FOREST DYNAMICS OF A SUB-XEROPHILOUS VEGETATION FORMATION IN CENTRAL PERU - CHANCHAMAYO VALLEY, PERU[1]

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ABSTRACT – Studies about the complex processes of forest dynamics in pre-montane and montane forests (between 600 – 3000 m altitude) are rare. This study contributes to our knowledge on changes in the floristic composition and population dynamics of woody species in a sub-xerophilous formation immersed in the humid pre-montane and montane forests of Peru. In 2015 we re-measured trees with diameter at breast height equal or greater than10cm in a permanent plot established in 2009. We recorded 31 species of 25 families, with a Fisher's Alpha diversity index of 7.5. The most abundant and dominant species (including *Heteropterys intermedia, Physocalymma scaberrimum, Sapium glandulosum, Tachigali peruviana* and *Machaerium hirtum*) represented 66.25% of all species in 2009 and 66.36% in 2015. The prevalence of these species and others ensures the maintenance of a characteristic seasonally dry forest formation within the census period (6.25 years). The dynamics of this forest, with a high rate of recruitment (3.82%) and a low rate of mortality (0.72%), show favorable conditions for the maintenance of this forest fragment.

Keywords: Dry forest; Mortality; Recruitment.

DINÂMICA FLORESTAL DE UMA FORMAÇÃO VEGETAIS SUB-XERÓFILA NO VALOR DE CHANCHAMAYO, DEPARTAMENTO JUNIN, PERU

RESUMO – Pesquisas sobre os complexos processos de dinâmica da floresta nas florestas montanas e premontanas úmidas (600 a 3000 msnm) são escassas. Este estudo tem como objetivo contribuir com o conhecimento de mudanças na composição florística e dinâmica populacional de espécies lenhosas em um tipo de formação de planta sub-xerofílica imerso nas florestas úmidas pré-posanas da Selva Central do Peru. Em 2015, todas as árvores com dap ≥ 10 cm foram novamente medidos em ums Parcela Permanente estabelecida em 2009. 31 espécies foram registradas em 25 famílias e um índice de diversidade Alpha-Fisher de 7.5 foi determinado. As espécies mais abundantes e dominantes em termos relativos mantiveram sua representatividade de 66.25% em 2009 e 66.36% em 2015, sendo ***Heteropterys intermedia****,* ***Physocalymma scaberrimum****,* ***Sapium glandulosum****,* ***Tachigali peruviana*** *e* ***Machaerium hirtum****. Uma composição florística é mantida com espécies de formações sazonalmente secas durante o período intercensal (6.25 anos). O dinamismo é influenciado pela alta taxa de recrutamento (3.82%), em oposição a uma baixa taxa de mortalidade (0.72%). Nossos resultados mostram condições favoráveis para a manutenção desse fragmento florestal.*

Palavras-Chave: Floresta seca; Mortalidade; Recrutamento.

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1.INTRODUCTION

The study of forest dynamics in the tropics has mainly focused on lowland rain forests in the Amazon revealing that their structure and dynamics are changing (Nebel et al., 2000; Lewis et al., 2004; Feeley et al., 2011). The species richness in these formations is mainly explained by their forest dynamics rather than by any other factor, showing that disturbance at smaller scales is functionally related with the species richness in a community (Phillips et al., 1994). In terms of tree growth, previous research has suggested that the availability of resources stimulates the net primary production, accelerating the dynamics of basal area and increasing the above-ground biomass (Lewis et al., 2004). However, the specific causes and consequences of such increases are still being discussed.

The study of ecological processes in forests, such as the dynamics of mortality and recruitment rates, and the changes in the floristic composition, can give us insight to and help understand the changing processes of the woody component. Studying the changes in composition improves not only our understanding about the ecology of tropical forests and their response to local and regional disturbances, but also our capacity to predict how future global changes can influence some vital services provided by these ecosystems (Feeley et al., 2011).

Examination of the changing patterns of species composition and their relation to carbon fertilization predictions, of past perturbations, of recovery from extreme drought caused by El Niño and of long-term climatic changes, showed that those changes increased the relative proportions of drought-tolerant species. These increases were determined by the occurrence of species along a soil humidity gradient and through a wider rainfall gradient (Feeley et al., 2011). Furthermore, additional research suggested that the compositional transition of tropical forests to more seasonal forest types is a consequence of increasingly dryer conditions which limit the distribution of species (Esquivel-Muelbert et al., 2017).

An optimal scenario to study the contrast between the humid flora and the flora from seasonally dry formations occurs in the central Peruvian rain forest in the Chanchamayo valley. This valley, part of the Perené River basin and located between 600 to 1200 m above sea level, harbors a sub-xerophilous floristic formation composed of small fragments embedded in a more extensive humid forest matrix. Since much of this valley is exposed to frequent slash and burn and land-use change events, it is important to study and monitor the remaining dry forest fragments over time to understand their dynamics and their contribution to diversity and conservation in these changing pre-montane landscapes in Central Peru. Especially considering the increase in intensity and length of dry seasons in the Amazon basin (Marengo et al., 2011).

Field observations in the study area suggested that the density of woody individuals was increasing. This could be the result of an increased recruitment rate, but not of mortality. This study sets out to prove this hypothesis. In addition, we also expected changes in the forest structure. These changes were also analyzed from a floristic composition perspective to explore species turnover.

2.MATERIALS AND METHODS

2.1 Study area

The study area is in the Perené River Valley, San Ramon District, Chanchamayo Province, Junin Region, in Central Peru. Average annual rainfall is between 1500 and 3000 mm, whilst average annual temperature is between 15 and 19 ºC. Soils are alluvial and support mainly rainforests that have 90 to 147 tree species/ha (Marcelo-Peña and Reynel, 2014). The valley also presents scattered seasonally dry vegetation formations with species that are characteristic of Neotropical dry forests and/or savannas, such as *Astronium fraxinifolium* (Anacardiaceae), *Curatella americana* (Dilleniaceae), *Machaerium pilosum* (Fabaceae), *Roupala montana* (Proteaceae), *Pseudobombax marginatum* (Malvaceae), *Luehea paniculata* (Malvaceae), *Dilodendron bipinnatum* (Sapindaceae), among others. Previous studies show that these species are absent or rare in the rainforest areas of the valley (Palacios-Ramos, 2017). Many of these areas are burned regularly for crop production.

One of us (SP) stablished a permanent plot for this drier type of vegetation within in a three-hectare area in 2009 (UTM WGS84: 18L 462779 E, 8772597 N). The last recorded fires of anthropic origin in the adjacent areas were in 2005 and 2009.

2.2 Methodology

This study compares tree census data from 2009 when the permanent plot (100x60m; composed of 15 sub-plots of 20x20m) was stablished (Palacios-Ramos and Reynel, 2011) with the second census in 2015, after six years with three months (6.25 years).

Both censuses included the assessment of all trees with DBH (diameter at breast height, 1.30m above ground) equal or above 10 cm, following the protocol of Phillips et al. (2009). The second census included: (i) recruits (individuals that reache or passed 10cm of DBH in the 2015 census) and (ii) dead individuals. Trees that could not be referred to a previously sampled specimen were collected to be identified later in the herbarium. The samples were processed and deposited in the Universidad Nacional Agraria La Molina Herbarium (MOL: Woody plants collection).

2.3 Data Analysis

We constructed a species accumulation curve using each 20x20m sub-plot within the permanent plot (100 permutation for each year we assessed) to show species richness values of the plot according to the size of the sample unit. To assess species diversity, we calculated Fisher's Alpha index, as it allows to compare data from sample units with different abundances. In both cases we used the R programming environment (R Development Core Team, 2017) and the ´vegan´ package (Oksanen et al., 2017).

We further calculated woody plant cover values by adding the relative densities (percentage of number of trees) and the relative dominances (percentage of basal area) to analyze the horizontal structure and representativeness of the species.

We analyzed forest dynamics by using mortality and recruitment rates. The mortality rate per annum was calculated according to the exponential growth model in continuous time (Nebel et al., 2000).

$$\text{Tm} = \frac{\ln(No) - \ln(No - Nm)}{\Delta t} \qquad \text{EQ-1}$$

where: Tm = annual mortality rate expressed in percentage; No = number of individuals recorded in the first census; Nm = number of individuals that died within the t time interval; Δt = time interval t expressed in years; ln = natural logarithm.

We calculated the recruitment rate per species by following an exponential function of population increase (Phillips et al., 1994; Nebel et al., 2000).

$$\text{Tr} = \frac{\ln(No - Nm + Nr) - \ln(No - Nm)}{\Delta t} \qquad \text{EQ-2}$$

where: Tr = recruitment rate or resettlement in percentage; No = number of individuals recorded during plots setup; Nr = number of individuals resettled within time interval t; Nm = number of individuals that died during time interval t; Δt = time interval t in years. ln = natural logarithm.

3.RESULTS

3.1 Diversity, floristic composition and structure

The species accumulation curve for the 2015 re-census shows a stabilization trend (Figure 1). This trend is similar to the estimated values calculated from the 2009 data. Fisher's Alpha diversity was 7.39 in 2009 and 7.5 in 2015. The number of woody individuals per hectare was 642, with an increase of 21% compared to the value estimated in 2009 (532 trees per hectare). In 2009 we recorded 22 families, and added three new families in 2015, each one with one species and only one individual (Annonaceae: *Guatteria sp*., Vochysiaceae: *Vochysia mapirensis* and Lacistemataceae: *Lacistema aggregatum*). Six of the seven species that were represented by only one tree in 2009 kept only one individual in 2015.

The most abundant and dominant species in the 2009 and 2015 censuses were *Heteropterys intermedia*, *Sapium glandulosum, Physocalymma scaberrimum*, *Tachigali peruviana* and *Machaerium hirtum*. These five species had similar cumulative plant cover values in both inventories (66.3% y 66.4%) (Table 1).

Abundance distribution by diametric categories in 2015 showed more individuals in the lower diametric categories, just as in 2009, resulting in

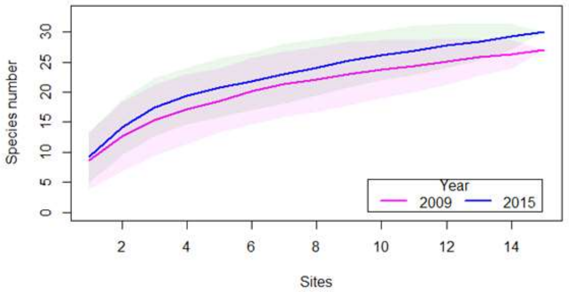

Figure 1 – Species accumulation curve for both censuses, green and pink shaded areas show 95% confidence envelopes, brown shade shows overlapping region.
Figura 1 – *Curvas de acumulação de espécies para os dois censos.*

Table 1 – Relative density (DR, individuals %), Relative dominance (DoR, basal área %) and Relative cover value (VC, cover %) of the 15 most abundant species for 2009 and 2015.
Tabela 1 *– Densidade relativa (DR, percentagem de indivíduos), Dominância relativa (DoR, percentagem de área basal) e Valor de Cobertura (VC, percentagem de cobertura) das 15 espécies mais abundantes para 2009 e 2015.*

Species	2009			2015		
	DR	DoR	VC	DR	DoR	VC
Heteropterys intermedia	28.84	29.55	29.20	27.53	27.47	27.50
Sapium glandulosum	13.79	13.43	13.61	14.29	13.62	13.96
Physocalymma scaberrimum	12.85	10.23	11.54	15.06	12.00	13.53
Tachigali peruviana	1.57	11.73	6.65	1.82	11.49	6.66
Machaerium hirtum	6.27	4.25	5.26	5.71	3.73	4.72
Cespedesia spathulata	4.70	4.24	4.47	3.90	4.13	4.02
Byrsonima spicata	3.76	3.18	3.47	3.90	3.51	3.71
Roupala montana	5.02	4.09	4.56	4.16	3.12	3.64
Cecropia polystachya	3.13	4.97	4.05	2.08	4.23	3.16
Luehea paniculata	3.45	3.20	3.33	3.12	3.07	3.10

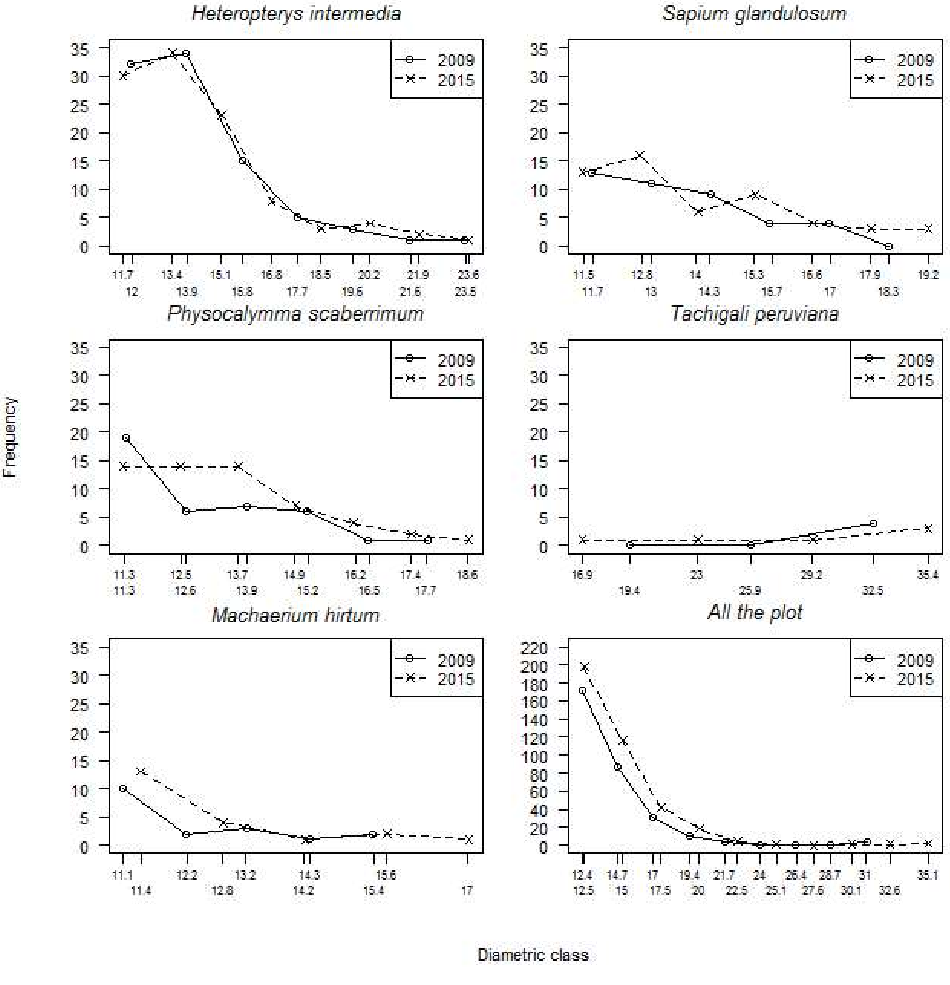

Figure 2 – Abundance distribution by diameter class of selected and pooled species during the 2009 and 2015 censuses.
Figura 2 *– Distribuição por classes diamétricas de 2009 e 2015.*

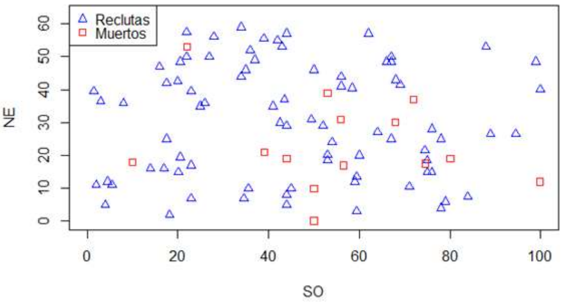

Figure 3 – Spatial distribution of dead and recruited individuals in the permanent plot.

***Figura 3** – Distribuição espacial de mortos e recrutas na parcela.*

an inverted-j trend. Two of the species with higher cover values kept the same distribution in both censuses (Figure 2).

3.2 Mortality and recruitment

Eleven species presented a total of 14 dead individuals in the second census. We also recorded 82 new individuals belonging to 18 species, three of them were species not recorded in the 2009 census. The relatively even distribution of dead individuals and recruits is slightly skewed towards the northwest of the plot (Figure 3). The recruitment of *Physocalymma scaberrimum* (17), *Heteropterys intermedia* (15) and *Sapium glandulosum* (14) represented 56% of all recruits.

There is a notorious difference between the high recruitment rates (8.82%) and the low mortality rates (0.72%). 18 of the 27 species registered in 2009 showed changes in their dynamics, primarily influenced by the high rate of recruitment (Table 2).

4.DISCUSSION

4.1 Diversity, floristic composition and forest structure

Four of the five most important species in the plot (*Heteropterys intermedia, Physocalymma scaberrimum, Tachigalii peruviana* and *Machaerium hirtum*) are characteristic of seasonally dry forests and/or wooded savannas (Palacios-Ramos and Reynel, 2011; Palacios-Ramos, 2017). *Luehea paniculata, Roupala montana* and *Byrsonima spicata* are common in seasonally dry formations (Weberbauer, 1945; Garcia-Villacorta, 2009;

Table 2 – Mortality and recruitment rates (2009 and 2015). N_0 original stems. N_m dead stems. N_s original stems surviving to final census. N_r recruited stems at final census. N_f: final stems. Tm: annual mortality rate. Tr: annual recruitment rate.

***Tabela 2** – Taxas de mortalidade e recrutamento para 2009 e 2015. N_0 individuos censo inicial. Nm número de indivíduos mortos. Ns indivíduos sobreviventes do censo final. Nr recrutas. Nf: indivíduos do censo final. Tm: taxa de mortalidade anual. Tr: taxa de recrutamento anual.*

Species	(N_0)	(N_m)	(N_s)	(N_r)	(N_f)	(Tm)	(Tr)
Allophylus floribundus	7		7	8	15	0.00	12.19
Guazuma ulmifolia	1		1	1	2	0.00	11.09
Maprounea guianensis	2		2	2	4	0.00	11.09
Mauria heterophylla	5		5	4	9	0.00	9.40
Schefflera morototoni	7		7	5	12	0.00	8.62
Physocalymma scaberrimum	41		41	17	58	0.00	5.55
Tachigali peruviana	5		5	2	7	0.00	5.38
Byrsonima spicata	12	1	11	4	15	1.39	4.96
Sapium glandulosum	44	3	41	14	55	1.13	4.70
Heteropterys intermedia	92	1	91	15	106	0.17	2.44
Machaerium hirtum	20	1	19	3	22	0.82	2.35
Luehea paniculata	11		11	1	12	0.00	1.39
Cespedesia spathulata	15	1	14	1	15	1.10	1.10
Roupala montana	16	1	15	1	16	1.03	1.03
Trema micrantha	2	1	1		1	11.09	0.00
Cecropia polystachya	10	2	8		8	3.57	0.00
Persea caerulea	6	1	5		5	2.92	0.00
Myrsine pellucida	10	1	9		9	1.69	0.00
Other	13	1	12	1	13	0.00	0.00
TOTAL	319	14	305	79	384	0.72	3.69

Linares-Palomino et al., 2011). All these belong to the ten species with the highest plant cover values in the plot, having maintained their representativeness since 2009 (Table 1). In our study area, they have only been registered in the sub-xerophilous formations (Palacios-Ramos and Reynel, 2011; Palacios-Ramos, 2017), except for *Sapium glandulosum* which is considered an ecological generalist species (Linares-Palomino et al., 2011) and also found in the adjacent more humid areas.

Studies have suggested that rainfall seasonality regulate the alpha diversity of Amazonian forests. However, the variation of diversity at local scales is the result of other factors (Ter Steege et al., 2003). For instance, even under high local humidity regimes, local edaphic conditions such as porous soils could increase hydrological stress and decrease diversity (Esquivel-Muelbert et al., 2017). A recent study in our area of interest compared soil diversity and characteristics of the different forest types and showed that the sub-xerophilous forest grew on soils different from those with humid forest growing on it. These different soils allow species to endure conditions with low organic material content, high levels of pH and interchangeable acidity (Romero, 2017). These conditions could be a limiting factor for the colonization of the adjacent humid forest species.

Another local factor that could influence the dynamics of species is fire. Fire exclusion trials in the Brazilian Cerrado showed that rainforest species are capable of colonizing savannas and compete with the local species assemblage adapted to fire (Geiger et al., 2011), suggesting that a closed canopy forest could develop on the low nutrient soil of the Brazilian Cerrado (Simon and Pennington, 2012). Time is of utmost relevance in this forest – savanna alternation. The transition from saplings to adult trees or from the savanna to forest requires long but unusual intervals without fire. The opposite transitions are favored by prolonged drought and when non-altered forests become flammable (Hoffmann et al., 2012). These statements are relevant for our study area considering that since 2005 and 2009 there have been no more fires. During those events, fires reached the plot border impacting the understory vegetation and the foliage of adjacent trees. However, many of the species in our plot, such as *Roupala montana, Byrsonima spicata, Luehea paniculata, Maprounea guianense* and *Pseudobombax marginatum* present adaptations to fire (Palacios-Ramos, 2017). And species such as *Curatella americana* require fire for reproduction (Penninton and Ratter, 2006). The absence of fire during these six years has not induced major changes in the horizontal structure of the forest (Table 1). The present status could be part of a cyclic succession between more open formations and closed canopy forests, although further censuses would be necessary to confirm it.

Despite the high overall number of recruits and low number of dead individuals, there is an increase of individuals in diametric classes higher than 10cm (Figure 1). However, unlike other forests in early successional states (Torres et al., 2012; Muñoz et al., 2014) this increase stabilizes above the 25cm diameter class. The smaller diametric classes kept the high number of trees and showed an inverted-j trend. This structure is characteristic of a forest with continuous recruitment and is particularly prevalent in some of the most important species of this forest (Figure 2), providing them whith good possibilities to remain in the plot over a longer term.

4.2 Mortality and Recruitment

The annual tree mortality rates reported for Neotropical dry and semi – deciduous forests ranges between 1.9% and 4.1% (for DBH ≥ 10 cm) (Felfili, 1995; Uslar et al., 2011; Torres et al., 2012) and between 1.3% and 4.9% (for DBH ≥ 5 cm) (Aquino et al., 2007; Carbajal and Calvo, 2013; Aguirre, 2016; Calvo-Rodriguez et al., 2017). These values are considerably higher than the mortality rate we report here (0.72%). In contrast, the recruitment rate reported for our plot (3.83%) is one of the highest for dry forest and semi – deciduous forest, which range between 0.73% and 7.9% (for DBH DAP ≥ 10 cm) (Swaine et al., 1990; Felfili, 1995; Uslar et al., 2011; Torres et al, 2012) and between 1.6% and 8.8% (for DBH ≥ 5cm) (Aquino et al., 2007; Carbajal and Clavo, 2013; Aguirre, 2016). In a savanna in Ghana Swaine et al. (1990) registered mortality and recruitment rates of 2.3% and 1.5%, respectively (for DBH ≥ 10 cm), values also different from those reported in the present study.

Curatella americana and *Pseudobombax marginatum* are species characteristic of the semi – deciduous Chiquitano forest and of the Brazilian Cerrados (Furley et al., 1988). They are also present in the sub-xerophilous formations in Central Peru, usually in areas with an open canopy and with predominance of grasses (Palacios-Ramos and Reynel, 2011). Long-term term permanence in these sub-xerophilous formations could be compromised since our plot data showed no recruitment. In addition, the increase in the density of trees per hectare of more than 20% between censuses provides an increasingly closed canopy.

Although the values we report for the mortality and recruitment rates could be strongly influenced by past locally provoked fires, they also show a floristic community with members adapted to those fires. In the dry forest, the floristic composition can be more sensitive to climatic changes associated to rainfall rather than past disturbances during relatively short time-scales (Enquist and Enquist, 2011). The intensity of mortality (mortality rate per annum is lower than 5%) and the distribution of dead individuals per species demonstrate that it is a background mortality. This is part of the processes that occur in the forest community, and could be influenced by auto-shading dependence and radiation capture, the position of trees in the canopy, the successional stage of the forest (Lugo and Scatena, 1996; Melo et al., 2016), the age or size of trees, or the mortality of each species (Lugo and Scatena, 1996). The reported mortality rate has a spatial distribution with no relationship to the limits where past fires occurred (NE vertex of the plot) (Figure 3). This means that the influence of these events does not appear to be evident in the trees we evaluated (with DBH bigger or equal than 10cm). At the same time, the slight decrease in the spatial distribution of recruitment towards the NW of the plot does not seem to be related to past fire events (NE vertex of the plot) (Figure 3).

The species with the highest recruitment rate constitute only 11% of the trees in the plot, while their recruitment constitutes less than 25% of the total recruits registered in 2015. In this context, the influence of these species in this forest could be questioned and we require a longer assessment period to value their relevance. Furthermore, although the most important species showed low recruitment rates, they dominated the forest during the period assessed.

4.3 Implication for conservation

Monitoring and assessment to detect patterns of change in the floristic composition of the populations that harbor these sub-xerophylous formations is out reach for the present study. However, the existence of these formations cannot be rejected during conservation planning of the pre- montane forests of the Chanchamayo Valley and the Perené Watershed. Especially when we consider the economic value of many of the species in these forests and their adaptation to dry conditions.

The constraint of most tree taxa in the western Neotropics to the more humid areas shows low generalized tolerance to dry conditions and low capability to acclimatize to them (Esquivel-Muelbert et al., 2017). In the present context of increase in the density and length of dry season in the Amazon Watershed (Marengo et al., 2011) and the increase of temperature (Jiménez-Muñoz et al., 2013), the results we are showing could be relevant. Particularly considering that the species that occupy a dominant position in the study area regarding dominance and relative density, are species from seasonally dry areas that have morphological adaptations to survive fire (Palacios-Ramos and Reynel, 2011; Palacios-Ramos, 2017), and are already growing in soils with low content of organic material, high levels of pH and interchangeable acidity (Romero, 2017). These species could be useful for restoration efforts of similar forest systems degraded by anthropic intervention and that are dispersed throughout the valley.

5.CONCLUSIONS

The population dynamics of the sub–xerophilous formation is mainly influenced by a high recruitment rate (3.82%) and a low mortality rate (0.72%). These values are different from other studies in Neotropical seasonally dry formations. These dynamics have not produced noticeable changes in the horizontal structure nor the floristic composition. The maintenance of these conditions suggest they are favorable for the existence of this forest.

The conservation of this sub–xerophilous forest will contribute to their recovery. And if the impact of the pressure over the forest fragments decreases, it can become a source of information for research and monitoring of the seasonally dry forests in Central Peru.

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