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Artículo

Tree ferns dominate secondary succession in abandoned pineapple plantations around Manu National Park, Peru

Olivia Schilling[1] and Adrian Tejedor[2*]
[1]The Evergreen State College. [2]The School for Field Studies

Correspondencia
A.Tejedor
e-mail: adriantejedor@gmail.com
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Abstract

Habitat management and restoration in buffer zones of national parks is critical for maintaining ecosystem services and biological connectivity in and around the parks' core protected areas. Vegetation succession in abandoned plantations in buffer zones may take different paths that reach climax ecosystems in more or less time depending on the conditions of initial succession, thus enhancing or hindering biological connectivity and ecosystem services. This study documents the dominance of tree ferns in the initial stages of vegetation succession on abandoned pineapple plantations on the Andean foothills around Manu National Park, Peru, and discusses the role it may have on ecosystem restoration. Four years after abandonment, tree fern gametophytes grow under the shade of pineapple plants and melastomes. After 6-10 years of succession, the vegetation is dominated by a tree fern community composed of at least eight species, of which the most common are by far *Cyathea delgadii* and *Cyathea microdonta*. *Cyathea microdonta* functions as a short-lived pioneer, reaching its peak of live stem density in 6 to10 years and dying off in older plots. *Cyathea delgadii*, on the other hand, continues to grow and persists beyond 10 years of succession. Areas adjacent to abandoned pineapple fields have few tree ferns and higher tree species diversity, suggesting that pineapple agriculture and the resulting tree fern community may be a longer pathway to reach climax vegetation stages than other types of plantation.

Key words: vegetation succession, tree ferns, Peru, Amazon, Manu National Park

Resumen

Los helechos arborescentes dominan la sucesión secundaria en plantaciones de piña abandonadas alrededor del Parque Nacional del Manu, Perú

El manejo y la restauración de hábitats en áreas de amortiguamiento de parques nacionales son críticos para mantener los servicios ecosistémicos y la conectividad biológica alrededor de las zonas núcleo de las áreas protegidas. La sucesión ecológica en plantaciones abandonadas en áreas de amortiguamiento pueden seguir cursos diferentes que alcanzan estabilidad en más o menos tiempo en dependencia de las condiciones iniciales de la sucesión, mejorando u obstaculizando los servicios ecosistémicos y la conectividad biológica. Este estudio documenta la dominancia de los helechos arborescentes en las etapas iniciales de la sucesión ecológica en piñales abandonados en el piedemonte Amazónico de los Andes en el Parque Nacional del Manu. Cuatro años después del abandono de las plantaciones, los gametofitos de helechos arborescentes se encuentran creciendo a la sombra de plantas de piña y de la familia Melastomataceae. Después de 6–10 años de sucesión, la vegetación aparece dominada por una comunidad de helechos arborescentes de al menos ocho especies, entre las cuales las más comunes son *Cyathea delgadii* y *Cyathea microdonta*. *Cyathea microdonta* funciona como una especie pionera de vida corta, alcanzando su pico de densidad a los 6–10 años y prácticamente desapareciendo en parcelas más antiguas. *Cyathea delgadii*, por otro lado, continua creciendo y persiste más allá de los diez años. Las áreas adyacentes a los piñales abandonados muestran relativamente pocos helechos arborescentes y mayor diversidad de árboles, lo cual sugiere que el cultivo de piña y la comunidad de helechos arborescentes que le sucede puede ser un mecanismo de sucesión más largo hacia la recuperación de la vegetación clímax que otros tipos de cultivos.

Palabras clave: sucesión ecológica, helechos arborescentes, Perú, Amazonia, Parque Nacional del Manu

Introduction

Under advancing degradation and fragmentation of the world habitats, conservation strategies will increasingly rely on active management and ecosystem restoration to ensure biological connectivity and maintenance of ecosystem services (Lindenmayer, 2008, Suding, 2011). Together with remnant patches of original habitats, restored habitats will likely be major components of biological corridors (Chazdon, 2008), and their management must include an understanding of pathways and mechanisms of ecological succession (Young et al., 2001). Buffer areas of national parks and other protected areas, are habitat restoration hotspots due to the higher degradation pressures they sustain (Sanchez-Azofeifa et al., 2003), and because, in the tropics, they mostly consist of highly dynamic rotational agriculture landscapes with the potential to revert to climax habitats (Chapman, 1999).

Manu National Park, in the Peruvian Amazon-Andes region, is the core protected area of Manu Biosphere Reserve, a UNESCO Natural World Heritage Site due to the high biological diversity encompassed in its 300–4020 m elevation gradient (Yallico and Suarez de Freitas, 1995). It is surrounded by a buffer zone that includes two different land uses. Along the northern and western boundaries, it is flanked by legally protected natural and indigenous reserves, mostly devoid of commercial large-scale land use change (Yallico and Suarez de Freitas, 1995). Along the eastern and southern boundaries, on the other hand, it is flanked by a more populous, 9 km wide Cultural Zone that is not legally protected but where sustainable economic activities are allowed, including low impact extraction of timber and other forest products, agriculture, ecotourism, and subsistence hunting (Shepard et al., 2010). As in much of Amazonian Peru, in the tropical belt of Manu's Cultural Zone, with the exception of coca cultivation, agriculture has remained almost entirely rotational (Bishop, 1982), allowing secondary forests to regenerate on abandoned crops for several years.

Beginning in the 1980s, private ecological reserves have sprung up in Manu's Cultural Zone (Yallico and Suarez de Freitas, 1995), some of which have inherited considerable degrees of habitat disturbance from previous timber extraction, cattle grazing, and rotational agriculture. Established in 2010, Villa Carmen Biological Station and Reserve is one of such private reserves, which, in addition to old growth forests, supports land continuously used for timber and rotational agriculture since the early 20th century (G. Muñiz, pers. comm.). Fallow plots that had been used for different crops in Villa Carmen, appear to support markedly different successional assemblages, among which nearly pure stands of tree ferns growing on abandoned pineapple fields at different stages of succession are particularly striking. This study aimed to investigate the composition and dynamics of the tree fern community established on abandoned pineapple at Villa Carmen Biological Station in order to document the vegetation succession on one of the most common crops around Manu National Park, and understand its role in forest regeneration and potential reversal to climax habitat in the buffer zone of this biosphere reserve.

Objectives

To document the composition and dynamics of tree fern successional communities on abandoned pineapple plantations in the buffer zone of Manu National Park and understand the role of these communities in the regeneration of climax forest.

Methods

Our study was conducted in November 2013 and February 2014 on the Villa Carmen Biological Station and Reserve (12º53"N, 71º24›W,), managed by the Amazon Conservation Association (ACA). The station is located near Pilcopata in the Kosñipata Valley, Cusco, Peru at an elevation of 520 m. The reserve protects premontane rainforest adjacent to Manu National Park, which shows increasing degrees of disturbance closer to the station. The average annual precipitation is 3000–5000 mm and the average annual temperature is 23°*C.*

Three plots were set up in each of four stages (4, 6, 10 and 12 years old) of abandoned pineapple fields. Plots were 10 x 10 m, where adult tree ferns were counted and measured, and each contained 25 subplots of 1 x 1 m each, randomly placed were gametophytes and young sporophytes were counted. All ferns were identified to species and very young sporophytes that could not be identified were counted separately. Subplots were accessed by 30 cm wide paths cut in one direction every two meters as well as around the borders. Trees and tree ferns were left undisturbed if within the 30 cm paths and pineapple plants were trimmed but not removed. Tree fern trunk height was measured in the individuals that could be identified to species from the ground to the tip of the trunk apex. Dead ferns were also measured, counted and identified. Mean heights and densities between ages and species were compared with ANOVA tests. All statistical analyses were conducted using JMP Pro 10 (JMP Statistics, SAS, Inc., Cary, NC).

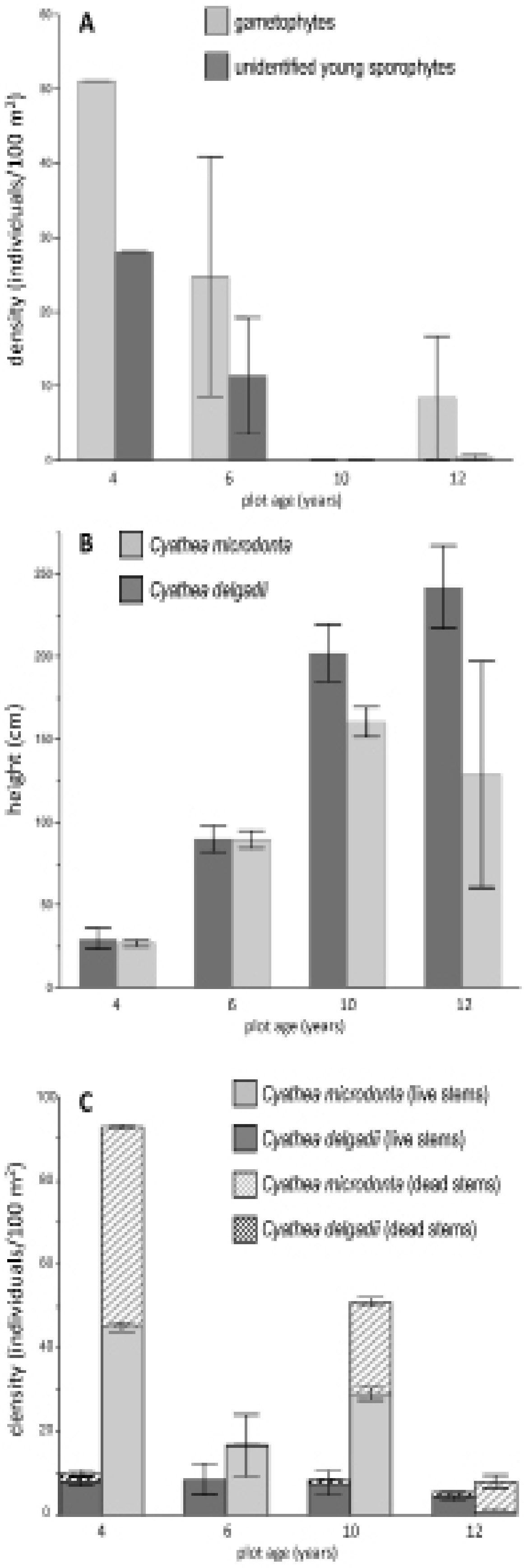


Figure 1. Changes in structure of a tree fern community in Pilcopata, Cusco, Peru, across 12 years of secondary succession. **A**). Decrease in density of earlier demographic classes, gametophytes and young sporophytes not identified to species (ANOVA, $p<0.05$). **B**). Mean increase in height of the two dominant species in the community, *C. delgadii* and *C. microdonta* (ANOVA, $p<0.05$). **C**). Density of adult sporophytes across 8 years of succession. *Cyathea microdonta* decreases in density and almost disappears by year 12 (ANOVA, $p<0.05$), whereas the density of *Cyathea delgadii* remains virtually unchanged (ANOVA, $p>0.05$). ***Figura 1****. Cambios en la estructura de una comunidad de helechos arborescentes en Pilcopata, Cusco, Perú, a lo largo de 12 años de sucesión secundaria.* ***A****). Disminución en la densidad de las clases etarias más jóvenes, gametofitos y esporofitos jóvenes no identificables (ANOVA, p<0.05).* ***B****). Incremento en promedio de la altura de las dos especies dominantes en la comunidad,* C. delgadii *y* C. microdonta *(ANOVA, p<0.05).* ***C****). Densidad de esporofitos adultos a lo largo de 8 años de sucesión.* Cyathea microdonta *disminuye en densidad y prácticamente desaparece al doceavo anho (ANOVA, p<0.05), mientras que la densidad de* C. delgadii *no cambia significativamente (ANOVA, p>0.05).*

Results

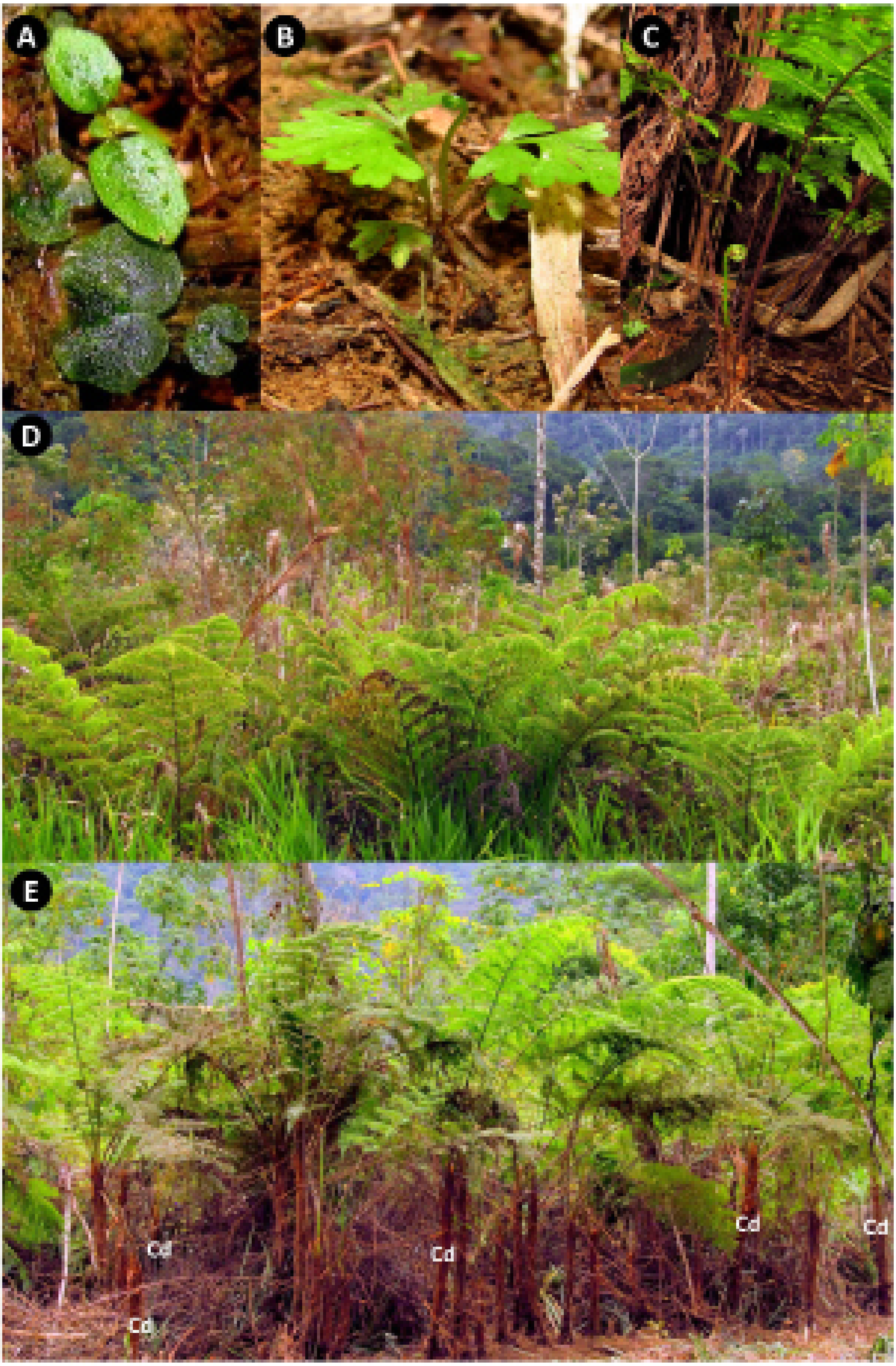
Eight species of tree ferns were found growing in 12 abandoned pineapple plots at Villa Carmen Biological Station: *Cyathea microdonta* (Desv.) Domin (258 individuals), *Cyathea delgadii* Sternb. (93), *Cyathea leucolepismata* Alston (5), *Cyathea pungens* (Willd.) Domin (3), *Cyathea subincisa* (Kunze) Domin (2), *Alsophila cuspidata* (Kunze) D.S. Conant (1), *Cyathea dombeyi* (Desv.) Lellinger (1), *Cyathea lasiosora* (Mett. ex Kuhn) Domin (1). After abandonment, tree fern establishment took place underneath the pineapple plants and a 60 cm tall cover of Melastomataceae. By the fourth year of abandonment, bare soil around pineapple plants was covered with a sparse carpet of gametophytes averaging 51 individuals/m^2, unidentified young sporophytes averaging 29 individuals/m^2, and a 25 cm tall layer of older sporophytes that could be identified to species, which averaged 5.3 individuals/m^2 (fig. 1, 2). Succession after four years was marked by a decrease in the number of gametophytes, a thinning of young and adult sporophytes, and growth of adult sporophytes at an average rate of 22.5 cm/year (fig 1, $p<0.05$).

The two most common tree ferns, *C. microdonta* and *C. delgadii* differed markedly in their life history. *Cyathea microdonta* functioned as short-lived pioneer species, with an initial highly dense population (45 individuals/100m^2) that accounted for 85% of all young sporophytes that could be identified to species. The number of live young sporophytes of *C. microdonta* was matched by a similar number (48 individuals/100m^2) of dead individuals, indicating a high juvenile mortality. After 6 years, it decreased on average in stem density and almost died off completely at 12 years of forest regrowth. Its trend of decreasing density, however, was broken by the production of 3–5 lateral trunks after the death of the main trunk (fig 2). Lateral trunks continued to grow until the eventual death of the entire plant in the 12 year old plot but never attained the height of 10 year old solitary trunks. *Cyathea delgadii*, on the other hand, did not change in stem density between 4 and 12 years of secondary succession and its solitary trunks grew linearly at an average rate of 23.75 cm/year(fig 1, $p>0.05$). Its juvenile mortality in the 4 year old plot was only 4% that of *C. microdonta*.

Discussion

The results presented here indicate that pineapple cultivation and subsequent abandonment at the Amazonian foothills of the Andes sets off a peculiar kind of vegetation succession involving a rich tree fern community with two densely represented, dominant species, *C. microdonta* and *C. delgadii*. The density of tree ferns in the abandoned pineapple fields at Villa Carmen is the highest reported from the Neotropics (Table 1), being 19 times higher than the average density found in neighboring secondary forest of the reserve (A. Min, unpublished data) and 1.5–42 times higher than densities found in lowland to premontane forests elsewhere in the New World (Table 1). Other sites with high tree fern densities, albeit still lagging far behind the abandoned pineapple fields at Villa Carmen, are at much higher elevations (La Planada, Colombia with 16

Figure 2. Five stages of tree fern dominated succession in Pilcopata, Cusco, Peru, across 12 years. **A**) Tree fern gametophytes (dark green kidney-shaped structures). Note young seedling of Melastomataceae at center top. **B**) young tree fern sporophyte of an unidentified species. **C**) young sporophyte identified to species, in this case, *Cyathea microdonta*. All young tree fern age classes were growing under the shade of 60 cm tall shrubby Melastomataceae and pineapple plants. **D**) six year old tree fern stand amid *Brachiaria* sp. and other grasses. Note isolated incipient pioneer angiosperm trees (*Cecropia* sp., *Trema* sp., and *Jacaranda copaia*). Shrubby Melastomataceae are still present in small numbers. **E**). ten year old plot overtaken by 1–2.5 m tall *Cyathea delgadii* (labelled Cd in photo) and *Cyathea microdonta* (all other trunks). Pioneer trees (*Cecropia* sp. and *Jacaranda copaia*) have increased in height and Melastomataceae are absent. Pineapple plants, the original crop, persist in the understory, now under the shade of the tree ferns. ***Figura 2**. Cinco estadios de sucesión dominada por helechos arborescentes en Pilcopata, Cusco, Perú, a lo largo de doce años. **A**) Gametofitos de helechos arborescentes (estructuras arriñonadas de color verde oscuro). Nótese la plántula de Melastomataceae en el centro superior. **B**) esporofito joven de helechos arborescente de especie no identificada. **C**) esporofito joven identificable, en este caso,* C. microdonta*. Todos los estadios jóvenes de helechos arborescentes en la sucesión estudiada crecían bajo la sombra de Melastomataceae arbustivas de 60 cm de altura y de plantas de piña. **D**) Helechos arborescentes en la sucesión de seis años entre* Brachiaria *sp., otros pastos, y angiospermas arborescentes pioneras (*Cecropia *sp.,* Trema *sp., y* Jacaranda copaia*). Las melastomatáceas arbustivas aún están presentes en pequeño número. **E**) sucesión de 10 años dominada por* C. delgadii *(Cd en la foto) y* C. microdonta *(todos los demás troncos) de 1–2.5 m de altura. Arboles pioneros (*Cecropia *sp. y* Jacaranda copaia*) tienen un mayor tamaño en este estadio y las melastomatáceas han desaparecido. Plantas de piña, el cultivo original, persisten en el sotobosque, ahora bajo la sombra de los helechos arborescentes.*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LOCALITY	REGION, COUNTRY	APPROXIMATE ELEVATION (m)	TAXA SAMPLED[a]	DENSITY (adults/100 m²)	SOURCE
Villa Carmen – pineapple	**CUS, Per**	**500**	**all tree ferns[b]**	**38.0**	**this study**
Villa Carmen – forest	CUS, Per	500	all tree ferns	2.0	A. Min, unpublished data
Quitacalzon – stream forest	CUS, Per	1000	all tree ferns	28.3	A. Min, unpublished data
La Planada	NAR, Col	2000	all tree ferns	16.0	Arens and Baracaldo, 1998
Una	BA, Bra	30	all tree ferns	0.9	Paciencia and Prado, 2005
Sapiranga	RS, Bra	570	*Alsophila setosa*	23.5	Schmitt and Windisch, 2005
Morro Reuter	RS, Bra	700	*Alsophila setosa*	17.4	Schmitt and Windisch, 2005
Novo Hamburgo	RS, Bra	20	*Cyathea delgadii*	2.1	Schmitt and Windisch, 2007
Vale do Ribera – old growth	SP, Bra	500	all tree ferns	1.8	Castello et al., 2017
Vale do Ribera – secondary	SP, Bra	500	all tree ferns	1.3	Castello et al., 2017
Cuyabeno	NA, Ecu	250	all tree ferns[c]	3.2	Poulsen and Nielsen, 1995
San Francisco Biol. Sta.	ZC, Ecu	2000	two species[d]	7.9	Chacón-Labella et al., 2015
La Selva	LIM, CR	60	four species	2.1	Jones et al., 2007

Table 1. Average density of tree ferns found after ten years of succession in abandoned pineapple plantations in Pilcopata, Cusco, Peru, compared to tree fern densities in lowland and middle elevation forests elsewhere in the Neotropics. In the Manu region, abandoned pineapple plantations support the highest tree fern densities found thus far in the New World. [a] Not all densities correspond to the entire tree fern community or samples were only a subset of the potential local diversity. [b] *C. delgadii* and *C. microdonta*. [c] *C. lasiosora*. [d] *Alsophila engelii* and *C. squamipes*/*C. lindeniana* (treated as *C. caracasana*). ***Tabla 1****. Densidad promedio de helechos arborescentes después de diez años de sucesión en plantaciones abandonadas de piña en Pilcopata, Cusco, Perú, comparada con densidades de helechos arborescentes de tierras ajas y elevaciones medias en otras localidades Neotropicales. Las plantaciones de piña abandonadas en la región del Manu muestran las mayores densidades de helechos arborescentes reportadas hasta la fecha en el Neotrópico.* [a] *No todas las densidades corresponden a la comunidad de helechos arborescentes en su totalidad o la muestra es solo una parte de la diversidad potencial local.* [b] C. delgadii *and* C. microdonta*.* [c] C. lasiosora*.* [d] Alsophila engelii *and* C. squamipes/C. lindeniana *(treated as* C. caracasana*).*

adults/100 m² in at 2000 m, Arens and Baracaldo, 1998), occur in wetter microenvironments such as ravines (Quitacalzon, Peru with 28.3 adults/100 m², A. Min unpublished data), or involve species that produce multiple trunks (*Alsophila setosa* Kaulf, Schmitt and Windisch, 2005). No doubt the fact that *C. microdonta* produces multiple trunks, between the sixth and tenth years of succession, contributes to the exceptionally high densities of tree ferns dominating abandoned pineapple fields around Manu National Park.

The difference in life history traits observed for the two dominant tree ferns, wherein *C. microdonta* gets established at high densities and tends to die off after approximately 12 years of forest regrowth whereas *C. delgadii* changes little if anything in density and continues growing under forest shade confirms previous observations about the ecology of these species. *Cyathea microdonta* is commonly found in cleared areas and swampy terrain (Large and Braggins, 2007) and seems to form part of the natural beach succession along large piedmont rivers (pers. observ.). *Cyathea delgadii*, on the other hand, even though it thrives in disturbed sites such as landslides and road cuts, tends to occur more often inside the forest (M. Lehnert, pers. comm.).

The fivefold decrease in the abundance of gametophytes in the 12 year old plots relative to the four year old plots, however, indicate that tree fern recruitment in the older plots should be lower than in younger ones. Therefore, over longer succession periods than those sampled here, even *Cyathea delgadii* might decrease in density from the average of 7.5 individuals/100 m² reported here to numbers closer to the background densities (1–2 individuals/100 m²) found in most Neotropical moist lowland forests.

The tree fern dominated succession on abandoned pineapple differs sharply in species composition from neighboring succession mosaics of the same age but on different crops such as pasture and banana. At the study site, abandoned pasture (*Brachiaria* sp.) tends to develop into a nearly monotypic secondary forest of bamboo

(*Guadua sarcocarpa* Londoño & P.M. Peterson) and abandoned banana plantations tend to develop into a mixed species secondary forest dominated by *Cecropia* spp., *Pourouma tomentosa* Mart. ex Miq., *Triplaris americana* L., *Acacia* sp., *Jacaranda copaia* (Aubl.) D. Don), *Socratea exhorriza* (Mart.) H. Wendl., and *Guarea guidonia* (L.) Sleumer (pers. observ.). Both the bamboo stands and the mixed-species associations are more similar to the composition of older-growth forest in the area (Huamantupa-Chuquimaco, 2010). In the tree fern succession, pineapple plants persist on the forest floor for over 12 years whereas in other abandoned crops the crop species disappear within 3–4 years (pers. observ.). All this suggests that abandoned pineapple and its succeeding tree fern community is a longer than optimal pathway to the regeneration of climax forest.

A possible reason for the unusual high density of tree ferns in abandoned pineapple fields around Manu may be the soil amendment techniques used in the region. Local farmers frequently apply ammonium sulfate ($(NH_4)_2SO_4$) as fertilizer to pineapple fields but rarely to other crops (Y. Espinosa, pers. comm.). As shown in studies of bean (Thomson et al., 1993), corn (Blevins et al. 1977), peach (Tagliavini et al., 1995), and natural temperate ecosystems (Van Miegroet and Cole, 1984) nitrogen fertilizers decrease soil pH. Acidic substrates (pH 4–5), in turn, have been shown to favor spore germination and the development of gametophytes in several tree fern species (Marcon et al., 2017, Medeiros et al., 2017, Rechenmacher et al. 2010). It is possible then that soil acidification following the fertilization of pineapple fields in the Manu region allow tree ferns to recruit more competitively than pioneer arborescent angiosperms such as *Cecropia* and *Jacaranda*. The observation that pineapple grown without nitrogen soil amendments become invaded by grasses rather than tree ferns (Y. Espinosa, pers. comm.) and the dominance of Melastomataceae in younger plots (4 year old) both support the soil acidity hypothesis. Melastomataceae richness and abundance have been found to be strongly correlated with low cation content in the soil (Tuomisto et al. 2002) which is in turn usually correlated with lower pH (Van Miegroet and Cole, 1984).

Conclusions

This study documents an unusual ecological succession pathway in the Amazonian foothills of the Andes, through which tree ferns, instead of angiosperm trees, take over abandoned pineapple plantations for the first 10 years of secondary succession. Tree fern communities in abandoned pineapple plantations are up to 42 times denser than those in other abandoned crops or mature forests in the Neotropical lowlands. Two species, *Cyathea microdonta* and *Cyathea delgadii* dominate these tree fern communities. Of the two, the more common *C. microdonta* behaves like a short-lived pioneer, starting out with a density ten times that of *C. delgadii* but largely disappearing from the vegetation after 12 years of succession. *Cyathea delgadii*, on the other hand, persists with almost no mortality and continues growing at a linear rate at least until 12 years of succession and probably beyond. The tree fern dominated succession appears to slow down the establishment of a rich angiosperm pioneer community and it seems to be triggered by soil acidification through nitrogen fertilization. This suggests that habitat management in buffer zones of protected areas in the Andes/Amazon region aimed to restore climax forest should avoid soil amendment with nitrogen fertilizers. Further studies involving soil pH manipulation are clearly necessary to confirm this recommendation.

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