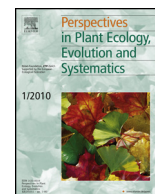




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## Research article

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

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## ARTICLE INFO

### Article history:

Received 26 March 2012

Received in revised form

22 December 2012

Accepted 18 March 2013

Available online 17 April 2013

### Keywords:

Competition

Community-level Allee effects

Facilitation

Fitness components

Interspecific interactions

Plant-animal interactions

## 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

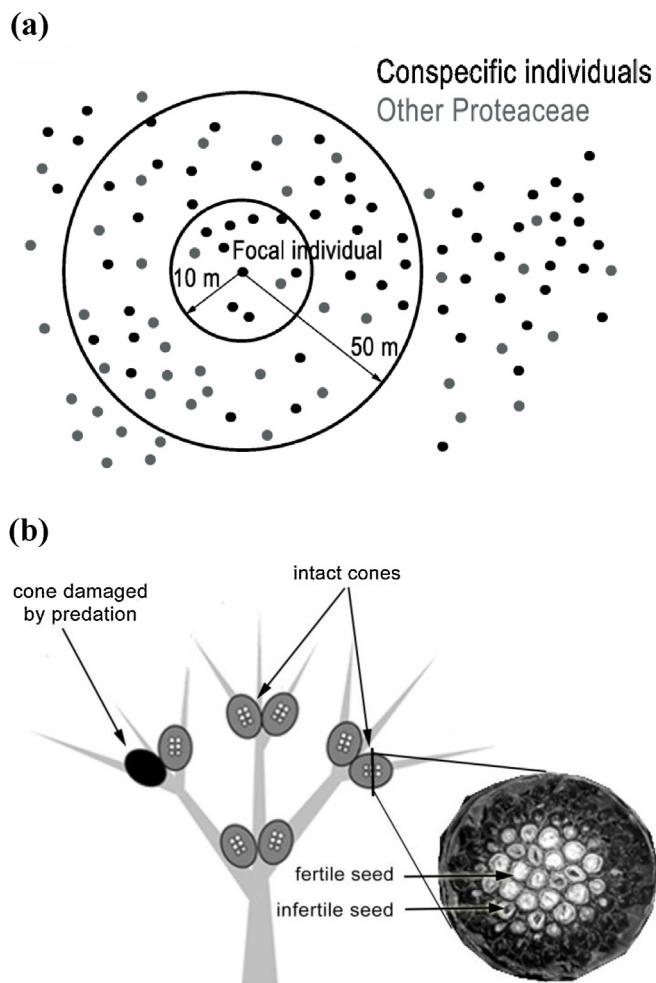
*P. repens* and *L. rubrum* are two common species of the Proteaceae family that co-occur in the Fynbos biome, a fire-prone Mediterranean-type vegetation in the CFR. Proteaceous shrubs play a key role for the functioning, conservation and economic use of Fynbos (Schurr et al., 2012a, 2012b). Both species 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. *Trichostetha* 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 km<sup>2</sup> (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



**Fig. 1.** The study design used to quantify the density-dependence of fecundity in serotinous Proteaceae from South African Fynbos. (a) The density of conspecifics and all overstorey Proteaceae was quantified in 10 m (small-scale) and 50 m (large-scale) radii around focal individuals. (b) Fecundity components that were used to quantify the lifetime fecundity of focal individuals belonging to two species of serotinous Proteaceae. The photograph on the bottom right shows a cross-sectioned *Protea repens* cone with fertile and infertile seeds.

Maitre, 1998). Hence, the mean size of individual seed reserves is a realistic measure of seed reserves at the expected time of the next fire and thus of expected lifetime fecundity.

For each focal individual, we counted the number of conspecific individuals and the number of overstorey Proteaceae individuals in circles of 10 m and 50 m radius (Fig. 1a). The 10 m radius (subsequently termed the small-scale neighbourhood) was chosen to reflect the area within which Proteaceae individuals interact for abiotic resources such as nutrients, water and light (10 m is approximately three times the average height of our study species, Rebelo, 2001). The 50 m radius (subsequently termed the large-scale neighbourhood) was chosen to reflect the pollination neighbourhood of the animal-pollinated *P. repens* (a circle of 50 m radius is close to the average territory size of Cape Sugarbirds, Calf et al., 2003) and seems a reasonable proxy for the pollination neighbourhood of the wind-pollinated *L. rubrum*. For the dioecious *L. rubrum* we initially distinguished between male and female conspecific neighbours. However, since male and female densities were highly correlated (Spearman's correlation coefficient between male and female density was 0.93 for both 10 m and 50 m radius), we only used the overall conspecific density for further analyses. In addition, we verified that the explicit inclusion of male and female density did not

improve models for seed set and seed predation, respectively. This underlines that overall conspecific density is a sufficient proxy for sex-specific densities.

The sum of conspecific and heterospecific density at each scale was our measure of community density.

For each focal plant, we determined individual age from node counts (Bond, 1985), quantified canopy volume from measures of canopy height and lateral extent, and counted the number of closed cones. Subsequently, we randomly harvested five closed cones of different ages. The harvested cones of *P. repens* were cut open with secateurs to count the numbers of fertile and infertile seeds (Fig. 1b), whereas the harvested cones of *L. rubrum* were bagged individually and placed in an oven at 50 °C for 5 days until they had released all seeds. Furthermore we checked the cones for signs of pre-dispersal seed predation such as infestation by beetles or stem-boring lepidopteran larvae. We distinguished between heavily damaged cones that did not contain any fertile seeds and "intact" cones that were not or only partly predated. The proportion of predation-damaged cones was used as a measure of pre-dispersal seed predation. Seemingly infertile seeds of *L. rubrum* were cut open to check whether they contained living embryonic tissue. Since each flower of our study species can only produce a single seed (Rebelo, 2001), the sum of fertile and infertile seeds per intact cone equals the number of flowers produced per inflorescence. Moreover, we measured seed set per intact cone as the mean number of fertile seeds.

In summary, we quantified three fecundity components for each focal individual: cone number per individual, the proportion of intact cones with no sign of predation, and seed set per intact cone. The lifetime fecundity of each individual was then determined as the product of these three components (Fig. 1b).

#### Statistical analyses

To analyse the density- and age-dependence of plant size, lifetime fecundity and its three components we used linear mixed-effects models (LME, package nlme, Pinheiro et al., 2007) in R 2.10.1 (R Development Core Team, 2009) with random effects of population that account for environmental variation between populations. We log-transformed all response variables except cone predation rate which was arcsine-square-root transformed. The maximal models for fecundity and its components included log-transformed plant age as well as linear and quadratic effects of intraspecific and community density in 10 m and 50 m radius. The maximal model for canopy volume included log-transformed plant age and its two way interactions with these density effects. Note that this maximal model did not include main effects of density; this is because cohort density may affect plant growth but is not expected to affect the initial size of seedlings. Following the procedure described in Crawley (2007), we simplified the maximal model by removing non-significant model terms ( $P > 0.05$ ) in a stepwise backward manner to obtain a minimal adequate model for each response variable. Main effects were not removed as long as the corresponding variable was still contained in an interaction (Venables and Ripley, 2002). In particular, linear density terms were not removed as long as the corresponding quadratic term was retained in the model. Minimal adequate models with linear and quadratic density terms can describe hump-shaped density dependence whereas models containing only linear density terms describe monotonic negative or positive density dependence.

#### Results

The sampled individuals showed considerable variation in neighbourhood density and composition. Small-scale

**Table 1**

Linear mixed-effects models for the density- and age-dependence of canopy volume, fecundity components and lifetime fecundity in the wind-pollinated *L. rubrum* and the animal-pollinated *P. repens*. For terms retained in the minimal adequate models, the table indicates the type of the effect (+: positive, -: negative,  $\cap$ : unimodal), and the associated parameter estimates for linear (L) and quadratic (Q) effects. Parameter estimates refer to the natural log of all response variables except cone predation (for which parameters refer to arcsine-square root transformed proportions). For models of canopy volume the entries in the density columns refer to density-age interactions, and significance values of age effects are not given since age interacts with density.

Response variables	<i>L. rubrum</i>						
	Intraspecific density (ind.)		Community density (ind.)		In Plant age (a)		
	10 m	50 m	10 m	50 m			
In Growth rate	n.s.		— <sup>***</sup>	L: -0.0040	n.s.	+	L: 3.761
In Cone number	— <sup>*</sup>	L: -0.006	n.s.		n.s.	+ <sup>***</sup>	L: 3.5912
arcsine Cone predation	n.s.		n.s.		n.s.	n.s.	
In Flowers per cone	n.s.		n.s.		n.s.	n.s.	
In Seed set per cone	n.s.		n.s.		n.s.	— <sup>*</sup>	L: -0.5264
In Lifetime fecundity	n.s.		n.s.		n.s.	+ <sup>***</sup>	L: 3.6501
Response variables	<i>P. repens</i>						
	Intraspecific density (ind.)		Community density (ind.)		In Plant age (a)		
	10 m	50 m	10 m	50 m			
In Growth rate	n.s.	n.s.	— <sup>***</sup>	L: -0.0048	n.s.	+	L: 3.434
In Cone number	n.s.	+ <sup>**</sup>	— <sup>**</sup>	L: -0.0110	n.s.	+ <sup>***</sup>	L: 2.5351
arcsine Cone predation	n.s.	$\cap$ <sup>*</sup>	n.s.		n.s.	n.s.	
							Q: -0.00002
In Flowers per cone	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	
In Seed set per cone	n.s.	n.s.	n.s.	$\cap$ <sup>***</sup>	L: 0.00510	— <sup>*</sup>	L: -0.4393
					Q: -0.00001		
In Lifetime fecundity	n.s.	+ <sup>*</sup>	n.s.	$\cap$ <sup>*</sup>	L: 0.00639	+ <sup>***</sup>	L: 2.2412
					Q: -0.00002		

\*  $P < 0.05$ .\*\*  $P < 0.01$ .\*\*\*  $P < 0.001$ .n.s.: not significant ( $P > 0.05$ ).

neighbourhoods (10 m radius) of the sampled *L. rubrum* plants contained 2–173 Proteaceae individuals, and their large-scale neighbourhoods (50 m radius) comprised 64–868 Proteaceae individuals. Small-scale neighbourhoods of *P. repens* held 0–105 Proteaceae, and large-scale neighbourhoods contained 0–420 Proteaceae. In both species, the proportion of conspecific neighbours varied widely between 0% and 100%. Moreover, the considered density measures did not show a clear relationship to plant age: with the exception of a weakly significant positive correlation between age and large-scale community density for *L. rubrum* (Spearman correlation,  $P = 0.04$ ), the density measures were not significantly correlated with age ( $P > 0.05$ ). The detected variation in density has direct consequences for plant growth. For both species, the minimal adequate models for canopy volume contain an interaction between plant age and small-scale community density (*L. rubrum*:  $\chi^2_{1df} = 19.7$ ,  $P < 0.001$ ; *P. repens*:  $\chi^2_{1df} = 13.2$ ,  $P < 0.001$ , Table 1). Plants with more small-scale neighbours thus had a lower growth rate.

#### Density dependence of fecundity in *L. rubrum*

Despite commonalities in the density dependence of growth rate, the two study species differ considerably in the density dependence of lifetime fecundity and its components (cone number, cone predation rate and seed set). In *L. rubrum*, fecundity and its components show relatively weak and monotonically negative density dependence (Table 1, Figs. 3 and 4). The minimal adequate model for cone number contains a negative effect of small-scale intraspecific density ( $\chi^2_{1df} = 6.3$ ,  $P < 0.05$ , Fig. 3a) and a positive effect of plant age ( $\chi^2_{1df} = 22.9$ ,  $P < 0.001$ ). Note, however, that alternative models in which small-scale intraspecific density was replaced by one of the three other density measures

provide similarly good explanations of variation in cone numbers ( $\Delta AIC < 1.2$  for all three alternative models). The proportion of predation damaged *L. rubrum* cones is generally low (median 0%, mean 6%) and independent of all density measures and age ( $P > 0.2$  for all explanatory variables). The same holds for the overall number of flowers per cone ( $P > 0.15$  for all explanatory variables). Seed set (the number of fertile seeds per cone) is also density-independent ( $P > 0.12$  for all density measures) but decreases significantly with plant age ( $\chi^2_{1df} = 5.1$ ,  $P < 0.05$ ). Consequently, the lifetime fecundity of *L. rubrum* as the product of cone number, proportion of undamaged cones and seed set shows a weak, non-significant negative response to small-scale community density ( $\chi^2_{1df} = 3.6$ ,  $P = 0.06$ , Fig. 4h). However, the minimal adequate model for *L. rubrum*'s lifetime fecundity only contains a positive effect of plant age ( $\chi^2_{1df} = 16.9$ ,  $P < 0.001$ ).

#### Density dependence of fecundity in *P. repens*

In contrast to the relatively simple patterns of density dependence observed for *L. rubrum*, the lifetime fecundity of *P. repens* and its components show rather complex responses to intraspecific and community density (Table 1, Figs. 5 and 6). Cone number per individual increases with large-scale intraspecific density ( $\chi^2_{1df} = 7.9$ ,  $P < 0.01$ , Fig. 5b), decreases with small-scale community density ( $\chi^2_{1df} = 9.0$ ,  $P < 0.01$ , Fig. 6a) and increases with plant age ( $\chi^2_{1df} = 39.8$ ,  $P < 0.001$ ). In contrast to *L. rubrum*, *P. repens* experienced a relatively high cone predation rate (median 20%, mean 19%) which showed a unimodal response to large-scale intraspecific density ( $\chi^2_{1df} = 5.4$ ,  $P < 0.05$ , Fig. 5d). As in *L. rubrum*, however, the number of flowers per *P. repens* cone is independent of plant age and all density measures ( $P > 0.3$  for all explanatory variables). Yet, the number of fertile seeds per *P. repens* cone shows a unimodal



response to large-scale community density ( $\chi^2_{1df} = 11.4$ ,  $P < 0.001$ , Fig. 6f) and decreases with plant age ( $\chi^2_{1df} = 6.2$ ,  $P < 0.05$ ). For the lifetime fecundity of *P. repens*, we found a unimodal effect of large-scale community density ( $\chi^2_{1df} = 5.5$ ,  $P < 0.05$ , Fig. 6h), and positive effects of large-scale intraspecific density ( $\chi^2_{1df} = 4.1$ ,  $P < 0.05$ , Fig. 5h) and plant age ( $\chi^2_{1df} = 23.2$ ,  $P < 0.001$ ).

#### Differences in the density dependence of lifetime fecundity

The two study species differ not only in that *P. repens* had significant density effects retained in the minimum adequate model for lifetime fecundity (Table 1); they also differ in the magnitude of the estimated density effects. In maximal models with scaled fecundity, density and age variables, the estimated effect of large-scale intraspecific density was 3.8 times larger for *P. repens* than for *L. rubrum*, and the linear and quadratic effects of large-scale community density were 2.6 and 2.3 times larger, respectively.

The lifetime fecundity of *P. repens* individuals is thus estimated to vary substantially as a function of large-scale intraspecific and community density (Fig. 7). In the absence of conspecific neighbours, the minimal adequate model predicts lifetime fecundity to increase 1.6-fold as large-scale community density increases from 0 to an optimal density of 146 individuals in 50 m radius. As community density increases further, lifetime fecundity is predicted to decrease: for the maximum community density observed in our study (420 individuals) it drops to 31% of the zero-density value. If all neighbours are conspecifics, the positive density dependence of fecundity is even more pronounced: in this case, lifetime fecundity increases 4.4-fold as large-scale density increases from 0 to an optimal density of 260 conspecifics in 50 m radius. Beyond this optimal density, fecundity is then extrapolated to decrease (Fig. 7, but note that this is an extrapolation as we did not sample conspecific densities above 244 individuals in 50 m radius).

#### Discussion

Our detailed analysis of lifetime fecundity in two species of long-lived Fynbos Proteaceae reveals both commonalities and striking differences between the study species. In both species, lifetime fecundity and its components show the same qualitative response to plant age (Table 1). Moreover, canopy volume and cone number of both species show similar negative density dependence. Yet, the two species differ markedly in the density dependence of pre-dispersal seed predation, seed set and lifetime fecundity (Table 1, Figs. 3–6). In the following, we first discuss which mechanisms are likely to cause these differences and commonalities, before highlighting some consequences of our findings for population and community dynamics.

#### Mechanisms of density dependence

A non-manipulative observational study like this cannot unequivocally identify mechanisms of density dependence. Yet, the presented detailed analysis of lifetime fecundity and its components together with the good understanding of the species' life history enables us to narrow down the suite of possible mechanisms underlying the observed patterns of density dependence.

In both species, individuals that experience a high small-scale community density grow less (Fig. 2), suggesting that they had fewer resources available for growth. Since the study species inhabit relatively infertile soils and Mediterranean climates with dry summers, they are likely to compete for nutrients and water. At high densities, small-scale competition for abiotic resources

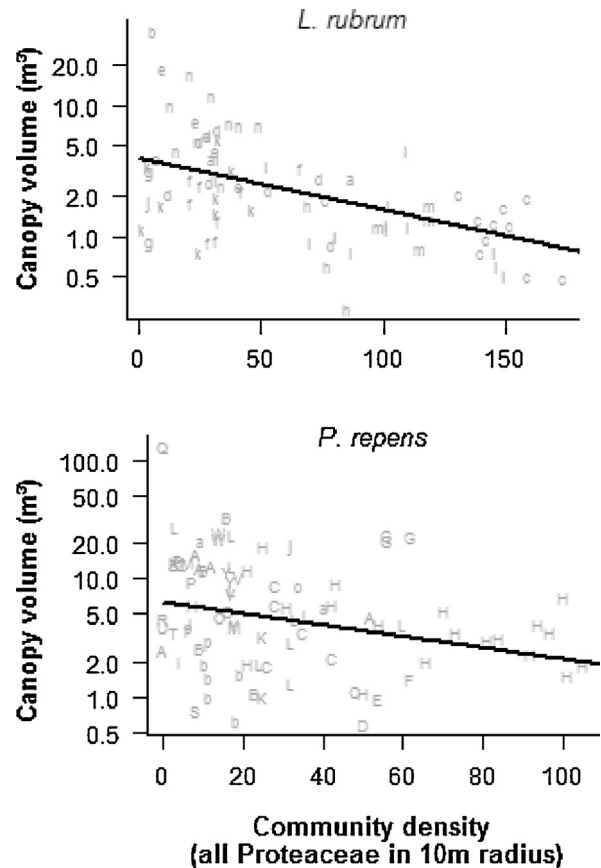
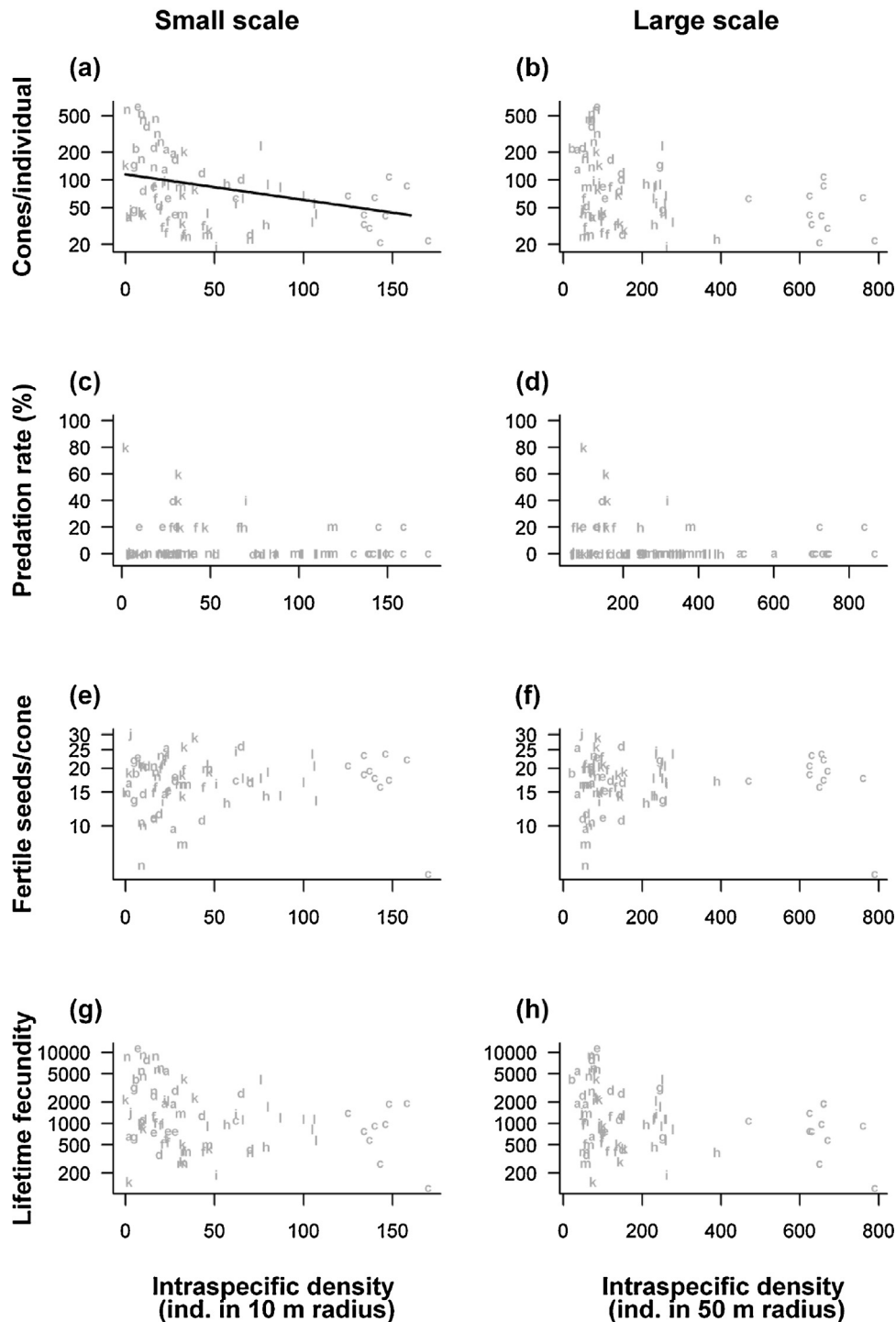


Fig. 2. Relationships between the canopy volume of *Leucadendron rubrum* and *Protea repens* individuals and small-scale community density around these focal individuals. Letters indicate different populations, and lines show predictions of minimal adequate LMEs. These predictions were calculated by setting plant age to its mean value (10 years for *L. rubrum*, 10.6 years for *P. repens*). Note that the y-axes are scaled logarithmically.

seems to lower not only the growth but also the cone production of both species: in *P. repens*, we found for cone number the same negative response to small-scale community density as for plant growth (Figs. 2 and 6, Table 1). In *L. rubrum*, growth and cone production also decrease with small-scale community density, although the minimal adequate model for cone production contains small-scale intraspecific rather than small-scale community density (Figs. 2 and 3, Table 1). However, due to the similar explanatory power of alternative density measures (see Results), we cannot conclude whether cone production of *L. rubrum* responds more strongly to intraspecific rather than heterospecific competition. In addition to such small-scale competitive effects, the cone production of *P. repens* also increases with large-scale intraspecific density (Fig. 5, Table 1). This could in principle result from variation in habitat quality: higher quality sites might both support higher densities and enable each individual to produce more cones. Yet, this explanation seems questionable since the growth of *P. repens* (as an alternative measure of plant performance) does not increase with large-scale intraspecific density (estimated effect of age-density interaction:  $-0.0001$ ,  $P = 0.74$ ). Thus, further research is needed to elucidate the mechanisms driving the positive relationship between cone number and large-scale intraspecific density of *P. repens*.

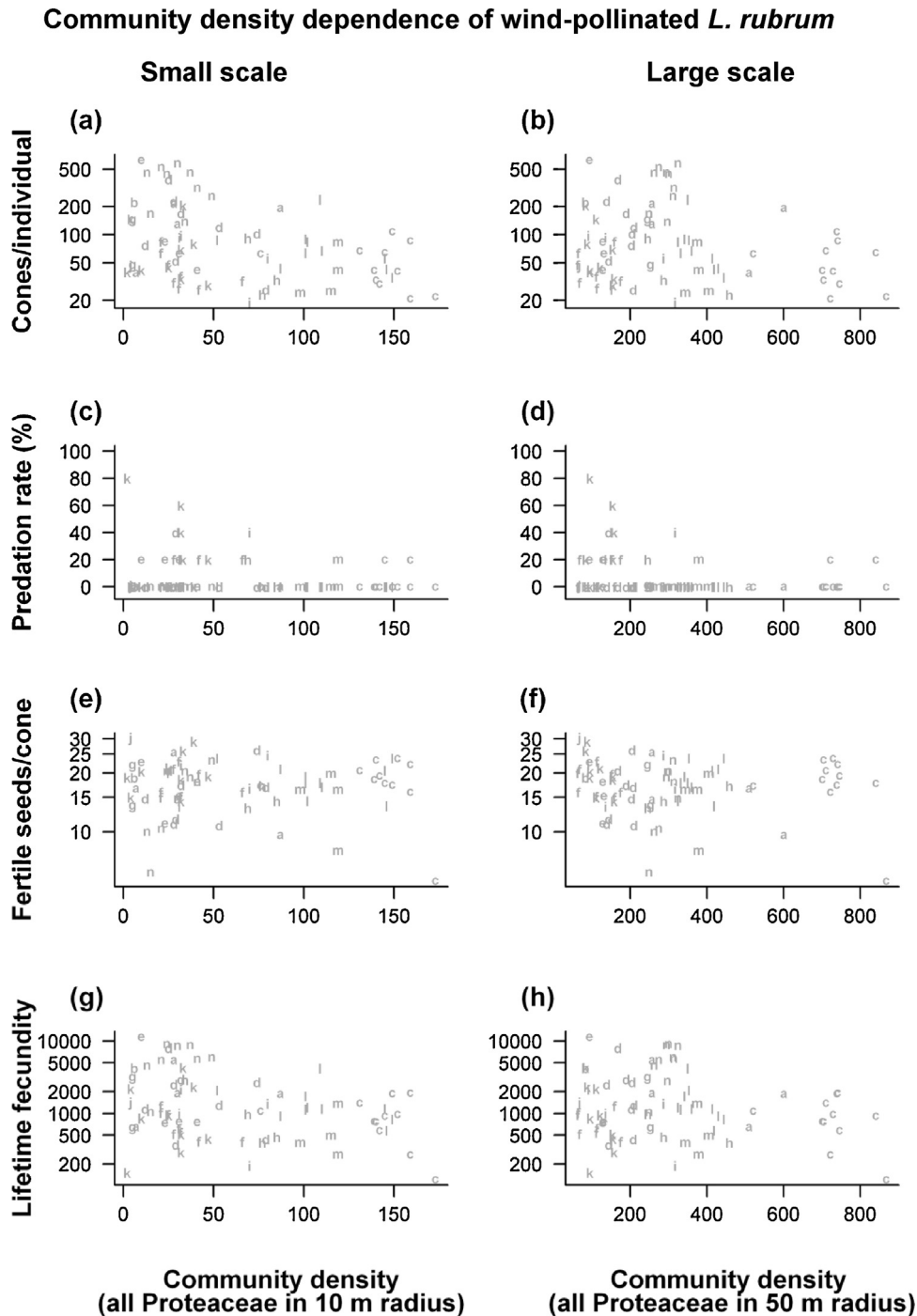
Since the number of flowers per inflorescence is age- and density-independent in both species (Table 1), age- and density dependence of seed set per cone is likely to arise from age and density effects on fertilization success and/or the survival of fertile

Intraspecific density dependence of wind-pollinated *L. rubrum*

**Fig. 3.** Cone number, cone predation rate, seed set and lifetime fecundity of 78 wind-pollinated *L. rubrum* individuals against intraspecific density on two spatial scales (10 m and 50 m radius). Letters indicate different populations, and lines represent LME predictions for terms retained in the minimal adequate model. These predictions were calculated by setting the retained age and density terms that were not plotted to their mean value. Note that all y-axes except those in (e) and (f) are scaled logarithmically.

seeds. In *P. repens*, seed set variation may additionally be shaped by a plant's allocation to pollen versus seed production. In both species we found average seed set per cone to decrease with plant age. This is a well-known phenomenon in serotinous Proteaceae: since seeds experience mortality in the canopy seed bank, older plants – in which mean cone age is higher – have less viable seeds per cone (Bond and van Wilgen, 1996).

Despite these similarities, the two species differ markedly in the density dependence of seed set per cone and cone predation: both fecundity components show unimodal density dependence in *P. repens* but are density-independent in *L. rubrum*. This is remarkable because the difference in sexual system should act in the opposite direction: in the dioecious *L. rubrum* low density neighbourhoods are likely to be dominated by a single sex, which should cause

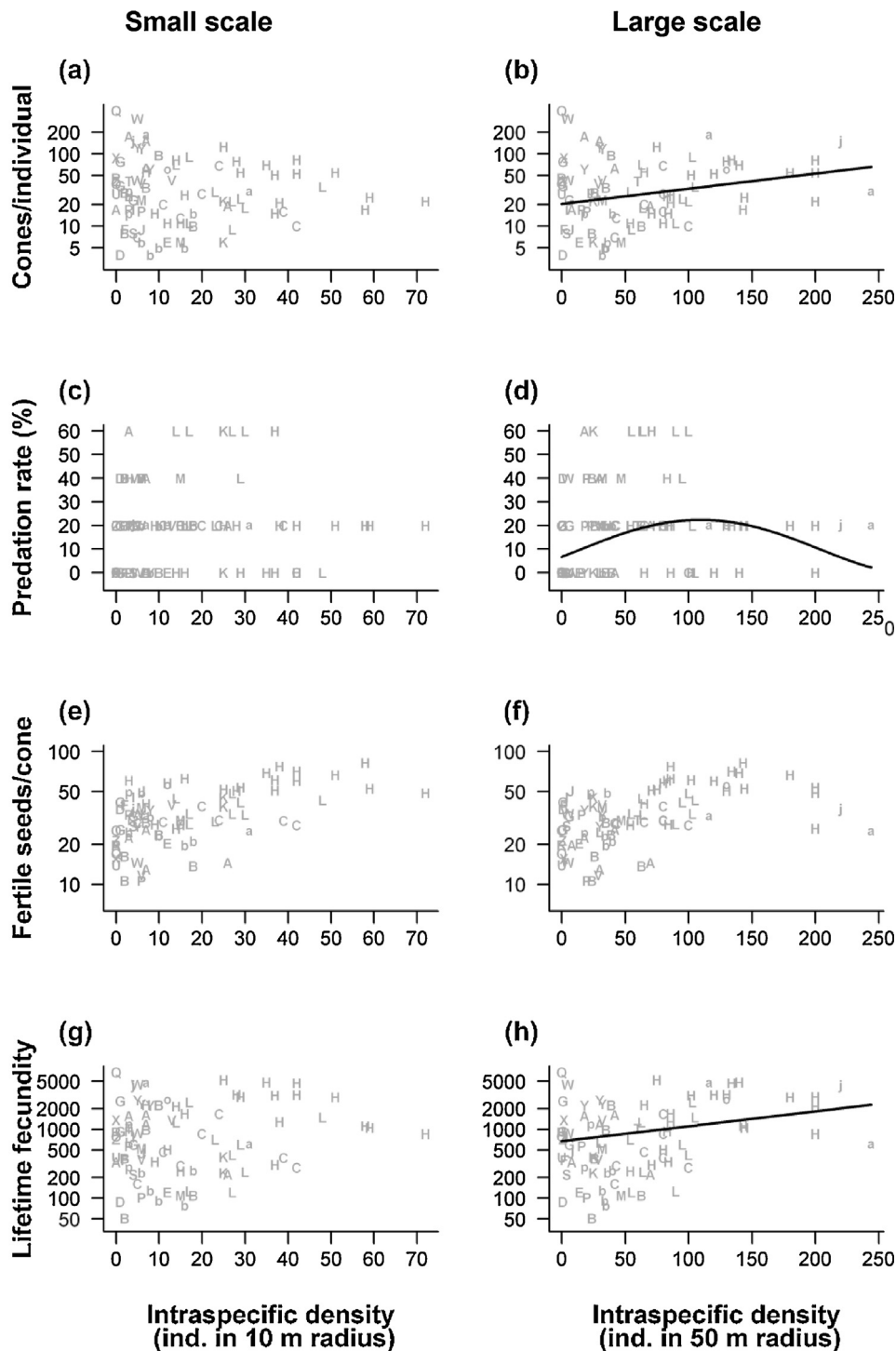


**Fig. 4.** Cone number, cone predation rate, seed set and lifetime fecundity of 78 wind-pollinated *L. rubrum* individuals against community density on two spatial scales (10 m and 50 m radius). For further details see Fig. 3.

positive intraspecific density dependence of seed set and cone predation. Species differences in sexual system thus cannot explain the differential density dependence of these fecundity components. In contrast, a likely explanation for the difference is that in *P. repens* both fecundity components are more strongly shaped by interactions with animals than in *L. rubrum*: *P. repens* not only depends on animals for pollination (Rebello, 2001), but its cones also harbour more insect seed predators (Roets et al., 2006), and consequently suffer from threefold higher rates of cone predation (Figs. 3–6). Possibly, the unimodal response of *P. repens*' seed set to large-scale

community density could arise from interactions with generalized pollinators (such as the Cape Sugarbird) that visit many species of nectar-producing Proteaceae (Collins and Rebello, 1987), whereas the unimodal dependence of *P. repens*' cone predation rates on large-scale intraspecific density may be caused by specialized seed predating insects.

Generally, the per-plant effect of plant-animal interactions may show unimodal density dependence if two conditions are met: (1) when plant stands are relatively sparse, an increase in plant density causes a disproportionate increase in animal density, e.g.

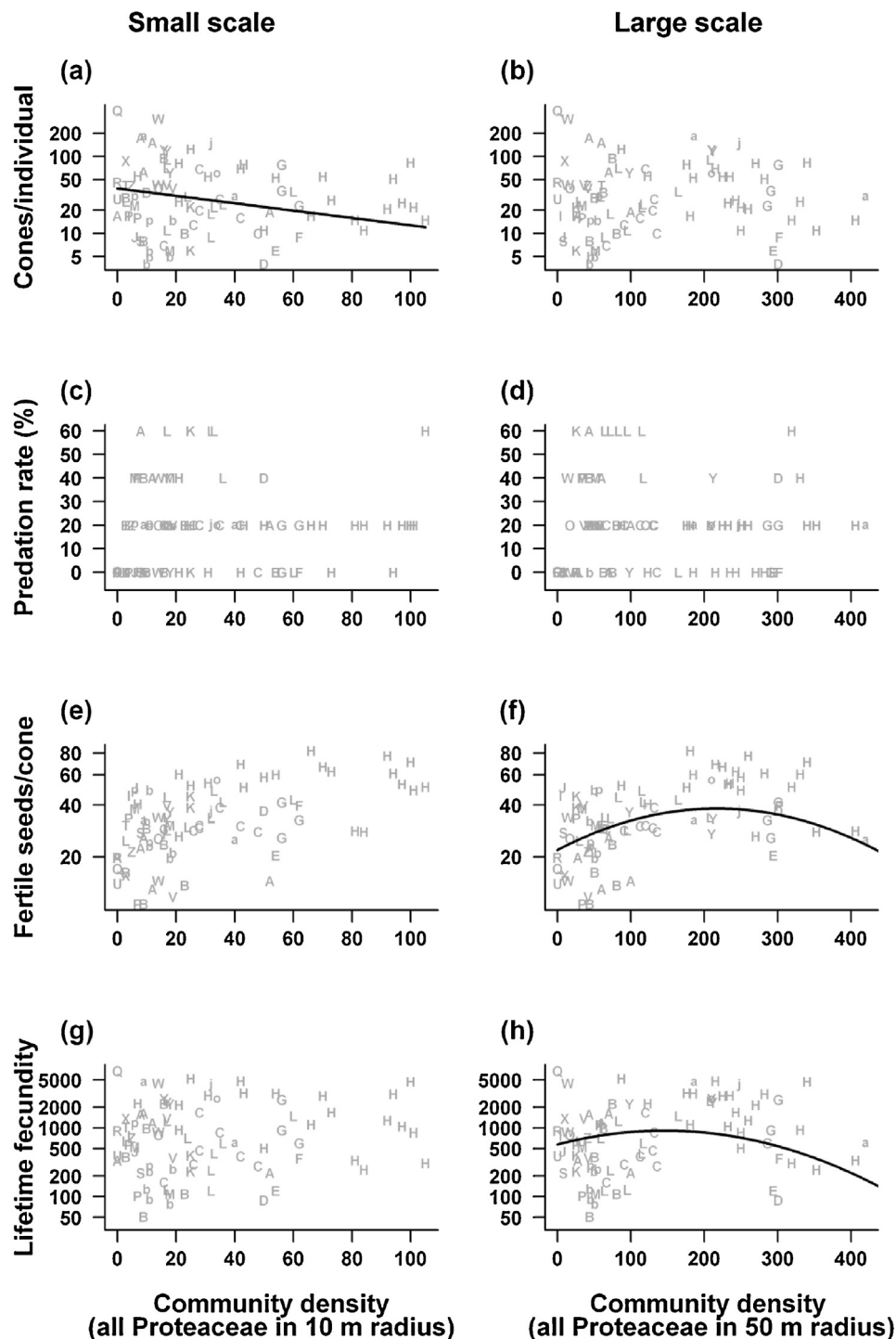
Intraspecific density dependence of animal-pollinated *P. repens*

**Fig. 5.** Cone number, cone predation rate, seed set and lifetime fecundity of 87 animal-pollinated *P. repens* individuals against intraspecific density on two spatial scales (10 m and 50 m radius). For further details see Fig. 3.

because the presence of animals requires a minimum level of plant-related resources that cannot be provided by a single plant and (2) at high plant densities, animal density is limited by resources that do not increase linearly with plant density. Both conditions are likely to be met for the interaction between (partly) bird-pollinated Proteaceae and the Cape Sugarbird. Cape Sugarbirds are typically absent from low-density Proteaceae stands in which

they cannot meet their daily energy requirements (Collins and Rebelo, 1987). However, in high-density Proteaceae stands that produce abundant nectar, the density of Cape Sugarbirds seems to be limited by territorial behaviour rather than nectar amounts (Calf et al., 2003) so that Sugarbird density should increase more slowly than the density of nectar-producing Proteaceae. Hence, the unimodal response of *P. repens*' seed set to community density



Community density dependence of animal-pollinated *P. repens*

**Fig. 6.** Cone number, cone predation rate, seed set and lifetime fecundity of 87 animal-pollinated *P. repens* individuals against community density on two spatial scales (10 m and 50 m radius). For further details see Fig. 3.

could arise because at low Proteaceae densities, pollination of an individual plant is first facilitated by neighbouring Proteaceae that help to attract Sugarbirds, whereas – as Proteaceae density increases further – plants increasingly compete for Sugarbird visits. Similar mechanisms could also act for insect pollinators and seed predators of *P. repens*: these insects may require a minimum density of plant resources (inflorescences or seeds) to build

up viable populations, whereas in high density stands their density may be limited by resources other than plant resources. Yet, this explanation is speculative because our knowledge about the insect pollinators and seed predators of *P. repens* and their resource requirements are much more limited than the respective knowledge about Cape Sugarbirds. It is worth noting that the seed set of *P. repens* did not drop to zero at low community densities. This

matches independent information that insects (which are likely to be present at Proteaceae densities too low for Sugarbirds) can effectively pollinate *P. repens* (Coetzee and Giliomee, 1985; B. Schmid, pers. comm.)

While the unimodal density dependence of both seed set and cone predation could potentially shape the lifetime fecundity of *P. repens*, we only detected a unimodal response of lifetime fecundity to large-scale community density. This suggests that *P. repens*' interactions with pollinators are more important for the density dependence of lifetime fecundity than its interactions with seed predators.

In summary, differences in pollination seem to be a key mechanism that causes our study species to differ in the density dependence of lifetime fecundity. In particular, animal pollination is likely to cause unimodal responses of *P. repens*' fecundity to community density. We speculate that this complex density dependence is not unique to *P. repens* but holds for many animal-pollinated serotinous Proteaceae and thus for the bulk of the Cape Proteaceae (only 3% of the serotinous species in this family are wind-pollinated, Rebelo, 2001). In the following, we explore how these differences in density dependence may affect the dynamics of serotinous Proteaceae populations and communities.

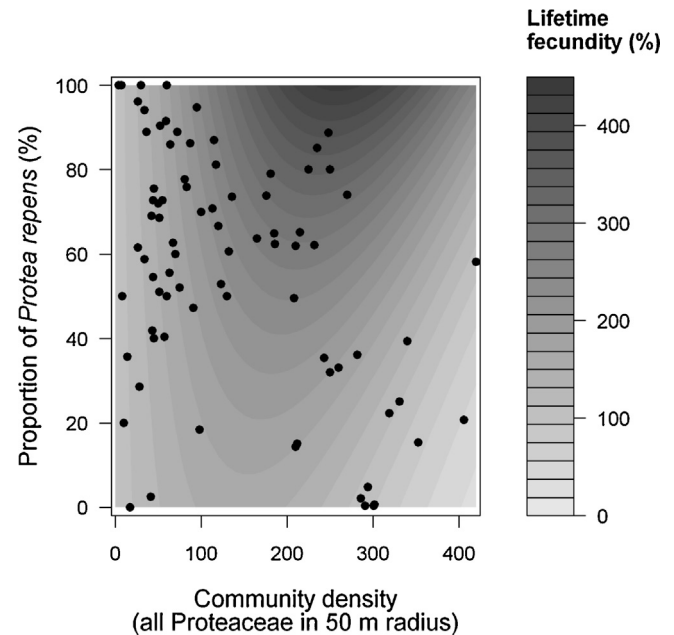
#### Consequences for population and community dynamics

For both study species, we found no evidence that lifetime fecundity is more negatively affected by conspecifics than by heterospecifics. Yet, this finding cannot directly be interpreted with respect to the coexistence of Proteaceae communities: to assess whether these communities can coexist locally (Esther et al., 2008), it will be necessary to quantify whether each species depresses its own population growth more than it depresses the population growth of other species (Chesson, 2000). Moreover, it seems promising to study whether the detected community-level Allee effects broaden the range of conditions under which multiple species can coexist in diverse Fynbos shrublands.

The detected interspecific differences in the density dependence of lifetime fecundity may not only affect species coexistence but also they are particularly likely to affect the response of our study species to environmental change. The absence of positive density dependence in *L. rubrum* suggests that this species is relatively robust to reductions in population or community density at the scales studied here. In particular, we found no positive density dependence of seed set which supports findings that wind-pollinated plants are generally less pollen-limited than animal-pollinated species (Friedman and Barrett, 2009). Potentially, the pollen limitation of *L. rubrum* could even be lowered further if global warming increases the probability of long-distance pollen transport by wind (Kuparinen et al., 2009).

In contrast, our results suggest that the lifetime fecundity of *P. repens* is likely to be reduced if factors such as increased fire frequency (e.g. Schurr et al., 2007; Wilson et al., 2010) or land transformation and climate change (Rouget et al., 2003; Cabral et al., 2012) lower either population or community density below certain critical levels (Fig. 7). This may even hold if these factors do not directly impact *P. repens* but rather lower the density of other Proteaceae. Moreover, since the community-level Allee effect seems to be caused by the response of pollinators to nectar resources, it seems likely that similar reductions of fecundity would also result from the commercial harvesting of Proteaceae inflorescences which can strongly reduce nectar provision in local Fynbos communities (e.g. Cabral et al., 2011).

Population and community-level Allee effects can have profound consequences for large-scale biogeographical dynamics (e.g. Keitt et al., 2001; Holt, 2009; Cabral and Schurr, 2010; Schurr



**Fig. 7.** Density dependence of lifetime fecundity in the animal-pollinated *P. repens*. Shades of grey indicate predictions of the minimal adequate model that describes how the fecundity of an individual varies with community density in 50 m radius and with the proportion of conspecifics in this radius. Fecundity is expressed relative to the fecundity of an individual growing at zero density. Points indicate observed variation in the density and composition of Proteaceae communities around *P. repens* individuals.

et al., 2012b). In fact, using a top-down approach Cabral and Schurr (2010) concluded that intraspecific Allee effects shape abundance variation across the geographical range of several Fynbos Proteaceae. This study now provides bottom-up evidence for the existence of such Allee effects in *P. repens*. Yet, to relate relatively small-scale studies like ours to large-scale models for biogeographical dynamics (e.g. Cabral and Schurr, 2010; Huntley et al., 2010), we need further research on the scaling of density dependence (Schurr et al., 2012b). This seems worthwhile since results like ours may help to predict the future dynamics of novel communities arising due to environmental change (Thuiller et al., 2008; Kissling et al., 2012). Predictions for such novel communities are particularly challenging in extremely species-rich systems like the CFR (Yates et al., 2010). So far studies of Fynbos Proteaceae only considered competitive effects on migration, showing that interspecific competition can markedly slow down migration rates under climate change (Higgins et al., 2008). Yet, our results suggest that pollinator-mediated facilitation by other species (Fig. 7) may promote the immigration of animal-pollinated species into areas that are already occupied by other animal-pollinated Proteaceae. In contrast, community-level Allee effects may slow down expansion into areas that are currently not occupied by nectar-producing Proteaceae.

#### Conclusions

The study of serotinous shrubs can provide insights into the patterns and mechanisms of density dependence, which are otherwise very difficult to obtain for long-lived plants. For two species of serotinous Proteaceae, we found striking differences in how lifetime fecundity depends on the density of conspecifics and all Proteaceae at two spatial scales. The decomposition of lifetime fecundity into its individual components (cone number, cone predation and seed set per cone) suggests that these

differences mainly arise from differences in how strongly these species interact with animals (notably pollinators). While fecundity of the wind-pollinated *L. rubrum* is density-independent, the unimodal response of *P. repens*' lifetime fecundity to large-scale community density may arise from interactions with generalized pollinators. The resulting community-level Allee effects might have profound consequences for the dynamics of Proteaceae communities. Understanding the mechanisms that cause such complex density dependence seems indispensable for predicting how plant communities will respond to future environmental change.

## Acknowledgements

We thank Mirijam Gaertner and Anne Horn for their helpful assistance during field work which was conducted under CapeNature permit AAA005-00074-0028. We are grateful to the reviewers for their insightful comments. HN thanks Jörn Pagel for inspiring comments and discussions. This work was supported by the German Ministry of Education and Research (BMBF) in the framework of Biota Southern Africa (FKZ: 54419938) and by the German Research Foundation (SCHU 2259/3-1). FMS additionally acknowledges support from the European Union through Marie Curie Transfer of Knowledge Project FEMMES (MTKD-CT-2006-042261). This is publication ISEM 2013-030 of the Institut des Sciences de l'Evolution de Montpellier.

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