Lachmuth, S., Henrichmann, C., **Horn, J.**, Pagel, J., Schurr, F.M. (2018):
Neighbourhood effects on plant reproduction: An experimental–analytical framework and its application to the invasive *Senecio inaequidens*
J. Ecol. **106** (2), 761 – 773

http://dx.doi.org/10.1111/1365-2745.12816

DR. SUSANNE LACHMUTH (Orcid ID : 0000-0002-4027-7632)
MR. JOERN PAGEL (Orcid ID : 0000-0002-4817-1920)
PROFESSOR FRANK M. SCHURR (Orcid ID : 0000-0002-4518-0602)

Article type : Standard Paper
Editor : Nicole Rafferty

Title: Neighbourhood effects on plant reproduction: an experimental-analytical framework and its application to the invasive *Senecio inaequidens*

Susanne Lachmuth[1,2,*], Colette Henrichmann[3], Juliane Horn[1,4], Jörn Pagel[3,5], Frank M. Schurr[3,5]

[1]Martin Luther University Halle Wittenberg, Plant Ecology, Am Kirchtor 1, 06108 Halle, Germany

[2]German Center for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103, Leipzig, Germany

[3]University of Potsdam, Plant Ecology and Nature Conservation, Am Neuen Palais 10, 14469 Potsdam, Germany

[4]Helmholtz-Centre for Environmental Research – UFZ, Department Ecological Modelling, Permoserstr. 15, 04318 Leipzig, Germany

[5]University of Hohenheim, Institute of Landscape Ecology and Plant Ecology, August von Hartmann-Str. 3, 70599 Stuttgart, Germany

[*]Corresponding author: Susanne Lachmuth; e-mail: susanne.lachmuth@botanik.uni-halle.de; phone: (+49) 345-55-26212; fax: (+49) 345-55-27228

Running headline: Neighbourhood effects on plant reproduction

Summary

1. Density-dependence is of fundamental importance for population and range dynamics. Density-dependent reproduction of plants arises from competitive and facilitative plant-plant interactions that can be pollination-independent or pollination-mediated. In small and sparse populations, conspecific density-dependence often turns from negative to positive and causes Allee effects. Reproduction may also increase with heterospecific density (community-level Allee effect), but the underlying mechanisms are poorly understood and the consequences for community dynamics can be complex. Allee effects have crucial consequences for the conservation of declining species, but also the dynamics of range edge populations. In invasive species, Allee effects may slow or stop range expansion.
2. Observational studies in natural plant communities cannot distinguish whether reproduction is limited by pollination-mediated interactions among plants or by other neighbourhood effects (e.g. competition for abiotic resources). Even experimental pollen supply cannot distinguish whether variation in reproduction is caused by direct density effects or by plant traits correlated with density. Finally, it is unknown over which spatial scales pollination-mediated interactions occur.
3. To circumvent these problems, we introduce a comprehensive experimental and analytical framework which simultaneously (1) manipulates pollen availability and quality by hand pollination and pollinator exclusion, (2) manipulates neighbourhoods by transplanting target plants, and (3) analyses the effects of con- and heterospecific neighbourhoods on reproduction with spatially-explicit trait-based neighbourhood models.

4. Applying this framework to *Senecio inaequidens*, one of Europe's fastest plant invaders, we found that the seed set was strongly pollen-limited. Reproduction had increased by pollinator-mediated facilitation by both con- and heterospecific neighbours which may lead to (community-level) Allee effects. Pollination-independent interactions, such as

amelioration of abiotic conditions through neighbours, contributed to additional positive neighbour effects. However, these pollination-independent interactions were weaker than the pollination-mediated interactions and they occurred over smaller spatial scales. Finally, the strength and direction of neighbourhood effects depended on neighbour traits and thus changed with the trait composition of the neighbourhood.

5. Synthesis. By manipulating both pollen availability and target plant locations within neighbourhoods, we can comprehensively analyse spatially-explicit density-dependence of plant reproduction. This experimental approach enhances our ability to understand the dynamics of sparse populations and of species' geographical ranges.

Keywords: Allee effect, biological invasion, density-dependence, competition, facilitation, plant-plant interactions, pollination, reproductive success, spatially-explicit model, trait-based neighbourhood model

Introduction

The fitness of plant individuals is strongly influenced by competitive and facilitative interactions with both con- and heterospecific neighbours. Whereas plant-plant competition and facilitation mediated by abiotic resources have been studied for decades (Stoll & Weiner 2000; Brooker *et al.* 2008), interactions mediated by other species are less well understood (Moeller 2004; Tur *et al.* 2016). This is particularly true for pollinator-mediated interactions and their effects on reproduction in small and sparse populations at range edges, or in habitats with adverse abiotic conditions, which can play a crucial role for range dynamics (Svenning *et al.* 2014; Tur *et al.* 2016).

In small or sparse populations, conspecific density-dependence is often positive and causes Allee effects (Allee 1931; Courchamp, Clutton-Brock & Grenfell 1999). This has critical implications for the conservation of declining species (Courchamp *et al.* 1999) as well as the dynamics of range edge populations (Liebhold & Bascompte 2003; Forsyth 2003; Cabral & Schurr 2010). Allee effects are also particularly important for invasive species since they may lead to propagation failure (invasion pinning), slow down rates of range expansion (Keitt, Lewis & Holt 2001; Taylor & Hastings 2005), and contribute to the lag-phases frequently observed in biological invasions (Taylor & Hastings 2005). When population density increases, density-dependence usually turns negative due to a prevalence of competitive plant-plant interactions (Taylor & Hastings 2005). Positive density-dependence has also been observed for heterospecific density (referred to as the community-level Allee effect by Nottebrock, Esler & Schurr (2013), see also Nottebrock *et al.* (2016)). For plants, which are immobile and rely on external vectors to achieve mating (e.g. wind, animal pollinators), intraspecific and community-level Allee effects often result from pollination-mediated plant-plant interactions (Lamont, Klinkhamer & Witkowski 1993; Moeller 2004; Nottebrock *et al.* 2013, 2016).

Pollination success is both a matter of conspecific pollen availability and of adequate pollination by external vectors (Pauw & Bond 2011; Ollerton, Winfree & Tarrant 2011; Pauw 2013). In animal-pollinated species, individuals growing in low-density floral neighbourhoods may benefit from noticeable conspecifics and heterospecifics, both of which can attract pollinators (Moeller 2004; Ghazoul 2006; Dauber *et al.* 2010; Nottebrock *et al.* 2013; Seifan *et al.* 2014; Tur *et al.* 2016). However, individuals growing in attractive neighbourhoods may suffer to compete for pollinators. Intra- and interspecific competition may decrease pollinator visits and thus the quantity of deposited pollen, and heterospecific neighbours may additionally decrease pollen quality by diluting the transferred pollen with incompatible pollen (Morales & Traveset 2008; Mitchell *et al.* 2009; Morales & Traveset 2009; Muchhala & Thomson 2012; Nottebrock *et al.* 2017). Pollen of both low quality and quantity can therefore reduce a plant’s reproductive success (Turnbull, Crawley & Rees 2000; Ashman *et al.* 2004; Knight *et al.* 2005).

Seed set not only depends on the abovementioned pollination-mediated interactions but also on pollination-independent interactions among plants. The most prevalent and consequently most studied pollination-independent plant-plant interaction is competition with con- and heterospecific neighbours for abiotic resources (Harper 1977). Furthermore, indirect plant-plant interactions may arise from "apparent competition" (Holt 1977) mediated by shared antagonists (Nottebrock *et al.* 2017). Under harsh environmental conditions, however, the negative effect of density often decreases and facilitative effects become relatively more important (Bertness & Callaway 1994, He et al. 2013). Positive density-dependence of reproduction may for example arise from the alleviation of biotic and abiotic conditions through con- or heterospecific neighbours (e.g. accumulation of nutrients, provision of shade, amelioration of disturbance, or protection from herbivores (Callaway *et al.* 2002)).

Studies investigating the density-dependence of reproduction in natural communities face the challenge to disentangle trait effects as well as pollination-mediated and pollination independent plant-plant interactions. Firstly, purely observational studies cannot unequivocally distinguish whether reproduction is limited by pollen availability or by other mechanisms such as the availability of abiotic resources. Consequently, statistical analyses cannot easily separate pollination-mediated plant-plant interactions from pollination-independent neighbourhood effects. This problem can be avoided by experimentally manipulating the quantity and quality of pollen supply. Secondly, it remains to be distinguished whether observed variation in reproduction is caused by direct density effects or by target plant traits correlated with density. For example, reproduction may be influenced by variation in plant size rather than by direct effects of site and neighbourhood-related resource and pollen availability. Transplant experiments provide a method to disentangle these effects. Here, we propose a comprehensive empirical approach towards the density-dependence of pollination that combines manipulating pollen availability (quantity and quality) and target plant locations within neighbourhoods (Fig. 1).

Not only can the effects of the aforementioned pollination-mediated and pollination-independent interactions be present over different spatial scales but also can the strength of these effects differ according to scale (Hegland 2014; Schmid et al. 2016; Nottebrock et al. 2016). Neighbourhood models (Weiner 1982; Pacala & Silander 1985), which analyse the response of performance traits of a plant individual to predictor variables derived from attributes of its neighbours, such as their number, distance, size or species identity, are a flexible and powerful tool to untangle and quantify these complex spatial interactions. Early neighbourhood models investigated plant-plant interactions by regressing the performance of target plants against the density and/or mean traits of neighbours at a predefined spatial scale (Pacala & Silander 1985, 1990). They thus ignored neighbourhood heterogeneity and the fact that neighbourhood effects generally decrease with spatial distance (Stoll & Weiner 2000). More recent statistical neighbourhood analyses have overcome these limitations by analysing plant performance with respect to spatially-explicit maps of individual plant locations (Stoll & Newbery 2005; Canham & Uriarte 2006). However, species-specific approaches soon face an intractable amount of parameters to be estimated as the number of interacting species increases (McGill *et al.* 2006). This has motivated attempts at replacing them by trait-based spatially-explicit neighbourhood analyses (Uriarte *et al.* 2004, 2010), which diminish the complexity of species-specific approaches and promote a mechanistic understanding of community dynamics (McGill *et al.* 2006).

Here, we report on a field study that used a combination of the above-described experimental manipulation and trait-based spatially-explicit neighbourhood analyses to explore the degree and underlying causes of pollen limitation in the invasive South-African ragwort *Senecio inaequidens* DC. by specifically addressing the following questions: (1) How do size and floral display affect the seed set of transplanted target *S. inaequidens* individuals (i.e. target effects)? (2) How do interactions with con- and heterospecific neighbours affect seed set (i.e. neighbourhood effects)? (3) How do these neighbourhood effects depend on neighbour size and floral display? (4) To which degree are the target and neighbourhood effects on reproduction mediated by pollination? (5) Over which spatial scales do pollination-mediated vs. pollination-independent interactions operate?

Materials and methods

Study species

Senecio inaequidens DC. (Asteraceae) is a perennial chamaephytic herb. The species is native to South Africa and Lesotho, where it mainly occurs in disturbed habitats with weak competition, such as steep rocky slopes, gravelly riverbeds, road verges and burnt areas (Heger & Böhmer 2005). *Senecio inaequidens* was unintentionally introduced to Europe in the late 19th – early 20th centuries and started spreading rapidly in the early 1970s (Lachmuth, Durka & Schurr 2010). In Germany, *S. inaequidens* is colonizing mostly ruderal habitats like railway tracks and road ditches and is occasionally present on fallow fields in early succession stages (Bossdorf, Lipowsky & Prati 2008). Individuals reach heights from 60-100 cm and develop up to 120 shoots bearing up to 3 500 capitula and 280 000 achenes during one flowering season lasting from May to December in Central Europe (S.L. personal observation). Florets are protandrous and mature in a centripetal manner in the capitulum (Heger & Böhmer 2005; López-García & Maillet 2005). The tetraploid cytotype occurring in Europe (Lafuma *et al.* 2003) is highly self-incompatible, presumably due to a homomorphic sporophytic self-incompatibility system which is commonly found for Asteraceae such as the closely related *S. squalidus* (Pelser, Gravendeel & Meijden 2002; Hiscock & Tabah 2003; Lafuma & Maurice 2007). However, single individuals have been observed to set seed following self-fertilisation (López-García & Maillet 2005; Lafuma & Maurice 2007; Vanparys *et al.* 2011). The species is pollinated by many generalist insects (such as Hymenoptera, Diptera and to a lesser extend Lepidoptera and Coleoptera) and seeds are mainly wind-dispersed (Lafuma & Maurice 2007; Vanparys, Meerts & Jacquemart 2008).

Study site

Field studies were carried out in the area of a former opencast mine near Zwenkau, Saxony, Germany (51°14’38.72’’, 12°18’34.79’’). Due to past mining work and recently performed recultivation activities (1999 - 2008), the dry and wind-exposed study site (210 x 145 m, Fig. S1 in supporting information) was sparsely vegetated, though it displayed variation in vegetation cover comprised of mainly rural herbs. The most dominant species were *Trifolium ssp*., *Matricaria chamomilla* L., *Lotus corniculatus* L., *Daucus carota* L., *Conyza canadensis* (L.) Cronquist, *Epilobium angustifolium* L. and several other Asteraceae species (see Table S1). Prior to our experiment, *S. inaequidens* was already established on the study site and was found mostly in the more vegetated parts. We specifically selected this study site as it contained large areas without any potential con- or heterospecific neighbours as well as all types of combinations of high to low con- and heterospecific densities.

Transplant experiment

At the end of July 2011, 81 individuals of *S. inaequidens* varying in size and amount of apparent capitula were collected from the nearby surroundings of our study site. Neither fungi nor herbivores were thought to have infested the selected individuals. We transplanted these target individuals into our study site and made sure to place those of various sizes and numbers of capitula into locations with differing neighbour densities of conspecifics as well as heterospecifics. This ensured a continuous variation in distances between target individuals and neighbours as well as in the trait composition of the floral neighbourhood. In particular, we established target plants in extreme isolation with no conspecific neighbour within 40 meters to cover a wide range of variation in both overall neighbour density and the proportion of conspecific neighbours. Before beginning the experiment, target individuals were watered for five days and allowed for another seven days to recover from transplanting. In order to minimise edge effects, we repeatedly removed all *S. inaequidens* from a 20 m broad buffer strip around our study site.

Neighbourhood mapping and measuring of covariates

For the neighbourhood analysis, we mapped every *S. inaequidens* individual (the 81 transplanted target individuals and 477 already established non-target individuals) within our study site (Fig. S1) with a highly accurate Differential GPS (DGPS) (© Leica GPS 1200 Series, Leica Geosystems AG, Heerbrugg, Switzerland). The following traits were measured as proxies for the size and floral display of these individuals: plant height from the ground to the tip of the canopy (height), the number of shoots originating within 1 cm from the soil surface (shoots), and the number of open and withered capitula. Histograms of these traits of *S. inaequidens* individuals are presented in Fig. S2.

Within our study site and the 20 m broad buffer zone, we mapped overall 3 257 single individuals of 25 insect-pollinated species co-flowering from July to October (according to BIOLFLOR database (Klotz, Kühn & Durka 2002), Table S1) to address the effects of heterospecific neighbours on the pollination success of *S. inaequidens.* The canopy diameter (at its broadest point) and the estimated floral cover (in %) within this diameter was recorded for each heterospecific individual. To increase mapping efficiency, high-density stands of five species were not mapped individually but rather the outline of polygons were mapped in which the respective species showed a constant density. For each polygon, we estimated the overall cover of the relevant species (in %) and then used this information to simulate regularly distributed individuals within the respective polygon. Mean values of canopy diameter and floral cover were assessed based on at least 30 randomly selected individuals per species and assigned to the overall 8034 simulated individuals.

Pollination experiments

Pollination experiments were performed during the period of August 6th to September 19th 2011 by applying the following four pollination treatments on different capitula of the transplanted target individuals: open pollinated (OPEN), cross-pollinated (CROSS), self-pollinated (SELF) and pollinator exclusion (EXCLUSION). Capitula chosen for these treatments were marked with plastic-collars, and, with the exception of the OPEN treatment, were bagged in transparent, air-permeable plastic foil prior to flowering (Fig. S3). Treatments commenced upon the opening of the first disk florets. To assess the seed set developed through natural pollination in neighbourhoods of varying densities, capitula were left open to pollination by insects (treatment OPEN). We applied pollen augmentation (treatment CROSS) in order to determine if *S. inaequidens* reproduction was pollen limited. These capitula received supplemental pollen for five consecutive days until the end of anthesis. Cross hand-pollinations were performed with each three pollen loaded capitula, which we harvested from three different individuals outside the study site. Directly after harvesting, we gently brushed these capitula onto the stigmas of the receptor capitulum until it was covered with pollen. Capitula were self-pollinated (treatment SELF) to test whether our study population displayed a high degree of self-incompatibility previously described for invasive *S. inaequidens* (López-García & Maillet 2005; Lafuma & Maurice 2007; Vanparys *et al.* 2011). To this end, pollen of anthers was carefully extracted with a wooden single-use spatula and applied to stigmas of the same capitulum for five days in a row. Further capitula were simply bagged, receiving no external pollination (treatment EXCLUSION) in order to check for the species' ability for spontaneous, pollinator-independent self-pollination.

These treatments were applied in three successive rounds (round 1, 2 and 3, see Table S2 for details) to achieve a high number and equal distribution of pollination across the target individuals. Round 1 encompassed the whole experimental period due to differences in individual flowering phenology. Individuals that received their first treatments early and flowered sufficiently throughout the whole period were included in the pollination experiments throughout (i.e. round 2 and 3). Sixteen individuals were excluded from the experiments under the condition that they either did not survive transplanting or failed to produce inflorescences. Data from three further individuals later had to be excluded from the analysis due to damaged exclusion bags. Whenever an individual simultaneously displayed at least two capitula in an early stage of flowering (i.e. no ray florets open), depending on the number of available capitula per plant, these were randomly assigned to treatments in the following order: OPEN, CROSS, OPEN, SELF, EXCLUSION. The OPEN treatment was thereby duplicated for individuals with at least three capitula to prevent data losses. Overall, there were 71 replicates for both the OPEN and CROSS treatment, 32 cases of self-pollination and 21 capitula were assigned to the EXCLUSION treatment. All treatments were always applied simultaneously for each individual per every round.

At the end of anthesis, all capitula assigned to treatments OPEN, CROSS, SELF and EXCLUSION were bagged in order to prevent seed loss and collected two weeks later when achenes were mature and near to release. Numbers of fertile and non-fertile seeds were counted under aid of a binocular microscope. The dark achenes filled with a fertile seed are easily distinguishable from the white and thin unfertilised ovules (Lafuma & Maurice 2007). Seed set was calculated as the ratio between the number of fertile seeds (*N.fert*) and the sum of fertile seeds and unfertilised ovules (*N.tot*). Whenever two capitula of an individual had been assigned to treatment OPEN, the sum of fertile seeds and unfertilised ovules of these capitula was taken. Fertile seeds of all treated capitula were weighed and mean seed masses per capitulum were calculated. To consider potential effects of transplanting on the fitness of target individuals, we collected an additional 55 open-pollinated capitula of non-target *S. inaequidens* individuals, which were processed in accordance to the method described above.

Statistical analysis

All statistical analyses were performed in R version 2.13.2 (R Development Core Team 2011). We compared the seed set and seed mass resulting from the different pollination treatments in the transplanted target plants using generalised (seed set, logit-link) and linear (seed mass) mixed models to assess the strength of self-incompatibility, overall pollen limitation and inbreeding depression (R package *lme4*, Bates, Maechler & Bolker (2011)). Plant identity and round were included as crossed random effects to account for pseudo-replication. We fit the models with a maximum likelihood (ML) approach and tested the significance of the fixed effect of pollination treatment by comparing the models containing this effect to the null models with a likelihood ratio test. Tukey post-hoc tests were used for pairwise treatment comparisons (R package *multcomp*, Hothorn, Bretz & Westfall (2008)). In addition, we used (generalised) linear models to compare seed set and seed mass from the (1st round) OPEN treatments of transplanted target individuals to those of the non-transplanted control *S. inaequidens*. The generalised linear model for seed set was fitted with a quasi - ML and a logit-link function. An F-test was used to test for significance in both cases. Correlation between (1st round) seed set as well as the absolute number of fertile seeds and seed mass of open-pollinated capitula in target individuals was assessed with Pearson's correlation coefficient.

To enhance our understanding of the processes which determine the seed set of *S. inaequidens,* we fitted a trait-based neighbourhood model of the following general form:

$$N.fert_i \sim Binomial(N.tot_i, p_i)$$

$$\operatorname{logit}(p_i) = b_i + \sum_j e_j * \exp(-f * D_{i,j})$$

where p_i is the seed set of target individual i associated with a binomial error distribution through a logit-link function. Parameter b_i describes the expected seed set of this individual irrespective of neighbourhood effects. e_j describes the effect of neighbour individual j, and f describes how steeply this effect decreases with distance D_{ij} between target individual i and neighbour j. The neighbourhood effects on each target individual are thus modelled as the summed interaction kernels of all neighbours.

For two model terms we defined regression submodels to explore how they are affected by plant traits. For the density-independent local term (*b*), seed set was modelled to depend on the target plant traits height, shoot number, capitula number and the categorical variable experimental round (to account for pseudo-replication and the timing of treatments relative to the target plant's individual phenology). For the effect term (*e*), neighbourhood interactions were modelled to depend on the height, shoot number, and capitula number of neighbouring *S. inaequidens,* as well as the canopy diameter and floral cover of heterospecific neighbours. For the neighbourhood analyses, capitula number as a covariate was not corrected for the number of capitula which were bagged during the experiment. Instead, we determined that capitula number was highly correlated to capitula number corrected for bagged capitula (Pearson's *r* of 0.999). This therefore supported our assumption that despite presence of bagged capitula, our covariate values were a valid proxy for the floral display available to foraging insects. The assignment of individuals as con- or heterospecific was used as an additional categorical variable. All continuous traits were log transformed and scaled before the analysis.

We used a Bayesian framework to fit the neighbourhood model. Posterior distributions of the model parameters were obtained using a Markov Chain Monte Carlo (MCMC) method. For each model we ran two chains with different initial values and 400 000 iterations with a thinning rate of 10. We considered the chains to be converged when the scale reduction factor of Gelman and Rubin (Brooks & Gelman 1998) dropped below 1.1, and then discarded previous iterations as burn-in, resulting in chains of 100 000 iterations each. We used non-informative priors for all parameters associated with our model. The analyses were carried out separately for the seed set of capitula of transplanted target *S. inaequidens* individuals in the treatments OPEN, CROSS and SELF.

Results

Experimental treatment effects

Seed mass of open-pollinated capitula in transplanted target *S. inaequidens* was neither significantly correlated with seed set (Pearson's $r = 0.1$, $p = 0.45$) nor with the absolute number of fertile seeds (Pearson's $r = 0.23$, $p = 0.08$). Pollination experiments significantly affected both seed set ($\chi^2_{(3)} = 6975.5$, $p < 0.001$, Fig. 2 a) and seed mass ($\chi^2_{(4)} = 68.5$, $p < 0.001$, Fig. 2 b). Seed set of open-pollinated capitula did not differ between transplanted target and un-transplanted non-target plants ($F_{(115,1)}$= 0.54, p = 0.46). However, the seed mass of transplanted plants was higher than that of non-transplanted plants ($F_{(109,1)}$ = 12.27, $p < 0.001$), which may have been an effect of watering after transplantation. Pollinator exclusion yielded a negligibly low seed set, suggesting that spontaneous, pollinator-independent self-pollination does not occur (Fig. 2 a). Ultimately, 56% of all selfed capitula developed viable seeds, although their seed set was very low (median =1 fertile seed, Fig. 2a), indicating a very low level of self-compatibility in our study population. Seed sets of 16 % and 21 % were, however, observed in two selfed capitula. The seed set of open-pollinated capitula was clearly pollen limited, as it was on average approximately 25 % lower than in cross-pollinated capitula (Fig. 2 a). Moreover, variation of seed set was largest within the open-pollination treatment. Seed mass of selfed capitula was about 30% lower than seed mass of open- and cross-pollinated capitula (Fig. 2 b).

Trait-based target and neighbourhood effects on seed set

Irrespective of interactions with the neighbourhood, the seed set of open-pollinated capitula decreased with plant height (Fig. 3). This effect was weaker in cross-pollinated and self-pollinated capitula (Fig. 3). Number of capitula had a significantly positive and shoots had a significantly negative effect on the seed set of open-pollinated as well as self-pollinated capitula. Moreover, number of capitula had a positive effect on seed set of cross-pollinated capitula. Additionally, both open- and cross-pollinated capitula treated later in the season had a lower seed set than those treated earlier (Table 1).

Our trait-based neighbourhood analyses showed no clear neighbourhood effects on the seed set of cross- and self-pollinated capitula (Table 1, Fig. S4). The credible intervals (CI) of effect parameters in these analyses were generally broad and included zero. The only exception was the positive effect of heterospecific canopy diameter on cross-pollinated individuals (Table 1). In the following paragraphs, we thus focus on results from the neighbourhood analyses of open-pollinated capitula.

Conspecific neighbours had a positive effect on the seed set of open-pollinated capitula when they had a height above 3.6 cm (Fig. 4 a), more than three shoots or less than four capitula. Overall, 53% of conspecific neighbours exhibited trait combinations that resulted in a positive neighbour effect despite the negative estimate for the conspecific intercept (Table 1). On the other hand, the effects of heterospecific neighbours turned negative when their floral cover exceeded 14.5 % (Fig. 4 b) or their diameter fell below 15.1 cm. Overall, 54 % of heterospecific neighbours exhibited trait combinations that resulted in a positive neighbour effect. Hence, heterospecific neighbours also had a predominantly positive effect on the seed set of *S. inaequidens* despite their negative intercept (Table 1).

Neighbourhood effects on the seed set of open-pollinated capitula were predicted to decrease rapidly with the spatial distance between the neighbouring plant and the target plant: at a distance of 2 m, neighbours with median trait values had only 9 % of their maximum effect (Fig. S5). Neighbourhood effects on cross- and self-pollinated capitula were predicted to decrease even faster and to thus have a smaller spatial extent than neighbourhood effects on open-pollinated seed set (Table 1). The short-range neighbourhood interactions detected in our analyses play an important role in the study population: non-target (i.e. non-transplanted) *S. inaequidens* were on average 1.64 meters from their nearest conspecific neighbour and 0.94 meters from their nearest heterospecific neighbour. In total, the 477 non-transplanted *S. inaequidens* plants had 1747 conspecific and 3379 heterospecific neighbours within 2 m distance. Partial residual plots confirmed that predominantly positive neighbourhood effects increased seed set in both the open (Fig. S6 a) and cross (Fig. S6 b) pollination treatment, with effects observed as generally stronger for the open-pollinated capitula (see also Fig. S4).

Discussion

We present a comprehensive framework that combines experimental manipulation and spatially-explicit trait-based neighbourhood analyses to identify mechanisms of density-dependence in plant reproduction (Fig. 1). Applying this experimental and analytical framework to the invasive *Senecio inaequidens*, we obtained three key results: (1) Neighbourhood analyses of open- in comparison to cross-pollinated capitula revealed that seed set is affected more strongly and across larger spatial scales by pollination-mediated than by pollination-independent neighbourhood effects (Table 1, Figs S4, S6). (2) The strength and direction of target and neighbourhood effects on seed set is trait-dependent (Table 1, Figs 3, 4). (3) Conspecific and heterospecific neighbours have predominantly positive effects on the reproduction of *S. inaequidens* (Table 1, Figs 4, S6). In the following, we first discuss the mechanisms which are likely to affect the reproductive success of *S. inaequidens*, before highlighting some consequences of our findings for invasion dynamics and community dynamics in general.

Self-incompatibility and pollen limitation of Senecio inaequidens

Senecio inaequidens was not able to self-pollinate, but still exhibited a low level of self-compatibility similar to the results of López-García & Maillet (2005) and Lafuma & Maurice (2007) (Fig. 2a). We did not record seed sets as high as those found by Vanparys *et al.* (2011) following self-pollination. A possible explanation for this variation in self-incompatibility could be pseudo-self-compatibility (Levin 1996; Brennan *et al.* 2011), although we are unable to ultimately exclude the occurrence of pollen contamination. Seeds that developed after selfing experienced a considerably reduced seed mass (Fig. 2b), presumably due to inbreeding depression (Brennan, Harris & Hiscock 2005).

The absence of spontaneous self-pollination and overall very low seed set following artificial self-pollination confirmed that *S. inaequidens* is very dependent on pollinator behaviour and the quantity and quality of pollen they are delivering. In fact, we found on average a 25% lower seed set in open than cross-pollinated capitula, but also high variation in the limitation of reproduction through the availability of out-crossed pollen. Our neighbourhood analyses gave light to several possible mechanisms acting on the degree of pollen limitation in target individuals on our sparsely and heterogeneously vegetated study site.

Effects of target and neighbour traits on pollination

The neighbourhood models revealed that the seed set of open-pollinated *S. inaequidens* diminishes as their height increases (Table 1, Fig. 3). This negative effect could result from a trade-off in resource allocation between vegetative growth and reproduction. However, when relieving pollen limitation in cross-pollinated capitula, we only found a slight negative effect of target plant height (Table 1, Fig. 3). This indicates that there is only a marginal influence of such a pollination-independent trade-off.

Consequently, the effects of target plant traits on reproduction are mainly pollination-mediated. Under these circumstances, the negative effects of *S. inaequidens* height, and shoot number (Table 1), is unexpected, as tall plants should be more visible and attractive for pollinators (Totland 2001; Carromero & Hamrick 2005; Dickson & Petit 2006; Schlinkert *et al.* 2015). The finding may actually reflect the significantly negative effect of the number of capitula - due to competition for pollinators between capitula or geitonogamous selfing - with the discrepancy that this variable was actually included in our neighbourhood models. In contrast to target plant size, the height and shoot number of conspecific neighbours had a positive effect on the seed set of open-pollinated capitula (Table 1, Fig. 4a) as tall conspecific neighbours may have driven pollinators to switch between different *S. inaequidens* host plants and provided compatible pollen. Furthermore, it is conceivable that target plants benefitted from the presence of tall conspecific neighbours based on the frequent finding that highly conspicuous plants strongly contribute to the attractiveness of their local neighbourhood (Seifan *et al.* 2014).

The effects of heterospecific neighbours on open-pollinated capitula remained positive as long as the floral cover of heterospecifics did not exceed 14.5 % (Table 1, Fig. 4b). Heterospecifics with a higher floral cover decreased the seed set of target individuals, which may be due to competition for pollinator visits (Caruso 1999; Seifan *et al.* 2014) or an increase in transfer of heterospecific pollen (Morales & Traveset 2008). As very few heterospecific individuals reached this critical value, heterospecific effects in our study population were largely positive, most likely due to the attraction of pollinators towards the target *S. inaequidens* (Moeller 2004; Ghazoul 2006; Hegland, Grytnes & Totland 2008).

Moreover, we found a larger canopy diameter of heterospecifics to significantly increase the seed set of both open- and cross-pollinated capitula (Table 1). Whereas for open-pollinated capitula this effect may again result from the attraction of pollinators to the local neighbourhood, neighbourhood effects on cross-pollinated capitula are caused by pollination-independent processes rather than pollen limitation. A possible explanation is that the occurrence of large heterospecific neighbours indicates a higher quality of post-transplant habitat, thereby increasing reproduction of *S. inaequidens*. Facilitation may also be behind the positive effect of large heterospecific neighbours. In fact, the stress-gradient hypothesis (Bertness & Callaway 1994; He, Bertness & Altieri 2013) proposed that facilitation by amelioration of abiotic conditions is generally more prevalent in stressful environments such as our study site in comparison to more benign environments. These positive effects on abiotic conditions presumably contributed to the overall facilitative effect of co-flowering heterospecifics on the seed set of open-pollinated target *S. inaequidens* individuals. Nevertheless, neighbourhood effects were in general much weaker in cross- than in open-pollinated capitula (Table 1). As both treatments (CROSS and OPEN) entered the analyses in equal numbers (see Table S2), differences in statistical power can be excluded as an explanation for this result. Moreover, these two treatments were always applied simultaneously to the same target individuals. Consequently, a phenological change of the neighbourhood, which may not be represented in our trait data since trait mapping of the neighbourhood was possible only once due to its enormous logistic effort, can be excluded as an explanation of this result. Thus, we conclude that within the ranges of con- and heterospecific densities investigated in this study, pollination-mediated neighbourhood effects clearly prevail under natural pollination.

Spatial range of neighbourhood effects

Our analyses showed that neighbourhood interactions operate at different scales, depending on the processes driving them (Table 1). The spatial range of interactions in the open-pollination treatment was limited to two meters for heterospecific and to four meters for conspecific neighbours (Fig. S5), which parallels the outcome of other studies on herbaceous plant species and shrubs that have demonstrated a positive relationship between density and reproductive success within a local spatial range of one to five meters (Spigler & Chang 2008; Jakobsson, Lázaro & Totland 2009; Hegland 2014; Schmid et al. 2016) . The spatial range of neighbourhood effects on reproduction in the cross-pollination treatment, which are driven exclusively by pollinator-independent plant-plant interactions, was much smaller (Table 1).

The observed scale difference between neighbourhood effects on the seed set of open and cross-pollinated capitula seems very plausible, considering that neighbourhood effects in the open-pollination treatment were largely pollination-mediated and therefore likely to extend beyond the spatial scales of direct plant-plant interactions that shape seed set in the cross-pollination treatment. This underlines the need for multi-scale neighbourhood analyses of plant reproduction, as neighbourhood analyses assessing neighbour interactions at predefined spatial scales might overlook ecological interactions on other scales (Stoll & Weiner 2000; Fedriani et al. 2015; Nottebrock et al. 2016).

Allee effects and invasion dynamics

Self-incompatible invasive species like *S. inaequidens* are sensitive to pollination-dependent Allee effects, especially during population establishment when population density is low (Drake 2004). Studies that aimed to detect pollination-mediated Allee effects in invasive plants yielded both negative (Kleunen & Johnson 2005; Monty & Mahy 2010; Rodger, van Kleunen & Johnson 2013) and positive (Davis *et al.* 2004; Elam *et al.* 2007; Firestone & Jasieniuk 2012; Anic *et al.* 2015) results. We revealed a component Allee effect (Stephens, Sutherland & Freckleton 1999), where the seed set, as one component of overall fitness, is reduced at low conspecific density. However, positive and/or negative density-dependence in other life stages can add to or compensate the positive density-dependence of pollination (Stephens *et al.* 1999). Thus, it remains to be clarified if and to which degree this component Allee effect translates into or contributes to a demographic Allee effect. Methods to consider could be the application of population models that incorporate Allee effects (Taylor & Hastings 2005) or population-scale seed edition experiments to show that population growth is actually limited by seed set (Kramer *et al.* 2009).

The density-dependent pollen limitation we detected is very likely to influence the invasion dynamics of *S. inaequidens*. An initially low seed set in sparse populations may increase markedly once the population density exceeds a rather high threshold (of about one individual per m^2). This can lead to a pronounced lag phase in local population growth with a rapid increase when the threshold density has been reached. Typically very dense populations along traffic routes (Garcia-Serrano *et al.* 2005; Blanchet *et al.* 2015), representing the major spread paths of the species (Blanchet *et al.* 2015), may benefit from positive conspecific neighbourhood interactions, which may contribute to their exceptionally rapid spread (Heger & Böhmer 2005).

Furthermore, seeds of this species are wind-dispersed and young individuals germinated from long-distance dispersed seeds are likely to be strongly isolated from conspecifics. *Senecio inaequidens* additionally suffers from negative fitness effects of reduced genetic diversity in founder populations (Lachmuth, Durka & Schurr 2011; Schrieber & Lachmuth 2017). Reduced *S*-allele diversity may further limit the availability of compatible mates and thus enhance pollination-mediated Allee effects (Levin, Kelley & Sarkar 2009; Rosche *et al.* 2017). Such interactive effects on population growth (Wittmann, Stuis & Metzler 2016) are expected to cause longer lag times in invasive species and to slow down the spatial spread of introduced populations (Taylor & Hastings 2005). A lag time of several decades has indeed been observed in *S. inaequidens* (Lachmuth *et al.* 2010), while variation in the invasion speed towards the leading edges still needs to be investigated.

Positive interactions with heterospecific neighbours might mitigate the detected pollination-mediated Allee effect due to the facilitation of pollination and therefore enhanced reproductive success. Yet due to its low competitive ability, *S. inaequidens* mostly spreads in ruderal habitats with sparse vegetation (Scherber, Crawley & Porembski 2003; Lachmuth *et al.* 2011) were it may, just as in our study site, experience community-level Allee effects (Nottebrock *et al.* 2013, 2016). Moreover, neighbourhood interactions will change in direction and magnitude as a function of the trait composition of the respective population and neighbourhood as they depend on target and neighbour traits. In denser vegetation comprising of multiple species with attractive floral displays, however, *S. inaequidens* might suffer more from competition for pollinators and full consequences of the Allee effect might become apparent. This could additionally explain as to why *S. inaequidens* is unable to invade denser vegetation and usually becomes displaced on ruderal sites during later stages of succession (Heger & Böhmer 2005).

More generally, heterospecific neighbourhood effects may change the strength of Allee effects and, in cases of so-called strong demographic Allee effects (*sensu* Taylor & Hastings 2005), may alter the conspecific density threshold at which population growth turns positive. Thus, as demonstrated by Walter *et al.* (2015), habitat heterogeneity may translate into heterogeneity in the strength of demographic Allee effects, which may be an underappreciated source of intraspecific variation in spread rates of range expanding species (Walter, Johnson & Haynes 2017). Considering that variation in the strength of demographic Allee effects increases the unpredictability of range dynamics, our methodological approach can provide a valuable tool to disentangle the underlying mechanisms and to gather the empirical information necessary to develop comprehensive mechanistic range models not only of invasive, but also of retreating, expanding or range shifting species. Future studies on other species and communities may thus benefit from the methodological advances described here, to gain a deeper understanding of the extent as well as scale- and trait-dependence of pollination-mediated plant-plant interactions and their ultimate effects on population, community and range dynamics.

Conclusions

The joint manipulation of pollen quantity, pollen quality and the location of target individuals within different neighbourhoods enabled us to disentangle various underlying mechanisms affecting the reproductive output of *S. inaequidens*. We found pollen limitation rather than abiotic resource limitation to be responsible for the decrease of *S. inaequidens* seed set at low densities. Results of our trait-based neighbourhood analyses suggest that interactions with both con- and heterospecific neighbours play a role. As the neighbourhood effects are trait-dependent, they may differ between populations and neighbourhoods with different size structure and species composition. Spatially-explicit neighbourhood models allowed us to delimit the relevant scales of these interactions and to show that pollination-independent plant-plant interactions occur on smaller spatial scales than pollination-mediated interactions. These findings improve the understanding of *S. inaequidens* population and invasion dynamics, which can be useful for the development of mechanistic population and range models (Schurr *et al.* 2012) as well as management schemes.

Authors' contributions

F.M.S. and S.L. conceived the idea and designed the experiment. C.H. and J.H. collected the data. J.P. developed the neighborhood models and significantly contributed to the analyses, which were performed by C.H., F.S.M. and S.L.. Finally, S.L., C.H. and F.S.M. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Acknowledgements

We thank U. Klee, M. Grau (Dept. Landtechnik, Umwelt- und Kommunaltechnik, MLU Halle Wittenberg) and J. Joshi (Dept. Biodiversity Research, University of Potsdam) for providing us with differential GPS devices. Isabell Hensen (Dept. Plant Ecology, MLU Halle Wittenberg) provided financial support. The German Research Foundation (DFG) supported the development of trait-based neighbourhood models (grant SCHU 2259/3-1 to FMS). Sächsisches Seebad Zwenkau GmbH & Co.KG gave permission and advice for conducting the study in a former daylight mining area. We are grateful to M. Hock and S. Träger for assistance during the field work and to C. Voigt for supporting the microscopy. Special thanks to two anonymous referees whose comments helped us to substantially improve this manuscript.

Data accessibility

All data as well as R code for the neighbourhood models are available at the dryad digital data repository: http://datadryad.org/resource/doi: 10.5061/dryad.sp012

Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1: Insect-pollinated heterospecific neighbours of *Senecio inaequidens* at our study site.

Table S2: Overview and time schedule of the pollination treatments performed in the different rounds.

Fig. S1: Individual based map of the study site illustrating the positions of *Senecio inaequidens* individuals (transplanted target and already established non-target individuals) and heterospecific neighbour plants.

Fig. S2: Histograms for the traits of *Senecio inaequidens* target (a-c) and neighbour (including target) individuals (d-f).

Fig. S3: Picture of exemplary *Senecio inaequidens* target individual with bagged capitula.

Fig. S4: Difference in percentage of predicted seed set in transplanted target *Senecio inaequidens* with and without neighbourhood effects for open-pollinated (OPEN) and cross-pollinated (CROSS) capitula.

Fig. S5: Predicted neighbourhood effects on the seed set in open-pollinated capitula of target individuals decay with distance from con- and heterospecific neighbours.

Fig. S6: Relationships of summed neighbourhood effects and seed set in (a) open-pollinated and (b) cross-pollinated capitula.

References

Allee, W.C. (1931) *Animal Aggregations, a Study in General Sociology.* The University of Chicago Press, Chicago.

Anic, V., Henríquez, C.A., Abades, S.R. & Bustamante, R.O. (2015) Number of conspecifics and reproduction in the invasive plant *Eschscholzia californica* (Papaveraceae): is there a pollinator-mediated Allee effect? *Plant Biology*, **17**, 720–727.

Ashman, T.-L., Knight, T.M., Steets, J.A., Amarasekare, P., Burd, M., Campbell, D.R., Dudash, M.R., Johnston, M.O., Mazer, S.J., Mitchell, R.J., Morgan, M.T. & Wilson, W.G. (2004) Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. *Ecology*, **85**, 2408–2421.

Bates, D., Maechler, M. & Bolker, B.M. (2011) *lme4: Linear Mixed-Effects Models Using S4 Classes*. R package version 0.999375-42. URL: http://CRAN.R-project.org/package=lme4.

Bertness, M.D. & Callaway, R. (1994) Positive interactions in communities. *Trends in Ecology & Evolution*, **9**, 191–193.

Blanchet, É., Penone, C., Maurel, N., Billot, C., Rivallan, R., Risterucci, A.-M., Maurice, S., Justy, F., Machon, N. & Noël, F. (2015) Multivariate analysis of polyploid data reveals the role of railways in the spread of the invasive South African Ragwort (*Senecio inaequidens*). *Conservation Genetics*, **16**, 523–533.

Bossdorf, O., Lipowsky, A. & Prati, D. (2008) Selection of preadapted populations allowed *Senecio inaequidens* to invade Central Europe. *Diversity and Distributions*, **14**, 676–685.

Brennan, A.C., Harris, S.A. & Hiscock, S.J. (2005) Modes and rates of selfing and associated inbreeding depression in the self-incompatible plant *Senecio squalidus* (Asteraceae): a successful colonizing species in the British Isles. *New Phytologist*, **168**, 475–486.

Brennan, A.C., Tabah, D.A., Harris, S.A. & Hiscock, S.J. (2011) Sporophytic self-incompatibility in *Senecio squalidus* (Asteraceae): S allele dominance interactions and modifiers of cross-compatibility and selfing rates. *Heredity*, **106**, 113–123.

Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G., Liancourt, P., Tielbörger, K., Travis, J.M.J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C.L., Saccone, P., Schiffers, K., Seifan, M., Touzard, B. & Michalet, R. (2008) Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology*, **96**, 18–34.

Brooks, S.P. & Gelman, A. (1998) General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, **7**, 434–455.

Cabral, J.S. & Schurr, F.M. (2010) Estimating demographic models for the range dynamics of plant species. *Global Ecology and Biogeography*, **19**, 85–97.

Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., Paolini, L., Pugnaire, F.I., Newingham, B., Aschehoug, E.T., Armas, C., Kikodze, D. & Cook, B.J. (2002) Positive interactions among alpine plants increase with stress. *Nature*, **417**, 844–848.

Canham, C.D. & Uriarte, M. (2006) Analysis of neighborhood dynamics of forest ecosystems using likelihood methods and modeling. *Ecological Applications*, **16**, 62–73.

Carromero, W. & Hamrick, J.L. (2005) The mating system of *Verbascum thapsus* (Scrophulariaceae): the effect of plant height. *International Journal of Plant Sciences*, **166**, 979–983.

Caruso, C.M. (1999) Pollination of *Ipomopsis aggregata* (Polemoniaceae): effects of intra- vs. interspecific competition. *American Journal of Botany*, **86**, 663–668.

Courchamp, F., Clutton-Brock, T. & Grenfell, B. (1999) Inverse density dependence and the Allee effect. *Trends in Ecology & Evolution*, **14**, 405–410.

Dauber, J., Biesmeijer, J.C., Gabriel, D., Kunin, W.E., Lamborn, E., Meyer, B., Nielsen, A., Potts, S.G., Roberts, S.P.M., Sõber, V., Settele, J., Steffan-Dewenter, I., Stout, J.C., Teder, T., Tscheulin, T., Vivarelli, D. & Petanidou, T. (2010) Effects of patch size and density on flower visitation and seed set of wild plants: a pan-European approach. *Journal of Ecology*, **98**, 188–196.

Davis, H.G., Taylor, C.M., Civille, J.C. & Strong, D.R. (2004) An Allee effect at the front of a plant invasion: *Spartina* in a Pacific estuary. *Journal of Ecology*, **92**, 321–327.

Dickson, C.R. & Petit, S. (2006) Effect of individual height and labellum colour on the pollination of *Caladenia* (syn. *Arachnorchis*) *behrii* (Orchidaceae) in the northern Adelaide region, South Australia. *Plant Systematics and Evolution*, **262**, 65–74.

Drake, J.M. (2004) Allee effects and the risk of biological invasion. *Risk Analysis*, **24**, 795–802.

Elam, D.R., Ridley, C.E., Goodell, K. & Ellstrand, N.C. (2007) Population size and relatedness affect fitness of a self-incompatible invasive plant. *Proceedings of the National Academy of Sciences*, **104**, 549–552.

Fedriani, J.M., Wiegand, T., Calvo, G., Suárez-Esteban, A., Jácome, M., Żywiec, M. & Delibes, M. (2015) Unravelling conflicting density- and distance-dependent effects on plant reproduction using a spatially explicit approach. *Journal of Ecology*, **103**, 1344–1353.

Firestone, J.L. & Jasieniuk, M. (2012) Small population size limits reproduction in an invasive grass through both demography and genetics. *Oecologia*, **172**, 109–117.

Forsyth, S.A. (2003) Density-dependent seed set in the Haleakala silversword: evidence for an Allee effect. *Oecologia*, **136**, 551–557.

Garcia-Serrano, H., Escarré, J., Garnier, É. & Sans, F.X. (2005) A comparative growth analysis between alien invader and native *Senecio* species with distinct distribution ranges. *Ecoscience*, **12**, 35–43.

Ghazoul, J. (2006) Floral diversity and the facilitation of pollination. *Journal of Ecology*, **94**, 295–304.

Harper, J. (1977) *Population Biology of Plants.* Blackburn Press, New Jersey.

He, Q., Bertness, M.D. & Altieri, A.H. (2013) Global shifts towards positive species interactions with increasing environmental stress. *Ecology Letters*, **16**, 695–706.

Heger, T. & Böhmer, H.J. (2005) The invasion of central Europe by *Senecio inaequidens* DC. — A complex biogeographical problem (Die Einwanderung des Schmalblättrigen Greiskrautes (*Senecio inaequidens* DC.) nach Mitteleuropa — Analyse eines komplexen biogeographischen Problems). *Erdkunde*, **59**, 34–49.

Hegland, S.J. (2014) Floral neighbourhood effects on pollination success in red clover are scale-dependent. *Functional Ecology*, **28**, 561–568.

Hegland, S.J., Grytnes, J.-A. & Totland, Ø. (2008) The relative importance of positive and negative interactions for pollinator attraction in a plant community. *Ecological Research*, **24**, 929–936.

Hiscock, S.J. & Tabah, D.A. (2003) The different mechanisms of sporophytic self–incompatibility. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **358**, 1037–1045.

Holt, R.D. (1977) Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology*, **12**, 197–229.

Hothorn, T., Bretz, F. & Westfall, P. (2008) Simultaneous inference in general parametric models. *Biometrical Journal. Biometrische Zeitschrift*, **50**, 346–363.

Jakobsson, A., Lázaro, A. & Totland, Ø. (2009) Relationships between the floral neighborhood and individual pollen limitation in two self-incompatible herbs. *Oecologia*, **160**, 707–719.

Kleunen, M. van & Johnson, S.D. (2005) Testing for ecological and genetic Allee effects in the invasive shrub *Senna didymobotrya* (Fabaceae). *American Journal of Botany*, **92**, 1124–1130.

Klotz, S., Kühn, I. & Durka, W. (2002) Biolflor : eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland., Schriftenreihe für Vegetationskunde, p. 334. Bundesamt für Naturschutz, Bonn.

Knight, T.M., Steets, J.A., Vamosi, J.C., Mazer, S.J., Burd, M., Campbell, D.R., Dudash, M.R., Johnston, M.O., Mitchell, R.J. & Ashman, T.-L. (2005) Pollen limitation of plant reproduction: pattern and process. *Annual Review of Ecology, Evolution, and Systematics*, **36**, 467–497.

Kramer, A.M., Dennis, B., Liebhold, A.M. & Drake, J.M. (2009) The evidence for Allee effects. *Population Ecology*, **51**, 341–354.

Lachmuth, S., Durka, W. & Schurr, F.M. (2010) The making of a rapid plant invader: genetic diversity and differentiation in the native and invaded range of *Senecio inaequidens*. *Molecular Ecology*, **19**, 3952–3967.

Lachmuth, S., Durka, W. & Schurr, F.M. (2011) Differentiation of reproductive and competitive ability in the invaded range of *Senecio inaequidens*: the role of genetic Allee effects, adaptive and non-adaptive evolution. *New Phytologist*, **192**, 529–541.

Lafuma, L., Balkwill, K., Imbert, E., Verlaque, R. & Maurice, S. (2003) Ploidy level and origin of the European invasive weed *Senecio inaequidens* (Asteraceae). *Plant Systematics and Evolution*, **243**, 59–72.

Lafuma, L. & Maurice, S. (2007) Increase in mate availability without loss of self-incompatibility in the invasive species *Senecio inaequidens* (Asteraceae). *Oikos*, **116**, 201–208.

Lamont, B.B., Klinkhamer, P.G.L. & Witkowski, E.T.F. (1993) Population fragmentation may reduce fertility to zero in *Banksia goodii* — a demonstration of the Allee effect. *Oecologia*, **94**, 446–450.

Levin, D.A. (1996) The evolutionary significance of pseudo-self-fertility. *The American Naturalist*, **148**, 321–332.

Levin, D.A., Kelley, C.D. & Sarkar, S. (2009) Enhancement of Allee effects in plants due to self-incompatibility alleles. *Journal of Ecology*, **97**, 518–527.

Liebhold, A. & Bascompte, J. (2003) The Allee effect, stochastic dynamics and the eradication of alien species. *Ecology Letters*, **6**, 133–140.

López-García, M.C. & Maillet, J. (2005) Biological characteristics of an invasive south African species. *Biological Invasions*, **7**, 181–194.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, **21**, 178–185.

Mitchell, R.J., Flanagan, R.J., Brown, B.J., Waser, N.M. & Karron, J.D. (2009) New frontiers in competition for pollination. *Annals of Botany*, **103**, 1403–1413.

Moeller, D.A. (2004) Facilitative interactions among plants via shared pollinators. *Ecology*, **85**, 3289–3301.

Monty, A. & Mahy, G. (2010) Evolution of dispersal traits along an invasion route in the wind-dispersed *Senecio inaequidens* (Asteraceae). *Oikos*, **119**, 1563–1570.

Morales, C.L. & Traveset, A. (2008) Interspecific pollen transfer: magnitude, prevalence and consequences for plant fitness. *Critical Reviews in Plant Sciences*, **27**, 221–238.

Morales, C.L. & Traveset, A. (2009) A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. *Ecology Letters*, **12**, 716–728.

Muchhala, N. & Thomson, J.D. (2012) Interspecific competition in pollination systems: costs to male fitness via pollen misplacement. *Functional Ecology*, **26**, 476–482.

Nottebrock, H., Esler, K.J. & Schurr, F.M. (2013) Effects of intraspecific and community density on the lifetime fecundity of long-lived shrubs. *Perspectives in Plant Ecology, Evolution and Systematics*, **15**, 150–161.

Nottebrock, H., Schmid, B., Mayer, K., Devaux, C., Esler, K.J., Böhning-Gaese, K., Schleuning, M., Pagel, J. & Schurr, F.M. (2016) Sugar landscapes and pollinator-mediated interactions in plant communities. *Ecography*, doi: 10.1111/ecog.02441.

Nottebrock, H., Schmid, B., Treurnicht, M., Pagel, J., Esler, K.J., Böhning-Gaese, K., Schleuning, M. & Schurr, F.M. (2017) Coexistence of plant species in a biodiversity hotspot is stabilized by competition but not by seed predation. *Oikos*, **126**, 276-284.

Ollerton, J., Winfree, R. & Tarrant, S. (2011) How many flowering plants are pollinated by animals? *Oikos*, **120**, 321–326.

Pacala, S.W. & Silander, J.A. (1985) Neighborhood models of plant population dynamics. I. Single-species models of annuals. *The American Naturalist*, **125**, 385–411.

Pacala, S.W. & Silander, J.A. (1990) Field tests of neighborhood population dynamic models of two annual weed species. *Ecological Monographs*, **60**, 113–134.

Pauw, A. (2013) Can pollination niches facilitate plant coexistence? *Trends in Ecology & Evolution*, **28**, 30–37.

Pauw, A. & Bond, W.J. (2011) Mutualisms matter: pollination rate limits the distribution of oil-secreting orchids. *Oikos*, **120**, 1531–1538.

Pelser, P.B., Gravendeel, B. & Meijden, R. van der. (2002) Tackling speciose genera: species composition and phylogenetic position of *Senecio* sect. *Jacobaea* (Asteraceae) based on plastid and nrDNA sequences. *American Journal of Botany*, **89**, 929–939.

R Development Core Team. (2011) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rodger, J.G., van Kleunen, M. & Johnson, S.D. (2013) Pollinators, mates and Allee effects: the importance of self-pollination for fecundity in an invasive lily. *Functional Ecology*, **27**, 1023–1033.

Rosche, C., Hensen, I., Mráz, P., Durka, W., Hartmann, M. & Lachmuth, S. (2017) Invasion success in polyploids: the role of inbreeding in the contrasting colonization abilities of diploid versus tetraploid populations of *Centaurea stoebe* s.l. *Journal of Ecology*, **105**, 425–435.

Scherber, C., Crawley, M.J. & Porembski, S. (2003) The effects of herbivory and competition on the invasive alien plant *Senecio inaequidens* (Asteraceae). *Diversity and Distributions*, **9**, 415–426.

Schlinkert, H., Westphal, C., Clough, Y., László, Z., Ludwig, M. & Tscharntke, T. (2015) Plant size as determinant of species richness of herbivores, natural enemies and pollinators across 21 Brassicaceae species. *PLOS ONE*, **10**, e0135928.

Schmid, B., Nottebrock, H., Esler, K.J., Pagel, J., Pauw, A., Böhning-Gaese, K., Schurr, F.M. & Schleuning, M. (2016) Responses of nectar-feeding birds to floral resources at multiple spatial scales. *Ecography*, **39**, 619-629.

Schrieber, K. & Lachmuth, S. (2017) The Genetic Paradox of Invasions revisited: the potential role of inbreeding × environment interactions in invasion success. *Biological Reviews*, **92**, 939–952.

Schurr, F.M., Pagel, J., Cabral, J.S., Groeneveld, J., Bykova, O., O'Hara, R.B., Hartig, F., Kissling, W.D., Linder, H.P., Midgley, G.F., Schroeder, B., Singer, A. & Zimmermann, N.E. (2012) How to understand species' niches and range dynamics: a demographic research agenda for biogeography. *Journal of Biogeography*, **39**, 2146–2162.

Seifan, M., Hoch, E.-M., Hanoteaux, S. & Tielbörger, K. (2014) The outcome of shared pollination services is affected by the density and spatial pattern of an attractive neighbour. *Journal of Ecology*, **102**, 953–962.

Spigler, R.B. & Chang, S.-M. (2008) Effects of plant abundance on reproductive success in the biennial *Sabatia angularis* (Gentianaceae): spatial scale matters. *Journal of Ecology*, **96**, 323–333.

Stephens, P.A., Sutherland, W.J. & Freckleton, R.P. (1999) What is the Allee effect? *Oikos*, **87**, 185–190.

Stoll, P. & Newbery, D.M. (2005) Evidence of species-specific neighborhood effects in the Dipterocarpaceae of a Bornean rain forest. *Ecology*, **86**, 3048–3062.

Stoll, P. & Weiner, J. (2000) A neighborhood view of interactions among individual plants. *The geometry of ecological interactions : simplifying spatial complexity*, (eds U. Dieckmann, R. Law & J.A.J. Metz), pp. 11-27. Cambridge University Press, Cambridge.

Svenning, J.-C., Gravel, D., Holt, R.D., Schurr, F.M., Thuiller, W., Münkemüller, T., Schiffers, K.H., Dullinger, S., Edwards, T.C., Hickler, T., Higgins, S.I., Nabel, J.E.M.S., Pagel, J. & Normand, S. (2014) The influence of interspecific interactions on species range expansion rates. *Ecography*, **37**, 1198–1209.

Taylor, C.M. & Hastings, A. (2005) Allee effects in biological invasions. *Ecology Letters*, **8**, 895–908.

Totland, Ø. (2001) Environment-dependent pollen limitation and selection on floral traits in an Alpine species. *Ecology*, **82**, 2233–2244.

Tur, C., Sáez, A., Traveset, A. & Aizen, M.A. (2016) Evaluating the effects of pollinator-mediated interactions using pollen transfer networks: evidence of widespread facilitation in south Andean plant communities. *Ecology Letters*, **19**, 576–586.

Turnbull, L.A., Crawley, M.J. & Rees, M. (2000) Are plant populations seed-limited? A review of seed sowing experiments. *Oikos*, **88**, 225–238.

Uriarte, M., Condit, R., Canham, C.D. & Hubbell, S.P. (2004) A spatially explicit model of sapling growth in a tropical forest: does the identity of neighbours matter? *Journal of Ecology*, **92**, 348–360.

Uriarte, M., Swenson, N.G., Chazdon, R.L., Comita, L.S., Kress, W.J., Erickson, D., Forero-Montana, J., Zimmerman, J.K. & Thompson, J. (2010) Trait similarity, shared ancestry and the structure of neighbourhood interactions in a subtropical wet forest: implications for community assembly. *Ecology Letters*, **13**, 1503–1514.

Vanparys, V., Cawoy, V., Mahaux, O. & Jacquemart, A.-L. (2011) Comparative study of the reproductive ecology of two co-occurring related plant species: the invasive *Senecio inaequidens* and the native *Jacobaea vulgaris*. *Plant Ecology and Evolution*, **144**, 3–11.

Vanparys, V., Meerts, P. & Jacquemart, A.-L. (2008) Plant–pollinator interactions: comparison between an invasive and a native congeneric species. *Acta Oecologica*, **34**, 361–369.

Walter, J.A., Johnson, D.M. & Haynes, K.J. (2017) Spatial variation in Allee effects influences patterns of range expansion. *Ecography*,**40**, 179-188 .

Walter, J.A., Meixler, M.S., Mueller, T., Fagan, W.F., Tobin, P.C. & Haynes, K.J. (2015) How topography induces reproductive asynchrony and alters gypsy moth invasion dynamics. *Journal of Animal Ecology*, **84**, 188–198.

Weiner, J. (1982) A neighborhood model of annual-plant interference. *Ecology*, **63**, 1237–1241.

Wittmann, M.J., Stuis, H. & Metzler, D. (2016) Genetic Allee effects and their interaction with ecological Allee effects. *Journal of Animal Ecology*, doi: 10.1111/1365-2656.12598.

Table 1: Posterior means of effect parameters from neighbourhood analyses for the treatments OPEN, CROSS and SELF. 95% credible intervals are given in parentheses. Seed set of *Senecio inaequidens* individuals (on logit scale) irrespective of neighbourhood effects (local model (b)) changes with parameters height, number of shoots, number of capitula and factor levels round 2/3 which account for pseudo-replication and the timing of treatments relative to the target plant's phenology. Effect strengths of neighbours (effect model (e)) are denoted for the parameters height, number of shoots, number of capitula and the heterospecific neighbour traits canopy diameter and floral cover. Positive parameter values of the effect model indicate facilitation whereas negative values indicate competition. The distance model gives the decay parameter f, determining the decrease of neighbourhood effects with increasing distance to target individuals. Note that all continuous explanatory variables have been log-transformed and scaled (x/sd(x)). Asterisks indicate that the credible interval did not include zero.

Parameters	Treatment OPEN	Treatment CROSS	Treatment SELF
Local model (b)			
Local intercept	1.90 (1.18 - 2.58)*	1.86 (0.84 - 2.82)*	5.70 (0.21 - 11.33)*
Height	-0.22 (-0.28 - -0.16)*	-0.14 (-0.22 - -0.05)*	-0.64 (-1.06 - -0.25)*
Nr. of shoots	-0.10 (-0.16 - -0.04)*	0.04 (-0.05 - 0.13)	-0.50 (-0.91 - -0.09)*
Nr. of capitula	0.29 (0.22 - 0.37)*	0.25 (0.14 - 0.37)*	0.53 (0.07 - 1.01)*
Round 2	- 0.04 (-0.19 - 0.10)	-0.83 (-1.01 - -0.65)*	-0.94 (-2.41 - 0.24)
Round 3	-1.05 (-1.43 - -0.69)*	-0.65 (-1.17 - -0.11)*	-8.56 (-22.63 - -0.60)*
Effect model (e) conspecific			
Conspecific intercept	-5.56 (-7.55 - -3.07)*	-9.99 (-27.41 - 8.84)	-0.01 (-19.69 - 19.43)
Height	0.36 (0.04 - 0.65)*	1.98 (-1.91 - 5.56)	-0.87 (-18.94 - 17.00)
Nr. of shoots	1.17 (0.83 - 1.43)*	0.37 (-2.05 - 1.97)	-1.42 (-19.26 - 16.33)
Nr. of capitula	-0.42 (-0.55 - -0.25)*	0.06 (-1.25 - 2.37)	-0.94 (-17.18 - 14.96)
Effect model (e) heterospecific			
Heterospecific intercept	-0.19 (-0.52 -0.17)	-4.99 (-17.11 - 1.21)	-2.65 (-21.71 - 16.64)
Diameter	0.22 (0.14 -0.29)*	1.56 (0.25 - 4.20)*	0.17 (-17.26 - 13.58)
Floral cover	-0.13 (-0.22 - -0.06)*	1.03 (-0.62 - 4.66)	-8.67 (-23.05 - 4.38)
Distance model			
Decay parameter (f)	0.17 (0.01 - 0.29)*	1.62 (0.71 - 2.29)*	2.31 (1.59 - 2.78)*

Figures

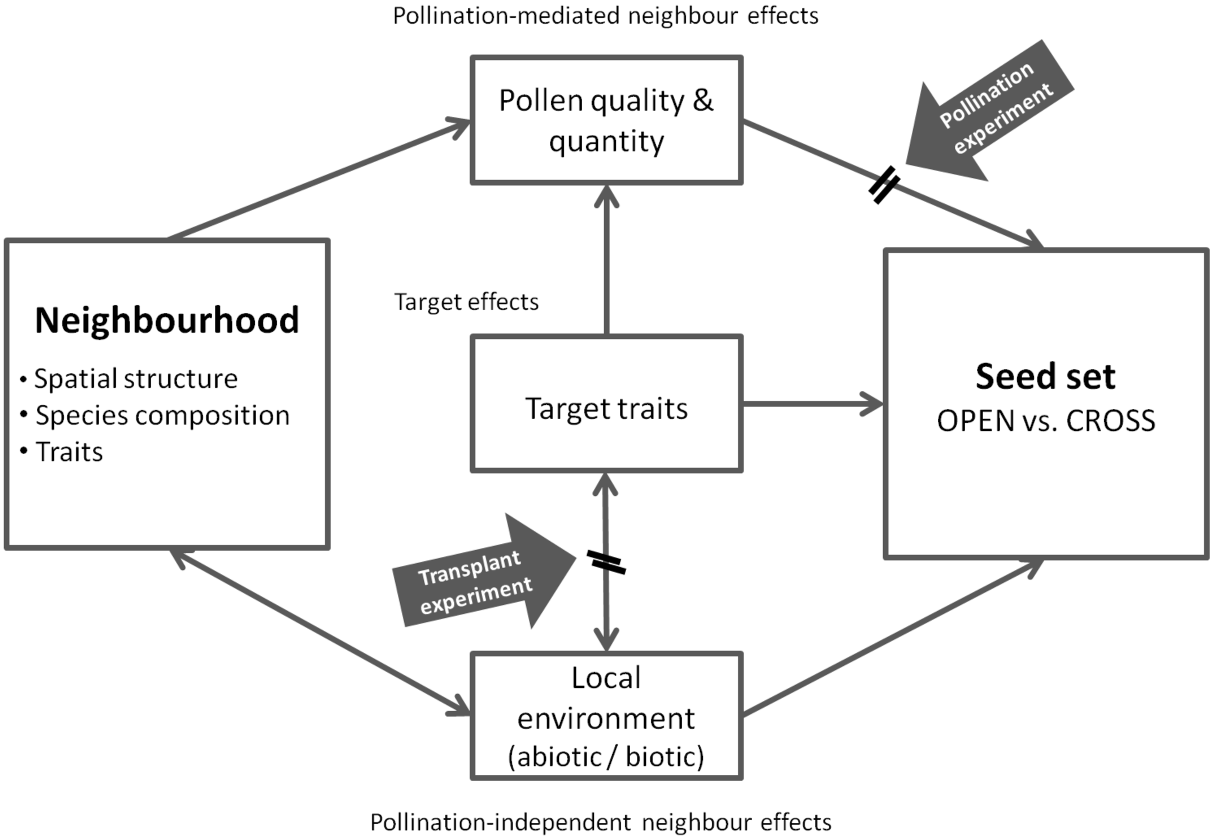

Fig. 1: Processes (thin arrows) that affect the seed set in animal pollinated plants: the graph illustrates how pollination-mediated (top) and pollination-independent (bottom) neighbourhood effects as well as effects of target plant traits (central) influence seed set in naturally pollinated flowers. Pollination-mediated interactions occur either through direct effects of con- and heterospecific neighbours as well as target plants on pollen quantity and quality, or through the attraction of and competition for pollination vectors. All of these effects depend on neighbour as well as on target traits. Pollination-independent plant-plant interactions occur through effects of neighbours and target plants, for example on the local abiotic (e.g. availability of resources) or biotic (e.g. herbivore abundances) environment. These effects, again, are trait dependent and cause feedback on community composition. Pollination-independent interactions may also influence seed set indirectly by effects on traits of the target plant which, in turn, affect pollen availability and seed set.

Experimental manipulation (fat arrows) helps disentangling these various processes. Artificial cross-pollination allows to separate effects of pollination mediated plant-plant interactions that influence exclusively the seed set of open pollinated flowers (OPEN) from effects of pollination-independent interactions and target traits that influence seed set in both, open and cross-pollinated (CROSS), flowers. Transplantation of target individuals into new neighbourhoods, moreover, allows excluding indirect effects of neighbours on seed set via their (past) effects on target traits. Spatially-explicit neighbourhood models can quantify neighbourhood as well as target effects on seed set in the different pollination treatments and how these effects change with neighbour distance.

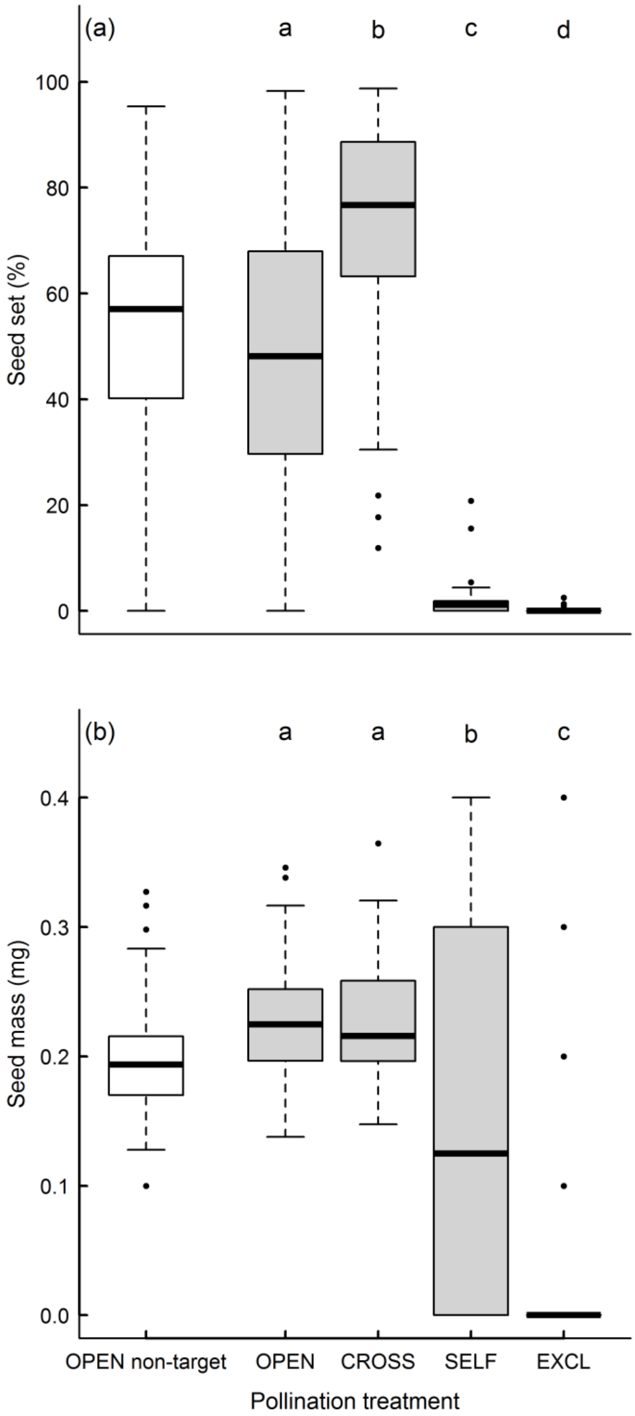

Fig. 2: Effect of pollination treatments on seed set (a) and average mass of fertile seeds (b) produced by the capitula of transplanted non-target (white) and target (grey) *Senecio inaequidens*: OPEN, open-pollinated; CROSS, cross-pollinated; SELF, self-pollinated; EXCL, pollinator exclusion. Mean values of target plant treatments marked with the same letter were not significantly different based on pair-wise comparisons with Tukey post-hoc tests (*p* > 0.05).

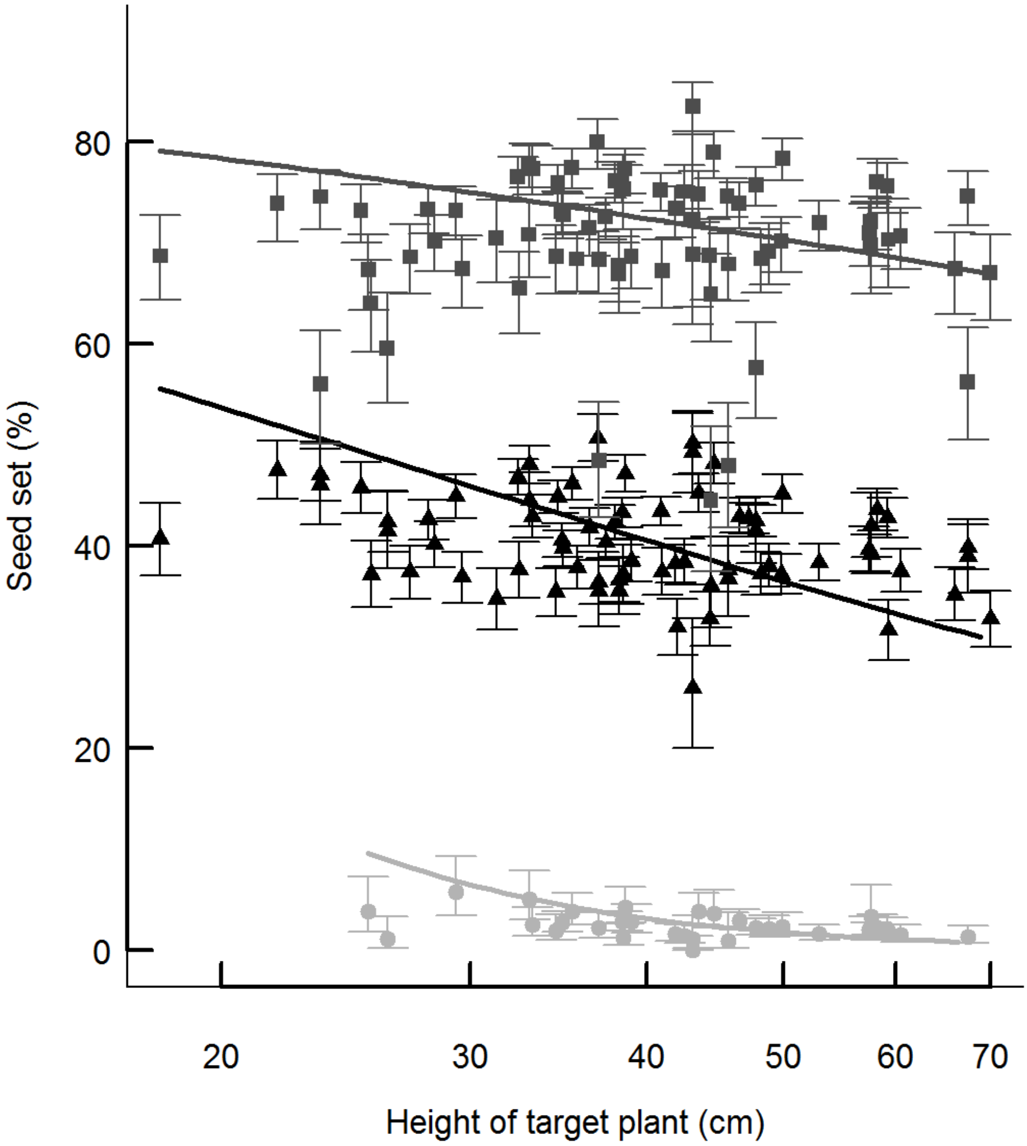

Fig. 3: Relationship between the median predicted seed set and the height of transplanted target *Senecio inaequidens* individuals for open-pollinated (OPEN, black triangles), cross-pollinated (CROSS, dark grey quadrates), and self-pollinated (SELF, light grey points) capitula. The 25 % and 75 % quantiles of predictions are represented by arrows.

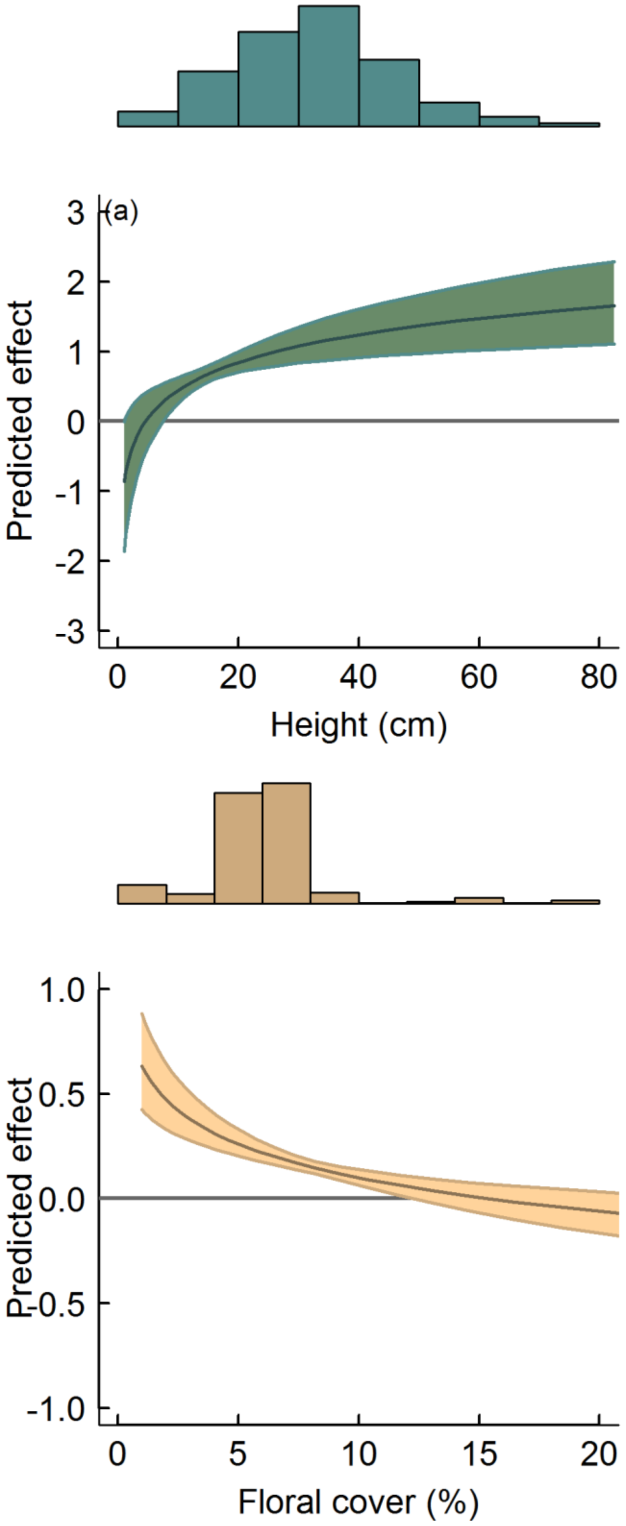

Fig. 4: Predicted effects of (a) conspecific neighbours of varying plant height and (b) heterospecific neighbours of varying floral cover on the seed set of open–pollinated capitula in target individuals. All remaining target and neighbour plant traits were set to their median values to generate the predictions. Positive predicted effects indicate facilitation whereas negative predicted effects indicate competition. Coloured areas represent the 25 % and 75 % inter-quantile-ranges of the predictions. Histograms present the frequencies of (a) height values of conspecific neighbours and (b) floral cover values of heterospecific neighbours on our study site.