Distributions of *Galipea trifoliata* (Rutaceae) and *Pausandra trianae* (Euphorbiaceae) in a Disturbed Region of the Peruvian Amazon; Testing the Janzen-Connell Explanation for Rarity with Two Common Amazonian Trees

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Abstract

The diversity of plants in tropical forests is a complex ecological phenomenon that is inextricably linked to the recruitment rates and life history traits of plant species. The Janzen Connell (J-C) hypothesis is one of the most prominent ecological hypotheses relating to the survivorship of seedlings. It posits that the survival rates of seeds and saplings increase as the distance from a conspecific, reproductive adult increases because seeds and saplings may be able to escape the impact of any specialized pathogens and herbivores which plague the parent plant. This model is particularly applicable to rare species, which have a greater sensitivity to species-specific pathogens. This study, however, explores the extent to which two common species of trees in the southwest Peruvian Amazon -- *Galipea trifoliata* Aubl. (Rutaceae) and *Pausandra trianae* (Müll.Arg.) Baill. (Euphorbiaceae) – provide empirical evidence for the J-C hypothesis in a disturbed forest. Samplings were conducted at Finca Las Piedras, a field station located on the edge of a terra-firme forest in an area that was selectively logged 25 years ago - logging and fragmentation throughout the Amazon in the last decades have changed forest dynamics due to the creation of edge effects and light gaps following the removal of large trees. The density of adults and the spatial distribution of saplings were measured. Here we show that the J-C hypothesis may be selectively applied to certain common species; *P. trianae* supported the veracity of the J-C model; results for *G. trifoliata* indicated the opposite - that sapling distribution does not follow any such pattern. These results contradict the expectation that common species, unlike rare species, do not often manifest specific distribution patterns in relation to their parent plants. Both study species are early successional species crucial to reestablishing forest cover. By studying the ecology of prevalent flora, this paper will shed light on the community dynamics of a regenerating forest.

Introduction

The Janzen Connell (J-C) hypothesis is one of the most prominent hypotheses describing the diversity of plants in tropical forests. It posits that the survival rates of seeds and saplings increase as the distance from a conspecific, reproductive adult increases. This is likely due in part to the fact that seeds and saplings are able to escape the impact of specialized pathogens and herbivores which plague the parent plant. The J-C hypothesis is crucial to understanding forest dynamics, particularly the diversity of tropical forests, as it brings to light the concept of negative density dependence (NDD). NDD is particularly applicable to rare species, as these have been found to have greater sensitivity to species-specific pathogens than common species (Comita et al., 2014). Common species, however, can serve as a conspicuous study group due to their high abundance, and can be used to characterize species-specific traits such as NDD. NDD may not, in fact, be strictly a prominent characteristic of rare species.

Logging and fragmentation throughout the Amazon in the last decades have changed forest dynamics due to the creation of edge effects and light gaps following the removal of large trees. Selective logging is the primary cause of forest degradation in the Amazon, and logging rates are rising rapidly in the world's tropics (Asner et al., 2005) This study took place in the Madre de Dios region of Peru, a hotspot for extractive activities including gold mining, logging, Brazil nut harvesting, and agriculture (Goodman, n.d.). The forest plot used in this study can be characterized as disturbed forest, as an abandoned logging road runs through it.

This study explores the extent to which two common species in the southwest Peruvian Amazon -- *Galipea trifoliata* Aubl. (Rutaceae) and *Pausandra trianae* (Müll.Arg.) Baill. (Euphorbiaceae) – provide empirical evidence for the J-C hypothesis in a disturbed forest. This preliminary assessment will supply a basis for understanding the ecological tendencies of common species in a non-pristine forest, which are not expected to exemplify any strong negative density dependence (Comita et al., 2014). Understanding the spatial distribution patterns of common species that do well in disturbed forests could elucidate the community dynamics of regenerating forests. Such information will be increasingly relevant as Madre de Dios faces ongoing environmental pressures. Ultimately, this study will contribute to understanding the applicability of a prominent ecological theory.

Methods

Study Site

This study takes place in Madre de Dios, Peru, at the Finca Las Piedras (FLP) Research Station (-12.2263°, -69.1126°). The station is located on the edge of a terra firme tropical moist forest. The area was selectively logged around 25 years ago and it is currently under protection by the NGO Alliance for a Sustainable Amazon. For this reason, we classify the forest as disturbed. The surrounding area is composed of mainly Brazil nut concessions, selectively logged forest, agricultural fields and cattle pastures, making it an ideal location to study the dynamics of a regenerating forest.

This study utilizes a 1-hectare permanent forest dynamics plot at FLP (see Table 1). The 1-hectare plot is divided into 100 subplots, each 10m x 10m. All stems ≥10cm diameter at breast height (DBH) were mapped, tagged, measured and identified to the species level as part of ongoing research on plant ecology in non-protected areas (R. Fortier, personal communication, July 15, 2021). For the purpose of the study, only data on the species of interest were retrieved.

Table 1: Chart indicating the GPS coordinates of the 1-ha plot.

	Latitude	Longitude
NW	-12.22634°	-69.11033°
NE	-12.22617°	-69.10929°
SW	-12.22713°	-69.11014°
SE	-12.22705°	-69.10924°

Study Species

The two species of interest -- *P. trianae* and *G. trifoliata* -- are abundant throughout the area of study. *P. trianae* is a subcanopy tree found throughout Central and South America from Honduras to Bolivia to Brazil. It is an important species in disturbed forest communities (Fujisaka et al.,1997). Its fleshy fruit implies that it is likely animal dispersed. The genus *Galipea* consists of shrubs or small trees that are typically found in disturbed areas (Gentry, 1996). *G. trifoliata* is widespread in Guyana, Venezuela, Colombia, Peru, Ecuador, Northern Brazil, and Bolivia (Pirani & Kallunki, 2007). It disperses its seeds by explosive dehiscence.

Data Collection and Analysis

For both *G. trifoliata* and *P. trianae*, ten subplots – 0.1-hectares in total - were chosen randomly and surveyed for saplings. Saplings are defined as any individual taller than one meter and <10cm DBH (cm). Diameter was not taken if the sapling was smaller than breast height (defined as 1.3 meters). The exact location of each sapling within the plot was determined in the field and mapped using the ggplot function in R (R Core Team, 2021). The plot was then georeferenced (Figure 1) based on the coordinates of the plot's corners (see Table 1) using QGIS (QGIS.org, 2021). The distance to the nearest parent plant for each sapling was determined using QGIS Distance to nearest hub (points). This algorithm determines the distance between a designated origin feature (source points layer) and the nearest individual of a designated destination feature (destination hubs layer). In this case, the source points layer was defined as saplings and the destination hubs layer was defined as adult trees. Individual distances for each sapling were averaged to establish a mean observed distance between saplings and parent plants for each species. An expected mean distance was established using the formula:

$$D_{exp} = \frac{1}{2}\sqrt{density}$$

where Dexp uses the density of parent plants in the plot to extrapolate the expected mean distance between saplings and conspecific adults assuming random assortment (Terborgh et al. 2008). A Chi Squared test was performed to establish whether there was a statistically significant

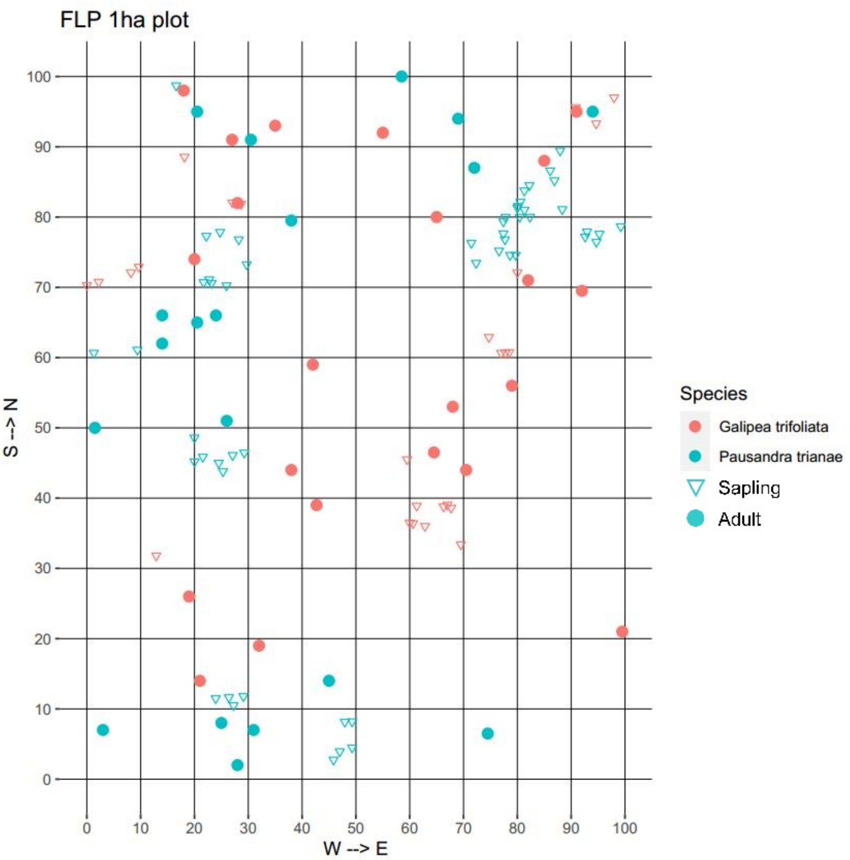

Figure 1: Grid map indicating the location of *G. trifoliata* and *P. trianae* adults and saplings within the 1-ha plot.

difference between the expected and observed mean distances, and therefore whether or not it is likely that the species are distributed non-randomly in relation to the parent plants. The J-C hypothesis is supported if the observed mean distance is significantly (p-value < 0.05) larger than an expected mean distance. In addition, an ANOVA was performed in R using the AOV function to compare the distances from saplings to adult trees between the two common species. Variances were assumed to be equal among species ($F = 0.73$, p-value $= 0.39$, n.s.) and distance data to be normally distributed ($W = 0.97$, p-value > 0.05). Therefore, ANOVA assumptions were met. Finally, a regression analysis was performed between distance from sapling to nearest adults and diameter of the sapling at breast height (if applicable).

Results

Within the 1-hectare plot, *P. trianae* has a density of 19 adult trees (trees ≥10cm DBH) per hectare and *G. trifoliata* has a density of 22 adult trees per hectare. Within the 0.1 hectare sample, 53 saplings of *P. trianae* and 25 saplings of *G. trifoliata* were found. *G. trifoliata* saplings were found at a minimum distance of 0.50m from the nearest adult tree and a maximum distance of 19.54m, with an average distance of 7.79m (s.d. = ±5.16). *P. trianae* saplings were found at a minimum distance of 3.48m from the nearest adult tree and a maximum distance of 17.97m, with an average distance of 9.58m (s.d. = ±3.94). *P. trianae* had an observed mean distance from a parent plant that was significantly greater than the expected mean distance (p-value < 0.025). *G. trifoliata* had an observed mean value that was also greater than the expected, but the difference was not statistically significant (p-value < 0.1). An ANOVA test compared the distances from saplings to adults between the two species. Distances between saplings and adult trees were found to have no significant variation between the two species ($F_{1,76} = 2.862$, p-value $= 0.09$).

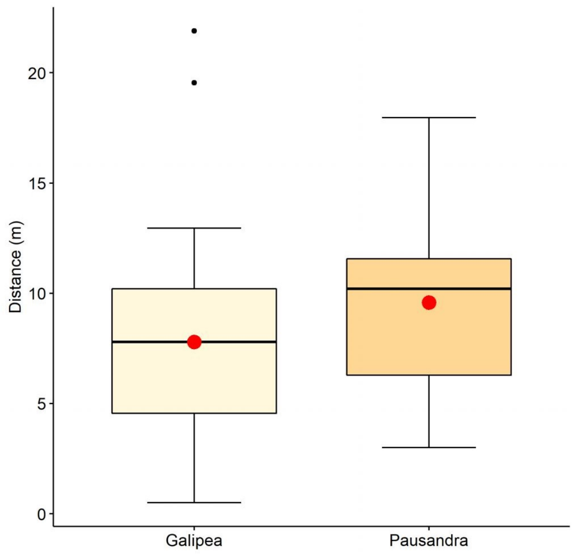

Figure 2: Box plot of the distances between saplings and adult trees for *G. trifoliata* and *P. trianae* ($F_{1,76} = 2.862$, p-value $= 0.09$)

Distance between saplings and adults versus diameter of the sapling was also analyzed for each species. *G. trifoliata* saplings had a minimum observed diameter of 0.45cm, and a maximum observed diameter of 6.3cm. *P. trianae* saplings had minimum observed diameter of 0.6cm, and a maximum observed diameter of 9.7cm. There was no association between distance from adult plant and diameter of the sapling for either *G. trifoliata* ($R^2 = 01651$) or *P. trianae* ($R^2 = 0.0197$).

Table 2: Data table of the relevant values from the Chi Squared test

	Observed (O)	Expected (E)	O-E	Chi Calc	d.f.	Chi Critical	p-value
P. trianae	9.58222	4.588	4.994	5.435	1	3.84	**0.01 < P < 0.025**
G. trifoliata	7.792974951	4.264	3.529	2.921	1	3.84	0.05 < P < 0.1

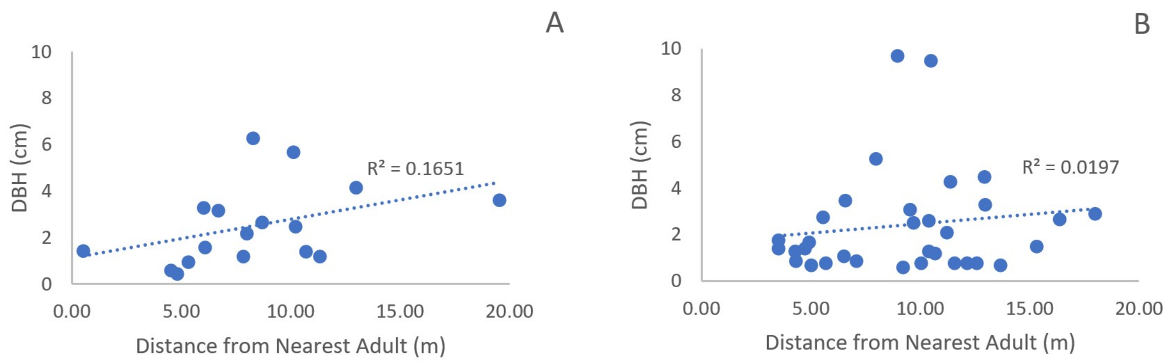

Figure 3: Scatterplot of distances of saplings from nearest adult versus diameter of the sapling at breast height (if applicable). ***G. trifoliata*** **(A; R^2 = 0.1651) and** ***P. trianae*** **(B; R^2 = 0.0197).**

Discussion

The primary implications of this study are ecological. The Janzen-Connell (J-C) hypothesis is expected to be more applicable to rare species due to the greater sensitivity to species-specific pathogens demonstrated in rare species as compared to common species (Comita et al., 2014). From this study, however, it can be inferred that the J-C hypothesis may be selectively applied to certain common species. Results for *P. trianae* support the J-C model, whereas results for *G. trifoliata* do not. The results for *G. trifoliata* might suggest that its sapling distribution does not follow any strong pattern. There is the potential that this difference may be due in part to the different dispersal mechanisms utilized by the two species. The J-C model has been tested extensively, but this ongoing research has provided few concrete conclusions regarding the specific size of the zone of reduced recruitment for different tree species, and the variance of this negative distance effect between species (Terborgh et al. 2008). By focusing on common species, we have shown that it is possible to characterize these traits. Future research would benefit from such characterizations of common species. Long term, larger-scale research on the fate of dispersed seeds and the impact of predation, sapling density, and parent density on seed survival would provide a deeper understanding of how biotic and abiotic factors do, or do not, provide empirical evidence to support the J-C model in specific species (Cintra, 1997).

The statistical analysis comparing distances from saplings to nearest adults between the two species provided further insight into the characterization of recruitment in each of these species. Distances between saplings and adult trees did not vary significantly between the two species – this implies that the distribution pattern found in both species should be almost identical. This interpretation, however, provides an interesting contrast to the previous result which showed the J-C model to be evident in only *P. trianae*. Despite the appearance of relative equivalence in tree distribution, it has been shown that important differences in spatial patterns may still exist. This highlights the importance of species-specific studies in forest ecosystems.

It is logical to assume that if the Janzen-Connell hypothesis is relevant to a species, then saplings that are further away from a conspecific, reproductive adult will have a higher probability of succeeding and growing to a larger size. The observation of size to determine species success presumes that plant diameter is an indicator of the age of the sapling and that surviving to an older age is indicative of sapling success. It was found, however, that diameter and distance from an adult tree were not associated for either species, even *P. trianae*, which seems to follow a J-C distribution. This result reinforces the idea that the majority of mortality occurs in the seedling stage. Seedlings are especially vulnerable to pathogens and predators, particularly when close to a parent plant (Hyatt et al., 2003). Once the sapling stage is reached, the plant becomes much less vulnerable to pathogen attacks. This concept is yet another facet of the J-C hypothesis.

The 1-ha plot used in this study is the first permanent monitoring plot in a terra firme forest in the Southern Peruvian Amazon (R. Fortier, personal communication, July 15, 2021). This research could be preliminary to a longer-term study documenting the life history traits of the diversity of flora in this region. The approach taken in this study was intended to be an easily repeatable method for surveying the small-scale spatial dynamics of a species-rich forest community. The two species studied are both integral members of the forest community, as both are native and their prevalence in disturbed forest communities allows them to be identified as early successional species crucial to reestablishing forest cover (Chechina & Hamann, 2015). By studying the ecology of prevalent flora, this paper has provided a small-scale basis for understanding the dynamics of a previously disturbed forest.

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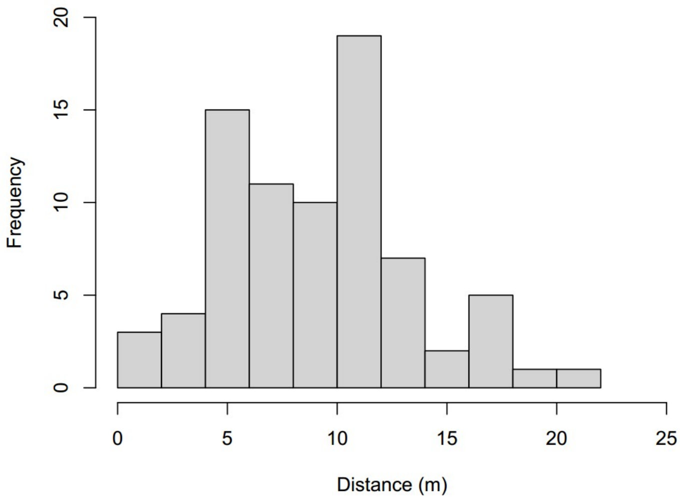
Supplementary Material

Appendix I: Histogram showing the distribution of distances to be normally distributed.



Supplementary Material

Appendix II: Study species guide.

Species	Identifying Features	Reference Image
G. trifoliata	Trifoliate (three leaflets) Alternate leaves Flattened petiole	
P. trianae	Serrated margin Long, alternate leaves Two glands at base of leaf