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Positive relationship between fruit removal by animals and seedling recruitment in a tropical forest

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Abstract

Fleshy-fruited plants rely on animal frugivores to disperse their seeds, and seed removal by frugivores may leave an imprint on seedling recruitment. However, to what extent plant–frugivore interactions are related to seedling recruitment has rarely been quantified at the community level, especially in species-rich tropical forests. In this study, we tested the effect of different plant traits on fruit removal by frugivores and tested the relative importance of fruit removal, plant traits and abiotic factors for seedling recruitment. We quantified plant–frugivore interactions of 22 fleshy-fruited plant species consumed by 56 diurnal frugivore species, and counted the number of seedlings that emerged along an elevational gradient in the Colombian Andes. We measured a set of plant traits (*i.e.*, crop size; fruit size; seed load and mass; fruit nutritional contents), estimated the density of adult plants and recorded relevant abiotic factors (light, temperature and humidity). We found that fruit removal by frugivores was positively associated with crop size, but negatively associated with fruit length and unrelated to seed load and fruit nutritional content. Seedling densities were positively related to the density of adult plants, seed mass and fruit removal by animals. We found no relationship between abiotic factors and seedling recruitment. Our results indicate that fruit abundance and morphology are important determinants of fruit removal and that fruit removal is positively associated with seedling recruitment accounting for effects of species abundance and plant traits. We conclude that plant traits shape fruit removal and seedling recruitment at the community level, while these two crucial processes of forest regeneration are directly linked by seed dispersal of animals.

Keywords: Fruit removal; Plant traits; Seed dispersal; Seedling recruitment; Colombian Andes

Introduction

Seed dispersal plays a crucial role in the reproductive cycle of plants, directly affecting plant population dynamics (Godínez-Alvarez & Jordano 2007). Plants and frugivorous

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animals interact in a mutualistic relationship: plants offer fruit resources and, in return, animals remove fruits and transport seeds with potentially positive effects on seedling recruitment (Jordano, García, Godoy, & García-Castaño 2007). Seedling recruitment is one of the most important phases in the life cycle of plants because it ensures plant regeneration, affects plant population, and community structure (Kitajima & Fenner 2000). The successful recruitment of new plant individuals depends upon a combination of biotic and abiotic factors (Howe & Miriti 2004). To date, little is known about how fruit removal and seedling recruitment are coupled (Balcomb & Chapman 2003; Donoso, Garcia, Rodríguez-Perez, & Martínez 2016). Furthermore, it is not understood how plant traits, fruit removal by animals and local environmental conditions jointly influence seedling recruitment at the community level.

Fruit removal from fleshy-fruited plants depends on the interplay between plant traits and the composition of the frugivore community. The number of fruits removed by animal frugivores determines the number of seeds dispersed and deposited on the ground (Parciak 2002). Crop size and fruit conspicuousness of fleshy-fruited plants typically promote fruit removal (Cazetta, Schaefer, & Galetti 2007; Blendinger & Villegas 2011), while fruit size may limit fruit removal. Notably, consumer gape width restricts small-sized seed dispersers to swallow small fruits only, whereas large-sized dispersers can swallow all fruit sizes (Muñoz, Schaefer, Böhning-Gaese, & Schleuning 2016). In addition, the ratio between digestible (pulp) and indigestible fruit components (seeds) determines the reward offered to frugivores (Herrera 1987). Other important plant traits are the various nutritional components found in fruit pulp (Herrera 1987). In general, frugivores prefer fruits rich in nutrients, such as lipids and carbohydrates (Lepczyk et al. 2000; Schaefer, Schmidt, & Winkler 2003). The effect of morphological and chemical fruit traits on fruit removal by animals has only rarely been analyzed simultaneously for species-rich plant communities. A recent study shows how fruit tracking by birds in the Southern Andes is related to nutrient availability although the nutritional quality of individual fruits only had a weak effect on fruit consumption (Blendinger et al. 2015). We therefore expect that fruit quantity (Moegenburg & Levey 2003) and morphology (Muñoz et al. 2016) may be more important than chemical fruit traits for explaining differences in fruit removal at the community level.

Seed size and seed predation are important factors influencing seedling recruitment (Baraloto, Forget, & Goldberg 2005). Most small-seeded species require more light than large-seeded species and depend upon specific microenvironmental conditions for germination (Ellison, Denslow, Loiselle, & M. 1993), whereas large-seeded species are generally less sensitive (Pearson, Burslem, Mullins, & Dalling 2002). Seed predation may also be influenced by seed size, for example, large seeds have a greater capacity to tolerate seed damage than small seeds (Leishman, Wright, Moles, & Westoby 2000). In addition, negative density-dependence may affect seedling recruitment, due to the effect of host-specific pathogens, parasites or predators (Terborgh 2012), and competition for resources (Wright 2002). Moreover, abiotic factors, such as light, temperature and humidity, influence seed germination, seedling growth and survival (Beckage & Clark 2003; Arx von, Graf Pannatier, Thimonier, & Rebetez 2013). Thus, seedling recruitment results from a combination of biotic and abiotic factors mediated by plant traits and the density of adult plants. Plant traits, fruit removal by animals and seedling recruitment are intricately interlinked and the traits that favour seed dispersal by animals may be disadvantageous for seedling recruitment. For example, large seed size can have a negative effect on seed removal, but increases seed germination and early recruitment in comparison to small seeds (Muñoz et al. 2016). Despite this multitude of competing factors, it has been shown for single species from a temperate ecosystem that seedling recruitment and fruit removal by animals are positively associated (Jordano & Herrera 1995).

So far, relatively little has been done to investigate the link between plant traits, fruit removal, and seedling recruitment, especially in species-rich, tropical communities (but see Wenny 2000; Blendinger, Blake, & Loiselle 2011 for studies focusing on particular plant families). In order to quantify the effect of plant traits on fruit removal and the effect of fruit removal on seedling recruitment, we followed a two-step approach reflecting the framework of seed dispersal effectiveness (Schupp, Jordano, & Gómez 2010). We first tested which plant traits promote fruit removal in a community of fleshy-fruited plants. (1) We hypothesize that fruit morphology and crop size affect plant–frugivore interactions more than fruit nutritional contents. Second, we tested the relative importance of fruit removal, seed size, density of adult plants and abiotic conditions for seedling recruitment of 22 plant species. (2) We hypothesize that fruit removal by animal frugivores is positively associated with seedling recruitment at the community level accounting for other biotic and abiotic factors.

Materials and methods

Study area

The study was conducted along an elevational gradient in the Central Andes of Colombia (1800 m up to 2700 m above sea level). The gradient covered two protected areas, the National Park Santuario de Fauna y Flora Otún Quimbaya (4°43′N, 75°34′W, 489 ha) and the adjacent Regional Park, Ucumarí (4°42′N, 75°29′W, 3980 ha). Both places are located on the western slope of the Cordillera Central in the Department of Risaralda. The forest vegetation comprises patches of mature forest as well as secondary forests at least 50 years old. The rainfall regime is bimodal, with mean annual precipitation ranging between 2000 and 4000 mm. Precipitation peaks occur in