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Short communication

Exclosure from browsing by invasive ungulates increases species richness and diversity of ground flora in rainforests of New Caledonia

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ABSTRACT

Introduced ungulates can impact forest structure and composition. We tested in rainforests of New Caledonia if exclosure of invasive ungulates (Javan rusa deer *Rusa timorensis russa* and feral pigs *Sus (scrofa) domesticus*) increased abundance, species richness and diversity of native plants by comparing 19 plots of 10 m^2 in four study areas that were protected from browsing for 7 years with 76 unprotected plots. Abundance, species richness and diversity of native plants of 20–60 cm of height were higher in protected plots compared to unprotected plots. We attribute the measured negative impact mainly to deer as the positive effect of exclosures was highest in the study area with the highest deer abundance and browsing rate. The exclosures were also beneficial in a secondary forest with medium deer abundance whereas in old-growth forest with medium deer abundance we could not detect an effect of the exclosures. We conclude that protecting even small areas from browsing by invasive ungulates can increase biodiversity and that exclosures are most beneficial at high deer abundance and in secondary habitats.

1. Introduction

In contrast to native ungulates, which can increase (e.g. Faison et al., 2016), sometimes to the benefit of non-forest species (Boulanger et al., 2018), or decrease (e.g. Ramirez et al., 2019) the diversity of plants in the herbaceous layer of forests, invasive ungulate browsers often have detrimental effects on vegetation (e.g. Husheer et al., 2006; Davis et al., 2016; Weller et al., 2018). European settlers introduced two invasive ungulates to New Caledonia at the end of the 18th century (Gargominy et al., 1996; Barrière and Fort, 2021), which can be found in rainforest at present time (Rouys and Theuerkauf, 2003): Javan rusa deer *Rusa timorensis russa* (further referred to as deer) and feral pigs *Sus (scrofa) domesticus* (further referred to as pigs). Keith and Pellow (2005) showed that deer had a negative impact on native plant species in New South Wales but did not assess if this affected plant diversity. In New Caledonia, we would expect an impact as in rainforest the main diet of deer consists of woody species (de Garine-Wichatitsky et al., 2005) and Le Bel et al. (2001) showed that deer affected the survival of kaori (*Agathis* spp.). Although in some areas significant efforts may be invested in deer culling, this does not necessarily decrease the impact of invasive browsers on forest plant species (Coomes et al., 2003; Ramsey et al., 2018). There is so far no specific study on the impact of pigs on ground vegetation in New Caledonia, but pigs threaten many species worldwide (Risch et al., 2021) and can have an important impact as seed predators (Gürtler et al., 2023) and on soil structure (Long et al., 2017). In Hawaii, pigs have far-reaching ecological impacts in rainforest (Nogueira-Filho et al., 2009). We therefore tested if the two introduced ungulates decreased plant abundance, species richness and diversity of ground vegetation in rainforest of New Caledonia by comparing understorey vegetation plots inside and outside exclosures.

2. Methods

We worked in four rainforest study areas of *Grande Terre*, the main island of New Caledonia (Table 1). The four study areas were between 13 and 150 km apart from each other and all located in the central mountain chain (Fig. 1). In 2011, *Centre de REgulation des gros Gibiers* (CREG) initiated the construction of 19 randomly-located exclosures of

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Table 1
Characteristics of the four study areas: *Parc Provincial des Grandes Fougères* (PPGF), *Ouengo*, *Mt Panié* and *Massif des Lèvres*. Driving census data from unpublished report (Collectif ICONE 2015, Eléments de cadrage pour une stratégie de régulation des cerfs sauvages et des cochons féraux envahissants en Province Nord), data on deer control from *Conservatoire d'Espaces Naturels* (New Caledonia).

Study area	PPGF	Ouengo	Mt Panié	Massif des Lèvres
Coordinates	21°30–39′S, 165°39–50′E	20°44–16′S, 164°43–47′E	20°37–38′S, 164°44–46′E	20°48–51′S, 165°04–09′E
Number of sites	8	4	4	3
Main habitat	secondary and formerly exploited primary forest	secondary forest	old-growth forest	old-growth forest
Elevation at sites (m)	340–670	420–500	480–580	250–360
Annual rainfall at sites (mm)	1500–2000	2000–3000	3000–3500	3000–3500
Average (±CI) proportion of savannah around sites	0.08 ± 0.04	0.17 ± 0.13	0.10 ± 0.04	0.06 ± 0.08
Periods of ungulate abundance estimate (length of transect)	Jan 2008, Nov 2016 (2.4 km)	Sep 2010, Jan 2012 (1.8 km)	Jan 2006, Nov 2010 (2.4 km)	Nov 2008 (0.6 km)
Deer dropping abundance/km	7.6	22.7	8.7	5.0
Average (±CI) deer browsing rate (number of plants checked)	8.6 % ± 5.4 % ($n = 787$)	30.1 % ± 46 % ($n = 198$)	2.0 % ± 0.4 % ($n = 580$)	1.7 % ± 1.0 % ($n = 467$)
Pig rooting abundance (proportion of area)	0.1 %	0.1 %	0.4 %	1.3 %
Deer/km^2 from driving censuses		116	21	
Deer culled annually per km^2 at site	2.6	2.5	4.2	Unknown

10 m^2 (3.16 m × 3.16 m) that were between 80 m and 5.8 km apart from each other within each respective study area. The exclosures consisted of metal wire fences (1.8 m high and 5 cm mesh size) that prevented browsing by deer as well as foraging and uprooting by pigs. At the time of their construction, CREG field helpers measured the height (from the ground to the highest bud or stipe as described in Hladik and Blanc, 1987) of every plant (including ferns, vines, woody and herbaceous plants) inside the exclosures. In 2018, we identified the species and measured the height of each plant of at least 20 cm within the exclosure. For analyses, we grouped heights into classes of [20–30[cm, [30–60[cm, [60–180[cm and ≥ 180 cm. Also in 2018, we added as controls to each of the 19 sites with an exclosure 4 plots of 10 m^2 surrounding the exclosure that were unprotected from browsing. We placed these 4 plots in the 4 directions parallel to the fence of the protected plot at a distance of 1 m, assuming that these unprotected plots matched the environmental conditions of the protected plot. As each of the 19 sites had 1 protected and 4 unprotected plots, the total number of plots was 95 (19 protected and 76 unprotected plots).

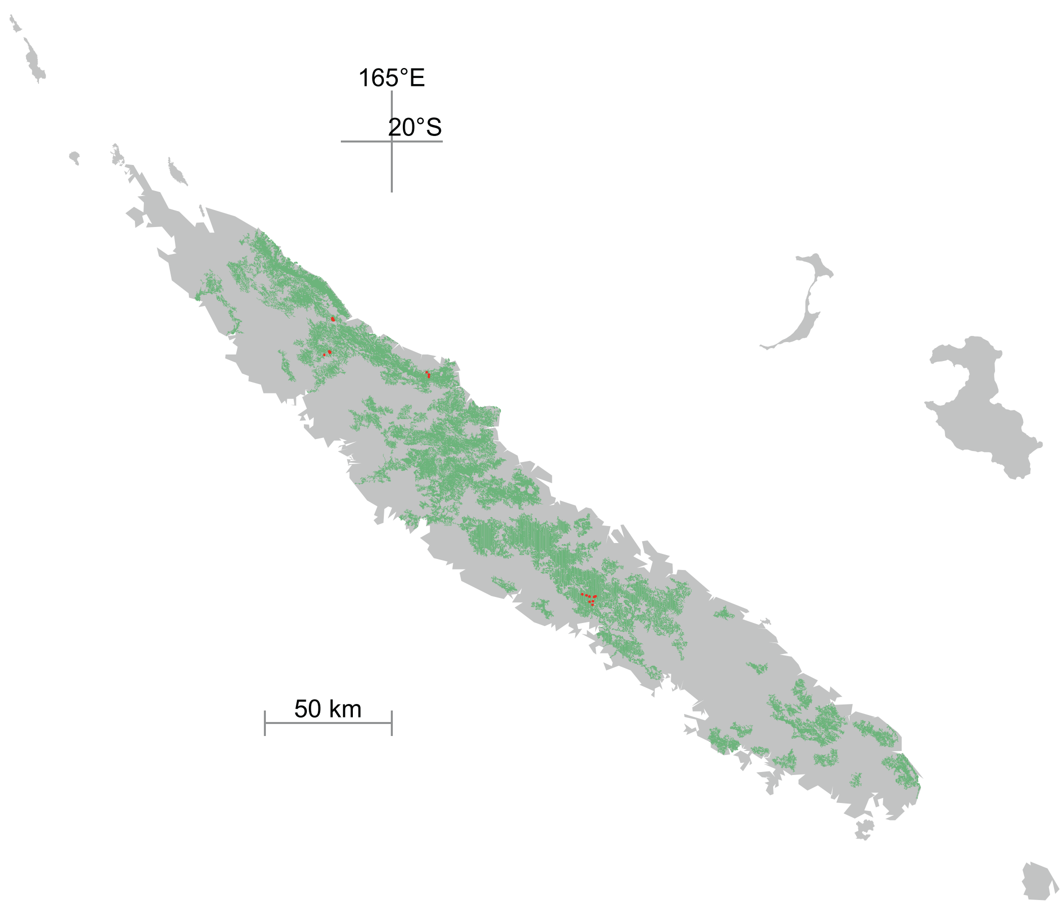

Fig. 1. Locations of the 19 sites (red dots) across the mainland of New Caledonia (in green forest area). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

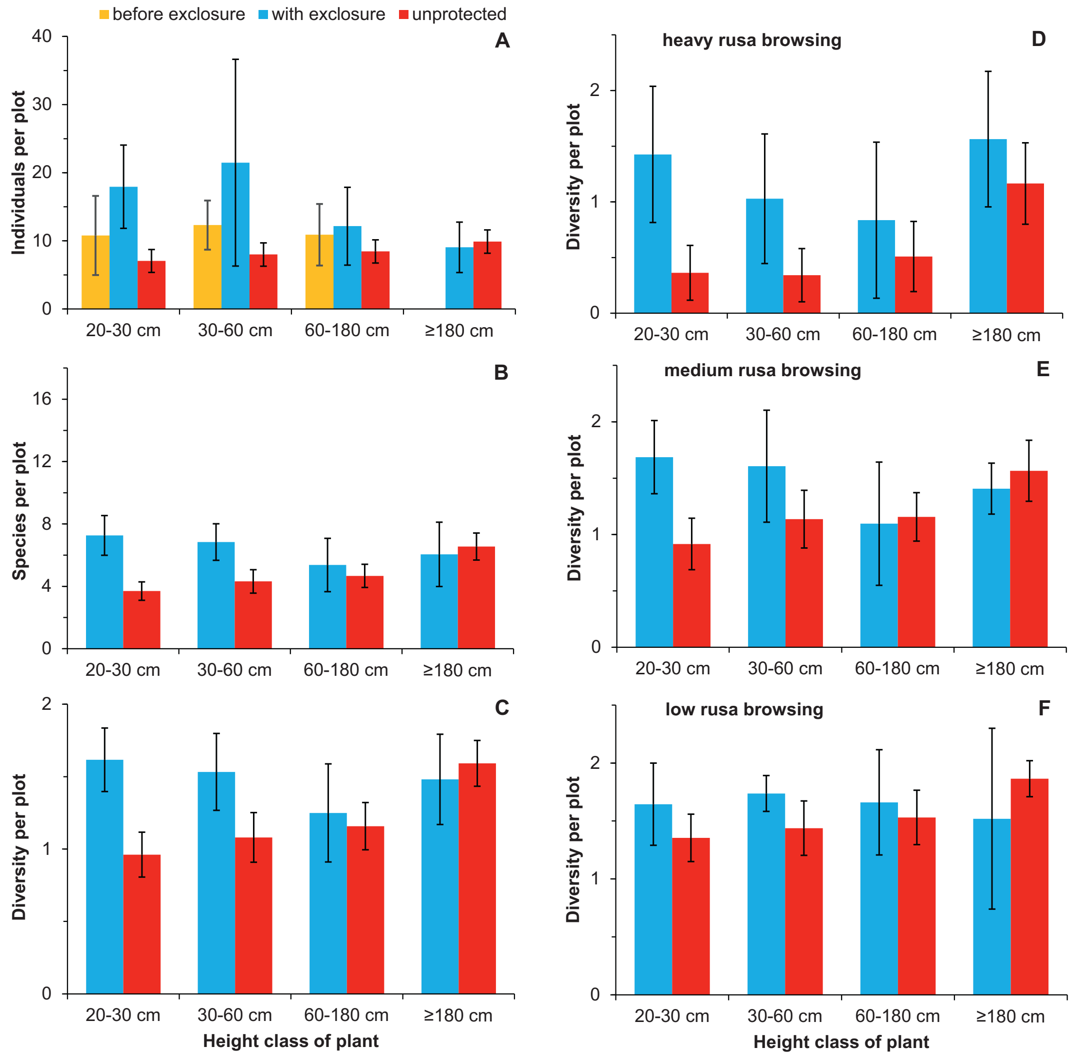

Fig. 2. Average (with 95 % confidence intervals) number of individuals (**A**), number of species (**B**), and diversity (Shannon-Wiener index) (**C**) of native plants in plots of 10 m^2 before (only for the number of individuals) and after being protected for 7 years from browsing by an exclosure (n = 19) and unprotected from browsing (n = 76) in four rainforest sites of New Caledonia. Average diversity at the site with heavy deer browsing, high deer abundance and secondary forest (*Ouengo*, n = 4 for protected and n = 16 for unprotected plots, **D**), the site with medium deer browsing, medium deer abundance and secondary forest (*Parc Provincial des Grandes Fougères*, n = 8 and n = 32, **E**) and the two sites with low deer browsing, medium deer abundance and old-growth forest (*Mt Panié* and *Massif des Lèvres* combined, n = 7 and n = 28, **F**).

Among a total of 3690 individual native plants found in the 95 plots, we identified 2162 individuals (59 %) at the species level (93 species). We could identify 616 individuals (17 %) only at the genus level, but could distinguish them as morpho-species (47 additional species). We treated the other 865 individuals (23 %) that we could identify at the genus level, but could not distinguish them as morpho-species, as one species per identified genus (58 species). Another 47 individuals (1 %), we could only identify at the family level and considered them as one species per identified family (11 species) in the analyses (complete data in Supplement 1). We then calculated, for each plot, the number of individuals, number of species and Shannon-Wiener diversity (Spellerberg and Fedor, 2003) of native species (we excluded the only individual out of 3691 that was from an introduced non-woody species). Based on 19 exclosure plots and 76 control plots, we then calculated averages with 95 % confidence intervals.

We estimated pig rooting abundance and deer faecal pellet group (further referred to as dropping) abundance on 1–4 (dependent on the size of the study area) transects of 0.6 km length in each of the four study areas (Table 1) as the proportion of area freshly rooted by pigs and as the number of recognisable deer droppings per km (detailed methods described in Rouys and Theuerkauf, 2003). To estimate browsing rate by deer, we examined all understorey plants under 180 cm of height in the 76 unprotected plots for signs of browsing. Then, we calculated browsing rate as the proportion of individuals with signs of browsing divided by the total number of individuals (varying from 198 to 787 individuals in the respective study areas: see Table 1). We used Generalized Linear Mixed-Models (GLMM) and Akaike's information criterion (AIC) ran in R version 4.3.1 with the package MuMIn version 1.47.5 (Bartoń, 2023) to assess the relative importance of the binominal parameter exclosure, as well as the continuous parameters deer dropping abundance, deer browsing rate, pig rooting abundance, and proportion of savannah around the sample plots on diversity of native plants. We included study area as random variable in the models. The proportion of savannah is a proxy of habitat suitability for deer, because savannah is the most important habitat for feeding. To estimate the proportion of savannah (non-forested area), we created 500-m buffers around the 19 sites (each with 1 protected and 4 unprotected plots) in ArcGIS 10 and assessed the proportion of forest in the buffer based on a 1:10000 vegetation map (date of data acquisition 1989–2007) by *Institut Géographique National* (IGN, Paris).

Table 2
Generalized Linear Mixed-Models ranked by Akaike weights (only models with ΔAICc <2) with Shannon-Wiener diversity index as dependent variable and study area as random variable (in all models), including the parameters **exclosure**, deer **browsing** rate, **deer** dropping abundance, **pig** rooting abundance, and proportion of **savannah** 500 m around 95 rainforest sample plots in New Caledonia for 4 plant height classes.

Rank	Parameters in model	AICc	ΔAICc	w
Plants of [20–30[cm				
1	Exclosure, browsing	183.7	0.00	0.247
2	Exclosure, browsing, savannah	183.8	0.11	0.233
3	Exclosure, savannah	185.0	1.24	0.132
4	Exclosure, browsing, pig	185.7	1.94	0.093
Plants of [30–60[cm				
1	Exclosure, savannah	198.2	0.00	0.186
2	Exclosure, browsing, savannah	198.7	0.54	0.142
3	Exclosure, browsing	198.8	0.60	0.138
4	Exclosure	199.6	1.43	0.091
5	Exclosure, savannah, pig	199.8	1.63	0.082
Plants of [60–180[cm				
1	Browsing, savannah	198.7	0.00	0.219
2	Browsing	199.5	0.80	0.147
3	Browsing, savannah, pig	200.1	1.42	0.108
4	Savannah	200.6	1.97	0.082
Plants of ≥180 cm				
1	Browsing, savannah, pig	188.3	0.00	0.255
2	Browsing, pig	188.4	0.11	0.242
3	Browsing, savannah	189.1	0.82	0.170
4	Browsing	189.3	1.06	0.150

3. Results and discussion

Abundance but particularly species richness and species diversity of native plants of 20–60 cm of height were higher in protected plots compared to unprotected plots (Fig. 2A-C). Abundance of plants was also lower in protected plots before compared to after 7 years of exclosure, but the difference is not proven as confidence intervals overlapped (Fig. 2A). For the plant height class of 20–30 cm, the most important parameter explaining diversity indices in the GLMM analysis (Table 2) was exclosure ($P < 0.001$), the next important parameter deer browsing rate ($P = 0.086$) was already not significant. This however indicates that protection by exclosure had the highest impact on plant diversity where deer browsing rate was highest. For the plant height class of 30–60 cm, results were similar but weakened and the most important parameter was again exclosure ($P = 0.005$), whereas the next important parameter deer dropping abundance ($P = 0.152$) was not significant. We could not detect differences in plants of height classes above 60 cm (Fig. 2). For the plant height class of 60–180 cm, the most important parameter explaining diversity indices in the GLMM analysis was deer browsing rate ($P = 0.058$) but the effect of exclosure was not detectable ($P = 0.576$). For the plant height class from 180 cm, the most important parameters explaining diversity indices were deer browsing rate ($P = 0.009$) and pig rooting abundance ($P = 0.018$), but the effect of pig rooting abundance was positive and probably related to pig abundance being highest where deer browsing rate was lowest. Exclosures increased diversity the most in the study area with the highest deer abundance and browsing (Fig. 2D), less in a secondary forest with average deer abundance and browsing (Fig. 2E) and lowest in old-growth forests with average deer abundance but low browsing (Fig. 2F).

Our observed results are the opposite to the effect of large mammals naturally occurring in Costa Rican rainforest, where the impact of mammals was highest in mature forest (Huanca-Nuñez et al., 2023). Deer are mainly browsers and grazers (de Garine-Wichatitsky et al., 2005), whereas pigs mainly feed on fruits and seeds (Montes-Sánchez et al., 2020). Considering this difference in feeding ecology between the two invasive ungulates, we suggest most of the differences demonstrated here are related to the browsing of deer. Additionally, pigs were the least abundant in the two study areas of higher impact on plants (Table 1), reinforcing our conclusion.

Invasive ungulates can facilitate the invasion of exotic plants (Vavra et al., 2007; Knight et al., 2009) or their success after invasion (Hoven et al., 2017). This could be of concern as the presence of alien plants often decrease abundance and species richness of native plant species in many ecosystems (Pyšek et al., 2012), including tropical rainforest (Rojas-Sandoval et al., 2022). However, we found no invasive woody and only one herbaceous plant among nearly 3700 individuals, suggesting that the interior of New Caledonian rainforests of these four study areas are not much affected by invasive plants. The majority of invasive plant species lack the life history traits necessary to invade undisturbed tropical rainforest (Fine, 2002). It is therefore likely that in old-growth rainforest of New Caledonia invasive ungulates do not play a significant role as dispersers or regulators of invasive woody plant species.

Given that even our small exclosures of 10 m^2 increased diversity of forest ground vegetation at least for 7 years, exclosures might be a practical alternative to replantation, which is usually the most expensive method in forest restoration (Brancalion et al., 2019). The model ranking by AIC showed that the parameter deer dropping abundance was less informative than deer browsing rate to explain plant diversity. Browsing rate puts the focus on the native plant species rather than the invasive species (in contrast to deer dropping abundance). Although an effective indicator of deer impact, it does not require high levels of botanical expertise allowing also citizens to engage in monitoring. We conclude that protecting even small areas from browsing by invasive ungulates can increase biodiversity in New Caledonia. Such exclosures are most effective at high deer abundance and in secondary habitats.

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CRediT authorship contribution statement

François Tron: Writing – review & editing, Writing – original draft, Conceptualization. **Maele Brisset:** Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **Cédric Haverkamp:** Writing – review & editing, Investigation, Formal analysis, Data curation, Conceptualization. **Romain Barrière:** Writing – review & editing, Investigation, Conceptualization, Methodology. **Marine Aubert:** Writing – review & editing, Formal analysis. **Jörn Theuerkauf:** Writing – review & editing, Writing – original draft, Formal analysis.

Declaration of competing interest

The authors have no relevant financial or non-financial interests to disclose.

Data availability

all data in supplement

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110675.

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