PROJECTIVE LEAF COVER PREDICTS PLANT SPECIES RICHNESS IN THE SACRED FIR FORESTS OF MONTE TLÁLOC, STATE OF MEXICO

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ABSTRACT

The establishment of relationships between the water balance coupled to the atmosphere and species richness, for a given ecosystem, allows characterizing the state of vegetation under stable conditions. The proposal by Specht and colleagues of the water relationship between actual evapotranspiration/potential evapotranspiration (Ea/Eo), mediated by the evaporative coefficient k, allows to establish empirical relationships, without implying a cause-effect relationship, between the projective leaf cover (CPF) and the richness of plant species in relation to k. These relationships were reviewed with information from sampling sites established in sacred fir [*Abies religiosa* (Kunth) Schltdl. & Cham.] forests of the warm temperate climatic region of Mount Tlaloc, State of Mexico. Species richness and CPF of the upper stratum of the forests were measured, and the aboveground biomass was estimated. The patterns of the relationship between the CPF of the upper stratum and the total number of species showed variations within the limits of Specht's equilibrium relationship, even though the levels of disturbing agents in the sites showed a greater dispersion of the data. Establishing a relationship between projective leaf cover and species richness facilitates estimates in plant diversity conservation projects.

Keywords: Specht's equilibrium relationship, evaporative coefficient k, relationships between k and projective leaf cover and species richness, relationship between projective leaf cover and species richness.

INTRODUCTION

Knowledge of the factors that predict species richness allows us to understand the functioning of ecosystems in relation to their stability under equilibrium conditions. Modern concepts of vegetation dynamics are based on resilience, resistance, and stability (Thompson *et al.*, 2009). A vegetation state is defined by the traits or

attributes of an ecosystem (species assemblage, functional roles, biomass, height, number of strata, etc.) and resilience refers to the ability of an ecosystem to return to its original state after a disturbance, maintaining its essential attributes, taxonomic composition, structure, ecosystem functions, and rates of processes (Holling, 1973). In the ecosystem perspective, ecological resilience is the ability of an ecosystem to withstand disturbances and reorganize to maintain its same functions, structures, and controls before reaching a threshold, where the ecosystem transitions to a different state (Zaccarrelli *et al.*, 2008, Roberts *et al.*, 2019).

Resilience is related to the concept of stability, in the sense that in the face of small perturbations it returns to the state of equilibrium or not within its operational limits, but it is not a dynamic characteristic of the response, but simply the magnitude of the response at a given time (Todman *et al.*, 2016). Ecological stability is the overall ability of a system to remain in the same domain of attraction (equilibrium) and retain its function and structure in the face of disturbances (Van Meerbeek *et al.*, 2021); it reflects the ability of an ecosystem to remain more or less within the same state, maintaining a dynamic equilibrium over time, while resisting a shift to a different state.

From the concepts discussed, in order to define equilibrium conditions of an ecosystem, it is necessary to have stability metrics, which is complex to define (Tilman, 1999; Thompson *et al.*, 2009). In relation to the stability of a system, May (1971) demonstrated that a random assembly of its components in systems is in general less stable than one associated with more complex assemblies. Elton (1958), in empirical and theoretical terms, argued that the stability of an ecosystem is roughly proportional to the number of links between species of a trophic level. In relation to multiple states in equilibrium, the work of May (1973 and 1977) at the theoretical level proposes that there are multiple alternative stable states when crossing disturbance thresholds.

With the use of resource competition models, Tilman (1982), Tilman *et al.* (1997) and Tilman (1999) proposed that productivity (biomass) increases with the number of species. In the case of competition for two resources, for example, water and nutrients, the pattern is the same as in the case of a single resource where, as the number of species increases, the resources are completely used, thus showing a saturation pattern. In an experiment on pasture plots, Tilman *et al.* (1996) showed that the number of species increases with the aerial cover of the vegetation, defining a specific relationship function, beyond the discussions between biomass and species richness.

Vilá *et al.* (2005) analyzed experimental evidence from forest systems, and proposed that there is a relationship between the number of species and productivity (biomass) of forests until before the closure of canopy cover given by the initial stages of succession or in forests with stress limitations, and then this relationship is modified by decline, if this occurs.

In general, species richness variability is best explained by water balance variables in warm, subtropical, and tropical regions, and energy variables such as evapotranspiration and energy fluxes are best at higher altitudes (Hawkins *et al.*, 2003). Plant water availability in 20 of 21 cases analyzed was a primary predictor of species richness. For

vertebrates and invertebrates, water and energy were the best predictors. In the case of reptiles (lizards) the best predictor was energy, but not in amphibians. Although several hypotheses have been put forward about the relationship between climate and species richness, the experimental evidence does not support any of them (Currie *et al.*, 2004). Collins (2010) suggests that the diversity of bird, mammal, amphibian, and reptile species has patterns related to Eo (water limitation) up to a certain level and then diversity does not respond to changes in Eo (energy limitation). Baldocchi (2005) proposed the existence of an inversely proportional relationship between the number of dominant plant species in plant communities with Ea/Eo, where Ea is the current evapotranspiration. The relationship between the total number of species with Ea/Eo shows much dispersion, unlike the case of the number of dominant species. Kirkman *et al.* (2001) defined an inversely proportional relationship between soil water potential and number of species, as well as a directly proportional relationship between aboveground biomass and number of species.

In a study based on an ecohydrological model, Eagleson (1982) proposed three hypotheses (ecological constraints) related to vegetation optimization under equilibrium conditions. The preliminary experimental evidence analyzed generated evidence in favor of the concept of climatic equilibrium (Eagleson and Tellers, 1982). The three hypotheses or constraints put forward by Eagleson (1982) are: a) at short time scales (within one or a few generations), vegetation canopy density will reach balance with climate and soil to maximize equilibrium soil moisture: minimum vegetation water stress; b) at long time scales (few generations), plant species will be selected on the basis of their potential transpiration efficiency resulting in maximum equilibrium soil moisture; and c) at very long time scales (landscape evolution), vegetation will alter soil physical properties toward equilibrium values, at which optimum foliage density will reach its maximum value.

The importance of Eagleson's (1982) proposal, regardless of the complexity of the model used, is that it proposes that the optimal foliage density of vegetation corresponds to the condition of maximum use of available water in the soil profile, which has been used to generate leaf area index (LAI) models with conditions of hydrological equilibrium: no underground water drainage, use of all the water infiltrated in the root depth of the vegetation (Ellis *et al.*, 2005). The use of vegetation optimization criteria reduces the complexity of models by defining constraints on their evolution (Eagleson, 1982), simplifying modeling schemes with minimal data. The optimization principle developed by Eagleson (1982) was stated in terms of the "vegetation carrying capacity considering soil water" (Xia and Shao, 2008; Fu *et al.*, 2012), which is equivalent to estimating the maximum IAF associated with a minimum stress level. This type of analysis was performed using coupled biophysical and hydrological models.

The objective of this contribution is to establish relationships between projective leaf cover, defined as the vertical projection of foliage on the ground, and plant species richness to facilitate its empirical use to characterize plant diversity in warm temperate ecosystems with easily measured variables. The relationship between water balance

and vascular plant species richness is analyzed with field data on species richness under conditions of no or low disturbance, in equilibrium conditions, in sacred fir forests on Monte Tláloc, State of Mexico.

MATERIALS AND METHODS

Plant balance

Specht (1972) proposed a model of plant balance with the atmosphere and water in the soil profile (flat topography):

$$\frac{Ea}{Eo} = S\,min + kW$$

$$W = P - Q - D + Sext \tag{1}$$

where *Smin* is the water storage in the root depth of vegetation not usable by vegetation, *k* is an evaporative coefficient (cm^{-1}) and *W* is the water balance, *Q* is surface runoff, *D* is subsurface drainage, and *Sext* is the water stored in the soil extractable by vegetation (at the beginning of the month). The soil stored water value (*Smax*) is between the field capacity value and the permanent wilting point. Precipitation *P* in excess of *Smax* is lost as subsurface drainage (D). The water balance values represent monthly data and balance is performed at the plot scale. The values of the variables in Equation (1) are in cm.

The behavior of Equation (1) is shown in Figure 1, where *Ea* is the current evapotranspiration and *Eo* is the potential evapotranspiration (atmospheric demand), and *Ea/Eo* has a maximum value of 1.0, a condition in which water is not limiting. In general terms, Specht's model proposes that water in the soil profile, coupled to the atmosphere-vegetation interaction, is the main limiting factor for the development of plant communities.
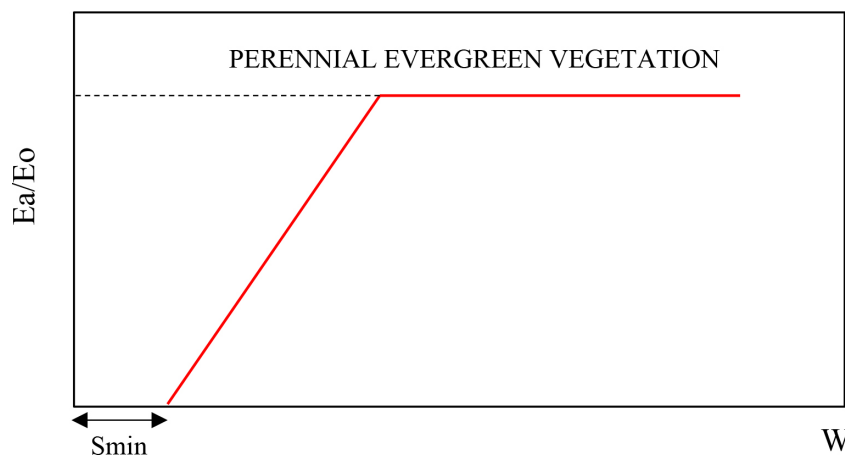

Figure 1. General Specht's model for non-climax evergreen perennial vegetation.

Specht (1972) proposed that stable evergreen perennial vegetation fully utilizes the available water, such that *Smin = 0* and *D = 0*:

$$\frac{Ea}{Eo} = kW \tag{2}$$

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

An apparent problem in the use of Specht's model is the need for plot-level information on water balance variables to determine k. Specht (1972) developed an iterative monthly balance algorithm using different *Sext* (and *Smax*) values to estimate k by converging under the condition that the vegetation uses all available water in the root depth such that *Sext* approaches zero, but never be equal, during the driest month of the year. This requires a minimum of three years of monthly *P* and *Eo* values as inputs. The iteration algorithm converges rapidly to the value of k, and is independent of the assumed value of *Smax*; except in very wet areas (Specht, 1972). Although Specht's model assumes a flat land condition, Specht (1972) discusses the consideration of the effects of different conditions in the algorithm for estimating k: slope and aspect of land topography, lateral water inputs, variation of *P* intercepted by foliage and flow over stems, variation of *Smax*, variation of root distribution, and variation of water distribution in the soil profile.

The coefficient k approaches by an evolutionary adjustment within the plant community to a maximum value close but never equal to zero. The assumption is that the stable community, in atmosphere-vegetation-soil equilibrium, fully exploits the available soil moisture for plant growth, so that roots must explore the soil to use all available water in any part of the soil profile.

Specht's model is similar to that of Eagleson (1982), but is based on empirical evidence and conceptual developments. An advantage of Specht's model is that the stability (and resilience) of a vegetation community can be characterized simply using *Smin*, so that the stable plant community is one with *Smin = 0*. In the case of nutrient limitation, Specht's model needs to be modified to consider a lower volume of available soil moisture.

If a plant community has a root distribution that does not explore the entire soil profile with available water, then it may be replaced by another community or different species composition, with roots that use all the water, becoming a stable community.

Plant succession towards stable communities proceeds in the direction of maximizing the evaporative coefficient k and minimizing *Smin*. Thus, the concept of plant "optimization", after considering the water resource as a critical factor becomes clearly operative.

In the case of the number of species and the composition of the plant community, the succession trajectory shows an increase in species richness in the process towards a

stable community. This is only one of the possible trajectories, since species richness and composition have a practically infinite number of combinations to achieve equilibrium or stable condition. This can be stated as:

Stable community = f (species, abundance)
Subject to:
Min(*Smin*) or Max(k) (3)

In the iterative algorithm for estimating k, the driest condition in a month, (where *Sext* tends to zero, but never equals it) determines the maximum foliage of the vegetation to adapt (survive) to the climate of the site. In this situation, although transpiration is small, it will continue during the year and simultaneously, there will be sufficient carbon fixation to balance the respiration of the entire plant community (Specht, 1972). In Specht's work, the projective canopy cover (*CPF*) of the plant community is divided into an upper stratum or *ES*, canopy cover = CPF_{ES}, and lower stratum or *EI*, canopy cover = CPF_{EI}. For communities dominated by tree species, the strata distinction is a height of two meters (Specht and Morgan, 1981; Specht and Specht, 1993; Specht and Tyler, 2010). In the case of shrublands, grasslands and crops, the separation between the upper and lower strata should use heights that reflect the partitioning of resources in the community (Specht and Morgan, 1981).

The most important structural feature of an evergreen (and deciduous) perennial plant community appears to be the distribution and orientation of 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 (mm^{-1}) (Specht, 1972). From these considerations, Specht (1972, 2008) proposed an empirical relationship between k and *CPF*:

CPF_{ES} = 9.770k - 7.15 (n = 54, R^2 = 0.95)
CPF_{EI} = 5.880k - 10.04 (n = 29, R^2 = 0.87) (4)
CPF_{T} = 15.350k - 5.80 (n = 29, R^2 = 0.93)

Specht *et al*. (1991) and Specht and Specht (1993) developed relationships between k (cm^{-1}) and species diversity in stable communities (S_T, number of species in both strata; S_{ES}, number of *ES* species):

Tropical Region ≥
In (S_T) = 2.19 + 34.79 k, (n = 20, R^2 = 0.94)
In (S_{ES}) = 0.92 + 40.02 k, (n = 29, R^2 = 0.98)

Subtropical Region ≥
In (S_T) = 2.54 + 28.10 k, (n = 15, R^2 = 0.91)
In (S_{ES}) = 0.01 + 45.90 k, (n = 9, R^2 = 0.93) (5)

Warm temprate Region $\geq$
In $(55 - S_T) = 4.55 - 64.23\ k,\ \ (n = 7, R^2 = 0.89)$
In $(S_{ES}) = 0.21 + 20.49\ k,\ \ (n = 16, R^2 = 0.71)$

In the case of the warm temperate region, *EI* makes up most of the community up to the humid climatic zone and then falls sharply as it is replaced by non-vascular plants (cryptogams).

The *CPF* of the upper stratum (CPF_{ES}) has a linear relationship with the average height of that stratum (Specht *et al.*, 2006) for non-wetland communities. With respect to wetlands, Specht (2009) showed that the percentage of annual precipitation retained in the soil is directly proportional to the height of the upper stratum.

Specht and Tyler (2010) show that the evaporative coefficient *k* has linear relationships directly proportional to the diversity of amphibians, snakes, small mammals, and birds by geographic region. Something similar happens in relation to the diversity of lizards, but with an inversely proportional relationship. The relationship between the number of plant and amphibian species shows linear patterns that are directly proportional and dependent on the climatic region. Amphibian diversity shows that the relationship with *k* is a function of soil nutrients (climatic regions).

In the case of small mammal diversity, Specht (2012) showed that the relationship with total vascular plant species richness (S_T) is linear and directly proportional, but dependent on climatic region. In the case of using S_{EI}, the relationship is unique.

The relationship between lower stratum species richness (S_{EI}) is linear and inversely proportional to CPF_{ES} (Specht and Morgan, 1981; Specht *et al.*, 2006).

Sampling data for analysis

The area studied is located on the western slope of Monte Tláloc, which is part of the northernmost region of the Sierra Nevada, in the municipality of Texcoco, State of Mexico. In this zone there are forests sacred fir [*Abies religiosa* (Kunth) Schltdl. & Cham.], in an altitudinal interval that goes from 3 100 to 3 500 m, in deep soils, of medium texture and rich in organic matter. Annual precipitation is 900 to 1000 mm and the mean annual temperature varies from 10 to 12 °C (Sánchez and López, 2005).

Location of sampling sites

The geographic location of the 30 sacred fir forest sampling sites considered in this study is shown in Table 1.

Site selection was not random due to the limitations imposed by accessibility. The locations selected were far from the main accesses to the forest, showing no evident signs of disturbance by fire, grazing or recent logging.

Two sampling campaigns were conducted, the first to define trends and the second for ratification. The 15 points of the first sampling were measured during May and July 2017, while the other 15 sites of the second sampling were measured from late September to early December 2018. The difference between the two samplings for annual species was not significant.

Table 1. Coordinates of the sampling sites in the oyamel forests of Monte Tláloc, State of Mexico.

Site	Longitude West	Latitude North	Altitude (m)
1	98° 45′ 01″	19° 26′ 38″	3318
2	98° 45′ 36″	19° 26′ 18″	3082
3	98° 45′ 13″	19° 26′ 01″	3296
4	98° 45′ 19″	19° 25′ 52″	3233
5	98° 45′ 19″	19° 25′ 57″	3232
6	98° 45′ 07″	19° 25′ 33″	3391
7	98° 45′ 52″	19° 25′ 47″	3398
8	98° 45′ 57″	19° 25′ 53″	3336
9	98° 44′ 54″	19° 26′ 31″	3374
10	98° 44′ 53″	19° 26′ 53″	3332
11	98° 44′ 39″	19° 27′ 03″	3264
12	98° 44′ 56″	19° 27′ 08″	3257
13	98° 45′ 11″	19° 26′ 59″	3222
14	98° 45′ 01″	19° 25′ 26″	3481
15	98° 45′ 07″	19° 25′ 46″	3372
16	98° 45′ 15″	19° 26′ 33″	3244
17	98° 45′ 24″	19° 26′ 28″	3194
18	98° 45′ 18″	19° 26′ 17″	3288
19	98° 45′ 11″	19° 26′ 11″	3333
20	98° 45′ 06″	19° 25′ 58″	3357
21	98° 45′ 09″	19° 26′ 46″	3247
22	98° 45′ 03″	19° 26′ 47″	3275
23	98° 44′ 47″	19° 26′ 01″	3484
24	98° 44′ 48″	19° 26′ 14″	3465
25	98° 44′ 40″	19° 25′ 55″	3540
26	98° 44′ 48″	19° 25′ 53″	3454
27	98° 44′ 45″	19° 25′ 45″	3455
28	98° 45′ 51″	19° 25′ 32″	3443
29	98° 45′ 39″	19° 25′ 18″	3409
30	98° 44′ 59″	19° 25′ 15″	3511

The sampling site was designed according to the PMC carbon and biodiversity inventory manual (2015). It was circular in shape and covered an area of 1000 m², it was in turn made up of four concentric circles of 400, 200, 100 and 12.56 m².

Species register

All vascular plant species present in each of the five concentric subunits of the sampling site were recorded, starting from the innermost circle (12.56 m²) to the outermost circle of 600 m². A photographic record was made of all taxa and only those in flowering or fruiting were collected using standard methods (Chiang and Lot, 1986). Cabinet taxonomic identification was carried out with the help of specialized literature.

The floristic composition (species, genera, and families) of the sampled sites was analyzed. The species catalog was taken with reference to the taxonomic classification system of angiosperms APG IV (APG, 2016). For the nomenclature of gymnosperms and pteridophytes, the Tropicos® world flora project of the Herbarium of the Missouri Botanical Garden (Missouri Botanical Garden, 2018) was consulted, which contains the most recent updates of taxonomic information concerning these types of plants.

Leaf projective coverage

Species richness has shown correlations with the development of plant cover, evaluated through its projective leaf cover (Specht and Specht, 1993; Specht, 1972; Specht and Specht, 1989). To evaluate these variables, the method developed by Salas *et al.* (2017) was implemented for the estimation of the forest cover fraction with the use of digital photography from its analysis with the Python 2.7 programming language and the Orfeo Toolbox (OTB) tool.

Estimation of aboveground biomass

At each 1,000 m^2 sampling site, data were collected by measuring the diameter at breast height (minimum diameter of 7.5 cm) of all the plants, and then estimating the aerial biomass using allometric equations for the species found.

Statistical analysis

The statistical analyses were simple comparisons and in the linear regressions the coefficient of determination was used as a metric of uncertainty.

RESULTS AND DISCUSSION

Derived from the graph presented by Specht and Specht (1989), regarding the relationship between CPF_{ES} and the total number of vascular species, Figure 2A shows the relationship and its limits.

Figure 2b shows the CPF_{ES} - S_T relationship for the first sampling sites (15), where the measured data adjust to the limits established by Specht and Specht (1989).

Estimates of the number of species by vegetation life form and by strata are shown in Table 2.

Figure 3 shows the relationship between CPF_{ES} with the species richness of the upper stratum (SES), where it is evident that there is a linear relationship, contrary to the non-linear relationship established using the CPF_{ES}-k and S_{ES}-k relationships.

Specht's equilibrium relationships assume an undisturbed condition of the vegetation, which is required to be verified at the sampling sites. Using a scale of levels from 1 to 3 (1 = little or no disturbance, 2 = medium, 3 = severe) of disturbance agents, Table 3 shows the assignments made for the 15 sites of the first sampling.

If sampling sites with a total value of disturbance agent reaches less than five, they are considered, Figure 4 shows the relationship between aboveground biomass in dry matter (M.S.) and the total number of species, in which a linear relationship is observed, which agrees with the results by Esparza *et al.* (2019) and Paz *et al.* (2022).
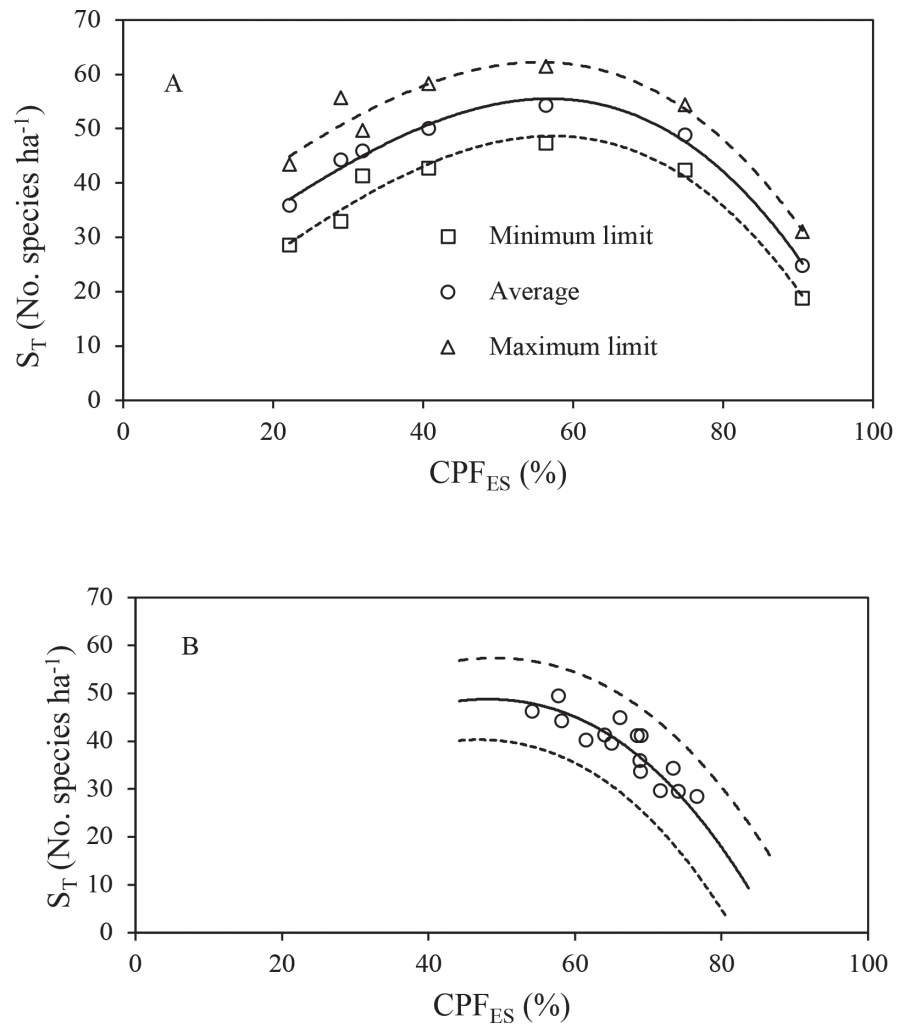
Figure 2. Relationships between CPF_{ES} - S_T for: (a) vegetation for the warm temperate region, and (b) the sacred fir forests, first sampling, of Monte Tláloc, State of Mexico.

The relationship between CPF_{ES} and the total number of species (S_T) for the totality of samples is defined in Figure 5A, which is similar to the case of the first sampling sites. In general, the relationship of Specht and Specht (1989) is adequately represented within its limits of variation, with the information from the sacred fir forest sampling sites of Monte Tláloc.

If total disturbance agents are less than or equal to 2 (minimum disturbance), they are considered, Figure 5B shows the relationship between CPF_{ES} and S_T.

Disturbance agents affect the dispersion of observed patterns, but do not modify trends, implying general conditions of equilibrium.

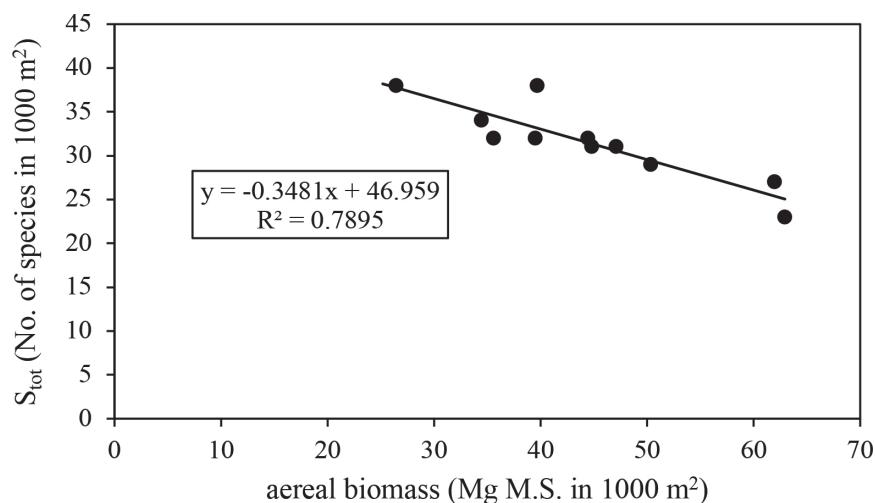**Table 2**. Number of species by life form and strata of sampling sites.

Site	CPF_{ES}	Trees	Shrubs	Woody plants	Herbaceous perennials	Herbaceous annuals	Herbaceous	Upper stratum species	Lower stratum species	Total species
1	74.1	2	11	13	8	1	9	6	16	22
2	64.0	4	20	24	6	2	8	8	24	32
3	71.7	1	11	12	7	4	11	5	18	23
4	68.5	2	16	18	12	3	15	7	26	33
5	61.5	2	11	13	12	7	19	7	25	32
6	73.5	3	10	13	13	2	15	6	22	28
7	69.0	2	12	14	11	2	13	6	21	27
8	69.1	2	11	13	13	5	18	6	25	31
9	65.0	2	9	11	14	6	20	**6**	25	31
10	66.2	2	13	15	13	4	17	6	26	32
11	54.2	2	11	13	15	10	25	**8**	30	38
12	58.2	4	17	21	9	4	13	9	25	34
13	57.7	4	17	21	13	4	17	8	30	38
14	76.7	1	6	7	13	3	16	4	19	23
15	68.9	2	12	14	12	3	15	6	23	29
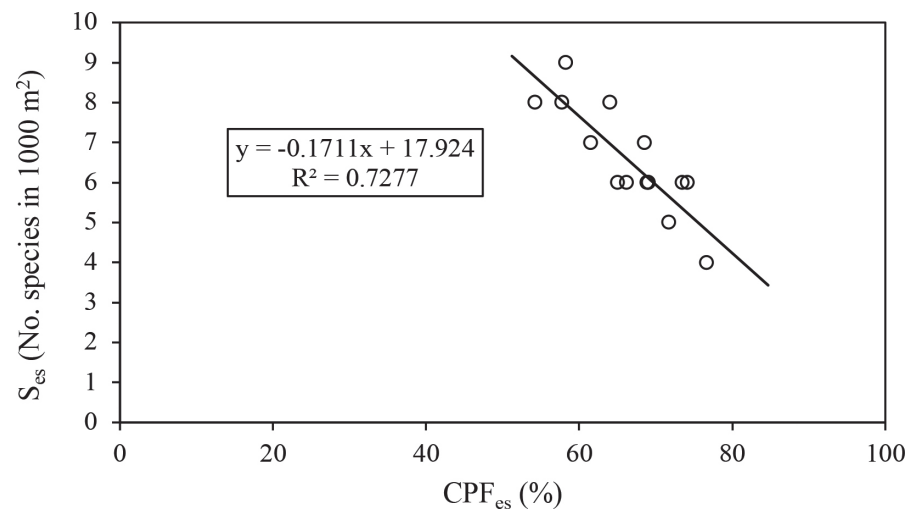
Figure 3. Relationship between CPF_{ES} - S_{ES} for oyamel forests, first sampling, Monte Tláloc, State of Mexico.

Table 3. Levels of disturbance agents in the first sampling sites on Monte Tláloc, State of Mexico.

Site	Sick, dead standing or fallen trees due to wind and ground inclination	Time of last use	Stumps	Firewood	Forestry work	Nearby sidewalks	Nearby main road	Total
1	0	2	3	2	0	1	0	8
2	0	0	0	0	1	2	0	3
3	0	1	2	0	0	1	1	5
4	0	1	2	1	2	1	0	7
5	0	0	1	0	0	1	0	2
6	4	1	1	1	1	0	0	8
7	0	0	1	0	0	2	0	3
8	0	0	1	0	0	1	0	2
9	0	1	0	0	0	1	1	3
10	0	1	1	0	0	1	0	3
11	1	0	0	0	0	1	0	2
12	0	0	1	1	1	1	0	4
13	0	0	0	0	1	1	1	3
14	0	0	2	0	0	1	1	4
15	0	1	1	0	0	1	0	3

Figure 4. Relationship between aboveground biomass and total number of species for the first sampling sites.

The assessment of species richness requires taxonomic knowledge, which implies sources of error in the estimates (Sánchez *et al.*, 2021), as well as time and resources. The use of indirect variables, such as projective leaf cover, facilitates the estimation process.
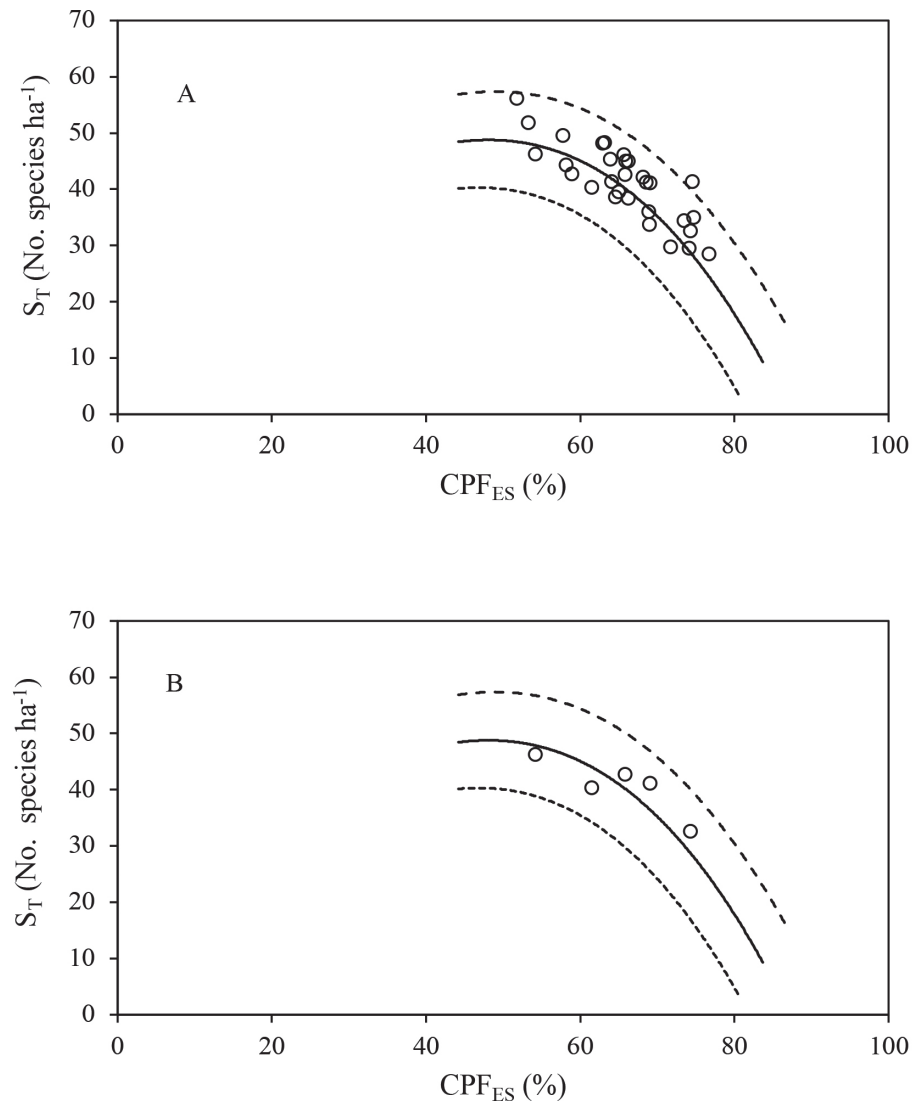
Figure 5. Relationships between CPF_{ES} - S_T for: A oyamel forests, all samples, of Monte Tláloc and B oyamel forests, all samples, with total disturbance agent levels ≤ 2.

Specht's vegetation equilibrium theory establishes relationships between the soil water balance and the atmospheric demand, represented by the evaporative coefficient *k*. From the relationship between *k* and *CPF* and *k* and species richness (*S*), non-linear relationships can be established between *CPF* and *S*, although only for the case of stable communities. The projective leaf cover is the variable that adequately considers the water-atmosphere interaction (Specht *et al.*, 2006).

Data from the *S* and *CPF* sampling sites were used to review the relationships established by Specht, finding that the patterns of the measurements agree with

Specht's limits, although disturbances associated with the measurement sites may represent non-stable vegetation manifested by variations in the defined patterns. The variations between the ratios of the projective foliar cover of the upper stratum (CPF_{ES}), with the total number of species S_T and the number of species of the upper stratum S_{ES}, show dispersion of data within the limits established by Specht's relationship.

CONCLUSIONS

The results obtained for Specht's relationship between projective leaf cover and species richness were congruent with the limits of this relationship, ratifying the general patterns, independently of the sites where the relationship was established.
The levels of disturbance agents at the sampling sites in the oyamel forests represented a dispersion of the data within the limits of Specht's relationship.

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