complexity (but see Peters 2001; Delnatte and Meyer 2012). It is possible that closed-canopy forest ecosystems found in islands may also show some resilience to plant

invasions. Therefore, long-term vegetation monitoring appears crucial to study island forest dynamics and vegetation changes in the presence of invasive alien species (Barbé et al. 2015; Li et al. 2015; Florens et al. 2017; Denslow et al. 2024) but also according to disturbance regime and forest types.

Here, we monitored rainforest dynamics in 10 plots established in the small tropical high volcanic island of Moorea (French Polynesia, South Pacific) over a 16-year (2006–2022) period to address the following questions: (1) How do woody invasive alien species alter the species richness, diversity and abundance of endemic and native plants over a long period of time, i.e. how vulnerable are island forest ecosystems to plant invasions? (2) Does this effect vary among different forest types and associated plant communities, depending on their relative resilience to natural and human disturbances? Those issues are crucial to prioritize control efforts in the most vulnerable habitats to plant invasions.

Methods

Study area

Moorea is a high volcanic island (17°32'33"S, 149°49'50"W) located ca. 18 km to the north-west of Tahiti, the main island of the Society archipelago in French Polynesia, South Pacific Ocean (Fig. 1A). The island is small (*ca.* 135 km²), between 1.15 and 2.45 My old, and its highest summit reaches 1,207 m (Mt Tohiea). The climate is tropical oceanic with a relatively dry and cool season between April and October and a warm and rainy season between November and March, when cyclones may occasionally occur (Laurent and Maamaatuaiahutapu 2019). The native vascular flora of Moorea comprises 300 species, including 122 ferns and 178 flowering plants (Meyer et al. 2015). Among them, 76 species are endemic (17 to French Polynesia or to Southeastern Polynesia, 47 to the Society Islands, six to the two islands of Tahiti and Moorea, and six are single island endemics). At least 767 alien species have been introduced on the island and half of them (327) are now naturalized, including 182 introduced as ornamentals or cultivated, and 145 agricultural weeds, adventives, and ruderals. The alien flora of Moorea also exceeds its native flora in terms of distributional range since 17% of the island are highly invaded, 45% are currently occupied by "hybrid" habitats where native species co-occur with alien species, and primary forests occurs on only 6% (8 km²), mainly on the highest summits of Mt Tohiea, Mt Rotui (899 m) and Mt Mouaputa (830 m) (Meyer et al., 2015).

Permanent plots

Ten 20 m × 20 m plots were set up in 2006 in three sites of the island of Moorea, near hiking trails (Chevillotte et al. 2014): Opunohu (OPU), Vaianae (VAI) and Mouaroa (MOU) (Fig. 1B). These plots are located at elevations ranging from 230 to 500 m. The vegetation is described as tropical low- to mid-elevation rainforests, also called « hygrophilous forests » (Florence 1993), or « valley forests » and « ridge forests » in Tahiti and Moorea (Mueller-Dombois and Fosberg 1998). Average annual temperature over the plots is *ca.* 25°C and annual precipitation *ca.* 3,000 mm (Laurent and Maamaatuaiahutapu 2019). The OPU site is made of valley forests on the north side of the island, the VAI site harbours a similar

vegetation on the south side and the MOU site is composed of ridge forests between both valleys (Fig. 1B). The composition and structure of woody species in each plot was first described in 2006 (Chevillotte et al. 2014). This first study showed that the three sites differ in their level of invasion, with OPU and VAI being more heavily invaded both in the canopy and understory strata and MOU having more abundant native and endemic species (Table 1). Since their establishment, the plots were monitored every four years until 2022 (2006, 2010, 2014, 2018 and 2022), *i.e.*, for a period of 16 years.

Table 1

Location and characteristics of the 10 permanent plots. Forest types with dominant woody species found in canopy and in the understory are taken from Chevillotte et al. (2014). *naturalized alien species (ancient Polynesian introduction); **invasive alien species (modern introductions)

Site	Plot name	Latitude S	Longitude W	Elev. (m)	Slope (°)	Forest type	Dominant woody species (by order or abundance)
Opunohu	OPU 1	17°32'36.24"	149°49'46.56"	250	8–12	Valley forest (north side)	<i>Spathodea campanulata</i> ** <i>Neonauclea forsteri</i> - <i>Talipariti tiliaceum</i> forest with <i>Ixora mooreensis</i> - <i>Cyclophyllum barbatum</i> in the understory
	OPU 2	17°32'37.32"	149°49'47.64"	230	8–10		<i>Neonauclea-Barringtonia asiatica</i> forest with <i>Ixora-Cyclophyllum</i>
	OPU 3	17°32'48.48"	149°50'22.56"	300	0–5		<i>Spathodea</i> ** <i>Aleurites moluccana</i> * forest with <i>Miconia calvescens</i> ** <i>Talipariti</i>
Mouaroa	MOU 1	17°32'50.64"	149°50'33.36"	420	15–25	Ridge forest	<i>Neonauclea-Talipariti</i> forest with <i>Ixora-Syzygium malaccense</i> *
	MOU 2	17°32'49.20"	149°50'44.16"	480	30–40		<i>Spathodea</i> ** <i>Neonauclea</i> forest with <i>Miconia</i> ** <i>Crossostylis biflora</i>
	MOU 3	17°32'49.20"	149°50'54.96"	500	30–40		<i>Weinmannia parviflora</i> - <i>Astronidium</i> sp. forest with <i>Miconia</i> **
Vaianae	VAI 1	17°33'04.32"	149°50'29.47"	230	12–18	Valley forest (south side)	<i>Spathodea</i> * <i>Neonauclea</i> forest with <i>Miconia</i> **
	VAI 2	17°32'53.81"	149°50'32.10"	340	0–5		<i>Neonauclea-Talipariti</i> forest

Site	Plot name	Latitude S	Longitude W	Elev. (m)	Slope (°)	Forest type	Dominant woody species (by order or abundance)
							with <i>Miconia</i> ** <i>Ixora</i>
	VAI 3	17°33'06.41"	149°50'30.48"	260	8–12		<i>Spathodea</i> ** <i>Neonauclea</i> forest with <i>Miconia</i> ** <i>Syzygium</i> *
	VAI 4	17°32'53.52"	149°50'25.08"	380	20–30		<i>Spathodea</i> ** <i>Neonauclea</i> forest with <i>Talipariti</i> <i>Miconia</i> **

Woody species richness, diversity and abundance

All endemic, native and alien woody species with a stem diameter at breast height (or dbh, taken at 1.3 m) ≥ 1 cm were identified. The number of species identified in each plot (alpha diversity) and the total number of species in the 10 plots (gamma diversity) were analyzed over time as well as two diversity indices:

- the Shannon index (Shannon and Weaver 1949), defined as: $H' = \sum_{i=1}^S p_i \log_2 p_i$ where S stands for the number of species and $p_i = n_i/N$ the relative importance of species;
- the Pielou evenness index (Pielou 1966): $J' = \frac{H'}{H'_{max}} = \frac{H'}{\log_2(S)}$

The Shannon index considers both species richness and evenness and represents the uncertainty with which we can predict which species will be one randomly selected individual in the community. If the community contains only one monodominant species, the uncertainty is zero then the more species-rich the community is, the more uncertainty increases. The maximum value of H' for community of given richness occurs at situation where all species represent the same relative proportion. The Pielou index is the ratio of the observed value of Shannon index to its maximum value. It is minimum ($J' = 0$) when one species dominates.

Diversity indices were calculated using the *diversity* function of the R package *vegan* (Oksanen et al. 2019). Woody plants were also measured and their basal area was calculated every four years between 2006 and 2022.

We analyzed how species richness, diversity and abundance (expressed in both number of stems and basal area) of endemic, native, naturalized and invasive alien plants changed from 2006 to 2022. We built a linear mixed-effects model with richness, diversity and abundance as response variables, time as explanatory variable and identities of the plots as random factors. Linear mixed-effects analyses were

performed using the R package 'lme4' (Bates et al. 2015). All data analyses were computed with the R software (R Core Team 2019).

Results

Changes in woody species richness and diversity

A total of 38 woody plant species were observed in the ten 400 m² permanent plots at the beginning of our survey in 2006, including 15 endemic species, 13 native species (excluding endemics), 8 naturalized alien species and two widespread invasive alien trees: *Miconia calvescens* (Melastomataceae) and *Spathodea campanulata* (Bignoniaceae). After 16 years, we observed a decrease in the gamma diversity of endemic and native species (falling from 28 species to 19) whereas the number of naturalized and invasive alien species remain stable (Fig. 2, Table S1). Four endemic and five native woody species have been extirpated in 2022 (Table S1): the endemic trees *Macaranga attenuata* (Euphorbiaceae), *Meryta lanceolata* (Araliaceae), and *Myrsine ovalis* (Myrsinaceae), the endemic shrub *Cyrtandra* sp. (Gesneriaceae), as well as the native trees *Serianthes myriadenia* (Fabaceae), *Tarenna sambucina* (Rubiaceae) and the shrubs *Boehmeria virgata* (Urticaceae), *Jossinia reinwardtiana* (Myrtaceae), and *Macropiper latifolium* (Piperaceae).

The alpha diversity reflected the same tendency with a significant decrease in the number of endemic and native species, especially for the higher-elevation plots (MOU), and no variation in the number of naturalized and invasive alien species (Fig. 3). Shannon and Pielou indices both decreased significantly with time, indicating a loss of diversity and equitability (Fig. 4). This was particularly so for the two sites most invaded by *M. calvescens*, i.e., VAI and MOU.

Changes in woody plant abundance

The number of stems of the two dominant invasive alien trees, *M. calvescens* and *S. campanulata*, increased by 50% over this 16-year vegetation survey, and this was associated with a significant decrease in the abundance of endemic species (loss of 20% in stem number) (Fig. 5). A similar tendency was observed with abundance as estimated with basal area (Fig. S1). Some woody species suffered serious population decrease such as the common endemic small tree *Phyllanthus manono* (syn. *Glochidion manono*, Euphorbiaceae) and the native trees *Crossostylis biflora* (Rhizophoraceae), *Alstonia costata* (Apocynaceae), as well as the tree fern *Cyathea affinis* (Cyatheaceae) especially in the higher-elevation plots located between 400–500 elevation in upper rainforest (Table S1).

Discussion

Forest vulnerability versus resilience to plant invasions

We monitored over a period of 16 years the composition and structure of 10 low- to mid-elevation rainforest plots in the island of Moorea. We found a strong increase in the abundance of the invasive

alien species *M. calvescens*, a shade-tolerant small tree with fleshy fruits actively dispersed by birds (Meyer 1998), and *S. campanulata*, a large tree with wind-dispersed seeds whose seedlings are also able to established in closed-canopy rainforests (Larrue et al. 2016), both introduced as garden ornamentals in the early 1930's in Tahiti, French Polynesia (Meyer and Florence 1996). In response, we revealed the extirpation of several endemic and native woody species, mainly small trees and shrubs found in the understory of these two major plant invaders. As a result, current plant communities appear less diverse and equitable than 16 years ago.

Three plots remained relatively stable with regard to Shannon and Pielou indices despite plant invasions. Some common native trees such as *Cyclophyllum barbatum* (Rubiaceae) and a small number of woody species such as the endemic shrub *Ixora moorensis* (Rubiaceae) and the relatively rare endemic trees *Ceodes taitensis* (syn. *Pisonia taitensis*, Nyctaginaceae), *Claoxylon taitense* (Euphorbiaceae), *Lepinia taitensis* (Apocynaceae), and *Pittosporum taitense* (Pittosporaceae) also persisted over time. This shows the relative resilience of a few number of native forest taxa (Table S1). The introduction and dispersal of a fungal pathogen to control *M. calvescens*, causing its partial defoliation in the canopy, might also explain the survival of some understory native and endemic shrubs and small trees (Meyer and Fourdrigniez 2011). By examining invasion dynamics of 480 plots over 40 years, Li et al. (2015) showed that native plants more closely related to invasive alien species were more likely to go locally extinct. This remains to be tested on islands and further work needs to be carried out to understand interspecific variations in plant responses to biological invasions, and functional ecology seems to be a promising approach (Barton and Fortunel 2023).

The role of natural and anthropogenic disturbances

Cyclones or hurricanes are perhaps the most important and large-scale natural disturbances in tropical islands, with huge impact on forest composition, structure, and dynamics, including the recruitment and spread of alien plant species (Walker et al. 1992; Horvitz et al. 1998; Thomson et al. 2007). However, these extreme climatic events are relatively rare in French Polynesia. Only 23 of them (with wind speed > 110 km/h) occurred between 1969 and 2018, *i.e.* a frequency of one cyclone every two years (Laurent and Maamaatuaiahutapu 2019). Among them, only one cyclone (named "Oli") hit Moorea in 2010 during our 16-year survey, causing some windfalls (to which *S. campanulata* was particularly prone) and partial defoliation of the canopy (especially that of *M. calvescens*) (pers. obs. 2010). This cyclone of moderate intensity was detrimental to some endemic woody species, such as *Meryta lanceolata* with observed broken stems or trunks, but has also promoted the seedling recruitment of a few other endemic species, such as the fast-growing and light-demanding pioneer tree *Macaranga attenuata* (unpub. data). Thus endemic, native and alien plants have complex responses to disturbances that can be hardly captured by a simplistic snapshot approach.

Furthermore, long-term vegetation monitoring allows to better document the impact of human disturbances at smaller scales. Although our study sites are located in forested areas without strong anthropogenic impacts (such as logging, agriculture, housing development), few forest changes were

caused by man activities near the hiking trails. We noticed a slight decrease in the number of stems of invasive alien species between 2018 and 2022 (Fig. 5) that was attributed to an operation carried out by a local nature protection group (called “Moorea Biodiversité”) aimed at controlling *M. calvescens* in the valley of Opunohu (cut marks were observed during field sampling at the OPU site, pers. obs.).

Our findings illustrate that long-term monitoring is crucial to study the impact of invasive alien woody species on forest structure, composition and dynamics according to forest types and associated plant communities. On Moorea, we demonstrated a continuous decline of native and endemic plant diversity, including species extirpation or local extinction, associated with increasingly abundant invasive alien trees in our higher elevation rainforest sites. This phenomenon, globally known as biodiversity erosion or biotic homogenization (Holden et al. 2004; Castro and Jaksic 2007), and well documented in many other tropical island rainforests (see e.g., Meyer 2004; Florens et al. 2016; Mascaro et al. 2008), could be slowed down, if not completely stopped, only by using adapted and efficient methods to control the dominant invasive species in the most vulnerable habitats.

Declarations

Funding

The Délégation à la Recherche (Research Department of the Government of French Polynesia) provided the funding support, and the Richard Gump biological research station (University of California ,Berkeley), the CRIOBE (EPHE-CNRS-Université de Perpignan) and the Eco-Musée “Te Fare Natura” in Moorea logistical support and accommodation for the monitoring team during the 16 years of survey.

Author Contribution

J.-Y. M. selected the study sites and designed the field protocol. S. F. B. and R. P. performed the statistical analyses. All authors conducted the field work, read and approved the final draft of the manuscript

Acknowledgements

We thank Hervé Chevillotte and Dr. Jacques Florence (formerly at IRD, now both retired) for the initial plant surveys conducted together in 2006, and Teva Maruhi (formerly at IRD, now deceased), Kevin Heimanu (formely at the Délégation à la Recherche) and Elie Poroi (“Te Rau Ati Ati a Tau a Hiti Noa Tu” nature protection group) for field assistance in 2010.

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Figures

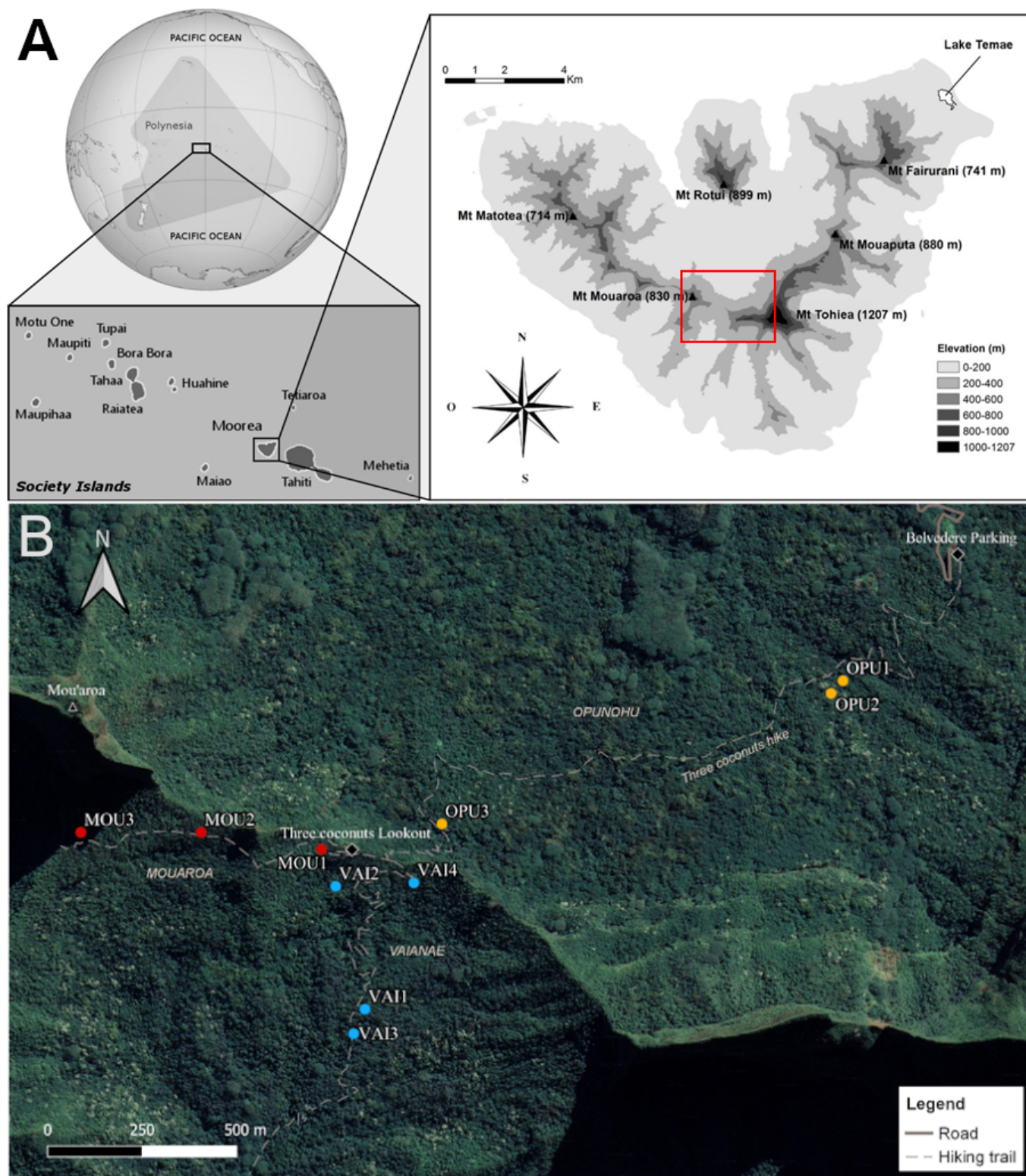


Figure 1

A Location of the island of Moorea (Society archipelago, French Polynesia) in the South Pacific Ocean. **B**: Location of the 10 permanent plots on the island of Moorea

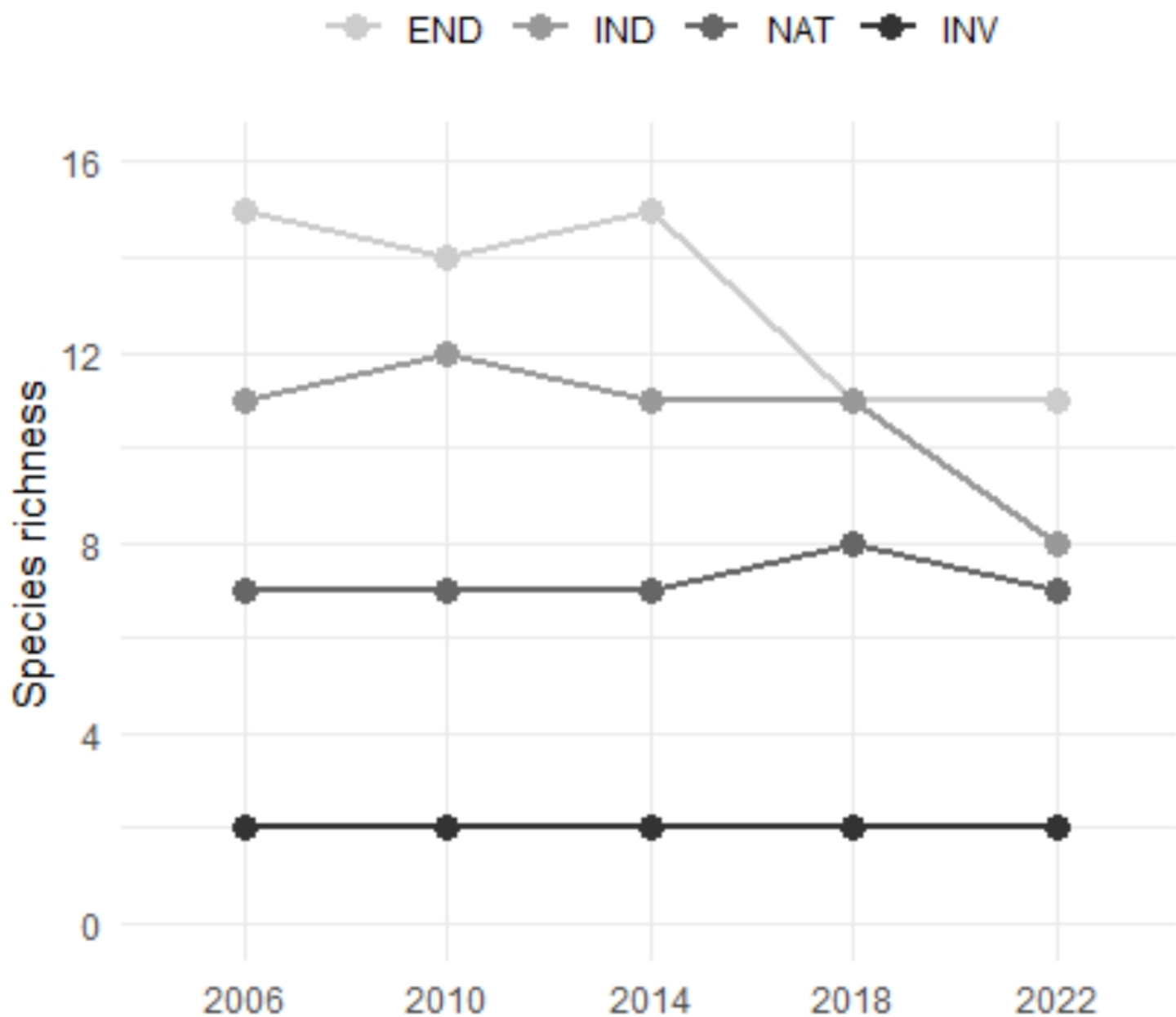


Figure 2

Change in species richness of the ten 400 m² plots combined (gamma diversity) between 2006 and 2022 by separating species based on their biogeographical status (END = endemic species, IND = indigenous species, NAT = naturalized alien species, INV = invasive alien species)

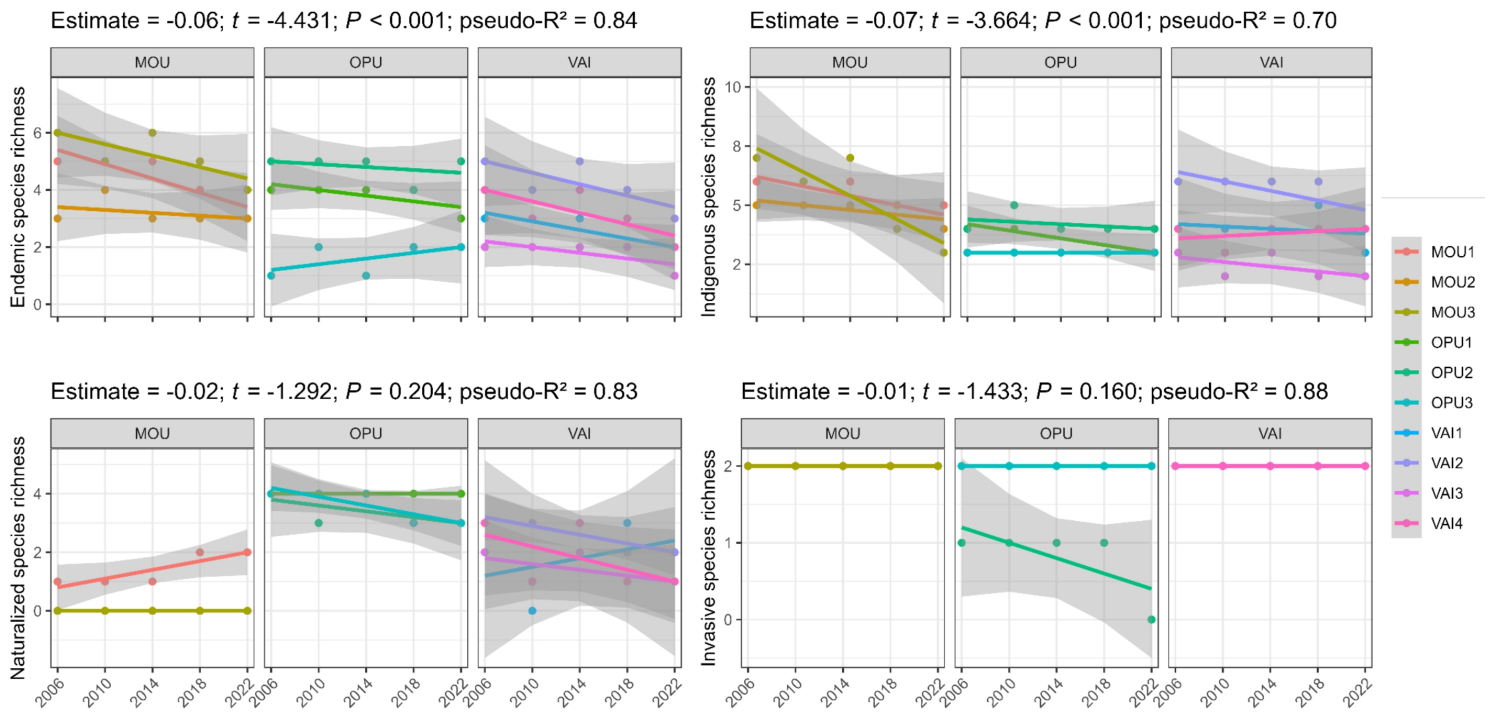
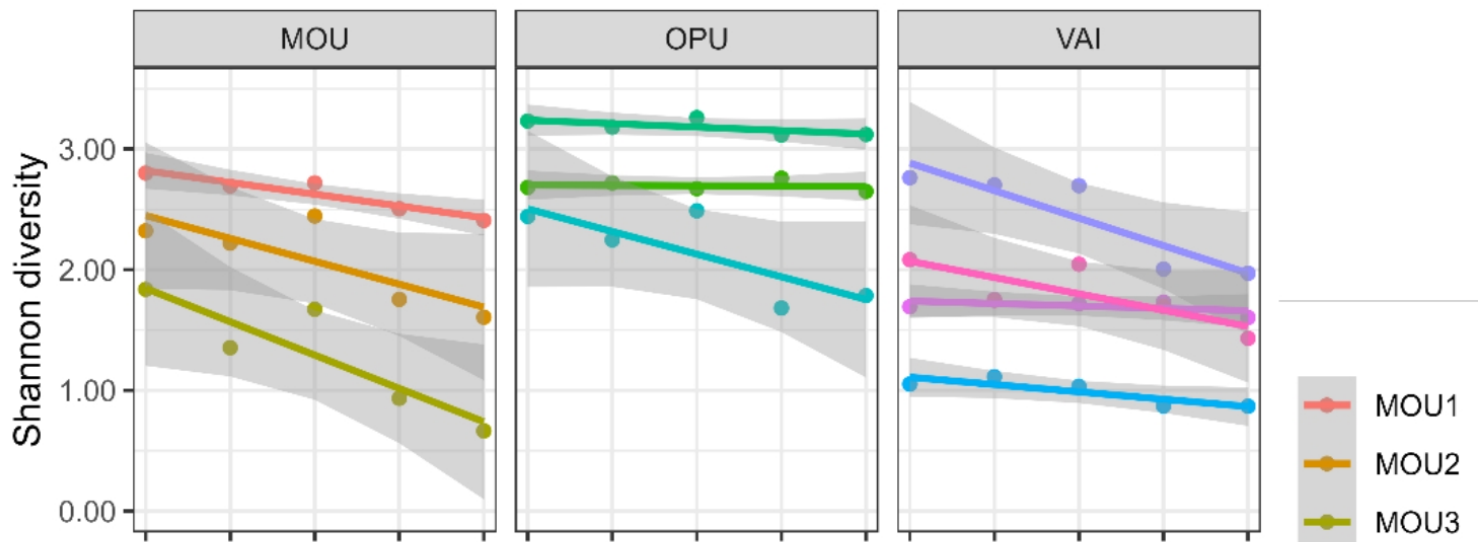


Figure 3

Change in species richness (alpha diversity) in the ten 400 m² plots between 2006 and 2022 by separating species based on their biogeographical status (endemic, indigenous, naturalized and invasive alien species). Plots are grouped by site: OPU (three plots), VAI (four plots) and MOU (three plots). Data have been fitted with linear mixed-effects models with species richness as response variable, time as explanatory variable and identities of the plots as random factors

Estimate = -0.03; $t = -5.891$; $P < 0.001$; pseudo- $R^2 = 0.92$



Estimate = -0.05; $t = -3.886$; $P < 0.001$; pseudo- $R^2 = 0.89$

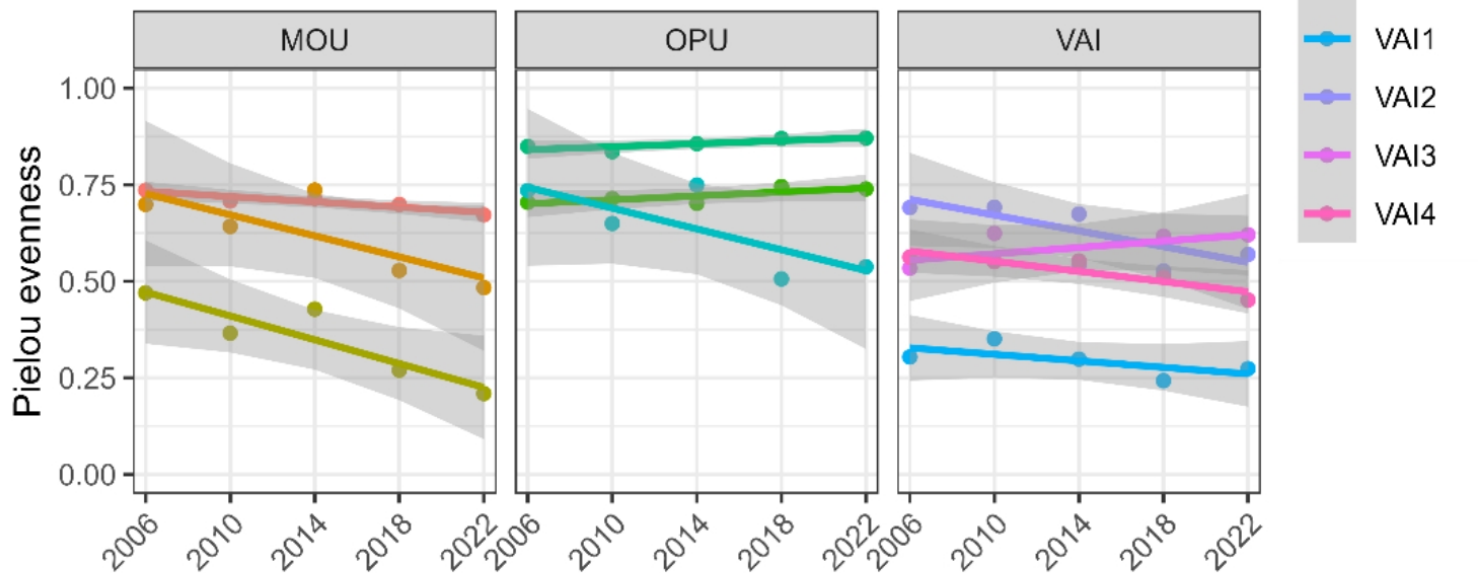


Figure 4

Change in Shannon and Pielou indices in the ten 400 m² plots between 2006 and 2022. Plots are grouped by site: OPU (three plots), VAI (four plots) and MOU (three plots). Data have been fitted with linear mixed-effects models with diversities as response variables, time as explanatory variable and identities of the plots as random factors

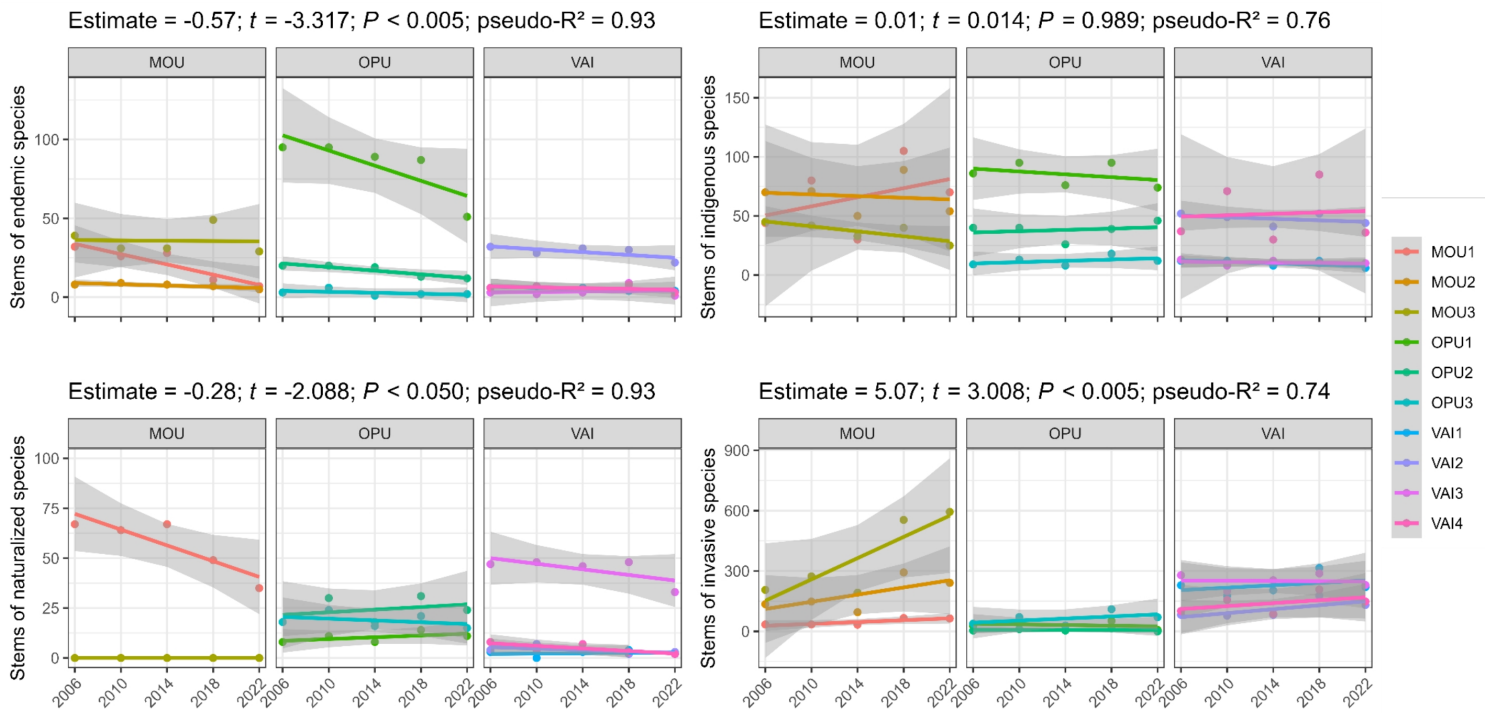


Figure 5

Change in stem number in the ten 400 m² plots between 2006 and 2022 by separating species based on their biogeographical status (endemic, indigenous, naturalized and invasive alien species). Plots are grouped by site: OPU (three plots), VAI (four plots) and MOU (three plots). Data have been fitted with linear mixed-effects models with stem number as response variable, time as explanatory variable and identities of the plots as random factors

Supplementary Files

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