



Cobertura proyectiva foliar y riqueza de especies de plantas vasculares en el Estado de México

Projective foliar cover and species richness of vascular plants in the State of Mexico

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Abstract

The relationship between vegetation productivity/production and vascular plant species richness is important in order to analyze the response of the vegetation to disturbances, which has been addressed by using different approaches and theoretical frameworks, although with insufficient results to explain the observed variability. Specht and collaborators propose non-linear relationships between projective foliar cover (*PFC*) and species richness (*S*) under equilibrium conditions and plant succession. In order to analyze the *PFC-S* relationships, sampling was carried out in different vegetation types in the eight forest regions defined by *Probosque* in the State of Mexico, in which 682 sampling plots of 1 000 m² each were established. The relationships established between *PFC* with respect to *S*, in the case of maximum values of *S*, exhibited patterns that are consistent with the empirical approaches of Specht and collaborators, particularly, as a function of the stages of forest/forest succession. In addition, the ratios were established for shrublands and grasslands. The results of the analyses showed potential relationships between *S* and the *PFC* of the upper and lower stratum, in which their parameters are related to each other, simplifying the estimation process to a single parameter.

Key words: Vegetal diversity, Specht's equilibrium, potential models, parameter relationships, maximum richness, forest succession.

Resumen

La relación entre la productividad/producción de la vegetación y la riqueza de especies de plantas vasculares es importante para analizar la respuesta de la vegetación ante disturbios, la cual se ha abordado con diferentes enfoques y marcos teóricos, aunque con resultados insuficientes para explicar la variabilidad observada. Las relaciones propuestas por *Specht* y colaboradores establecen relaciones no lineales entre la cobertura proyectiva foliar (*CPF*) y la riqueza de especies (*S*) bajo condiciones de equilibrio y de sucesión vegetal. Para analizar las relaciones *CPF-S* se realizaron muestreos en diferentes tipos de vegetación en las ocho regiones forestales definidas por *Probosque* en el Estado de México, en las que se establecieron 682 parcelas de muestreo de 1 000

m² cada una. La relación establecida entre la *CPF* con respecto a *S*, caso de valores máximos de *S*, evidenció patrones congruentes con los planteamientos empíricos de *Specht* y colaboradores, particularmente, en función de los estados de la sucesión de bosques/selvas. Adicionalmente, las relaciones para matorrales y pastizales están establecidas. Los resultados de los análisis mostraron relaciones potenciales entre *S* y la *CPF* del estrato superior e inferior, en las cuales sus parámetros están relacionados entre sí, lo que simplifica el proceso de estimación a un solo parámetro.

Palabras clave: Diversidad vegetal, equilibrio de *Specht*, modelos potenciales, relación entre parámetros, riqueza máxima, sucesión forestal.

Introduction

Species richness has been related to vegetation productivity and production through different approaches and theoretical frameworks in order to explain the underlying processes and their driving factors (LaRue *et al.*, 2019; Sheil and Bongers, 2020; Wang *et al.*, 2020); however, these associations have proven insufficient to account for the observed variability (Wang *et al.*, 2019).

Regarding the functioning of ecosystems, an increase in the productivity or production of vegetation has been cited as concurrent with the diversity of plant species (Liang *et al.*, 2016). In this respect, using resource competition models, Tilman (1982, 1999) and Tilman *et al.* (1997) proposed that (biomass) production increases in direct proportion to the number of species competing for a single resource. Thus, the variation in biomass production is high, and its variance decreases as the number of species increases. The same pattern may be observed in the case of competition for two resources (*e.g.*, water and nutrients), therefore, a higher number of species results in full use of the resources and a saturation pattern.

In an experiment on the relationship between productivity/production and species richness in grassland, Tilman *et al.* (1996) proved that the projective foliar cover

increases with the number of species, which is indicative of a specific functional relationship beyond the one existing between biomass and species richness.

Vilá *et al.* (2005) analyzed experimental evidence in forest systems and proposed that there is a connection between the number of taxa and the productivity/production of forests before canopy closure (early stages of succession or in forests with stress limitations), which changes when (and if) the forest declines. At the beginning of the succession, the shrub cover increased with the increasing tree species richness, which meant that they did not interfere with the tree production.

Wang *et al.* (2020) analyzed the relationship between productivity/production and species richness and determined concave, asymptotic, positive, negative, and irregular patterns with a positive effect on productivity. Ónodi *et al.* (2021) registered different relationships before and after a fire, thereby proving that the influence of disturbances on plant succession conditions the stability of ecosystems.

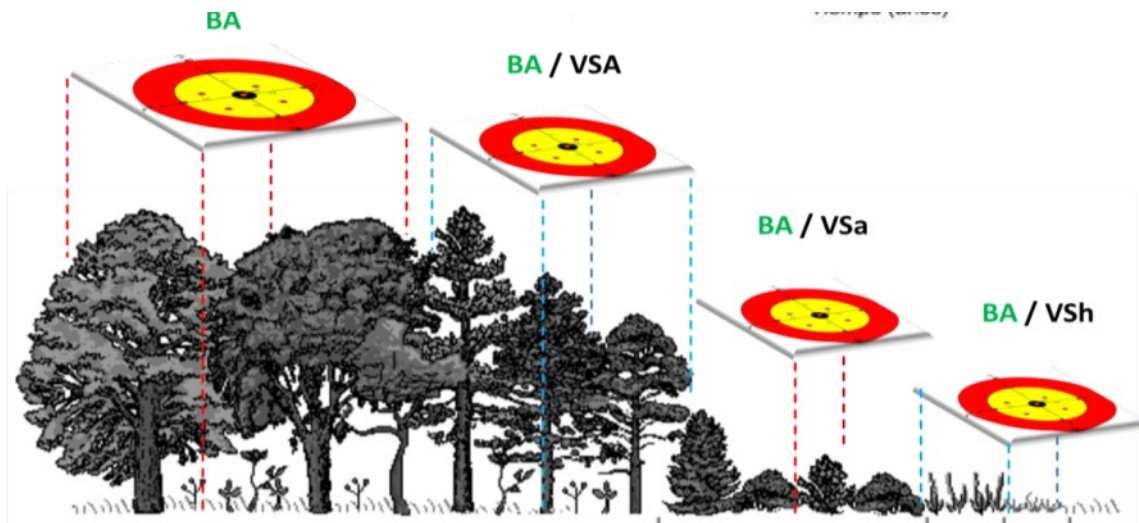
The aerial vegetation canopy cover has a positive effect on species diversity; the intensity of disturbance has a negative effect on the aerial cover and a variable impact on the species richness (Sanaei *et al.*, 2018). The aerial canopy cover, measured as the availability of radiation illumination, is positively and strongly correlated with species richness (Dormann *et al.*, 2020).

The objective of this work was to analyze the relationship between the plant productivity/production and the species richness for the establishment of the necessary conditions for the increase of the aerial biomass and projective foliar cover, as well as the relationship between the projective foliar cover and the number of species for the different types of vegetation of the State of Mexico, based on extensive sampling of its various plant communities.

Materials and Methods

Sampling campaign in the State of Mexico

In 2014, a field campaign was implemented to carry out an inventory of carbon storage and vascular plant richness in the different vegetation types of the State of Mexico. In order to optimize resources, a chronosequential sampling strategy was followed in which primary (undisturbed) vegetation was sampled first, followed by disturbed vegetation (secondary vegetation, in succession), and finally, by vegetation associated with permanent changes in land use mainly as a result of anthropogenic activities (Figure 1).



- Phase I** Reference forests (initial state)
- Phase II** Disturbed vegetation (transition/degradation)
- Phase III** Agricultural and livestock vegetation (end state)

Source: Self made.

The red and yellow circles represent the sampling sites in a fir (*Abies* spp.) forest at different stages of succession. BA = Primary fir forest; BA/VSA = Fir forest with secondary arboreal vegetation; BA/VSa = Fir forest with secondary shrub vegetation; BA/VSh = Fir forest with secondary herbaceous vegetation.

Figure 1. Sampling phases based on the stratification of land use and vegetation homologated for the State of Mexico.

The types of vegetation and land use were classified according to the system of the *Instituto Nacional de Estadística y Geografía, Inegi* (National Institute of Statistics and Geography), included in the FAO FRA 2010 (Paz-Pellat *et al.*, 2019), according to which secondary vegetation (SV) has three succession stages, depending on the dominance of the stratum: (A) tree, (a) shrub, or (h) herbaceous. The phases of plant succession make it possible to quantify the level of disturbance of the ecosystem as a measure of its stability.

Sampling distribution

A total of 682 sampling sites 1 000 m² each were established randomly; Table 1 shows the number of these sites measured in each phase of the campaign. The sample size was estimated according to the protocol for calculating the number of sampling points used in Afforestation and Reforestation Clean Development Mechanism projects (A/R CMD project activity) of the United Nations Framework Convention on Climate Change (UNFCCC), using of the A/R CDM methodological tool

(2014), developed by Winrock International (Pearson *et al.*, 2005). The sites were distributed according to the regions into which the *Proteccion de Bosques del Estado de México, Probosque* (Protector of Forests of the State of Mexico) divides that federal state. The use of the sampling phase allows the analysis of vegetation by dominance of the secondary succession stage.

Table 1. Number of plots sampled in each region and stage.

<i>Probosque</i> region	Sampling phase		
	I	II	III
01 <i>Toluca</i>	40	45	16
02 <i>Zumpango</i>	22	28	12
03 <i>Texcoco</i>	56	65	20
04 <i>Tejupilco</i>	9	44	10
05 <i>Atacomulco</i>	42	50	23
06 <i>Coatepec Harinas</i>	23	30	11
07 <i>Valle de Bravo</i>	26	27	13
08 <i>Jilotepec</i>	19	35	16
Total	237	324	121

Figure 2 shows the spatial location of the measured sites, both by region and by sampling phase. The spatial variability of the samples reflects that of the vegetation types registered in each region. The particular types of vegetation are not shown in Figure 2, since the analyses are presented in general terms.

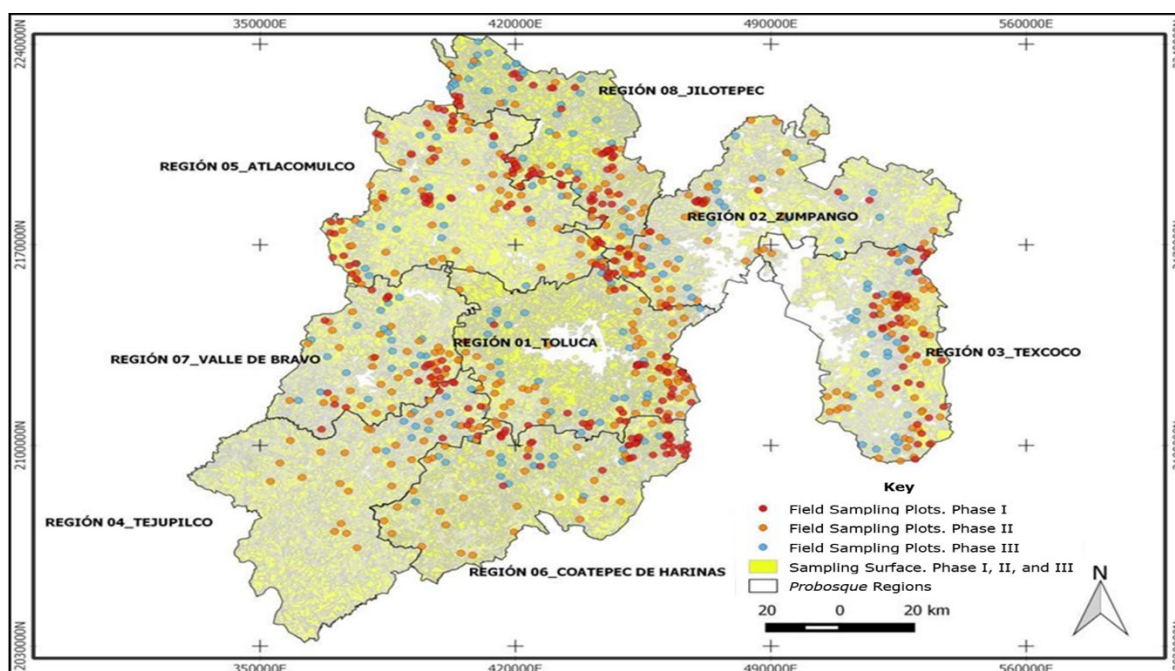


Figure 2. Location of the sampling plots in the *Probosque* regions, by phases of the sampling campaign.

Species record

All vascular plant species present at each sampling site were considered. A photographic record of the taxa was taken, and only those that were flowering or fruiting were collected by standard methods (Lot and Chiang, 1986). Taxonomic identification in the laboratory was carried out with the help of specialized literature (Lot and Chiang, 1986).

The floristic composition (species, genera, and families) of the sampled sites was analyzed. The APG IV angiosperm taxonomic classification system was used as a

reference for the species catalog (2016). For the nomenclature of gymnosperms and pteridophytes, the Tropicos™ world flora project of the Missouri Botanical Garden Herbarium was consulted (Missouri Botanical Garden, 2018), which contains the most recent updates of taxonomic information concerning this type of plants. Taxon records were made using field information and integrated into databases for analysis.

Projective foliar cover

The projective foliar cover (*PFC*) was evaluated with the method developed by Salas-Aguilar *et al.* (2017) for estimating the fraction of forest cover using digital photography: the images were taken with a Canon® Eos Rebel T5 camera set at the highest spatial resolution (17 915 904 pixels). The camera lens was set to an ISO of 200, and the aperture and exposure were used in automatic mode. In order to take the photograph, the lens was leveled upwards, at a 1.5 m height from the ground, at radii of 17.84, 11.28, and 5.65 m, respectively, and clockwise: north to south, northeast to southwest, east to west, and southeast to northwest (Figure 3).

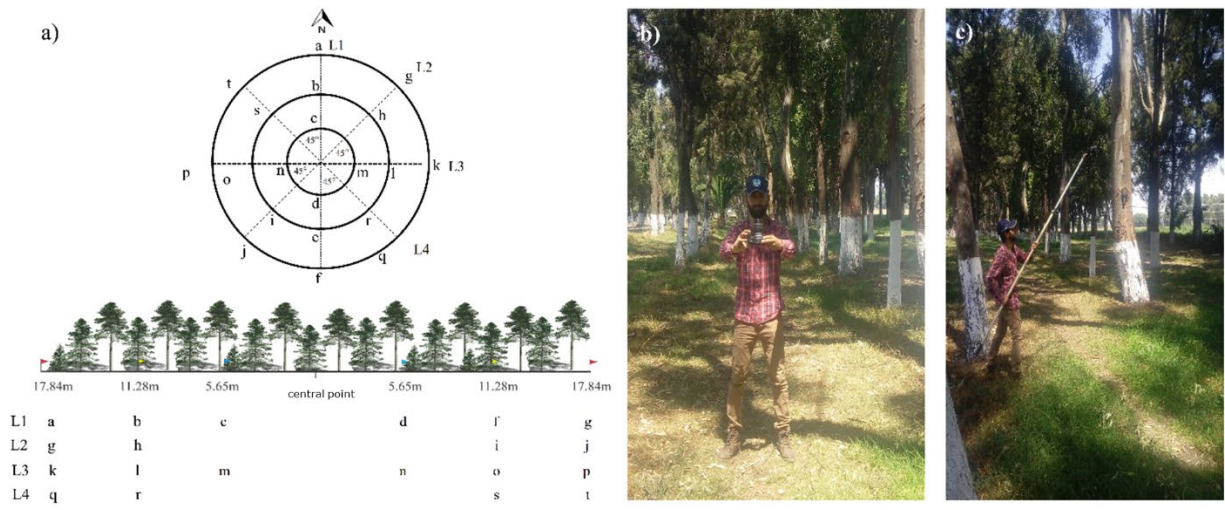


Figure 3. Photographic capture process at the sampling sites: a) PMCB design: the letters correspond to the distance of the capture from the center of the sampling site, b) Photographic capture at zenith, c) Photographic capture at nadir.

Vegetation balance

Specht (1972) proposed a model of vegetation equilibrium with the atmosphere and water in the soil profile:

$$\frac{C_e}{P_e} = S \min + kW \quad (1)$$

$$W = P - Q - D + Sext$$

Where:

C_e = Current evapotranspiration

P_e = Potential evapotranspiration (atmospheric demand)

S_{min} = Water storage in the root depth of vegetation that cannot be used by vegetation

k = Evaporative coefficient (cm^{-1})

W = Water balance

P = Precipitation

Q = Surface runoff

D = Subsurface drainage

S_{ext} = Water stored in the soil extractable by vegetation (at the beginning of the month)

The value of the water stored in the soil (S_{max}) is estimated by dividing the root-zone water storage capacity value by the permanent wilting point. The precipitation P exceeding S_{max} is lost as subsurface drainage (D). The water balance (Equation 1) is performed at plot scale; its values correspond to monthly data, and its units are cm.

Specht (1972) proposed that the climax evergreen perennial vegetation utilizes the total available water through the balance of soil water and the atmospheric demand, modulated by the evaporative coefficient k , so that $S_{min} = 0$ ($y D = 0$):

$$\frac{C_e}{P_e} = kW \quad (2)$$

Where:

C_e = Current evapotranspiration

P_e = Potential evapotranspiration (atmospheric demand)

k = Evaporative coefficient (cm^{-1})

W = Water balance

The evaporative coefficient k integrates the effects of the vegetation's aerial geometry (mostly foliar) and the plants' resistance (mostly stomatal and leaf boundary layer) to water movement (Specht, 1972). A high k value implies a densely structured plant community (low resistance).

Coefficient k is approximated through an evolutionary adjustment within the plant community to a maximum value that is very close but never equal to zero. The assumption is that the climax community (in equilibrium between atmosphere, vegetation, and soil) fully utilizes the available soil moisture for plant growth (biomass accumulation); for this purpose, the roots must explore the soil to use all available water in any part of the soil profile.

In Specht's work, the PFC of the plant community is divided into an upper stratum or US (projective canopy cover= PFC_{US}) and a lower stratum or LS (projective canopy cover= PFC_{LS}). For communities dominated by tree species, the difference in height between these strata is two meters (Specht and Morgan, 1981; Specht and Specht, 1993; Specht and Tyler, 2010). In the case of shrublands, grasslands, and agricultural lands, heights that reflect the partitioning of resources in the community are utilized to determine the distinction between the upper and the lower strata (Specht and Morgan, 1981).

The most important structural feature of an evergreen (and deciduous) perennial plant community is the distribution and orientation of the leaf area from the top to

the bottom of the community, in relation to the direct and diffuse component of radiation. These structural attributes, together with the resistance to water flow, determine the value of k (Specht, 1972). Based on these considerations, Specht (1972; 2000) posited an empirical relationship between k (mm^{-1}) and PFC :

$$\begin{aligned} PFC_{US} &= 9\,770k - 7.15(n = 54, R^2 = 0.95) \\ PFC_{LS} &= 5\,880k + 10.04(n = 29, R^2 = 0.87) \\ PFC_T &= 15\,350k + 5.80(n = 29, R^2 = 0.93) \end{aligned} \quad (3)$$

Where:

PFC_{US} = Projective foliar cover of the upper stratum

PFC_{LS} = Projective foliar cover of the lower stratum

PFC_T = Projective foliar cover of total foliage

k = Evaporative coefficient (cm^{-1})

n = Data number

R^2 = Coefficient of determination

Specht *et al.* (1991), and Specht and Specht (1993) developed relationships between the evaporative coefficient k (cm^{-1}) and the species diversity in climax communities:

$$\begin{aligned} & \textit{Tropical Region} \Rightarrow \\ & \ln(S_T) = 2.19 + 34.79k, (n = 20, R^2 = 0.94) \\ & \ln(S_{US}) = 0.92 + 40.02k, (n = 29, R^2 = 0.98) \\ & \textit{Subtropical Region} \Rightarrow \\ & \ln(S_T) = 2.54 + 28.10k, (n = 15, R^2 = 0.91) \quad (4) \\ & \ln(S_{US}) = 0.01 + 45.90k, (n = 9, R^2 = 0.93) \\ & \textit{Warm Temperate Region} \Rightarrow \\ & \ln(55 - S_T) = 4.55 - 64.23k, (n = 7, R^2 = 0.89) \\ & \ln(S_{US}) = 0.21 + 20.49k, (n = 16, R^2 = 0.71) \end{aligned}$$

Where:

$\ln()$ = Logarithm function

k = Evaporative coefficient (cm^{-1})

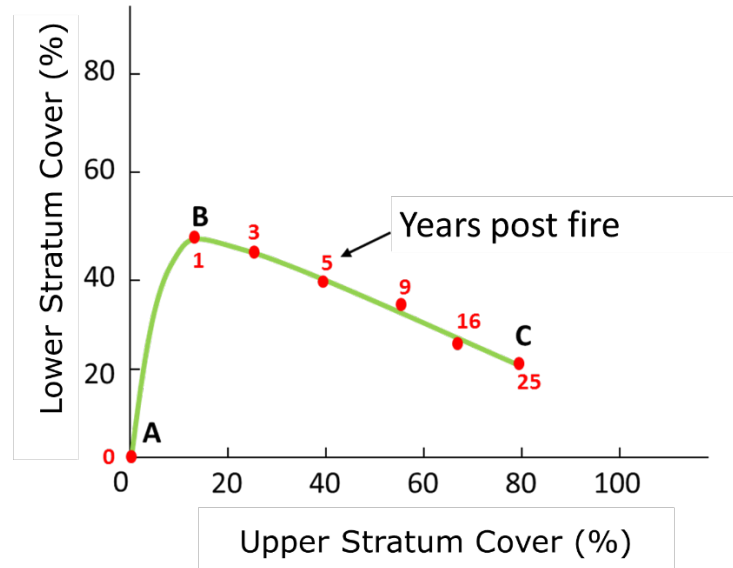
S_T = Species richness

S_{US} = Species richness of the upper stratum

n = Data number

R^2 = Coefficient of determination

The relationship between species richness of the lower stratum (S_{LS}) is linear and inversely proportional to PFC_{US} (Specht and Morgan, 1981; Specht *et al.*, 2006). This pattern is observed in the post-fire succession of a plant community (Specht and Jones, 1971) (Figure 4), which shows that, as the forest tends to mature, the species diversity of the *LS* decreases and that of the *US* increases.



Source: Adapted from Specht and Jones (1971)

Figure 4. Schematization of the evolution of the projective foliar cover in a post-fire succession.

Regarding the number of species and the composition of the community, the succession trajectory shows an increase in species richness in the process towards a climax community. This is only one of the potential trajectories, given that species richness and composition have a virtually infinite number of combinations by which to achieve the equilibrium condition (climax). In general terms, Specht's model states that water in the soil profile, coupled with the atmosphere-vegetation interaction, is the main constraint for the development of plant communities.

The ratio of canopy cover between the upper and lower strata has also been observed in mature plant communities in the United States of America (Tausch *et al.*, 1981; Tausch and Tueller, 1990).

Based on the linear relationship between k and PFC and the exponential relationship between the number of species and the evaporative coefficient k , we expect an exponential (non-linear) relationship between PFC and the number of taxa, which

increases with disturbance in the vegetation and is reflected in the state of plant succession. This is particularly true in the case of climax communities.

Data processing

In order to analyze the relationship between the *PFC* and the *S* of vascular plants (variables of analysis) the following procedure was followed:

- a) First, analyses of the projective foliar cover and species richness relationships were carried out for each individual region (*Probosque* regionalization).
- b) For each general vegetation type and land use, the site with the highest number of species was identified by region, and the corresponding *PFC* was measured in the field was associated with it.
- c) All sites in the *Probosque* regions were selected and grouped by vegetation type: forests/rainforest (with their succession stages), shrublands, grasslands, and agricultural lands.

Results

Figure 5 shows the results obtained for forests/rainforest and their succession stages. The relationship between S and the PFC_{US} of the upper stratum was fitted to a linear model:

$$S = A + B(PFC_{US}) \quad (5)$$

Where:

S = Species richness

A = Empirical constant

B = Empirical constant

PFC_{US} = Projective foliar cover of the upper stratum

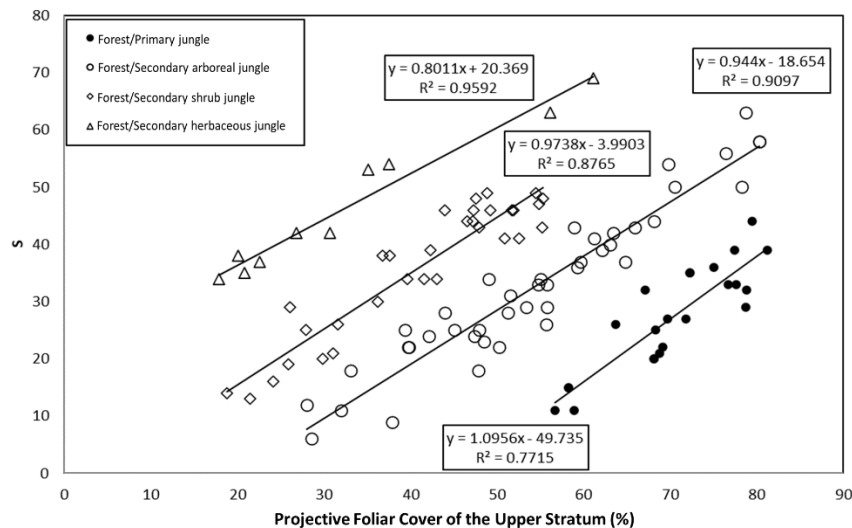


Figure 5. Linear relationships between PFC_{US} and S for forests/rainforest and their succession stages.

The number of sample plots represented in the study is 108; however, eight extreme values in the upper part and four extreme values in the lower part are not shown herein, as they were outside the analyzed limits and had patterns with little experimental data.

Given that a nonlinear relationship between PFC_{US-k} , relationships (3) and (4) were expected, Figure 6 shows the relationships established by potential models.

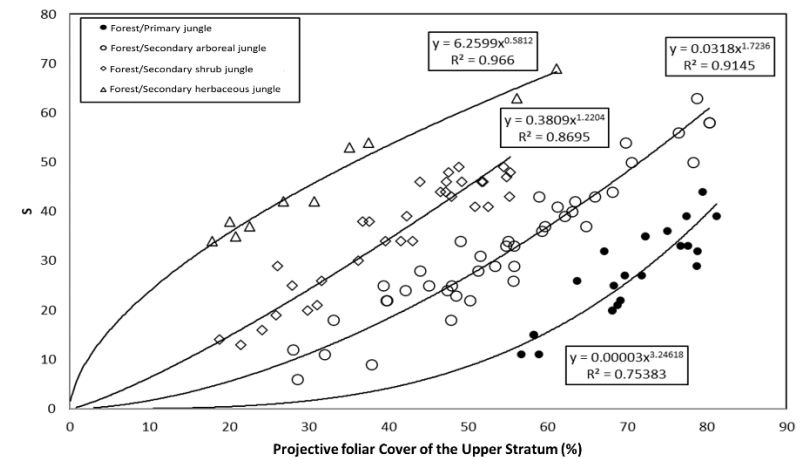


Figure 6. Potential relationships between PFC_{US} and S for forests/jungles and their succession stages.

When analyzing the potential model $S=A(PFC_{US})^B$, it was observed that the parameters $nl(A)$ and B are related to each other, as they intersect at a common point $(0,1)$. Figure 7 shows the relationship between the parameters of the potential models fitted in Figure 6; the straight line passes through the point $(0,1)$, since $nl(A=1)=0$ in the case of $B=1$. Thus, the relationship between the parameters of the potential models requires only one piece of information to establish the relationships between the different stages of forest/forest succession.

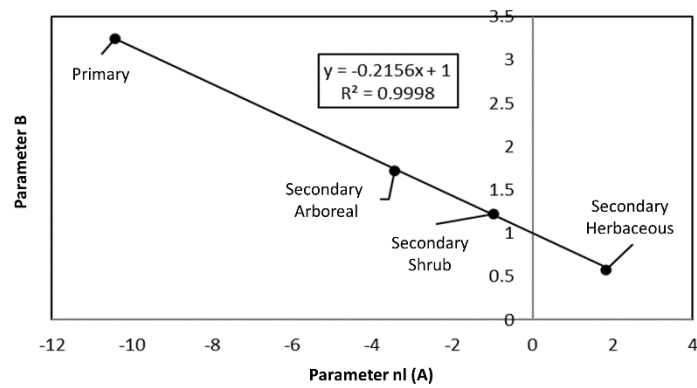


Figure 7. Relationship between the parameters of the potential models for forests/rainforest and their succession stages.

For non-forest/forest vegetation, the number of plots sampled was limited. Figure 8 shows the relationship between PFC_{LS} and S in the case of shrublands.

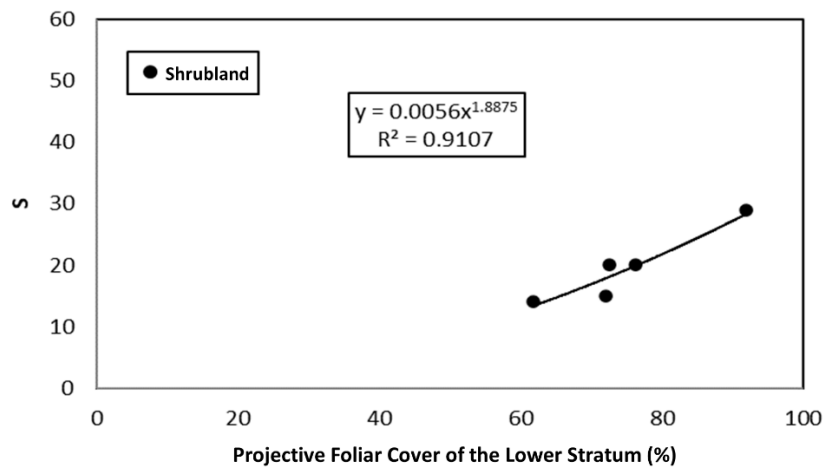


Figure 8. Relationship between PFC_{LS} and S for shrublands.

Figures 9 and 10 show the relationships between PFC_{LS} and S for grasslands and agricultural lands, respectively.

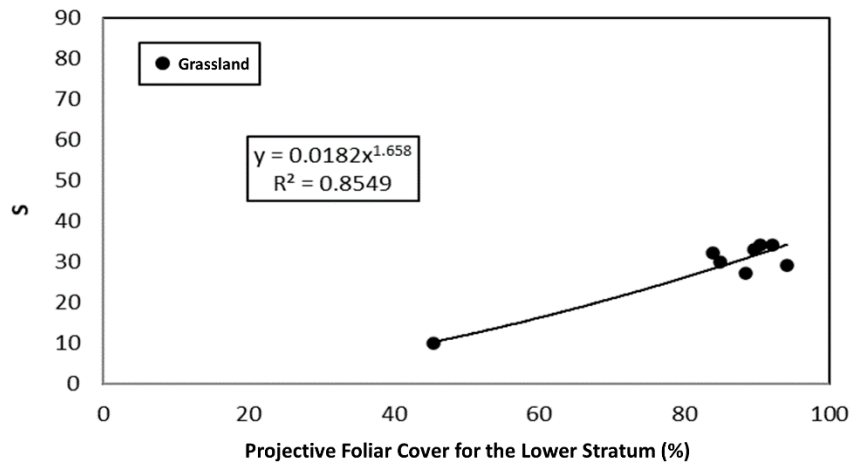


Figure 9. Relationship between PFC_{LS} and S for grasslands.

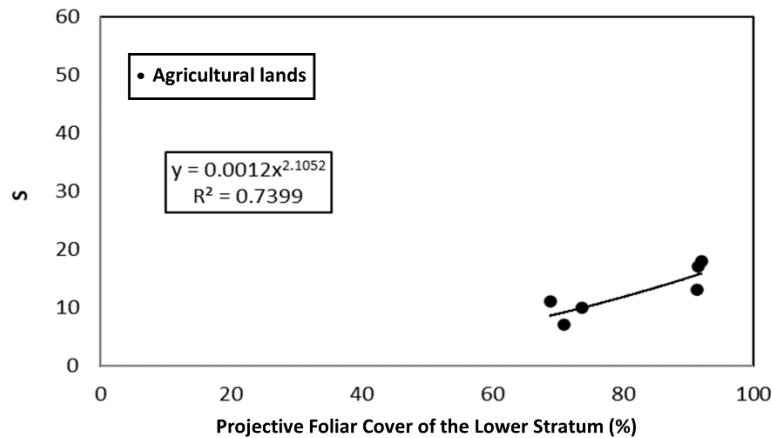


Figure 10. Relationship between PFC_{LS} and S for agricultural lands.

Figure 11 shows the relationship between the parameters of the potential models fitted for the relationship of S to PFC_{LS} for shrubs, grasslands, and agricultural lands which, in a similar way to forests/rainforest, were fitted to a straight line passing through the point (0,1).

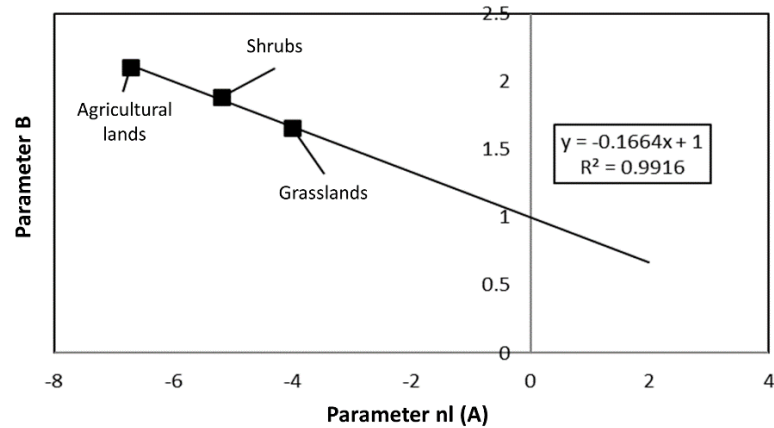


Figure 11. Relationship between the parameters of the potential models for shrubs, grasslands, and agricultural lands.

Discussion

The relationship between species richness and projective foliage cover for climax communities has been determined by Specht and Morgan (1981) through the use of undisturbed gradients. In the present study, this relationship exhibited patterns that are consistent with the empirical approaches of Specht and Specht (1993), particularly in terms of the forest/rainforest succession stages. It should be noted that studies on this subject are practically restricted to Mediterranean climate ecosystems; the literature includes certain works that make reference to temperate forests (Tausch *et al.*, 1981; Tausch and Tueller, 1990) in sequences of plant succession. According to these reviews, the application of the *PFC-S* relationship to other types of environments, such as the temperate and subtropical forests of the

State of Mexico, extends the previously defined developments and allows establishing general patterns of the relationship between $PFC_{US}(k)$ and the species richness (S), as demonstrated in the research documented here.

The relationship between aerial cover and species richness can be determined for undisturbed climax vegetation (Sánchez-Sánchez *et al.*, 2021); however, its generalization to stages of succession or disruption is still a pending task.

The criterion of using the maximum number of species to characterize a vegetation type and land use establishes a more equilibrium-oriented condition, even in succession stages, as it considers vegetation whose cover ratio to species richness is optimal. A high variability of the experimental data is expected in relation to the fit of potential models, given that the criteria for defining succession stages are qualitative (dominance of strata), varying during the time of plant succession and being subject to a certain level of subjective characterization of the succession.

The dynamics of the evolution of the relationship between the cover and the number of species is the result of the balance between the upper and lower strata (Figure 4) of the vegetation canopy.

The $PFC-S$ relationship reflects the water balance of ecosystems and the trajectories of forest succession, as well as of other vegetation types. Although no variables related to the water balance were measured, the results indirectly support its dynamics.

Conclusions

The models proposed in this work to explain the relationship between the projective foliar cover of the upper and lower vegetation strata in relation to the richness of vascular plant species are consistent with the relationships cited in the literature.

The relationships between the parameters of the potential models simplifies the estimations, as only one value is required for their parameterization, given the relationships between the parameters. The relationship between the two parameters is a consequence of the fact that various linearly transformed curves intersect at a common point.

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Conflict of interest

The authors declare that they have no conflict of interest.

Contribution by author

Fernando Paz Pellat: conceptualization, drafting of the manuscript, and formal analysis; Víctor Salas Aguilar: revision of the manuscript, methodology; Alma Velázquez Rodríguez: revision of the manuscript, data curation; Cristóbal Sánchez

Sánchez: revision of the manuscript, research; Martín A. Bolaños González: revision of the manuscript and management of the project.

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