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Population and genetic structure of two dioecious timber species *Virola surinamensis* and *Virola koschnyi* (Myristicaceae) in southwestern Costa Rica

Pablo Riba-Hernández [a,*], Jorge Lobo Segura [b], Eric J. Fuchs [b], Juan Moreira [a]

[a] *Proyecto Carey, Península de Osa, Puntarenas, Costa Rica. Apdo, 10672-1000 San José, Costa Rica*
[b] *Escuela de Biología, Universidad de Costa Rica, 2600 San Pedro, Costa Rica*

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ABSTRACT

Selective logging regulations generally fail to account for sex ratios, sex size distribution, spatial patterns and genetic structure in dioecious timber species. Furthermore, sympatric congeneric dioecious tropical species are harvested under the same vernacular name, failing to account for potential variation in species population traits. This practice is expected to have deleterious consequences in the population density and reproduction of the least abundant species. Here we document density, sex ratios, sex size distribution, spatial patterns and genetic structure in two dioecious timber tree species, *Virola surinamensis* and *V. koschnyi* in southwestern Costa Rica. In addition, we assessed the probability that harvesting these two species under the same vernacular name will cause a significant decline in either sex density of the least abundant species, which is expected to unbalance sex ratios, therefore, reducing the reproductive potential of the species. In a 62 ha plot we tagged, geo-referenced and sampled for cambium tissue all adults of the two species (dbh > 30 cm) for genetic analyses. Microsatellites loci were used to describe genetic diversity parameters and spatial genetic structure. In a nuclear subplot (42 ha) we measured dbh and monitored sex expression during two reproductive events to describe population density, sex ratios, sex size distribution and spatial patterns. Adult density was twofold higher for *V. surinamensis* than *V. koschnyi*. The proportion of flowering males and females and diametric size distribution did not differ within species. Adults of both *Virola* species were spatially aggregated, but sexes were distributed randomly. We found a significant but weak spatial genetic structure for *V. surinamensis*, but not for *V. koschnyi*. Finally, there is a high probability (Multivariate hypergeometric distribution, $p = 0.47$) that harvesting these two species under the same vernacular name will cause a drastic decline in the density of male or female trees of *V. koschnyi*. Overall our results suggest that dioecy does not influence tree size or spatial distribution of these two timber species. The weak spatial genetic structure in *V. surinamensis* is likely due to clumped seed dispersal and absence of thinning during the recruitment of genetically related seeds to the adult stage. Harvesting these two species under the same vernacular name will have important consequences in the reproduction of *V. koschnyi*. We suggest that selective logging regulations for dioecious species should encourage appropriated species identification, ascertain the sex of reproductive individuals, harvest these species in proportion to their sex ratios and reduce the proportion of harvested individuals in the population.

1. Introduction

Dioecy is the separation of male and female functions in different individuals. This reproductive strategy has higher incidence in woody plants from tropical area and island (Bawa, 1980; Sobrevila and Kalin Arroyo, 1982; Kress and Beach, 1994). Conservation and management strategies of tropical forest areas must take into account this reproductive strategy as a factor that influences population structure parameters and reproduction of many tropical plants, in particular, tree species. In undisturbed conditions the population structure of dioecious plants is expected to be influenced by intersexual differences on life history traits (Lloyd and Webb, 1977). For instances, it has been shown that females allocate more resources (e.g. biomass) to reproduction than males (see Obeso, 2002, for a review). This sex-biased resources

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[*] Corresponding author. Tel.: +506 88506222; fax: +506 2330151.
E-mail address: pabloribah@gmail.com (P. Riba-Hernández).

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allocation is predicted to affect not only flowering frequency (e.g. Bullock and Bawa, 1981; Armstrong and Irvine, 1989; Thomas and LaFrankie, 1993), but also female resources investment for growth and protection against herbivores. Generally, female plants are expected to have lower growth rates (e.g. Cipollini and Whigham, 1994) or higher mortality (e.g. Allen and Antos, 1988) than males. In addition, it is expected that females predominate were resources are limited to compensate for the investment on reproduction, which may lead to generate spatial segregation of sexes (SSS) along environmental gradients (Bierzychudek and Eckhart, 1988).

For tropical dioecious trees, biased and balanced sex ratios have been found to be equally likely (Opler and Bawa, 1978; Ackerly et al., 1990; Wheelwright and Bruneau, 1992; Thomas and LaFrankie, 1993; Queenborough et al., 2007a; Amorim et al., 2011; Fernandez-Otarola et al., 2013). Whenever sex ratio is unbalanced, male bias is expected (Opler and Bawa, 1978; Armstrong and Irvine, 1989; Ackerly et al., 1990; Thomas and LaFrankie, 1993; Nicotra, 1998; Somanathan and Borges, 2000; Lenza and Oliveira, 2006; Queenborough et al., 2007a). However, female-biased sex ratios have also been reported (Melampy and Howe, 1977; Thomas, 1997; Forero-Montaña et al., 2010). Males have not shown either "precocious" reproduction (Thomas and LaFrankie, 1993; Forero-Montaña et al., 2010), or size differences relative to female plants (Queenborough et al., 2007a; Pavón and Ramírez, 2008; Forero-Montaña et al., 2010). Finally, spatial segregation of sexes (SSS) seems to be rare in tropical tree species (Bullock, 1982; Queenborough et al., 2007a; Forero-Montaña et al., 2010). In general, the above exceptions to theoretical expectations regarding sex ratios, plant size and spatial segregation of sexes suggest that not all tropical dioecious trees species respond similarly to reproduction costs, rather it appears that other sex-independent factors may shape the population structure of dioecious trees (Thomas and LaFrankie, 1993; Forero-Montaña et al., 2010; Field et al., 2012).

Spatial aggregation is a common feature of tropical trees, including dioecious species (Condit et al., 2000; Queenborough et al., 2007b). Spatial aggregation is also common between sexes in tropical dioecious species (Bullock, 1982; Mack, 1997; Queenborough et al., 2007a; Forero-Montaña et al., 2010). In tropical tree species it has been attributed to seed dispersal limitation, as most seeds fall in close proximity of maternal trees (Janzen, 1970; Schupp et al., 2002). One potential consequence of an aggregated spatial arrangement is the non-random distribution of related individuals over short distances, resulting in spatial genetic structure (SGS). In spite of the potential of SGS on inbreeding and genetic drift in plant populations (Schnabel et al., 1998), few studies have evaluated the presence of SGS in tropical dioecious trees. Current evidences suggest weak SGS in adults of tropical vertebrate-dispersed dioecious trees (Hardesty et al., 2005; Hardy et al., 2006).

Dioecy is expected to increase the vulnerability of trees threatened by anthropogenic disturbances (Vamosi and Vamosi, 2005). In species with this obligated outcrossing breeding system, reproduction is susceptible to changes in population structure such as sex ratio (House, 1992; Osunka, 1999), male–female distance (de Jong et al., 2005), individual size (Bullock and Bawa, 1981; Somanathan and Borges, 2000; Fernandez-Otarola et al., 2013) and pollinator abundance or behavior (House, 1993; Somanathan and Borges, 2000). Therefore, any anthropogenic activity that modifies any of these factors could affect the long-term viability of dioecious plants. Selective logging is by far the most common management strategies to exploit commercial timber trees in tropical regions (Putz et al., 2012). Harvesting strategies are based on two main parameters, the proportion of adult trees extracted per species per area over a minimum dbh size threshold and the frequency of cutting cycles. Frequently, these technical parameters are applied regardless of the species reproductive biology; as a consequence it is difficult to predict the viability of residual populations after logging. This problem is emphasized in dioecious trees, because selective logging is conducted without any information on the sex of harvested individuals. Information on the effect of selective logging on tropical dioecious timber trees is still limited, but a few studies suggest that sex ratios, size and spatial distributions are modified in residual populations after extraction (Macedo and Anderson, 1993; Somanathan and Borges, 2000; Sebbenn et al., 2008).

The use of vernacular names is a common non-technical tree identification system used by logging companies to conduct forestry inventories. This system is well established in a few tropical regions (Swaine and Agyeman, 2008), however it has been shown to be highly inaccurate (Lacerda and Nimmo, 2010). One of the fundamental flaws of this system is the variation of local knowledge on tree species identification; common names may represent several species within a genus or even represent species from different genera (Barrantes et al., 1999; Lacerda and Nimmo, 2010). Consequently, the use of vernacular names generates misleading harvesting parameters, compromising the long-term viability of harvested species. In particular, its impact is expected to be higher on timber species that occurs at lower densities (Lacerda and Nimmo, 2010).

In this study, we describe the population structure and adult spatial genetic structure of two timber dioecious tree species in the *Virola* genus in a continuous forest. In particular we evaluate the following questions; 1) Do population sex ratios deviate from unity? 2) Do males have a different size distribution than females? 3) Are sexes spatially segregated? 4) Are these two species spatially aggregated at the population level? and 5) Is there any evidence of spatial genetic structure in the adult population of these two dioecious trees species? Finally, we estimated the likelihood that harvesting these two species under the same vernacular name will cause a significant decline in the density of male or female trees of the less abundant species.

2. Methods

2.1. Study site

This study was conducted in a tropical humid forest (Holdridge et al., 1971), located at the Punta Rio Claro Wildlife Refuge, Osa Peninsula, southwestern Costa Rica (8°39′N, 83°44′E), adjacent to the Golfo Dulce Forest Reserve (61,702 ha). This Refuge encompasses a total area of 247 ha, with about 90% of it covered by mature forest, while the rest is represented by secondary forest in advance stages of regeneration and open areas. The climate of the Osa Peninsula is characterized by high precipitation levels (3500–5000 mm), with a dry season between January and March, and the highest precipitation occurs during August to October. The temperature ranges from 21 to 33.5 °C (Lobo et al., 2008). Steep slopes dominate the topography and soils are mostly ultisols (Weissenhofer and Huber, 2001).

2.2. Study species

Virola surinamensis (Rol.) Warb., is a dioecious canopy tree distributed from Costa Rica to the Amazon basin. In Costa Rica it is found in both the Pacific and Atlantic slopes (Quesada et al., 1997). In Panama this species is associated with slopes and streams (Harms et al., 2001). Flowering occurs between November and January (P. Riba-Hernández, unpubl. data). In Brazil, flowers are reported to be pollinated by two species of flies, *Copestylum sp.* and *Erystalys* sp. in the Syrphidae family (Jardim and Mota, 2007). In the Osa Peninsula fruits mature between May and July (P. Riba-Hernandez, unpubl. data). Fruits are woody capsules containing a