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Research article

Effects of intraspecific and community density on the lifetime fecundity of long-lived shrubs

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ABSTRACT

Intra- and interspecific density dependence has profound consequences for plant population and community dynamics. In long-lived plants, however, lifetime patterns and mechanisms of density dependence are difficult to study. Here, we examine effects of intraspecific and community density on the lifetime fecundity of two long-lived shrub species from South African Fynbos: *Protea repens* (animal-pollinated, hermaphroditic) and *Leucadendron rubrum* (wind-pollinated, dioecious). Both species are serotinous, retaining seeds in cones until fire kills the mother plant. We measured lifetime fecundity as the product of cone number, proportion of cones that are not damaged by predation and seed set (fertile seeds per intact cone). Intraspecific and community densities were quantified by counting individuals of target species and all Proteaceae in small- and large-scale neighbourhoods (10 m and 50 m radius) around each focal individual. Additionally, we determined the age and size of focal individuals. We found that lifetime fecundity of the wind-pollinated *L. rubrum* is density independent. In contrast, the lifetime fecundity of the animal-pollinated *P. repens* increases with large-scale intraspecific density and shows a hump-shaped relationship to large-scale community density. Community density has a hump-shaped effect on seed set (probably through partial absence of generalized pollinators at low and competition for pollinators at high densities) and negatively affects cone number per individual. For both species, plant age decreases seed set while increasing lifetime fecundity. The qualitative differences in the density dependence of lifetime fecundity may arise from differences between animal and wind pollination. In particular, interactions with generalized animal pollinators may cause community-level Allee effects with profound consequences for the future dynamics of long-lived plant populations and communities.

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Introduction

The density dependence of fecundity and reproduction strongly shapes the dynamics of populations and communities. Negative density dependence determines the carrying capacity of populations, and the strength of negative density dependence affects the intrinsic stability of population dynamics (May, 1974). Moreover, the relative strength of negative intra- versus interspecific density dependence is important for community dynamics and species co-existence (Tilman, 1994; Chesson, 1994). However, density dependence is not necessarily negative: there is now substantial evidence that reproductive success decreases at low intraspecific densities (Lamont et al., 1993; Roll et al., 1997; Groom, 1998; Kery

et al., 2000; Hackney and McGraw, 2001). The resulting positive density dependence at low densities (a so-called Allee effect) can reduce population persistence, and has substantial consequences for the conservation and management of small populations (e.g. Courchamp et al., 2008).

Sessile plants interact over limited spatial scales (e.g. Silander, 1978; Law and Dieckmann, 2000; Gunton and Kunin, 2007). The dynamics of plant populations and communities thus depend on the spatial scales over which intra- and interspecific density effects act (Kunin, 1997; Groom, 1998; Bolker and Pacala, 1999; Moeller, 2004; Schurr et al., 2008). To understand and predict the dynamics of plant communities, we have to determine the magnitude, spatial scale and direction (positive or negative) of intra- and interspecific density dependence. This requires an understanding of the mechanisms that generate different types of density dependence.

A major mechanism causing negative density dependence of plant reproduction is competition for abiotic resources such as

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nutrients or light (e.g. Stoll and Weiner, 2000). However, negative density dependence can also arise from plant-animal interactions, for instance if pre-dispersal seed predators are attracted to high-density stands or if plants compete for flower visits by pollinating animals. At the same time, biotic and abiotic pollination is also a common cause for positive density dependence: plants in small populations often have reduced reproductive success because of decreased pollination quantity or quality (Ghazoul, 2005).

At low intraspecific densities, both wind- and animal-pollinated plants may show positive density dependence of pollination because the presence of conspecifics increases pollen production and reduces pollen loss, which may decrease pollen limitation (Ghazoul, 2005). In animal-pollinated plants, this positive density dependence may be further enforced if pollinators are absent from low-density populations (Sih and Baltus, 1987; Kunin, 1997). Above a certain intraspecific density, however, wind- and animal-pollinated plants may differ in the density effect on pollination: wind pollination is likely to become density-independent (unless conspecifics lower wind speeds, Kuparinen et al., 2007; Schurr et al., 2008), whereas animal-pollinated plants may increasingly compete for pollinator visits (Goulson, 2000; Ghazoul, 2005). Moreover, animal and wind pollination are expected to respond differently to the density of other plant species: heterospecific neighbours may either have no effect on wind pollination or they may decrease wind pollination by intercepting airborne pollen (Kuparinen et al., 2007) or enhancing interspecific pollen transfer (Friedman and Barrett, 2009). In contrast, pollination by animals can show complex responses to the density of other plant species. Animal-pollinated plants may suffer from competition for pollinators against more common flowering species (Levin and Anderson, 1970; Waser, 1978; Rathcke, 1988) or from interspecific pollen transfer (Ghazoul, 2005). However, they may also benefit from co-occurring plant species that attract shared pollinators, thereby increasing pollinator visits and enhancing seed production (Moeller, 2004; Ghazoul, 2006). In summary, wind pollination is expected to be independent of interspecific density and to show positive or no responses to intraspecific density, whereas animal pollination may show more complex responses to both intra- and interspecific density.

While experiments and observational studies have thus established multiple mechanisms of density dependence in plant communities, it is largely unclear how these different mechanisms interact to shape the lifetime fecundity or fitness of plants. In particular, we know very little about the density dependence of lifetime fecundity in long-lived plants. This is because the lifetime fecundity of long-lived species is typically difficult to measure. Our knowledge about the density dependence of fecundity thus originates largely from short-lived plants (especially annuals) or from short-term studies of long-lived plants (Ghazoul, 2005). However, the population and community dynamics of long-lived plants ultimately depends on lifetime rather than short-term effects on fecundity and reproduction. Hence, we need to know the density dependence of lifetime fecundity if we want to understand how interactions shape the population and community dynamics of long-lived plants.

Here we present a study of the density dependence of lifetime fecundity in two long-lived shrub species (*Protea repens* (L.) L. and *Leucadendron rubrum* Burm. f.) from the South African Cape Floristic Region (CFR). They are common members of the Proteaceae family which has developed into a model system for biodiversity research and is frequently used as an indicator group for conservation in the CFR (Schurr et al., 2012a). The serotinous habit of our study species enables direct measurements of lifetime fecundity (Bond et al., 1995): because they form canopy seed banks but no long-lived soil seed banks (Bond et al., 1984; Rebelo, 2001), the total fecundity of an individual can be measured as the product of cone number, the

proportion of intact, undamaged cones, and seed set per intact cone. Fire triggers seed release from the canopy and subsequent seedling recruitment while killing adult plants. Hence, the total fecundity of a plant is identical to the plant's lifetime fecundity given that it burns before the next flowering season (Bond et al., 1995). These long-lived shrubs are thus ideally suited to quantify how lifetime fecundity and its components vary with intraspecific and community (intra- and interspecific) density at different spatial scales.

Methods

Study system and study species

P. repens and *L. rubrum* are two common species of the Proteaceae family that co-occur in the Fynbos biome, a fire-prone Mediterranean-type vegetation in the CFR. Proteaceous shrubs play a key role for the functioning, conservation and economic use of Fynbos (Schurr et al., 2012a, 2012b). Both species produce inflorescences that consist of many individual flowers. Each flower contains a single ovule, so that – after successful fertilization – each fruit contains a single seed (Rebelo, 2001). Selfing is impossible in the dioecious *L. rubrum* and seems to be rare in the hermaphroditic and protandrous *P. repens* (Colins and Rebelo, 1987). Moreover, both species are serotinous: after flowering, their inflorescences develop into woody, fire-proof cones in which seeds are typically retained for many years until the mother plant burns or except when predated. In contrast, the survival and establishment probabilities of seeds released between fires are very low. Hence, the study species have long-lived canopy seed banks but no persistent soil seed banks (Bond et al., 1984; Rebelo, 2001). Pre-dispersal predation of the canopy seed bank is mostly caused by insects: for *P. repens* it has been shown that endophagous beetle and butterfly larvae (*Sphenoptera* spp. (Buprestidae), *Genuchus hottentottus* (Scarabaeidae), *Argyroplote* spp. (Olethreutidae), *Tinea* spp. (Tineidae)) are major seed predators (Coetzee and Giliomee, 1987a, 1987b; Wright and Samways, 1999).

Fire not only triggers seed release from cones, but also kills the adult plants of both study species (Rebelo, 2001). Hence, the total number of seeds that an individual retains at the time of a fire is a close proxy of the individual's lifetime fecundity, and has direct consequences for rates of post-fire population growth (Bond et al., 1995; Bond and van Wilgen, 1996; Rebelo, 2001; Schurr et al., 2005, 2007).

Our study species have a very similar life history which they share with many other species of CFR Proteaceae (Rebelo, 2001). Yet, they differ in sexual system (*L. rubrum* is dioecious whereas *P. repens* is hermaphroditic, see above) and in pollination syndrome: *L. rubrum* is wind-pollinated, whereas *P. repens* is animal-pollinated (Rebelo, 2001). The pollinator of *P. repens'* showy inflorescences comprise the Cape Sugarbird (*Promerops cafer*), sunbirds (*Nectarinia* spp.) and flying insects such as beetles (e.g. *Trichosteta* spp., *Hopliniidae*; Coetzee and Giliomee, 1985; Collins and Rebelo, 1987).

Study design

We studied 87 and 78 seed-bearing focal individuals of *P. repens* and *L. rubrum*, respectively. These focal individuals belonged to 30 and 15 populations, respectively, that were situated in an area of ca. 6000 km² (extending from 33°41'23" S to 34°31'34" S and from 18°30'39" E to 19°27'36" E) in the winter-rainfall area of the south-western Fynbos biome. The mean post-fire age of our study populations (~12 years) and minimum of 5 and maximum of 19 years falls well within the range of mean fire return intervals reported for Fynbos (10–20 years, Bond and van Wilgen, 1996; Le

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