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Ferns and Lycophytes as new challenges

Temporal dynamics of the superdominant bracken fern *Pteridium arachnoideum* in Neotropical savanna-riparian forest transitions

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Abstract
Clonal growth can be especially advantageous in spatially heterogeneous environments and some clonal plants are highly invasive or superdominant, especially in disturbed environments. However, their temporal dynamics in the absence of large disturbances are not well known. We assessed whether patches dominated by the native bracken fern *Pteridium arachnoideum* expanded or retracted in area over six years. We mapped the contour of eight patches occupied by *P. arachnoideum* in a savanna-forest transition every two years from 2009 to 2015. The area occupied by most patches was overall stable, indicating that forested patch boundaries may be unsuitable for an effective vegetative spread of *P. arachnoideum*. One patch fully retracted during the study period, possibly due to extensive herbivory by leafcutter ants. Thus, although clonal foraging may enable the spread of the species to more suitable sites from these patches, these results indicate that *P. arachnoideum* does not represent a threat to the biodiversity of savanna-riparian forest transitions in the absence of extensive disturbances, as the area of the largest patches remained stable or decreased during our study. These findings highlight that specific characteristics of the local disturbance regime may be key to the cost-effective management of some superdominant native species.
Key words: cerrado, clonal growth, disturbance, *Pteridium esculentum* subsp. *arachnoideum*, riparian forest.

Resumo
O crescimento clonal tende a ser especialmente vantajoso em ambientes espacialmente heterogêneos e algumas plantas clonais são altamente invasivas ou superdominantes, especialmente em ambientes perturbados. No entanto, a sua dinâmica temporal na ausência de distúrbios maiores não é bem conhecida. Nós acompanhamos manchas dominadas pela samambaia nativa *Pteridium arachnoideum* ao longo de um período de seis anos para avaliar se elas aumentaram ou diminuíram de tamanho durante este tempo. Nós amostramos seis manchas ocupadas por *P. arachnoideum* em uma transição entre floresta e savana e mapeamos o seu contorno de dois em dois anos, de 2009 a 2015. Não houve incêndios na área de estudo durante este período e a área ocupada pela maioria das manchas se manteve no geral estável, indicando que limites de manchas de floresta parecem não serem adequadas para uma expansão vegetativa efetiva do *P. arachnoideum*. Além disso, uma mancha retraiu completamente durante o tempo de estudo, possivelmente devido a herbivoria intensa por formigas-cortadeiras. Assim, embora forrageamento clonal possa permitir o espalhamento desta espécie para sítios mais adequados a partir das manchas já ocupadas, estes resultados indicam que *P. arachnoideum* não é uma ameaça à biodiversidade em transições entre savana e floresta ripária na ausência de grandes distúrbios, já que a área das manchas permaneceu estável ou diminuiu durante o estudo. Estas descobertas enfatizam que decisões relacionadas ao manejo de espécies nativas superdominantes (*e.g.*, controle ativo ou regeneração natural) devem considerar como estas espécies respondem ao regime local de distúrbios.
Palavras-chave: cerrado, crescimento clonal, distúrbio, *Pteridium esculentum* subsp. *arachnoideum*, floresta ripária.

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Introduction

The ecological advantages of clonal growth have been extensively studied during the last decades, particularly for herbs from temperate plant communities (Pennings & Callaway 2000; Roiloa *et al.* 2010; Xu *et al.* 2010). Newly emerged modules (hereafter called ramets) of clonal species often receive stored resources previously produced by mature ramets, thus exhibiting high growth and survival rates and making these species more likely to occur where growing conditions are poor (Stuefer *et al.* 1994; Hutchings & Wijesinghe 1997; Amsberry *et al.* 2000). Clonal growth also enables certain stoloniferous and rhizomatous species to originate new patches by changing internode distance (spacing between ramets) and branching intensity according to local environmental conditions (De Kroon & Hutchings 1995; Duchoslavová & Weiser 2017). However, this local spread may be less effective where environmental conditions are more stable and spatially homogeneous (Hutchings & Wijesinghe 1997; Hutchings & Wijesinghe 2008). In addition, it may also depend on the efficiency and duration of the clonal integration (D'hertefeldt & Ingibjo 2003; Klimeš 2008), as well on the response to local environmental variation at the ramet level (Evans 1992; Dong 1993; Xu *et al.* 2010).

Clonal growth may favor the formation of large monospecific stands of native species, especially clonal perennial herbs (*e.g.*, Amsberry *et al.* 2000; Griscom & Ashton 2006; Rother *et al.* 2009; Lima *et al.* 2012; Stevens *et al.* 2015). Even though these stands often occur in sites naturally subjected to either large disturbances or strong environmental filters (Walker 1994; Amsberry *et al.* 2000; Gagnon *et al.* 2007), they have also been found in diverse disturbed tropical rainforests as a result of large-scale natural disturbances or of anthropogenic activities (Griscom & Ashton 2003; Larpkern *et al.* 2011; Lima *et al.* 2012). Many of these clonal plants dominating tropical ecosystems are perennial species with efficient clonal growth, such as a number of bamboo species (Campanello *et al.* 2007; Larpkern *et al.* 2011; Lima *et al.* 2012) and ferns from the *Pteridium* genus (Marrs & Watt 2006). These mono-specific stands may persist for long periods, as, for some of these species, a single genetically identical individual (genet) has been shown to survive for hundreds to thousands of years (Marrs & Watt 2006), and conditions within the stand are often unsuitable for the establishment of other native species (Walker 1994; Rother *et al.* 2009; Larpkern *et al.* 2011).

Pteridium arachnoideum (Kaulf.) Maxon is considered a threat to the local biodiversity of certain disturbed Neotropical ecosystems, where its long-term persistence and expansion has been especially associated with fire occurrence (Hartig & Beck 2003; Silva & Silva Matos 2006; Portela *et al.* 2009; Roos *et al.* 2010; Menezes *et al.* 2019; Xavier *et al.* 2023). A better knowledge of its patch dynamics in the absence of disturbances, for example whether patches dominated by it tend to expand or to decrease in size, may aid decision making regarding the control of this species. We monitored for six years the variation in the size of patches dominated by *P. arachnoideum* in a Neotropical savanna-riparian forest transition protected from disturbances in South-eastern Brazil, in order to determine whether (1) *Pteridum arachnoideum* patches would enlarge, thus overthrowing the surrounding vegetation; (2) the patches would remain stable during the study period, indicating that this species is in equilibrium with the surrounding communities; or (3) the patches would diminish, being replaced by the surrounding vegetation. Degeneration of *Pteridum* patches has been identified at a time scale of decades (Marrs & Hicks 1986; Marrs & Watt 2006), and the growth of *P. arachnoideum* has been shown to be negatively affected by shading (Xavier *et al.* 2019). Accordingly, we expected that the patches would remain stable during the study period, corroborating with the definition of *P. arachoideum* as a native species that only becomes dominant under specific conditions.

Material and Methods

Study species

Several clonal ferns from the genus *Pteridium* are native in multiple ecosystems from all continents except Antarctica (Marrs & Watt 2006). Even though there are ecological differences among these species (Silva Matos *et al.* 2014), they produce an extensive rhizome system, so that visible aboveground parts are in effects emergent fronds (petiole and laminae) often connected underground (Marrs & Watt 2006). Such rhizome system allows for large resource storage and efficient translocation between fronds (hereafter referred to as ramets), thus being a major dispersion mechanism of these species, since sexual reproduction is rare (Marrs & Watt 2006). Once established, stands dominated by *Pteridum* exhibit a dense canopy and a deep litter layer (den Ouden 2000; Ghorbani *et al.* 2006), hampering the establishment of other species. Species from the genus are dominant in large degraded temperate

(Marrs & Watt 2006; Stevens *et al.* 2015; Alday *et al.* 2023) and tropical ecosystems (Alonso-Amelot & Rodulfo-Baechler 1996; Hartig & Beck 2003; Silva Matos & Belinato 2010; Silva Matos *et al.* 2014; Menezes *et al.* 2019; Levi-Tacher & Morón-Ríos 2023; Xavier *et al.* 2023).

There are several synonyms for the common bracken ferns of south-eastern Brazil, such as *Pteridium arachnoideum*, *P. aquilinum* var. *arachnoideum*, *P. esculentum* subsp. *arachnoideum*, and *P. esculentum* subsp. *arachnoideum* var. *arachnoideum* (Schwartsburd *et al.* 2018). The most recent phylogenetic studies suggest a close relationship between the South American *P. arachnoideum* and the Australasian *P. esculentum*, thus supporting the name *P. esculentum* subsp. *arachnoideum* (Thomson 2012; Schwartsburd *et al.* 2018). Here, for practical reasons, we adopted the classification of *P. arachnoideum* at species level. *P. arachnoideum* is a rhizomatosous and perennial species, with fronds (ramets) reaching up to 3–4 m in height and with a leaf morphology clearly different from the northern bracken fern *P. aquilinum* (Thomson 2012; Xavier *et al.* 2019).

Study site

We performed this study in a transition area between a dense savanna and a riparian forest in São Carlos, São Paulo state, South-Eastern Brazil. Average annual precipitation and temperature are 1,500 mm and 21 °C, respectively. The area is located within the Federal University of São Carlos, between a riparian forest around a narrow second-order stream (width of 0.7 to 2.5 m - Sabbag & Zina 2011), with continuous canopy height of up to 25 m (P. Dodonov, unpublished data), and a dense savanna classified as *cerrado denso*, a phytophysiognomy with 50 to 70% of canopy cover and average canopy height of 5 to 8 m (Ribeiro & Walter 1998). We selected seven *P. arachnoideum*-dominated patches of different areas in this site (Fig. 1a; Tab. 1). Data on ramet density, biomass production and ramet growth in some of these sites were obtained in previous studies (Silva Matos *et al.* 2014; Xavier *et al.* 2016, 2019). These patches are characterized by a nearly continuous *P. arachnoideum* cover; however, they also contain native tree species, albeit with a lower diversity than adjacent non-invaded areas (Fig. 1b-c) (Miatto *et al.* 2011). Two of the smaller patches included in our study were connected to larger patches. According to managers, before the study period these sites have not been subject to fire or other large disturbances during the last 20 years.

Data collection

In 2009, 2011, 2013, and 2015, we mapped the contour of each patch (Fig. 1a) with a hand-held GPS device by walking around it as close as

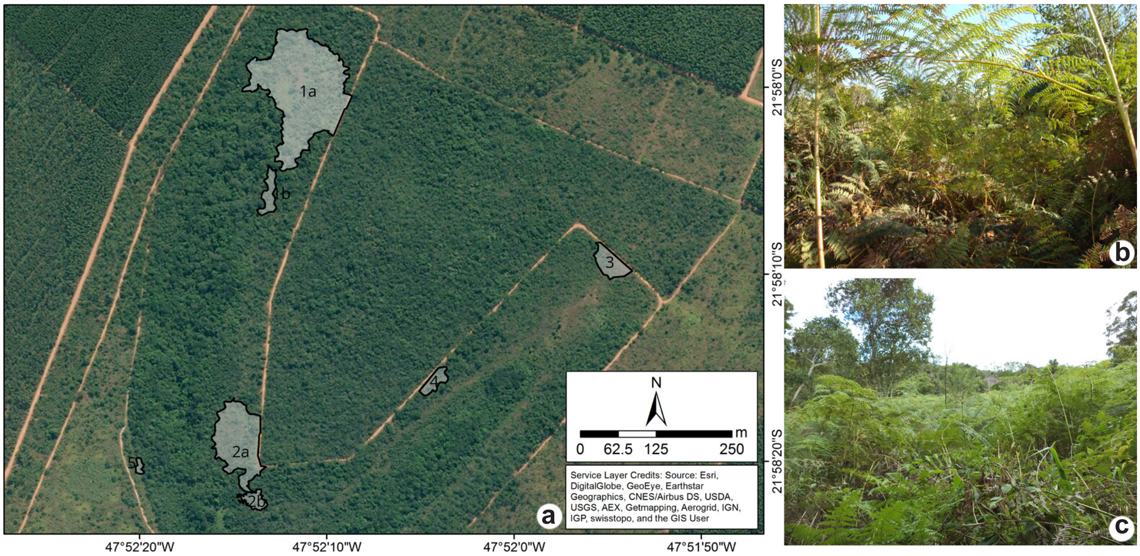

Figure 1 – a. Satellite image showing the size and shape of patches dominated by the southern bracken (*Pteridium arachnoideum*) in a savanna-riparian forest transition in the Brazilian southeast (the shaded areas represent each patch with their maximum size during a 6-year monitoring period; the letters within or next to the patches correspond to the codes (unique identifiers) given to each patch). b-c. view from within the patches.

Table 1 – Area (in m^2) of the six *Pteridium arachnoideum*-dominated patches along the six-year period. Refer to Figure 1 for the location and shape of the patches.

Patch	Year			
	2009	**2011**	**2013**	**2015**
1a	20069	20360	19174	19616
1b	N/A [a]	1121	1146	1178
2a	6825	6550	7102	7424
2b	NA [a]	849	762	840
3	1758	0 [b]	12	0
4	470	802	937	802
5	95	235	200	224

[a] = This patch was not sampled in this year.

[b] = In this year, this patch was occupied by only a few *P. arachnoideum* ramets.

possible to the continuous *P. arachnoideum* cover (Fig. 1b-c), on non-rainy days to minimize the GPS error. Considering the overlap between the cover of this species and of native species, we believe this method to be more precise than the use of satellite imagery, which has been showed to be ineffective for the definition of bracken boundaries (Holland & Aplin 2013); in addition, some of our patches were too small to be detected on satellite images. As we only identified two secondary smaller patches during the second mapping, they were sampled only from 2011 forth.

Data analysis

We used Quantum Gis 2.6 (Quantum Development Team 2013) to create polygons for each patch in each year based on the GPS data and calculated their area. We used mixed-effects linear models to assess temporal trends, including year as fixed variable and patch as random factor, in the lme4 package (Bates *et al.* 2015). We used log-transformed patch sizes due to non-normality of the residuals with non-transformed data. We performed two analyses, one including all patches and years 2011–2015 and another including all years and only the patches that were measured since 2009. One patch had nearly completely retracted after the first year and was excluded from the analyses; its inclusion, however, did not modify the results. We used Akaike's information criterion corrected for small sample size (AICc) to compare the adjusted models with null models, which did not contain year but contained patch as random factor, with the bbmle (Bolker & R Development Core Team 2017) package.

Results

Patch dynamics

Maximum patch size was observed in 2009 for one patch, in 2011 for three patches, in 2013 for one patch, and in 2015 for two patches; the smaller patches exhibited a twofold increase from 2009 to 2011, but this increase did not continue over time (Tab. 1; Fig. 1). Conversely, the variation in size of the two larger patches between 2009 and 2015 was of approximately 2% to 9% of their original size in 2009. Some changes in patch shape were observed at the patch borders (Fig. 2). In general, the area occupied by the *P. arachnoideum* patches was overall stable, with expansion and retraction periods but no clear overall trends (Tab. 1; Fig. 2). However, one patch, where the ramets were apparently subjected to severe herbivory by leafcutter ants (*Atta* sp.), had occupied 0.17 ha in 2009 but completely retracted by 2015 (Tab. 1; Fig. 2). No temporal trends were observed, as the null model had the lowest AICc in both analyses, with the alternative model having a ΔAICc of 10.8 and 4.4 for the years 2011–2015 and 2009–2015, respectively.

Discussion

In this study we showed that undisturbed patches dominated by *P. arachnoideum* generally remained stable during a six-year period. We only observed little advance and retreat around the patch borders, reflecting an equilibrium state between this species and the surrounding plant community. Similar results were observed in undisturbed patches dominated by *P. aquilinum* during over 50 years of monitoring (Marrs & Hicks 1986). We believe that this stability is consistent with the response of individual ramets to canopy cover, with increased growth in height under high canopy cover (Xavier *et al.* 2019), as a greater investment in ramet height under lower light availability is not an adequate strategy to promote vegetative spread under an undisturbed forest canopy. First, *P. arachnoideum* ramets are unable to achieve enough height to capture light in the upper layer, as the average tree height in our sites is higher than 10 m (Miatto *et al.* 2011). In addition, because ramets of *Pteridium* exhibit very low diameter variability (Xavier *et al.* 2019), very high ramets are more subjected to damage by wind and prostration (Marrs & Watt 2006), which would increase mortality rates and decrease light absorption. Thus, our findings suggest that preventing large disturbances would be the best strategy to avoid the dominance of *P. arachnoideum* in tropical forest communities.

In addition to low photosynthetic capacity under low light availability, the high mortality of newly emerged ramets may play a role on the size stability of undisturbed *P. arachnoideum* dominated patches. Xavier *et al.* (2019) found over 50% of ramet mortality of *P. arachnoideum* at our study site; in their study, there was nearly no survival where ramets either emerged under canopy with more 75% closure or were subjected to herbivory by leaf cutting ants during the phase of expansion of pinnae, which appears to have contributed to the full retraction of *P. arachnoideum* in one patch. High ramet mortality in the early stages of development of *P. arachnoideum* has also been reported for *P. aquilinum* (Hara *et al.* 1993). This is surprising because clonal species often exhibit lower mortality rates (Cain 1990; Pennings & Callaway 2000) and higher resilience to herbivory (Schmid *et al.* 1988; Gao *et al.* 2013) than non-clonal species during the early development as a result of clonal integration. However, ramet

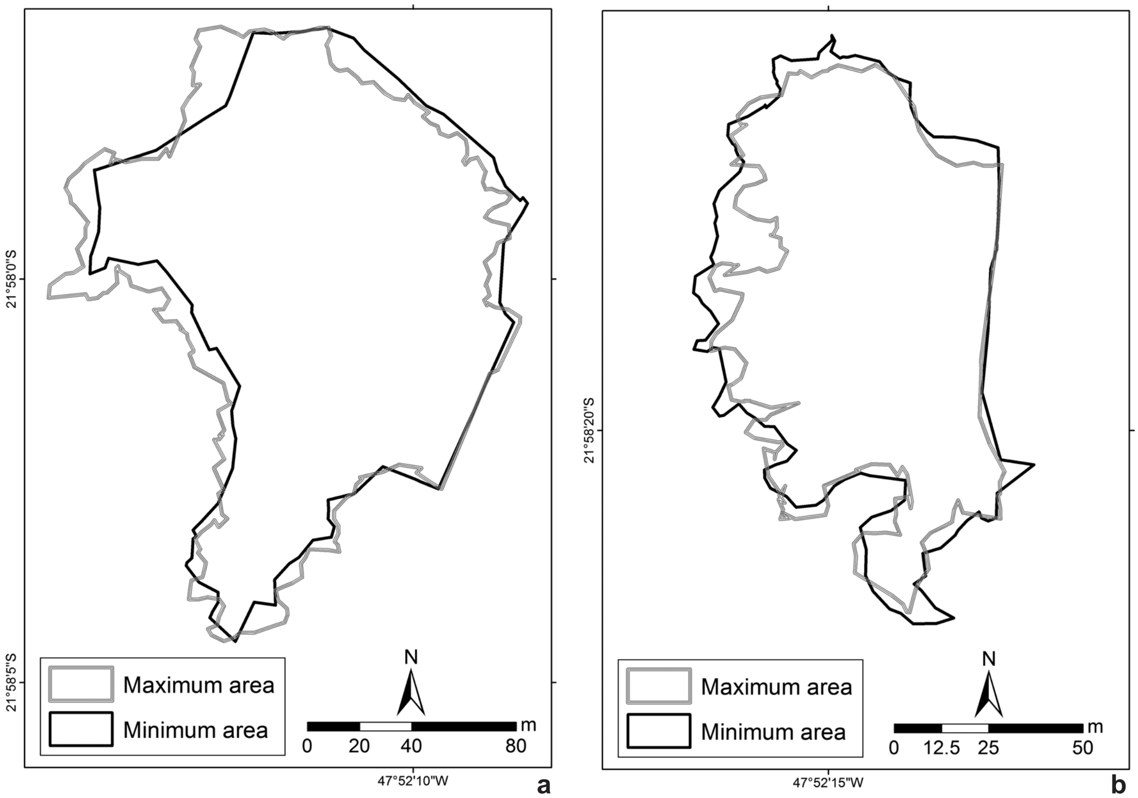

Figure 2 – a-b. Size variation of the two largest patches dominated by *Pteridium arachnoideum* in a savanna-riparian forest transition in the Brazilian southeast. Polygons represent the minimum and maximum size of each patch, corresponding respectively to the years 2013 and 2011 for patch 1a (left) and 2011 and 2015 for patch 2a (right).

mortality often increases during the transition from the use of rhizome reserves to self-supported primary production, particularly when there is no generation overlap or this is very little (Harper 1977), such as in species of the genus *Pteridium* (Marrs & Watt 2006). On the one hand, the very high ramet mortality where canopy cover was high (Xavier *et al.* 2019) suggests that *P. arachnoideum* ramet survival may be partially dependent on self-supported primary production (Marrs & Watt 2006). On the other hand, considering the potential sharing of defense signals between ramets (Stuefer *et al.* 2004; Gómez & Stuefer 2006), it is also possible that very low light availability and herbivory are cues to self-induced ramet mortality, as translocating resources to support additional growth of damaged ramets would be less advantageous. Further ecophysiological studies should investigate the relative importance of the photosynthetic rates of bracken ramets to their own survival under multiple environmental conditions. Regardless, our results show that adequate abiotic conditions, especially regarding light incidence, are essential for the expansion of *P. arachnoideum* into forested areas, which is therefore unlikely to occur in the absence of disturbances.

The retreat of *P. arachnoideum* associated with plant herbivory was accompanied by an expansion of the African grass *Urochloa eminii* (Mez) Davidse, which is highly resistant to defoliation (Klink 1994), and then by native shrub species (RO Xavier, personal observation). These changes disagree with our original hypothesis, according to which a six-year period would be too brief for retraction to be detected. However, all other patches remained stable during a period of 6 years, suggesting that in the absence of external factors they will maintain a stable size in the medium term. Gradual retraction of *Pteridium* and replacement by woody species had been previously reported based on decades of satellite imagery from undisturbed sites of cerrado (Pinheiro & Durigan 2012) and heathlands (Marrs & Watt 2006). These successional changes are more probable to occur after a longer period because they likely depend on both a natural decline in the performance of the clonal species (Marrs & Hicks 1986; de Witte & Stöcklin 2010) and effective seed rain from the surrounding vegetation. Here we only mapped the contour of the *Pteridium*-dominated patches, while some indications of decline could also be related to lower ramet density and higher density of other species within the patches (Marrs & Hicks 1986). Even though a precise prediction about the future of these sites also depends on monitoring both these characteristics, field excursions carried out in 2009 within the patches indicated that the cover of *Pteridium* was nearly continuous, suggesting that the patches that remained stable could be effectively in a phase of equilibrium with the surrounding vegetation.

Even though no bracken patch spread during the study period, the presence of smaller patches adjacent to the larger ones highlights the importance of vegetative spread ability for the dispersal of *P. arachnoideum*. Considering the little distance between these secondary patches, we believe that they resulted from the vegetative spread of larger patches to more suitable sites. This successful spread may be related to foraging ability, which may be defined as the ability to detect better growing conditions in spatially heterogeneous ecosystems, and has been reported for a number of clonal species (De Kroon & Hutchings 1995). Spatial and temporal variation in habitat suitability for ramet growth is expected to occur even in undisturbed riparian forests and dense savannas (MacDougall & Kellman 1992; Lemos-Filho *et al.* 2010), and effective resource translocation and an extensive underground reserves system may support clonal dispersion in spatially heterogeneous environments (Stuefer *et al.* 1994; De Kroon *et al.* 2005). Therefore, our findings are consistent with the prevalence of vegetative spread as a mechanism to small local spread of *P. arachnoideum* even in undisturbed riparian sites.

In conclusion, we observed stability of patches dominated by *Pteridium arachnoideum* during a period of 6 years, suggesting that their spread to these forest-savanna transitions is unlikely in the absence of large canopy disturbances. Although high canopy cover and ant herbivory may also constrain the survival of newly emergent ramets and hence the persistence and spread of these patches and although we observed full retraction of one patch, the formation of new patches by means of vegetative growth is likely to ensure long-term persistence of *P. arachnoideum*. Further studies should investigate strategies to limit the growth and survival of newly emergent ramets, which seems to be the critical phase for the spread of this species. However, our results suggest that under a lack of large canopy disturbances this species is not a threat to the biodiversity of these savanna-riparian forest transitions. Considering that controlling *P. arachnoideum* to promote forest recovery tends to be expensive and may favour the spread of invasive non-native species (Xavier *et al.* 2023), our study shows that relying on tree regeneration and a natural decline of clonal patches may be the most appropriate strategy to manage this species in tropical forest sites protected from fire.

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Data availability statement

In accordance with Open Science communication practices, the authors inform that additional data is available on the first author's Github repository: <https://github.com/pdodonov/publications>.

References

Alday JG, Cox ES, Santana VM, Lee H, Ghorbani J, Milligan G, McAllister HA, Pakeman RJ, Le Duc MG & Marrs RH (2023) Recovery of upland acid grasslands after successful *Pteridium aquilinum* control: long-term effectiveness of cutting, repeated herbicide treatment and bruising. Journal of Environmental Management 342: 118273.

Alonso-Amelot ME & Rodulfo-Baechler S (1996) Comparative spatial distribution, size, biomass and growth rate of two varieties of bracken fern (*Pteridium aquilinum* L. Kuhn) in a Neotropical Montane Habitat. Plant Ecology 125: 137-147.

Amsberry L, Michael AB, Patrick JE & Mark DB (2000) Clonal integration and the expansion of phragmites australis. Ecological Applications 10: 1110-1118.

Bates D, Mächler M, Bolker B & Walker S (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67: 1-48.

Bolker B & R Development Core Team (2017). bbmle: tools for general maximum likelihood estimation. R package version 1.0.25. Available at <https://CRAN.R-project.org/package=bbmle>. Access on 23 Oct 2023.

Cain ML (1990) Patterns of *Solidago altissima* ramet growth and mortality: the role of below-ground ramet connections. Oecologia 82: 201-209.

Campanello PI, Gatti MG, Ares A, Montti L & Goldstein G (2007) Tree regeneration and microclimate in a liana and Bamboo-Dominated Semideciduous Atlantic Forest. Forest Ecology and Management 252: 108-117.

D'hertefeldt T & Ingibjo RSJ (2003) Extensive Physiological integration in intact clonal systems of *Carex arenaria*. Journal of Ecology 87: 258-264.

De Kroon H & Hutchings MJ (1995) Morphological plasticity in clonal plants: the foraging concept reconsidered. Journal of Ecology 83: 143-152.

De Kroon H, Huber H, Stuefer JF & Van Groenendael JM (2005) A modular concept of phenotypic plasticity in plants. New Phytologist 166: 73-82.

de Witte LC & J Stöcklin J (2010) Longevity of clonal plants: why it matters and how to measure it. Annals of Botany 106: 859-870.

den Ouden J (2000) The role of bracken (*Pteridium aquilinum*) in forest dynamics. Wageningen University, Wageningen. 218p.

Dong M (1993) Morphological plasticity of the clonal herb *Lamiastrum galeobdolon* (L.) Ehrend. & Polatschek in response to partial shading. New Phytologist 124: 291-300.

Duchoslavová J & Weiser M (2017) Evidence for unexpected higher benefits of clonal integration in nutrient-rich conditions. Folia Geobotanica 52: 283-294.

Evans JP (1992) The effect of local resource availability and clonal integration on ramet functional morphology in *Hydrocotyle bonariensis*. Oecologia 89: 265-276.

Gagnon PR, Platt WJ & Moser EB (2007) Response of a native bamboo [*Arundinaria gigantea* (Walt.) Muhl.] in a wind-disturbed forest. Forest Ecology and Management 241: 288-294.

Gao Y, Wang D, Xing F, Liu J, Wang L & Elzenga T (2013) Combined effects of resource heterogeneity and simulated herbivory on plasticity of clonal integration in a rhizomatous perennial herb. Plant Biology 16: 774-782.

Ghorbani, J, Le Duc MG, Mcallister HA, Pakeman RJ & Marrs RH (2006) Effects of the litter layer of *Pteridium aquilinum* on seed banks under experimental restoration. Applied Vegetation Science 9: 127-136.

Gómez S & Stuefer JF (2006) Members only: induced systemic resistance to herbivory in a clonal plant network. Oecologia 147: 461-468.

Griscom BW & Ashton PMS (2003) Bamboo control of forest succession: *Guadua sarcocarpa* in Southeastern Peru. Forest Ecology and Management 175: 445-454.

Griscom BW & Ashton PMS (2006) A self-perpetuating bamboo disturbance cycle in a neotropical forest. Journal of Tropical Ecology 22: 587-597.

Hara T, Toorn JVD & Mook JH (1993) Growth dynamics and size structure of shoots of *Phragmites australis*, a clonal plant. Journal of Ecology 81: 47-60.

Harper JL (1977) Population biology of plants. Academic Press, London. 892p.

Hartig K & Beck E (2003) The bracken fern (*Pteridium arachnoideum* (Kaulf.) (Maxon) in the Andes of Southern Ecuador. Ecotropica: 3-13.

Holland J & Aplin P (2013) Super-resolution image analysis as a means of monitoring bracken (*Pteridium aquilinum*) distributions. ISPRS Journal of Photogrammetry and Remote Sensing 75: 48-63.

Hutchings MJ & Wijesinghe DK (1997) Patchy habitats, division of labour and growth dividends in clonal plants. Trends in Ecology and Evolution 12: 390-394.

Hutchings MJ & Wijesinghe DK (2008) Performance of a clonal species in patchy environments: effects of environmental context on yield at local and whole-plant scales. Evolutionary Ecology 22: 313-324.

Klimeš L (2008) Clonal splitters and integrators in harsh environments of the trans-himalaya. Evolutionary Ecology 22: 351-367.

Klink CA (1994) Effects of clipping on size and tillering of native and African grasses of the Brazilian Savannas (the Cerrado). Oikos 70: 365-376.

Larpkern P, Moe S & Totland O (2011) Bamboo dominance reduces tree regeneration in a disturbed Tropical Forest. Oecologia 165: 161-168.

Lemos-Filho J, Barros C, Dantas G, Dias L & Mendes R (2010) Spatial and temporal variability of canopy cover and understory light in a *cerrado* of Southern Brazil. Brazilian Journal of Biology 70: 19-24.

Lima RAF, Rother DC, Muler AE, Lepsch IF & Rodrigues RR (2012) Bamboo overabundance alters forest structure and dynamics in the Atlantic Forest hotspot. Biological Conservation 147: 32-39.

Macdougall A & Kellman M (1992) The understorey light regime and patterns of tree seedlings in tropical riparian forest patches. Journal of Biogeography: 667-675.

Marrs RH & Hicks MJ (1986) Study of vegetation change at lakenheath warren: a re-examination of A.S. Watt's theories of bracken dynamics in relation to succession and vegetation management. Journal of Applied Ecology 23: 1029-1046.

Marrs RH & Watt AS (2006) Biological flora of the British Isles: *Pteridium aquilinum* (L.) Kuhn. Journal of Ecology 94: 1272-1321.

Menezes GS, Cazetta E & Dodonov P (2019) Vegetation structure across fire edges in a Neotropical rain forest. Forest Ecology and Management 453: 117587.

Miatto RC, Silva IA, Silva-Matos DM & Marrs RH (2011) Woody vegetation structure of Brazilian cerrado invaded by *Pteridium arachnoideum* (Kaulf.) Maxon (Dennstaedtiaceae). Flora - Morphology, Distribution, Functional Ecology of Plants 206: 757-762.

Pennings SC & Callaway RM (2000) The advantages of clonal integration under different ecological Conditions: a community-wide test. Ecology 81: 709-716.

Pinheiro ES & Durigan G (2012) Diferenças florísticas e estruturais entre fitofisionomias do *cerrado* em Assis, SP, Brasil. Revista Árvore 36: 181-193.

Portela RCSQ, Silva Matos DM, Siqueira LPD, Braz MIG, Silva-Lima L & Marrs RH (2009) Variation in aboveground biomass and necromass of two invasive species in the Atlantic Rainforest, Southeast Brazil. Acta Botanica Brasilica 23: 571-577.

Quantum Development Team (2013) Quantum Gis Geographic Information System. Open Source Geospatial Foundation Project. Free Software Foundation, India. Available at <https://www.qgis.org/en/site/>. Access on 23 Oct 2023.

Ribeiro J & Walter B (1998) Fitofisionomias do Bioma Cerrado. *In*: Sano SM & Almeida SP (eds.) Cerrado: ambiente e flora. Embrapa Cerrado, Planaltina. Pp. 89-166.

Roiloa SR, Rodríguez-Echeverría S, de la Pena E & Freitas H (2010) Physiological integration increases the survival and growth of the clonal invader *Carpobrotus edulis*. Biological Invasions 12: 1815-1823.

Roos K, Rollenbeck R, Peters T, Bendix J & Beck E (2010) Growth of tropical bracken (*Pteridium arachnoideum*): response to weather variations and burning. Invasive Plant Science Management 3: 402-411.

Rother DC, Rodrigues RR & Pizo MA (2009) Effects of bamboo stands on seed rain and seed limitation in a Rainforest. Forest Ecology and Management 257: 885-892.

Sabbag AF & Zina J (2011) Anurans of a Riparian Forest in Sao Carlos, state of Sao Paulo, Brazil. Biota Neotropica 11: 179-188.

Schmid B, Puttick GM, Burgess KH & Bazzaz FA (1988) Clonal integration and effects of simulated herbivory in old-field perennials. Oecologia 75: 465-471.

Schwartsburd PB, Yanez A & Prado J (2018) Formal recognition of six subordinate taxa within the South American bracken fern, *Pteridium esculentum* (*P. esculentum* subsp. *arachnoideum s.l.* - Dennstaedtiaceae), based on morphology and geography. Phytotaxa 333: 22-40.

Silva Matos DM & Belinato TA (2010) Interference of *Pteridium arachnoideum* (Kaulf.) Maxon. (Dennstaedtiaceae) on the establishment of rainforest trees. Brazilian Journal of Biology 70: 311-316.

Silva Matos DM, Xavier RO, Tiberio FCS & Marrs RH (2014) A comparative study of resource allocation in *Pteridium* in different Brazilian ecosystems and its relationship with European studies. Brazilian Journal of Biology 74: 156-165.

Silva Ú & Silva Matos DM (2006) The invasion of *Pteridium aquilinum* and the impoverishment of the seed bank in fire prone areas of Brazilian Atlantic Forest. Biodiversity and Conservation 15: 3035-3043.

Stevens CJ, Ceulemans T, Hodgson JG, Jarvis S, Grime JP & Smart SM (2015) Drivers of vegetation change in grasslands of the Sheffield region, Northern England, between 1965 and 2012/13. Applied Vegetation Science 19: 187-195.

Stuefer JF, During HJ & De Kroon H (1994) High benefits of clonal integration in two stoloniferous species, in response to heterogeneous light environments. Journal of Ecology: 511-518.

Stuefer JF, Gómez S & Mölken TV (2004) Clonal integration beyond resource sharing: implications for defence signalling and disease transmission in clonal plant networks. Evolutionary Ecology 18: 647-667.

Thomson J (2012) Taxonomic status of diploid southern hemisphere brackens (*Pteridium*: Dennstaedtiaceae). Telopea 14: 43-48.

Walker LR (1994) Effects of fern thickets on woodland development on landslides in Puerto Rico. Journal of Vegetation Science 5: 525-532.

Xavier RO, Alday JG, Marrs RH & Matos DMS (2016) The Role of *Pteridium arachnoideum*(Kaulf) on the seed bank of the endangered Brazilian Cerrado. Brazilian Journal of Biology 76: 256-267.

Xavier RO, Dodonov P & Silva Matos DM (2019) Growth and mortality patterns of the Neotropical bracken (*Pteridium arachnoideum*) and their response to shading in a savanna-riparian forest transition. Flora 252: 36-43.

Xavier RO, Melo UM, Pivello VR, Marrs RH, Castro, PGA, Nascimento JL & Silva Matos DM (2023) Combining mechanical control and tree planting to restore montane Atlantic forests dominated by the Neotropical bracken (*Pteridium arachnoideum*). Forest Ecology and Management 529: 120657.

Xu CY, Schooler SS & Van Klinken (2010) Effects of clonal integration and light availability on the growth and physiology of two invasive herbs. Journal of Ecology 98: 833-844.

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