

Research Article

Spatial Patterns of *Ceroxylon parvifrons* (Engel) H.Wendl of the Montane Forests in Southern Ecuador

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The species of the genus *Ceroxylon* have narrow geographical ranges, and subsequently, their populations are subjected to a high degree of fragmentation due to deforestation and land conversion. *Ceroxylon parvifrons* (Engel) H. Wendl is a representative floristic species of the Andean rainforest; however, little information related to its natural history, ecology, biology, and conservation status is available, making it difficult to assess its biological relationship with the environmental factors and the current status of their populations in natural environments. Here, we studied the spatial pattern of adults, rosettes, and seedlings of *C. parvifrons* in the montane rainforest and assessed the role of populations' spatial structure and intraspecific interactions on plant performance. A total of 460 individuals were categorized according to their size, with 11 adults, 10 juveniles, 336 rosettes, and 103 seedlings being recorded. *C. parvifrons* showed that the population is expanding during the first two stages of the plant (seedling and rosette). After this, there is a significant decrease where the frequency of individuals of the juvenile and adult categories tend to disappear from the population. The $L(r)$ function shows a robust clustering throughout the entire scale for seedlings, rosettes, and adult palms. Also, the Poisson cluster process describes a patchy distribution in which plant individuals are distributed in clumps (clusters). Thus, this approximation related to spatial patterns of *C. parvifrons* will provide an important step for the conservation of this species in tropical zones.

1. Introduction

Species of the genus *Ceroxylon* have narrow geographical ranges, and subsequently, their populations are exposed to a high degree of fragmentation due to deforestation [1]. Deforestation is currently one of the main factors explaining the significant reduction of natural *Ceroxylon* spp. In some cases, populations have been reduced to small forest remnants, whereas in others, they have reached their extinction [2, 3]. The *Ceroxylon* genus is endemic to the Andean mountains, encompassing approximately 12 species [4, 5]; however, their persistence is seriously threatened by the uncontrolled leaf harvesting for the Palm Sunday celebration [1, 6, 7].

Ceroxylon parvifrons (Engel) H. Wendl is a representative floristic species of the Andean rainforest. *C. parvifrons* is distributed from Venezuela to Peru and is also found in Colombia, Ecuador, and Bolivia between 2100 and 3500 m.a.s.l. [4]. In Venezuela and Colombia, *C. parvifrons* is listed according to IUCN criteria as endangered and near threatened, respectively [8, 9]. In Ecuador, this species is listed as vulnerable [10].

Previous studies have documented that species of the genus *Ceroxylon* have spatially restricted dispersion of its seeds (low removal rates and short dispersal distances), which is identified as one of the limitations in their recruitment. Thus, dispersal processes condition the formation

of an aggregate pattern in tropical zones [11–14]. Nonetheless, several factors such as selective management, age of forest disturbance, and dense-dependent factors can influence a clustered distribution [13].

Population studies have been conducted for some *Ceroxylon* species [15]. For instance, in Bolivia, the population status, exploitation, and commercialization chain of *Ceroxylon pityrophyllum* Mart. ex H. Wendl. have been studied [16]. In Ecuador, the population structure of *Ceroxylon echinulatum* Galeano and *Prestoea acuminata* (Willd.) H. E. Moore has also been documented [17]; however, to date, the population structure and spatial distribution of *C. parvifrons* have not been documented. On the other hand, the distribution of *Ceroxylon* palms is influenced by both small and large-scale environmental factors [13] and by dispersal processes [18]. Thus, an idoneous way towards understanding ecological processes is to identify spatial patterns (SP) [19] since most of the mechanisms acting upon plant populations and communities are related to their spatial structure [20]. Spatial patterns have been widely employed to understand processes in the dynamics of plant species [21]. Also, the plants are considered the result of the interactions among environmental factors, plant characteristics, and intraspecific or interspecific interactions between plants [22]. They can also be identified as the result of subjacent ecological processes [23] and negative dense-dependence processes, among others, with greater evident spatial signals [24]. These processes would reduce the aggregation between conspecifics, particularly during the early stages of the plants, when seedlings or juveniles are located in the vicinity of the mother plant at high density [25]. Thus, studying spatial distribution requires the most commonly used methods in the praxis based on point patterns, i.e., data sets that include the spatial location of individuals or plants and marks or covariates associated with individuals [26]. With this baseline information, summary functions such as Ripley's K-function or the pair correlation function (g) are used, based on analyzing the distance between pairs of points as well as the description of spatial relationships at different scales [22, 27]. These methods allow typifying point patterns and identifying processes that generate clustering of plants in spatial distribution that may be the result of limited dispersion and the effect of environmental heterogeneity [29].

Thus, the main purpose of this study was to determine the population structure and spatial distribution of *C. parvifrons* individuals in a tropical montane forest fragment in Southern Ecuador. We also aimed at answering the following questions: (1) does environmental heterogeneity affect the formation of the spatial pattern of each class? and (2) do spatial patterns of *C. parvifrons* vary with ontogeny?

2. Materials and Methods

2.1. Study Area. The study was conducted in a fragment of tropical montane forest "Aguarnudas," located in the southern region of Ecuador, Saraguro, Loja Province (03°39'37" S 79°08'17" W, 2800–3300 m a.s.l.), with an

approximate area of 429 ha (Figure 1). The climate is tropical-humid with an average annual rainfall of 1250–1500 mm and an average annual temperature between 10 and 12°C (Meteorological Station "Saraguro").

2.2. Experimental Design and Data Collection. We conducted a complete census of all *C. parvifrons* individuals. We coded each individual and also categorized them based on their size (height in m), and we divided according to four size categories as follows: seedling (0.1–0.50 m), rosette (0.51–5 m), juvenile (5.1–8 m), and adult (8.1–15 m). We mapped all *C. parvifrons* plants in this study forest using a Leica total station, model TS02-5power with a precision of <5 cm.

2.3. Spatial Analysis. For the spatial analysis, we considered three categories: adult, rosette, and seedling. In this study, the adult category consisted of all individuals >8 m to reach the minimum number of 20 individuals and obtain a representative spatial pattern [28]. Spatial patterns of *C. parvifrons* were analyzed using the univariate Ripley's K-function [27, 30] and the bivariate pair correlation function [22, 30]. The pattern of homogeneous points was denoted by the intensity of the pattern λ . We used the linearized estimator to facilitate the spatial pattern type interpretation as a distance function $L(r) = \sqrt{K(r)/\pi}$ [31]. The pair correlation function $g(r)$ is related to the derivative of the K-function, i.e., $g(r) = K'(r)/(2\lambda r)$, and it is defined as the expected number of points at an approximately equal distance to r from an arbitrary point, divided by the intensity of the pattern [30]. In addition, we used the K-inhomogeneous function [$K_{inhom}(r)$] to quantify environmental heterogeneity. To construct the K-function, we assumed that the observed pattern is generated by a two-step process [32], where an originally homogeneous pattern is refined according to a surface area $\lambda(x)$, which only depends on the spatial location. This surface describes the environmental heterogeneity and is proportional to the intensity of a two-step process. Thus, the inhomogeneous K function was calculated as a homogeneous K but pondering each point by $1/\lambda(x)$ [33]. If the pattern was homogeneous or Poisson inhomogeneous, with intensity function $\lambda(u)$, then $K_{inhom}(r) = \lambda r^2$, and $L(r) = L_{inhom}(r) = 0$, i.e., graphically, the L-function should be a horizontal line. Empirical K functions were estimated using an isotropic Ripley edge correction [34], and they were calculated up to a distance of $r = 300$ m.

2.3.1. Characterization of the Spatial Pattern of Adults, Rosettes, and Seedlings. To characterize the aggregated patterns as effects of limited dispersal, we fit a Poisson cluster (PC) process using the minimum contrast method. A PC process describes pattern formation as a two-step process: first, a homogeneous Poisson pattern of "parents" points is generated with intensity ρ [57]. Then, each parent point produces "descendants" that are distributed according to the Poisson law, and their locations are independent and normally distributed around each parent, with zero mean and

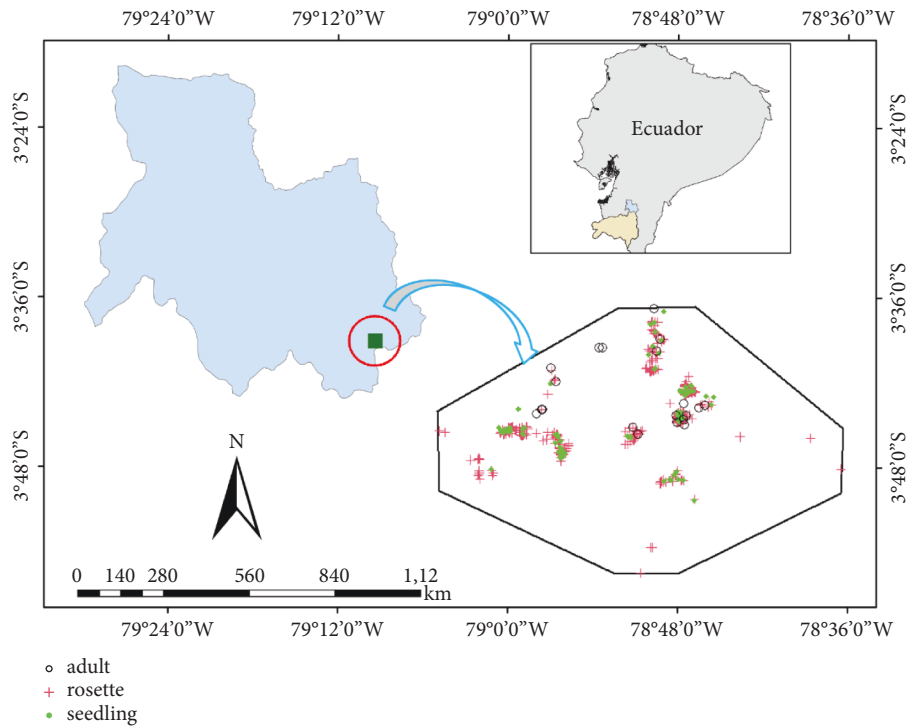


FIGURE 1: Site of study (Aguarnudas montane forest, Saraguro).

deviation σ . Estimations of ρ y σ will serve to measure the magnitude of aggregation as well as identify possible differences between populations and classes of states [35]. We analyzed the spatial pattern of individuals in each of the stages (seedling, rosette, and adult) of *C. parvifrons* using the univariate function $L(r)$ and compared it to a homogeneous Poisson null model with 399 Monte-Carlo simulations.

2.3.2. Differences in Aggregation and Spatial Relationships between Classes. We employed a null model of random labeling within a case-control design to test whether the strength of aggregation varies between classes (adult-seedling, adult-rosette, rosette-seedling; Lara-Romero et al., 2017 [57]). This model assumes that cases are aleatory subsets of the population composed of cases and controls [33]. We used seedlings as cases and compared them to adults and rosettes (controls). The rosette class was also considered as a case when compared to the adult. To identify if clustering changed with the stage of the plant, we compared differences of pair correlation functions $g_a - g_p$, $g_s - g_p$, $g_a - g_s$. To test if the seedling pattern was significantly associated with the adult pattern, we employed the differences $g_a(r) - g_p(r)$, which have an expected value of zero under random labeling, where subscript a denotes adult individuals and p denotes seedling individuals. Thus, if $g_a(r) - g_p(r) = 0$, for adults were surrounded by the same density of adults and seedlings at the same time [25], illustrating equality in habitat utilization by the two classes. Negative deviations indicated the attraction of seedlings to adults, while positive deviations indicated segregation between adults and seedlings [33]. A value of

$g_p(r)g_a(r) > 0$ demonstrated the existence of additional aggregation mechanisms within seedlings independent of adults [33].

It is crucial to be able to differentiate the effects of clustering, which may be attributed to dispersal processes or interactions, or also to the effects of environmental heterogeneity, to understand the mechanisms of species distribution and coexistence. In tropical forests, plant aggregation at large scales (>50 m) was interpreted as the effect of environmental heterogeneity, and at small scales, it is thought to be a response to interactions between plants [36, 37].

The edge effect was rectified using Ripley's isotropic method [34]. The observed and expected patterns (null) were compared utilizing envelopes from 399 Monte-Carlo simulations with the corresponding goodness-of-fit test (GoF-test) [38, 39]. All calculations were executed using R 4.0.3 software [40] and the packages "spatstat" [41] and "ecspa" [42].

3. Results

3.1. Population Characterization of *C. parvifrons*. A total of 460 individuals of *C. parvifrons* were identified in the study area, which included 10 adults, 11 juveniles, 336 rosettes, and 103 seedlings. The corresponding population structure of the individuals shows that the population is expanding during the first two stages of the plant (seedling and rosette). After this, there is a significant decrease (chi-square test $X^2 = 615.88$, $df = 3$, $p < 0.0001$) where the frequency of individuals of the juvenile and adult categories tend to disappear from the population.

3.2. *Analysis of the Spatial Patterns of C. parvifrons in the Adult, Rosette, and Seedling Categories.* L (r) functions show robust clustering throughout the entire scale both for seedlings and rosettes (Figures 2(a) and 2(b)) and for adult palms (Figure 2(c)), thus rejecting the hypothesis of the randomness of the pattern (GoF-test, $p < 0.0001$, Figure 2).

3.3. *Evaluating the Effect of Environmental Heterogeneity.* After including the effect of environmental heterogeneity (inhomogeneous L-function) in the null model, the pattern of adults fitted most scales, except in the range of 50–10 m (Figure 3(c)). However, the pattern of seedlings and rosettes did not fit the heterogeneous process in most of the distances (Figures 3(a) and 3(b)) (GoF-test, $p < 0.001$), which suggests that heterogeneity affects more in the final stages of the plant.

3.4. *Evaluating the Effect of Limited Dispersion.* The Poisson cluster process describes a patchy distribution in which plant individuals are distributed in clumps (clusters). The number of estimated clusters was 6, 6, and 9 for seedlings, rosettes, and adults, respectively. On the other hand, the estimated cluster's average radius was 47 m, 52 m, and 3 m for seedlings, rosettes, and adults, in that order. According to medium cluster size, the pattern was more clumped for seedlings than adults and rosettes. Adult individuals of *C. parvifrons* were less aggregated than expected by a Poisson cluster process on scales of 0–50 m (Figure 4).

3.5. *Differences in Aggregation and Spatial Relationship between Seedlings, Rosettes, and Adult Plants.* Differences $g_a - g_p$, $g_s - g_p$, $g_a - g_s$, with the random labeling null model showed that seedlings, juveniles, and adults of *C. parvifrons* presented similar aggregation at all scales (GOF p value > 0.05 , Figures 5(a), 5(d), and 5(g)). The $g_p - g_a$ difference differed significantly from the null model of random labeling up to $r = 50$ m (GOF p value < 0.0001), stating strong seedlings segregation, i.e., seedling clustering is independent of the adult individual pattern. Seedlings surround adults at the same intensity as adults surround each other (GOF p value = 0.19202, Figure 5). Similarly, rosettes surround adults and seedlings surround rosettes. Nevertheless, seedlings tend to separate from adults, more than would be expected by random labeling, i.e., the pattern of seedlings is aggregated regarding the pattern of adult plants.

4. Discussion

C. parvifrons populations showed a clustered spatial distribution, as shown by the Poisson cluster process model which incorporates the effect of limited dispersal [43, 44]. Thus, aggregate patterns probably correspond to distances between nearby clusters [45], where adult individuals showed clusters more numerous at short distances. In this scenario, species that regenerate in patches or aggregates have recruitment of seedlings apparently adaptable to the

intense competition with the progenitor individuals. Rimachi and Oliva [46] showed an aggregate pattern for *C. parvifrons* in tropical forests of Perú. Following this pattern previous studies have shown an aggregate pattern in the wax palm in tropical zones [11–14].

A possible cause of this pattern at small scales is related to the fraction of seeds that settle around the parent for dispersal processes. Similarly, Cabrera and Wallace [47] showed that in a tropical forest, aggregate patterns in palm trees are related to the low dispersal and predation of seeds. Nanami et al. [48] proposed that small dispersal distances could explain the aggregate pattern. We found many seeds in the surrounding adults, which possibly gave rise to seedlings and rosettes and also possibly gave rise to seedlings and rosettes at short distances. This observation suggests that earlier life stages can exploit more of the available space than higher ones [33], due to that, a plant's increase in size and biomass and the effects of competition for resources begin to be noticed, and only the dominant individuals become established.

We also observed a few aggregated populations in sites where falling trees have caused clearings related to specific topographic and edaphic factors [13, 49–51]. As shown here, *C. parvifrons* exhibited that the populations' environmental heterogeneity effect related inversely to the plant stage, where seedlings are affected on a larger scale (> 200 m) and adults on a smaller scale (> 100 m).

The demographic structure of *C. parvifrons* showed an increasing pattern due to the higher number of rosettes and seedlings recruited to the next stage, or age class, under natural conditions. The difference in aggregation between recruits and adults suggests that recruits and rosettes are subjected to self-thinning once established. Thus, adults were less aggregated than rosettes, probably due to the impact of mortality in the transition from rosette to adult and the impact of excessive palm leaves' harvest. In this context, Borchsenius and Moraes [1] show that *Ceroxylon* palms are mostly used for ceremonial purposes on "Palm Sunday" at the moment. Unfortunately, leaf harvest is not performed appropriately. For instance, immature leaves are harvested from juvenile individuals who have not yet developed a trunk and produce approximately two new leaves per year. Further harvesting causes a decrease in the crown of leaves and consequently the death of the individual if it persists over time. Similarly, previous studies have shown that *C. alpinum* DC., *C. pityrophyllum*, and *C. quindiuense* (H.Karst.) H.Wendl. palm populations are affected by the amount of leaf harvest [16, 52, 53].

On the other hand, several species of the *Ceroxylon* genus have narrow geographical ranges, and their populations undergo a high degree of fragmentation [1, 54, 55]. Thus, habitat fragmentation and the impact of excessive palm leaves' harvest are modifying the population structure of *C. parvifrons* directly. This is probably why there are so few adults. In this context, Cayuela et al. [56] emphasized that habitat fragmentation affects each species in a different way and intensity and that this will depend directly on the species' characteristics, requirements, and sensitivity.

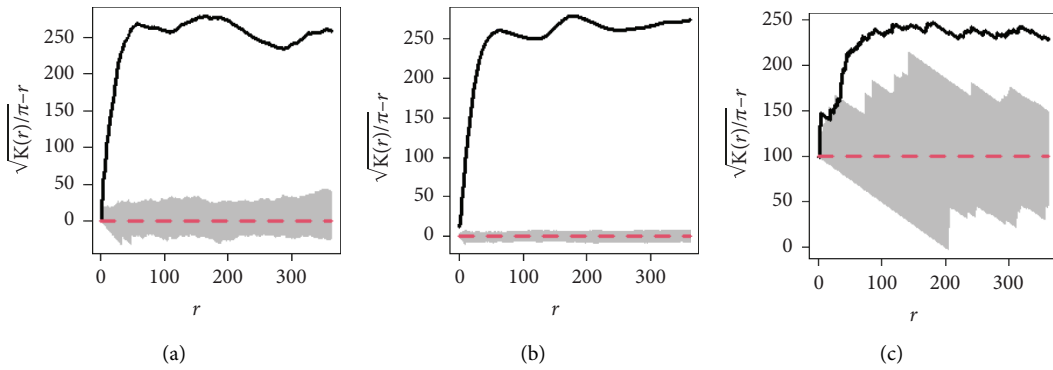


FIGURE 2: $L(r)$ functions of *C. parvifrons* compared to a homogeneous Poisson null model, (a) seedlings, (b) rosettes, and (c) adults. The solid black line represents the homogeneous $L(r)$ function observed in each case. The gray region represents the envelopes obtained by the simulation of the null model, and the dotted line represents the expected value of the null model (homogeneous Poisson process).

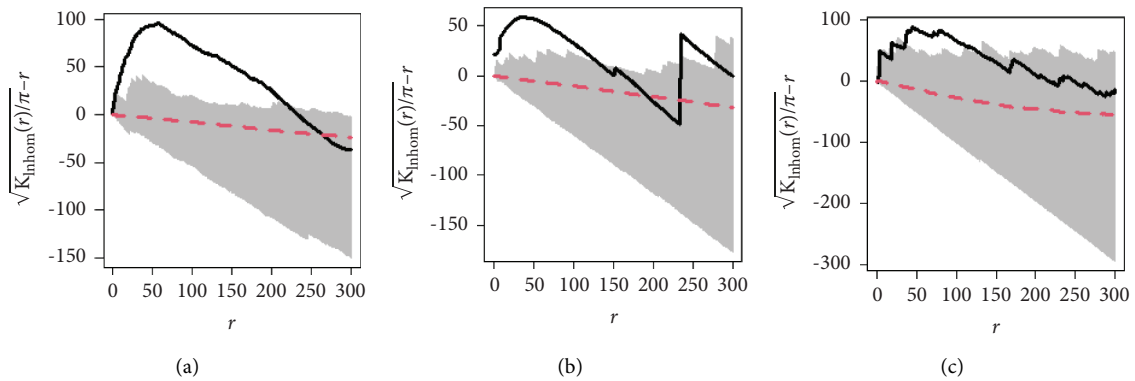


FIGURE 3: L-functions compared to an inhomogeneous Poisson null model, with estimated intensity through Gaussian kernel. (a), (b), and (c) as in the previous figure.

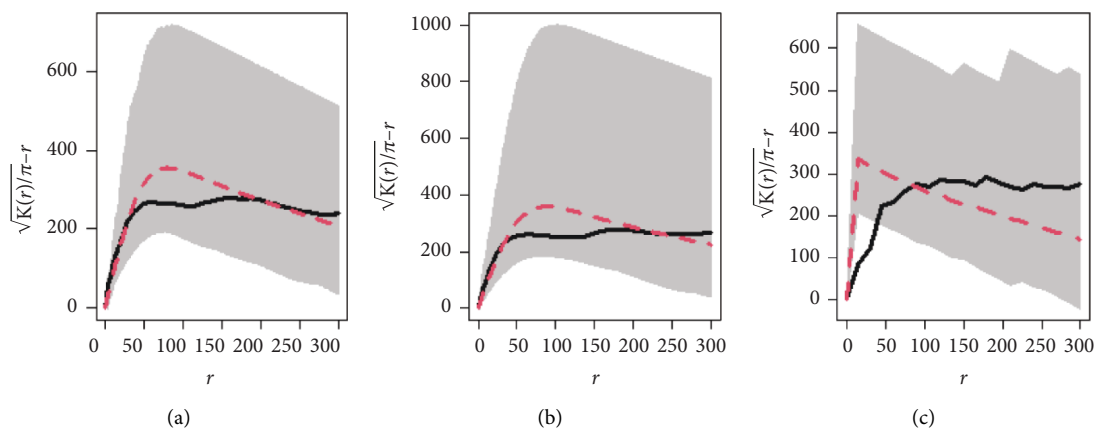


FIGURE 4: Spatial distribution of (a) seedlings, (b) rosettes, and (c) adults of *C. parvifrons*. Patterns contrasted with the null Poisson cluster (PC) model using Ripley's K function. The gray region represents simulation envelopes constructed using 399 simulations of the PC process. The solid and dotted lines indicate the observed and expected patterns, respectively.

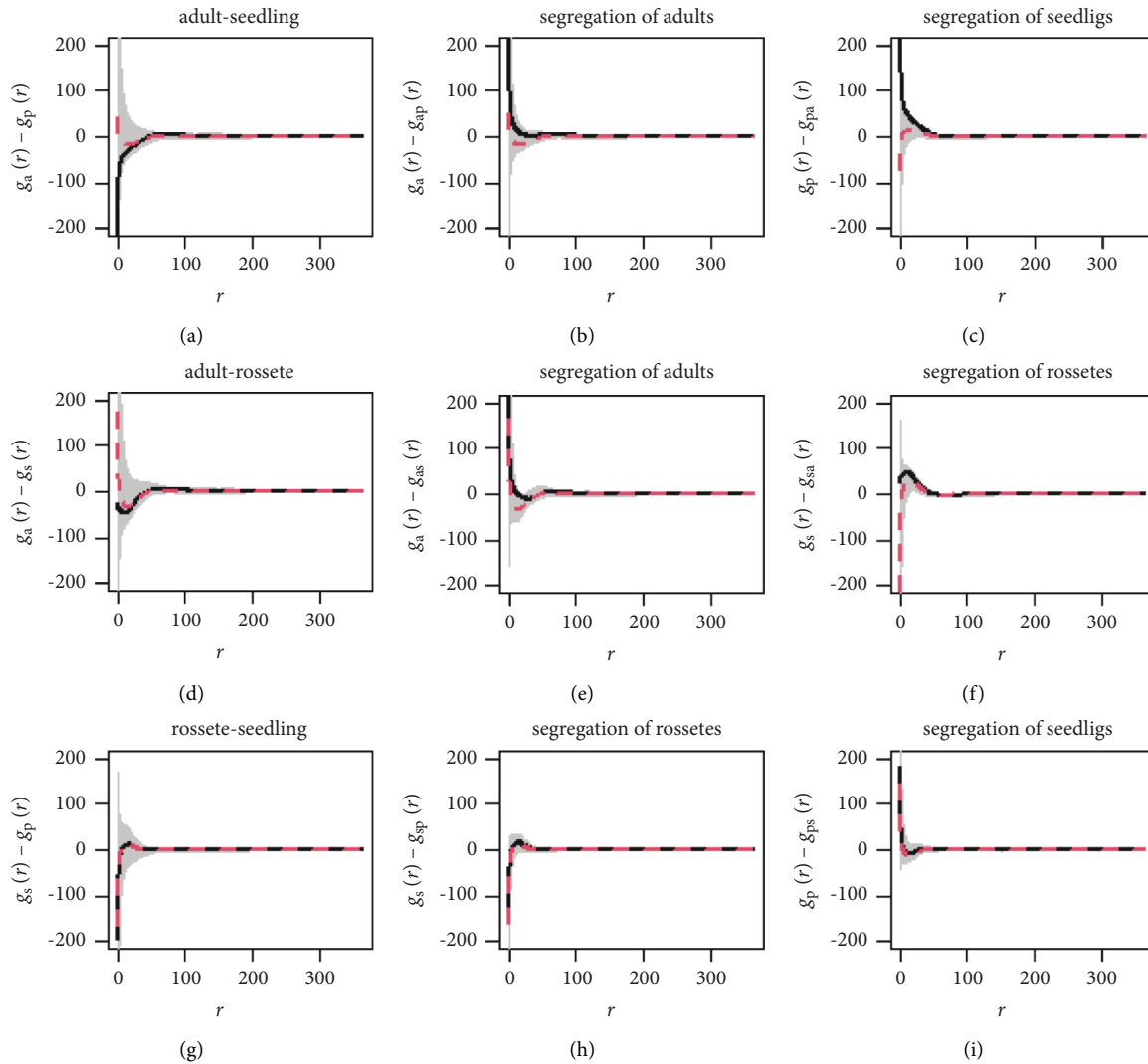


FIGURE 5: Differences in the aggregation strength of seedlings to rosettes and adults and analysis of the relationship between stages. The figure illustrates differences between the pair correlation function $g(r)$ using a randomly labeled null model, where subscripts “p,” “s,” and “a” represent seedlings, rosettes, and adults of *C. parvifrons*, respectively. Simulation wraps (gray region) were constructed employing 399 simulations of the random labeling model. Solid and dotted lines denote the observed and expected patterns, respectively. (a) Adult-seedling, (b) segregation of adults, (c) segregation of seedlings, (d) adult-rosette, (e) segregation of adults, (f) segregation of rosettes, (g) rosette-seedling, (h) segregation of rosettes, and (i) segregation of seedlings.

5. Conclusion

In conclusion, the results presented here support the idea that *C. parvifrons* population expands during the first two stages of the plant life cycle (seedling and rosette). We also found that *C. parvifrons* seedlings remain aggregated in clusters, while rosettes and adults separate from each other, which suggests a modification of their pattern of distribution and density throughout the available space. Apart from the impact caused to *C. parvifrons* adult populations by human harvesting for ceremonial purposes, a self-thinning mechanism also seems to be responsible for this segregation pattern. This conclusion is the result of the combination of the statistical analyses performed. Thus, this methodological approach can be considered a valuable and robust tool that will allow an adequate management and conservation of the

species. To the best of our knowledge, this is the first study of its kind concerning an endangered species in the Ecuadorian mountain forests.

Data Availability

The data are freely available within the manuscript.

Conflicts of Interest

The authors declare no conflicts of interest.

Authors' Contributions

Ángel Benítez, Pablo Ramón, Martha Sarango, Esteban Torracchi-Carrasco conducted conceptualization,

methodology, validation, investigation, and data curation; they analyzed the data, wrote the original draft, and conducted writing, review, and editing.

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