



## Seed-deposition and recruitment patterns of *Clusia* species in a disturbed tropical montane forest in Bolivia



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### ABSTRACT

Spatial patterns of seed dispersal and recruitment of fleshy-fruited plants in tropical forests are supposed to be driven by the activity of animal seed dispersers, but the spatial patterns of seed dispersal, seedlings and saplings have rarely been analyzed simultaneously. We studied seed deposition and recruitment patterns of three *Clusia* species in a tropical montane forest of the Bolivian Andes and tested whether these patterns changed between habitat types (forest edge vs. forest interior), distance to the fruiting tree and consecutive recruitment stages of the seedlings. We recorded the number of seeds deposited in seed traps to assess the local seed-deposition pattern and the abundance and distribution of seedlings and saplings to evaluate the spatial pattern of recruitment. More seeds were removed and deposited at the forest edge than in the interior. The number of deposited seeds decreased with distance from the fruiting tree and was spatially clustered in both habitat types. The density of 1-yr-old seedlings and saplings was higher at forest edges, whereas the density of 2-yr-old seedlings was similar in both habitat types. While seedlings were almost randomly distributed, seeds and saplings were spatially clustered in both habitat types. Our findings demonstrate systematic changes in spatial patterns of recruits across the plant regeneration cycle and suggest that the differential effects of biotic and abiotic factors determine plant recruitment at the edges and in the interior of tropical montane forests. These differences in the spatial distribution of individuals across recruitment stages may have strong effects on plant community dynamics and influence plant species coexistence in disturbed tropical forests.

### 1. Introduction

Seed dispersal by animals is an important mechanism that influences the structure and diversity of plant communities in tropical ecosystems (Howe and Smallwood, 1982; Nathan and Muller-Landau, 2000). For fleshy-fruited plants, frugivorous animals are the most important vectors to disperse and deposit seeds at specific locations in the environment (Jordano et al., 2011). Seed-deposition patterns generated by frugivorous bird communities can depend on many factors, such as the diversity of the local bird assemblage (Jordano et al., 2007), avian foraging behavior (Sinu et al., 2012) and movement patterns (Lenz et al., 2011) which, in turn, may depend on habitat conditions (Breitbach et al., 2012). It is largely unclear whether the spatial pattern of seed deposition by animals is modified at later stages of plant recruitment.

While the number and distribution of seeds dispersed from a focal

fruiting tree represent the initial seed-deposition pattern (Werner, 1975; Beckman et al., 2012), the spatial distribution of recruited individuals is also the consequence of successive secondary processes, such as secondary seed dispersal (Gallegos et al., 2014), seed predation, germination, herbivory and growth that all affect the recruitment of new individuals (Wang and Smith, 2002). Consequently, a multitude of factors influences whether an animal-dispersed seed has the chance to recruit and to establish an adult plant at its deposition site (Schupp et al., 2010). Habitat suitability of seed-deposition sites is a particularly important determinant of the probability of seedlings to establish, as most seeds require specific biotic and abiotic conditions to germinate and survive (e.g., Wenny and Levey, 1998; Carlo and Tewksbury, 2014). Furthermore, different recruitment stages of the same plant species may differ in their requirements for optimal environmental conditions (Schupp, 1995, 2007). In order to quantify the effects of seed dispersers on the recruitment success of a plant species, the

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effectiveness of seed dispersal has been defined as the contribution of seed dispersers to the establishment of new individuals in terms of quantity (*i.e.*, number of seeds dispersed by each seed disperser) and quality (*i.e.*, the probability that a viable dispersed seed generates a new individual) (Schupp, 1993; Schupp et al., 2010).

Different hypotheses about the processes affecting the recruitment of plant species in tropical ecosystems have been proposed (Howe and Smallwood, 1982) and tested with models (Nathan and Casagrandi, 2004). Field studies and experiments testing these predictions have shown that seed dispersal by animals generally improves the establishment of new individuals and hence shapes spatial recruitment patterns (Beckman et al., 2012; Spiegel and Nathan, 2012). However, there are few studies that simultaneously describe and compare the spatial patterns of seed deposition and plant recruitment (Carlo and Tewksbury, 2014). Because the spatial distribution of plant individuals could affect processes of community dynamics and species coexistence (Wiegand et al., 2007; Kraft and Ackerly, 2010), studies on the spatial distribution of plants at different stages in the regeneration cycle are important to understand the processes shaping the spatial distribution of plants in tropical ecosystems.

Andean tropical montane forests are one of the 25 hotspots of biodiversity, measured in terms of species richness and endemism (Myers et al., 2000). However, at the same time these forests are one of the most threatened by deforestation (Kessler and Beck, 2001; Killeen et al., 2005). As a result, large areas of human-induced forest edges of forest remnants have been created. Given their ubiquity, it is important to study the effects of forest edges on ecological processes in the forest remnants. Previous studies in the Bolivian Andes have shown that ecological processes, such as seed dispersal, can be maintained at forest edges (Saavedra et al., 2014), which potentially contributes to the recovery of disturbed areas surrounding the forest remnants (Lippok et al., 2013).

In this study, we investigate changes in seed deposition and recruitment patterns across different recruitment stages (seeds vs. seedlings vs. saplings) of three *Clusia* species that are widespread elements of tropical montane forests (de Roca, 1993; Zenteno-Ruiz, 2007). Previously, we have reported differences in the genetic structure of two species of *Clusia* between forest edge and forest interior and between recruitment stages (Apaza et al., 2013). Changes in population genetic structure of *Clusia* may be associated with differences in seed deposition and recruitment between habitat types. Here we compare recruitment of three species of *Clusia* between forest edge and forest interior in a tropical montane forest of the Bolivian Andes. We addressed the following questions: (1) Are there differences in seed deposition and plant recruitment between forest edge and interior? We expected that the higher number of seeds removed at forest edges than in the interior (Saavedra et al., 2014) lead to a larger number of deposited seeds and recruited individuals at forest edges than in the forest interior. (2) Are there differences in the spatial distribution of seeds and recruits between forest edge and interior and among recruitment stages? We hypothesized that the spatial structure of seeds and recruits will change across recruitment stages and will be highly clustered for seeds and less clustered for later recruitment stages, due to the action of post-dispersal processes (Beckman et al., 2012; Gallegos et al., 2014) and environmental filters such as water availability and seasonality (Comita and Engelbrecht, 2009).

## 2. Materials and methods

### 2.1. Study area and species

Field work was carried out in a tropical montane forest in the Bolivian Andes, near the town of Chulumani (1900–2500 m asl 16° 24' 37.10" S. 67° 31' 37.08" W). Most of the forests in the area have been disturbed by human activities such as selective logging, the expansion of coca fields (*Erythroxylum coca* Lam.) and uncontrolled fires.

Currently, there are two forest remnants in the region, surrounded by large deforested areas: one is a private Ecological Reserve under the administration of a local community (Apa-apa forest 16° 20' 50.60" S 67° 30' 48.46" W) and the other is a non-protected forest remnant (Cala-cala forest 16° 24' 39.12" S 67° 34' 00.91" W). The climate in the study area is seasonal, with a short dry season from May to September and a wet season from November to April. The mean annual precipitation is 2300 mm and the mean annual temperature is 16.8 °C (Schawe et al., 2010).

As study species we selected three *Clusia* species (*Clusia lechleri* Rusby, *Clusia sphaerocarpa* Planch. & Triana and *Clusia trochiformis* Vesque [Clusiaceae Lindl]). The selected species are a common component of the tropical montane forest in the region (de Roca, 1993), growing naturally in clumps in the forest (F. Saavedra, pers. obs.). All species are dioecious trees up to 11 m tall with evergreen foliage (de Roca, 1993). After the flowering period between March and August, fruits are ripe between November and February (Zenteno-Ruiz, 2007). The fruits of the three species are fleshy globular capsules of different size aggregated in racemes. Fruits open to expose several red fleshy and lipid-rich arils covering several seeds. Arils constitute the seed-dispersal unit (Gallegos et al., 2014). The fleshy arils of all studied *Clusia* species are consumed by frugivorous bird species that usually defecate intact seeds (Saavedra et al., 2015). *Clusia* seedlings and saplings can be readily identified by their typical leaf texture and shape. However, *Clusia* seeds, seedlings and saplings could not be distinguished among species in the field. We thus jointly analyzed these data across *Clusia* species which is justified as the species share most ecological characteristics (Gallegos et al., 2015): (1) a similar assemblage of avian seed dispersers has been recorded in all three species (Saavedra et al., 2014), (2) the size of the arils is comparable among species (mean  $\pm$  SE): *Clusia lechleri* (12  $\pm$  0.28 mm, n = 50 arils), *Clusia sphaerocarpa* (13.5  $\pm$  0.5 mm, n = 50 arils) and *Clusia trochiformis* (9.83  $\pm$  0.22 mm, n = 50 arils), and (3) the fruiting period of all three *Clusia* species overlaps in the study region (F. Saavedra, pers. obs.).

### 2.2. Study design

We recorded the local seed-deposition and recruitment pattern of *Clusia* species at seven study sites. We selected three sites in Cala-cala forest and four sites in Apa-apa forest, separated from each other by at least 2 km. At each site, we established one plot of 20  $\times$  100 m size parallel to the forest edge (10 m from the forest margin), and another plot of the same size in the forest interior (160 m from the forest margin). The distance between forest interior and forest edge was consistent with earlier studies (*e.g.*, Laurance et al., 2002; Saavedra et al., 2014, 2015). Forest edge and interior differed due to effects of human activities on (1) plant species composition and diversity (Lippok et al., 2013), (2) plant traits (Apaza-Quevedo et al., 2015) (3) the assemblage of frugivorous bird species (Saavedra et al., 2014), and (4) abiotic conditions, *e.g.* an increase in temperature (mean  $\pm$  SE: 15.52  $\pm$  0.35 vs. 14.94  $\pm$  0.26;  $t = 2.86$ ,  $P = 0.01$ ) and a decrease in humidity (mean  $\pm$  SE: 65.24  $\pm$  5.26 vs. 79.32  $\pm$  3.60;  $t = -2.68$ ,  $P = 0.01$ ) at forest edges in comparison to the forest interior (Lippok et al., 2014). Within each plot, one adult fruiting tree of one of the three *Clusia* species was selected as a focal tree in order to measure the local seed shadow. Individuals of the same *Clusia* species were selected in both habitat types, but were different between study sites. We selected *Clusia trochiformis* at three sites and *Clusia sphaerocarpa* and *Clusia lechleri* at two sites, respectively. Because *Clusia* species are dioecious species, relatively few trees were fruiting during the 4-month study period and thus seed shadows derived almost exclusively from the selected focal tree.

### 2.3. Seed removal of *Clusia*

To assess the potential disperser community of *Clusia*, frugivorous

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