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Article

Influence of invasive species on ecological succession routes in disturbed seasonal dry tropical forests in southeastern Mexico.

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Abstract: Understanding the role of invasive species in ecosystem functioning represents one of the main challenges in ecology. *Pteridium aquilinum* is a successful cosmopolitan invasive species with negative effects on the ecological mechanisms that allow secondary succession. In this study we evaluated whether *P. aquilinum* favours the establishment of alternative states, as well as the effect of recovery strategies on the secondary succession. A random stratified sampling was established with three treatments, each one with at least 50 year of fern invasion and with variations on the periodicity of fires and cuttings (chapeos) vs one control without fern bracken We determined the species richness and composition, as well as the relative importance value (IVI) in each treatment. We found that *P. aquilinum* decreases the action of the mechanisms that allow secondary succession, particularly facilitation. The recovery strategies consist in monthly cuttings and control fires allow to recover the secondary succession and eventually, the regeneration of areas invaded by *P. aquilinum*. Our study has relevant implications on the ecology of alternative state, and in practical strategies to maintain tropical forests, as well as for the maintenance of environmental services and sustainability.

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Keywords: Alternative states; secondary succession; tropical dry forest; *Pteridium aquilinum*.

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1. Introduction

One of the great challenges for the conservation of biodiversity is the control of invasive species. It has been widely documented that the introduction of exotic or invasive species has negative implications on the dynamics of ecosystems through the modification of the composition and decrease in species richness with effects on ecological interactions (intra and interspecific), and effects on competition and facilitation, among others [1–5]. It has been observed that invasive species indirectly modify the physical-chemical properties of the soil, affecting the accumulation of organic matter, nutrients cycling, and they can influence the frequency and intensity of fires [6,7]. It is estimated that the introduction of invasive species and the change of land use are the main threats to

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ecosystem services and species diversity in the world [8,9]and are considered one of the main promoters of the greatest extinction of species in the last century [10].

Disturbance is associated with the dynamics of tropical forests, being the result of the recent and historical disturbance regimes [11]. Through the process of secondary succession, attributes of structure and composition can be recovered after disturbances at different spatio-temporal scales, such as hurricanes, fires, felling, agricultural agriculture or livestock [11–13]. However, it has been observed that secondary succession is one of the processes that is mainly affected by the introduction of invasive species. It has been observed that the introduction of invasive species can modify the patterns of dominance and establishment of species from the initial phase of succession [14]. Moreover, the introduction of non-native species can alter the composition of soil microorganisms [6,7], as well as (alterations of the biological factors, and the physical-chemical environment [14]; and generate a new *status quo* inside of the plant community that lead to the establishment of an alternative state which affects the feedback processes returning to the original state [15–17]. .

The theory of alternative stable states (SSA) predicts that ecosystems can exist in multiple states under the same external environmental conditions, transiting from a stable state from disturbance events where state variables (e.g. composition of species) change [18]. A stable ecosystem has enough resistance to remain unchanged. From the perspective of restoration ecology, degraded communities can be seen as stable (quarries, mine sites, communities invaded for exotic species) and will not change unless a force is applied that reactivates, accelerates and directs the succession path.

Pteridium aquilinum (L.) Kuhn is considered one of the most successful global invasive species. Its distribution is related to processes of land use change derived from human activities, e.g. agricultural and livestock activities [19]. This species is particularly successful when light is not a limiting resource [20,21]. Due to its mechanism of dispersal by spores, its allelopathic characteristics, and its ability to tolerate a wide range of environmental and soil conditions have helped to colonize almost all terrestrial ecosystems, except for deserts [22,23]. Additionally, through the creation of a physical barrier generated by the density of its canopy it hinders the establishment of native species [24]. Similarly, it has been observed that the accumulation of biomass from the dry fronds of individuals modifies the frequency and intensity of fires [25,26]. This exhausts the seed bank and limits the growth of seedlings [27]. Finally, the lack of competitors for limiting resources [28], and the absence of pests and herbivory, their resistance to fire due to their ability to regrow from their rhizomes, give them strategic advantages over native species [29]. Studies from Brazil, Ecuador, the Dominican Republic and Rwanda found that former agricultural active regions are currently disabled due to the interruption of secondary succession processes [30–33]. In Mexico, most of the studies have been carried out in the south, mainly in the states of Quintana Roo, Campeche and Oaxaca [21,34]. Likewise, it has been observed that, the lack of strategies for their control, can generate a substantial growth in a relatively short time, for e.g. Schneider and Fernando, [35] found that their coverage increased between 1982 and 2010, from 40 km^2 to 80km^2. It was also observed that landscapes with invaded areas are less productive, have a reduced biological diversity and show severe impacts in the socio-economic dynamics of the affected regions, because the areas cannot be used by the owners [21,34,36]. Currently there are insufficient studies that have been developed in seasonally dry tropical forests that provide information on the historical effect and management of areas invaded by *P. aquilinum*, and its impact on richness and floristic composition, and their influence on succession. We

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believe that this may be a priority for strategies to restore areas affected by one of the most important invasive species in the world. Finally, it is important to mention that the establishment of invasive species affects the possibility of maintaining the net primary production of the ecosystems [37,38] . Consequently, the aim of this work was to determine the effect of the invasion of *P. aquilinum* on the generation of alternative states that modify the routes of secondary succession in a seasonally dry forest; and to determine if the different treatments contribute to restore the original secondary succession of the system.

2. Materials and Methods

Study area

The study was carried out in the ejido (communally managed land) Laguna Om (-89.15 W 18.70 N, -88.87 W 18.40 N WGS 84) in south of the state of Quintana Roo, Mexico with an area of 84,998 ha (RAN-INEGI, 1997).

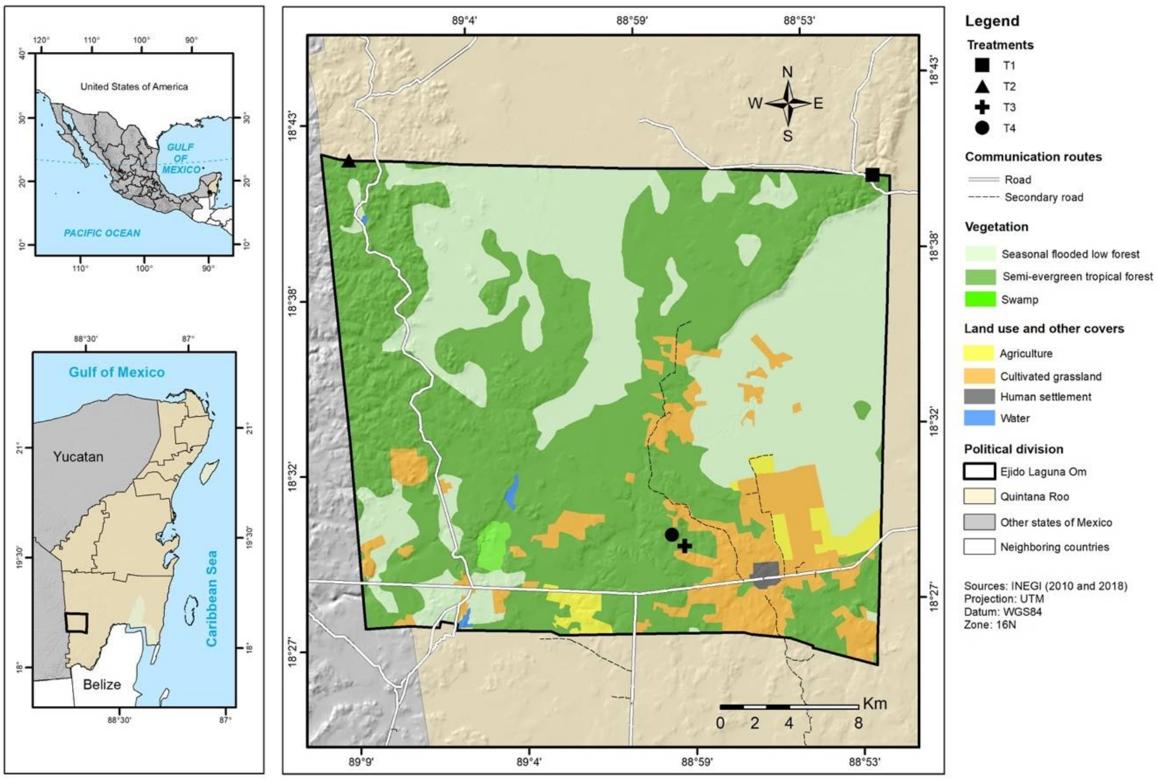

Figure 1. Study site, Ejido Laguna Om

The ejido is located in the geological formation called "Petén", which belongs to the Paleocene-Eocene and is characterized by compact macro and microcrystalline massive limestones, with yellow to white coloring, with stained parts of brown color by iron oxides [39,40]. The terrain is flat with an ondulated microrelief, and with wide depressions that present small plains. Its altitude above sea level varies between 100 and 150 m [40–42]. The climate is Aw (x') i, warm subhumid, with precipitation in summer and some part during winter [43]. The climatological station located in the center-south part of the ejido reports 1290 mm of precipitation and an average annual temperature of 26ºC. Soils are Leptosols, Vertisols and Gleysols [44,45]. The dominant vegetation in the study area is semi-evergreen tropical forest, and by a low seasonal flooded forest and savanna [46].

Sampling design

A stratified random design was used [47,48]. This sampling design was used considering the characteristics of the experiment, which consisted of three different treatments. Additionally, the species richness and composition of the treatments were compared with a control which is a acahual (secondary forest plot, and a consequence of slash and burn for the establishment of a traditional milpa) that has never presented an invasion of *Pteridium* and similar to the treatments was abandoned some 50 years. Each of the treatments plus the control were considered as the stratum, and within each of them, eight sampling units (UM) of 10 x 10 m (100m2) were randomly selected.

Experiment (Treatments)

Three treatments were established in areas invaded by *P. aquilinum* for approximately 50 years (from 1960 till present) (Figure 1). Treatment one (T1) consisted of areas without mechanical removal of the ferns with regular periods of burning, every two or three years during the last fifty years; the last recorded fire occurred in 2015. Vegetation sampling was done one year after the last burn (2016). Treatment two (T2) was established in areas invaded by ferns during the last 50 years, but the last burning occurred 7 years ago (2009), this treatment was not mechanically removed. Treatment three (T3) was established in areas with a similar land use history, but since 2010 burning was controlled and the removal method applied by Macario [49] was applied, which consists of weekly cuttings (locally known as chapeos) during for two months, followed by monthly chapeos until the year, and later quarterly and semi-annual chapeos depending on the density of the fern. Additionally, a control treatment (T4) was established in areas that were burned for the last time in 2007 for the establishment of the milpa system, which was abandoned after two years of use. These areas never presented invasion by ferns. All the plots presented similar conditions in relation to climate, stoniness, slope, altitude.

Sampling

The sampling was carried out between May and June 2016 in the areas mentioned in the experimental design section. In each of the sampling units the following variables were recorded: the diameter at breast height (DBH) of all woody species > 0.5 cm and the taxonomic identity of each of them [Wyatt-Smith, 1962]. All registered individuals were identified from dichotomous botanical keys [50] and existing floristic listings [51,52]. The community of plant species was characterized in each of the four established treatments through the determination of the floristic composition, the richness and abundance, as well as the forms of growth. The Importance Value Index (IVI) was determined in each of the treatments. IVI = relative density + relative basal area + relative frequency. Where: relative density = (number of individuals of species/total number of individuals)*100; relative basal area = (basal area of a species/basal area of all species)*100; relative frequency = (frequency of a species/ frequency of all species)*100 [53].

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Data analysis

To compare the taxonomic diversity of the treatments, a rarefaction analysis (interpolation) and extrapolation (prediction) of the Hill numbers were performed, based on sample size and coverage, which represents a unified criterion to contrast the diversity of multiple assemblages [54], 2016]. The analysis was carried out based on the order q (richness of species) and richness estimators were determined with the iNEXT software package R [54,55].

The variation in the composition of species was analyzed through an analysis of correspondence: The abundance was established with a transformation of Hellinger, which minimizes the weight of rare species. In addition, a canonical correspondence analysis was carried out to determine the relative influence of soil nutrients on the composition of species. The analysis was carried out with the CANOCO 4.56 package [56]. Additionally, statistically significant differences in the composition of woody species between the different treatments with a dissimilarity analysis (ANOSIM) in PRIMER-E 6.1.12 [57] were calculated. Finally, regression analyzes were carried out between the diversity of species found in each treatment and the soil variables. The diversity of species usually presents a Poisson distribution, a generalized linear model (GLM) was used .

3. Results

Composition and floristic richness

There were 2162 individuals belonging to 33 families, 56 genera and 63 species, recorded in the 32 sampled plots (T1 to T4). Of the total recorded individuals, 1884 (87.14%) were trees and 278 (12.86%) shrubs. The treatment with most diversity was T4 with 32 families, 49 genera, 54 species and 1091 individuals, of which 882 were trees and 209 shrubs. On the other hand, T1 showed the lowest species richness with 11 species, belonging to nine families, and a total of 193 individuals (trees) without presence of shrubby species (Table 1). The families with higher richness of recorded species were Fabaceae with 11 species, followed by Asteraceae, Meliaceae, Rubiaceae, Sapindaceae and Verbenaceae with three species each, contributing 41.26% of the total of the species registered in the treatments. The genera that presented the highest number of species were *Lonchocarpus* with five, *Thevetia*, *Eugenia* and *Coccoloba* with two species respectively. The largest number of individuals was distributed among the following families Rubiaceae with 572, Araliaceae (237), Fabaceae (233), Polygonaceae (159), Cecropiaceae (134), Asteraceae (115), Ulmaceae (110) and Sapindaceae with 104. Species with higher densities were *Guettarda combsii* Urb. (522), *Dendropanax arboreus* (L.) Decne. & Planch. (237), *Coccoloba spicata* Lundel (158), *Cecropia peltata* L. (134) and *Trema micrantha* (L.) Blume (108), and together formed 53.60% of the inventoried species.

The variation gradient observed between the treatments is wide (4.622 SD), which suggests a wide variation in the composition of species between treatments. The first two axes captured 56 and 44% of the variation, respectively (Figure 2). The dissimilarity of species is a good measure to identify the distribution of the ecological niche between the species. The dissimilarity analysis (ANOSIM) determined that there are significant differences in the dissimilarity between the different treatments, meaning that beta diversity varied between treatments. In this case, the variation percentage ranged between 60% and 91% between the treatments. Our results showed that the treatments T1 and T3 are the treatments with greater degree of differentiation in the composition of species, and T1 and T2 those that presented the lower percentage of differentiation (Table 2).

Table 1. Taxa and life form composition per treatment

Treatments	Family	Genus	Species	Shrubs	Trees	Ind. Num.
T1	9	10	11	0	193	193
T2	13	18	20	13	57	70
T3	20	31	34	56	752	808
T4	32	49	54	209	882	1091
Total	33	56	63	278	1884	2162

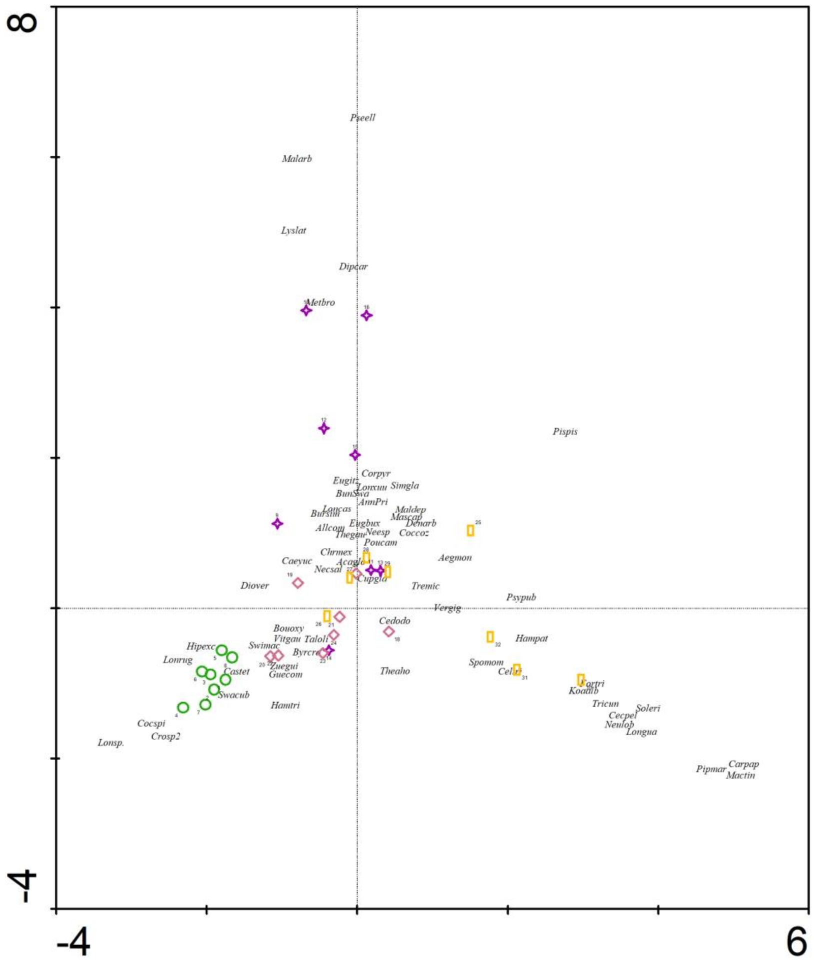

Figure 2. Correspondence analysis biplot for the first and second axes.

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Table 2. Results of ANOSIM comparisons of community composition among treatments, showing test statistics for global and pair-wise comparisons.

	r	*P*
All treatments	0.0714	0.01
1,2	0.68	0.02
1,3	0.917	0.02
1,4	0.845	0.02
2,3	0.635	0.05
2,4	0.607	0.02
3,4	0.652	0.03

Statistically significant differences were observed for species richness among the evaluated treatments. It was observed that the species richness decreased from T4 to T1, respectively. Likewise, abundance showed the same pattern, except for T2 which presented the lowest abundance. It was also observed that the sampling effort performed is representative for the richness and composition of the biota of the region (between 98 and 99% for T1, T3 and T4 and 88% for T2) under different management approaches (Table 3).

Table 3. Observed and estimated species richness for all woody plants > 0.5 cm dbh. Different letters indicate significant differences. Raref., rarefaction (for 70 individuals); S.obs. observed; dD., estimated (with 70 individuals), qD.LCL, qD.UCL the bootstrap lower and upper confidence limits for the diversity of order q at the specified level in the setting (with a default value of 0.95); SC.LCL, SC.UCL = the bootstrap lower and upper confidence limits for the expected sample coverage at the specified level in the setting (with a default value of 0.95).

Treat.	M	N	S.obs	qD.LCL, qD.UCL	qD	SC.LCL, SC.UCL	SC
T1	8	193	11	9.40-12.62	9.4	8.40-10.32	0.99
T2	8	70	20	16.4-25.86	18.78	15.53-22.03	0.88
T3	8	808	34	29.63-38.37	15.21	14.28-16.19	0.99
T4	8	1091	54	47.47-60.53	22.41	21.45-23.38	0.98
Total	32	2162	63				

Relative Importance value index (IVI) of the species.

The IVI was obtained in each of the four treatments and (Figure 3) IVI data of each of the species is presented. In T1, the species with the highest IVI are *Coccoloba spicata* Lundell, *Lonchocarpus rugosus* Benth., *Croton* Spp, *Hippocratea excelsa* Kunth. and *Diospyros verae-crucis* Standley. Regarding T2, the species that characterize this community due to its higher IVI are: *Lysiloma latisiliquum* (L.) Benth., *Bursera simaruba* (L) Sarg., *Malvaviscus arboreus* Cav., *Trema micrantha* (L.) Blume., *Metopium brownei* (

Jacq.) Urb., *Simarouba glauca* DC and *Guettarda combsii* Urb. The characteristic species of T3 based on IVI were *Guettarda combsii* Urb., *Hampea trilobata* Stand., *Zuelania guidonia* (Sw.) Britton & Millsp., *Coccoloba spicata* Lundel, *Lonchocarpus rugosus* Benth., *Lysiloma latisiliquum* (L.) Benth., *Bursera simaruba* (L.) Sarg., *Swietenia macrophylla* King, *Trema micrantha* (L.) Blume and *Croton* spp. Finally, the species with greater relative importance in T4 were *Cecropia peltata* L., *Dendropanax arboreus* (L.) Decne. & Planch., *Trema micrantha* (L.) Blume, *Bursera simaruba* (L) Sarg., *Kaonophyllon albicaulis* (Sch. Bip. Ex Klatt) RM King & H. Rob., *Piscidia piscipula* (L.) Sarg., *Hamelia patens* Jacq ., *Allophylus cominia* (L.) Sw., *Lonchocarpus guatemalensis* Benth., *Nectandra salicifolia* Kunth., *Coccoloba spicata* Lundell, *Aegiphyla montrosa* Moldenke, *Bourreria oxyphylla* Stand., *Verbesina gigante* (L.) Kuntze and *Guettarda combsii* Urb.

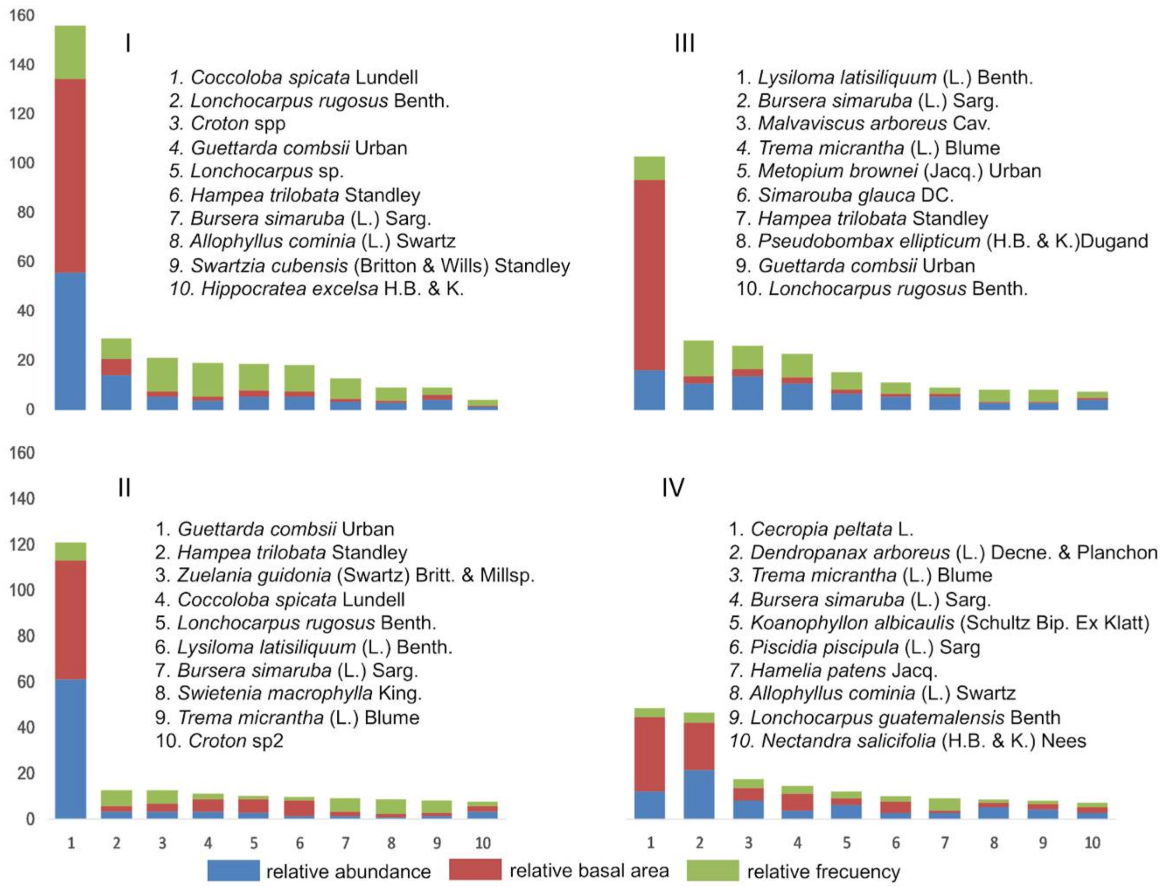

Figure 3. List of the woody species with the 90% of the Relative Importance Value Index (IVI) in each treatment.

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Effect of treatment on diversity and abundance.

The generalized linear model showed an important relationship between the diversity of woody species and abundance with explanatory variables (r2 = .57.86, P <0.001 and R2 = 67.46, P <0.001, respectively). In particular, it was observed that there is a clear relationship between the management of the areas and the species richness, particularly that the estimator of T3 is almost twice than in T1 and T2. When analyzing the effect of soil nutrients on species richness, it is observed that there are no significant differences between them (Table 4). The abundance of individuals, and the richness of species, showed significant differences between abundance and treatments; and to a much lesser extent differences were observed in abundance with respect to soil nutrients, except for phosphorus and potassium (Table 4). It was observed that abundance increases related to the intensity of the treatment, with the exception for the T2 that showed the lowest abundance of individuals (Table 2).

Table 4. Variation partitioning of woody species richness and abundance through General Lineal Model (GLM) and influence of each variable in the model.

	Richness	**Abundance**
	% Explained	
Total explain variation model	57.86	67.46
Total unexplained variation model	42.14	32.54
Variables	% contribution of total explained variation	
Treatment	16.25	-
K	12.48	-
Na	-	31.69
Ca	-	34.87
Among variables interaction	29.13	0.9

	Variable	**df**	**Deviance**	**df**	**P**
Richness	Treatment	3	80.1	28	0.00100
	SOM	***1***	***0.032***	***27***	***0.85765***
	N	1	0.164	26	0.68508
	pH	1	0.16	25	0.68961
	P	1	0.062	24	0.80361
	K	***1***	***3.259***	***23***	***0.07103***
	Na	1	0.744	22	0.38849
	Ca	1	0.029	21	0.86495
Abundance	Treatment	3	52491	28	**< 0.001**

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SOM	1	4588	27	**< 0.001**
N	1	2912	26	**< 0.001**
pH	1	1248	25	**< 0.001**
P	1	4	24	0.04
K	1	2	23	0.16
Na	1	2209	22	**< 0.001**
Ca	1	9198	21	**< 0.001**

4. Discussion

Identifying and understanding the influence of the invasive species on the secondary succession, as well as to understand its influence on the establishment of alternative states is of major importance from a theoretical perspective, and of immense practical significance for the restoration of the ecosystems and sustainable management of biodiversity.

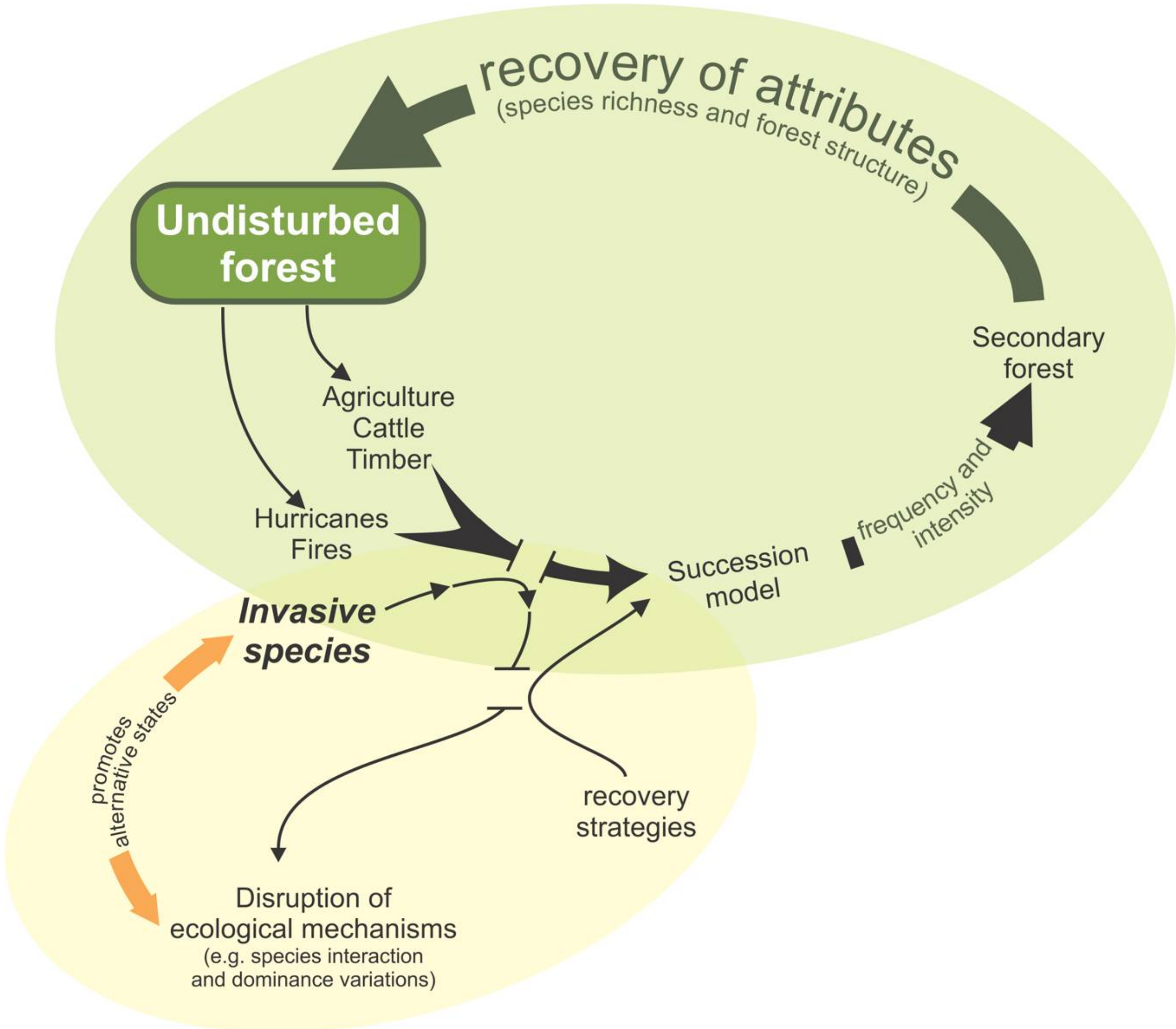

Figure 4. Conceptual model of influence of the invasive species on the secondary succession model.

Effects of *P. aquilinum* on the vegetation structure

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The floristic composition in the three evaluated treatments (T1 to T3), and in the control treatment (T4) was represented mainly by species of the Fabaceae family. This agrees with results of secondary vegetation studies carried out in the Yucatan Peninsula [58–63]. Other authors like and Sánchez & Islebe [64] and De Stefano et al [65] found that the Fabaceae family is particularly diverse in the southern region of the Yucatan Peninsula due to the precipitation gradient and its biogeographical affinity to the biota of Central America. Furthermore, it has been widely reported that it is the dominant family in secondary vegetation at different successional stages [66–69].

The species with the highest densities recorded in the four treatments is a group of species with resprouting capacities (*G. combsii* Urb., *D. arboreus* (L.) Decne. & Planch. and *C. spicata* Lundell) and sufficient seed reserve like *C. peltata* L. and *T. micrantha* (L.) Blume) which facilitate the establishment in the treatment areas. The densities of those species are distributed unequally considering the influence of the different types of treatments evaluated in the area. This agrees with species data by Macario-Mendoza (2003) in the control area.

The species that yielded the highest IVI values and are dominant of the different treatments are: *C. spicata* Lundell, *L. latisiliquum* (L.) Benth, G. combsii Urb., *C. peltata* L. Those trees are common species in secondary forest patches in seasonal dry forests. The low values of the IVI in most of the recorded species indicate specific traits like fast growth and differential adaptation to soil and site characteristics. Similar conditions were observed in a seasonal dry tropical forest of northern Quintana Roo where in hurricane damaged areas few species dominated [70].

The variation of species richness and abundance recorded by the rarefaction results is attributed to the invasion of *P. aquilinum* (L.) Kuhn and the history of land use in the area.

The results show that the species richness in T1 and its low diversity are best explained given that T1 was frequently burnt and the absence of seed bank. The low richness of species can be explained by the different edaphic conditions present in each type of treatment (depth, stoniness among others). Fires, occasional or frequent, favor the spread of bracken fern, but is also dependent on the seasonality of burning. The establishment of species in T1 and T2 is limited by shallow soils with little organic matter and characterized by species of secondary forest patches [71,72].

The dissimilarity between treatments T1 and T2 was the highest and was the consequence of the invasion of *P. aquilinum* (L.) Kuhn. The species composition was not similar between treatments, not even in the areas that were invaded by P. aquilinum (L.) Kuhn. Although, at three of the treatments were *Pteridium* dominated their history of use contributes to the non-similarity of species richness. The level of dissimilarity in the area explains why the age of the vegetation could influence the results and restricts the regeneration in T1 due to the absence of seed banks and to the frequency of burning and eventually interrupts the succession. The T2 treatment and its management allows the development of a seed bank and self-thinning of the species after of fire. The surviving species manage to facilitate secondary succession, with increased shaded areas affecting bracken fern cover. It can be observed that there was a high floristic dissimilarity among all studied treatments (Table 3). The high dissimilarities explain that most species of one treatment do not repeat in the other treatments.

The T2, T3 and T4 treatment were almost of the same age but T4 was not invaded by P. aquilinum (L.) Kuhn. T1, T2 and T3 were invaded, since the different types of management circumscribe this dissimilarity. The T1 is the treatment with the highest dissimilarity compared to the previous treatments, which evidences the successional age in the area. López-Martínez [68] reported that significant differences in the dissimilarity between successional age classes indicate that the composition of the species changes during the succession. From other studies analyzing succession in seasonal dry tropical forests in the Yucatán Peninsula we observe a similar trend [70,73].

The treatments differ in richness outlined previously, however, the evaluation of the nutrients on the treatments did not present significant differences (Table 4).

The results of this work do not show that soil nutrients (N, P and K) have a relationship with species richness, it differs with richness of the evaluated species. Table 5 indicates that N and P were slightly significant. The content of K on the density of species is significant and negative. This would indicate that the presence of K the probability of increasing species richness is lower. Finally, the level of N is significant but positive which means that it increases the abundance of species in the treatments. The results of the present investigation coincide with John et al [74] where soil resource availability is relevant to tree species composition.

Figure 4 represents a schematic view on the different of succession caused by bracken fern. The main danger for conservation and land use is the disruption of ecological mechanisms controlling succession invaded by *Pteridium*. Without active to strategies of control bracken fern causes a disruption in natural recovery, making it nearly impossible to recover the affected areas for future planning.

Changes in bracken cover and abundance in secondary forests are also influenced by competitive interactions with trees and thus directly with dynamics of the forest canopy. Additionally, in managed or human impacted forest ecosystems like southern Mexico, the dominance of bracken is closely connected to stand development (e.g. management) by the local communities. Figure 4 also highlights one of the main problems caused by bracken, which is the lack of tree recruitment for longer time periods. If the dominance of bracken is not hindered, there are few possibilities for individual tree species to grow on bracken stands and eventually establish with a closed canopy.

Our data have shown that the presence of a tree canopy reduces the area covered by bracken. However, effective growth of tree seedling like *Lysiloma latisiliqua* requires sufficient light on soils. Some disturbance is therefore positive to an improved establishment of seeds at given times during the succession. The resprouting tree species reach sufficient heights compared to the bracken canopy, under specific recovery strategies.

Large scale bracken dominance in areas formerly covered by seasonal dry tropical forest is the consequence of prior deforestation or bad forestry practices. To achieve sustainable forest management we recommend considering past land use practices to avoid future increase in bracken dominated former forest areas.

Alternative states and recovery strategies

From a traditional perspective of the succession model, mechanisms such as competition and facilitation have modulated the plant communities [75–78]. Particularly, it has been postulated that facilitation acts on the direction of succession and is the main mechanism in conditions of high abiotic stress [79]. It has been observed that pioneer or light-demanding species are the first to colonize disturbed areas, and eventually generate conditions for the establishment of shade-tolerant or long-lived species. [77,79–83]. P. aquilinum is a highly competitive species with its invasive and toxic conditions, and does not present interactions (eg herbivory) that regulate the development of its populations. Bracken presents a high productivity of biomass that accumulates in the soil, limiting light for native pioneer species, and its spores are fire tolerant to regular burning.

[84]. This set of characteristics change the ecological mechanisms that drive the process of secondary succession in plant communities, and generates the establishment of an alternative state that favors the establishment of bracken (Figure 4). This study clearly shows that the introduction of P. aquilinum leads to the establishment of an alternative state (T1), because, even though the site has been abandoned for more than 50 years, the dominant species is P. aquilinum. The composition of woody species that managed to survive the last burning are species with resprouting capacities. This study showed that the application of community recovery strategies break the alternative state (Figure 4) and re-establish the processes of secondary succession, increasing the species richness and the establishment of resprouting species, and those coming from seed rain of the surrounding vegetation matrix.

5. Conclusions

Our study has important theoretical and practical implications for the recovery of sites invaded by P. aquilinum in southeastern Mexico. The results of this study demonstrated that invasive species disrupt the ecological mechanisms that drive secondary succession, but through recovery strategies it is possible to foster secondary succession (Figure 4). Our conceptual model can serve as a tool that allows the recovery of areas invaded by non-native species. Finally, the increase in species richness and composition made it possible to evaluate the effectiveness of the recovery strategy used in this study, so the use of controlled burning and regular cutting are efficient strategies for the eradication and recovery of areas invaded by P. aquilinum. Recovery strategies for bracken invaded areas provide improved land use strategies and finally improve sustainability of rural areas.

Author Contributions: A. J-B executed the field work, J.O.L-M conceived the research design, analysis, and wrote the manuscript. G.I. revised and wrote the manuscript. P.M. conducted the field data collection. B.V-L, L.P. and M.V-H assisted in analysis of the results and revised the manuscript.

Funding: This research was funded by COMISION NACIONAL FORESTAL, Programa de Compensación Ambiental, grant number XXX" Check carefully that the details given are accurate and use the standard spelling of funding agency names at https://search.crossref.org/funding, any errors may affect your future funding.

Acknowledgments:

Conflicts of Interest: The authors declare no conflict of interest.

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