Received: 14 April 2022 | Accepted: 8 September 2022

DOI: 10.1111/1365-2745.14018

Journal of Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Effects of biotic interactions on plant fecundity depend on spatial and functional structure of communities and time since disturbance

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Funding information
Deutsche Forschungsgemeinschaft, Grant/Award Number: SCHL 1934/1-3 and SCHU 2259/3-3; German Academic Scholarship Foundation

Handling Editor: Michal Bogdziewicz

Abstract

1. Biotic interactions in plant communities affect individual fitness and community dynamics. Interactions between plants vary in space, over time and with organisational complexity. Yet it is challenging to quantify temporal, spatial and functional determinants of different types of interactions between long-lived perennial plant species and their effect on lifetime fecundity.
2. We studied how plant–plant, pollinator- and seed predator-mediated interactions affect year-to-year variation in three fecundity components (cone production, seed set and seed survival) during post-fire recovery. Age-stratified data on the three fecundity components were collected in 19 even-aged communities comprising 20 serotinous *Protea* shrub species in the South African Fynbos. We analyse data on these fecundity components with neighbourhood models to infer the sign and strength of interactions throughout post-disturbance recovery, the neighbour plant traits that shape them and the spatial scale at which interactions take place. For each fecundity component, these models describe how neighbourhood effects change over time and with spatial distance between plants. We then predicted neighbourhood effects on individual fecundity components and cumulative reproductive output at different post-fire stand ages for each focal plant.
3. Competitive effects on cone production and seed set increased with post-fire stand age as biomass and floral resources for pollinators build up. In contrast, neighbourhood effects on seed survival were weak throughout post-disturbance recovery. Plant–plant interactions were shaped by neighbour traits related to resource acquisition, whereas animal-mediated interactions depended on neighbour traits related to resource availability for pollinators and seed predators. The spatial scale of the interactions increased from plant–plant over predator-mediated to pollinator-mediated interactions. The joint effect of these interactions on cumulative reproductive output caused the proportion of focal plants experiencing competition to increase with time since fire.

4. *Synthesis*. We show that temporal changes in biotic interactions throughout post-disturbance recovery of perennial plant communities depend on functional traits and can be integrated into neighbourhood effects on lifetime fecundity. Studying the temporal, spatial and functional determinants of neighbourhood effects on lifetime fecundity is important for predicting not only individual plant fitness but also population and community dynamics in changing environments.

KEYWORDS
disturbance-driven, fecundity components, functional traits, multi-species communities, neighbourhood effects, plant population and community dynamics, plant–plant and animal-mediated interactions, temporal dynamics

1 | INTRODUCTION

Biotic interactions in plant communities play an important role in community dynamics and species coexistence (Armas & Pugnaire, 2009; Benadi et al., 2012; Chesson, 2000; Kinlock, 2021; Kraft et al., 2015; Levine et al., 2017). However, the study of biotic interactions is challenging because they vary in space, over time, and with organisational complexity (Callaway & Walker, 1997; Forrester, 2014; Levine et al., 2017; Tilman & Kareiva, 1997).

Complexity in interactions in plant communities arises not only from the co-occurrence of multiple species but also from the joint action of different types of plant–plant and animal-mediated interactions (Callaway & Walker, 1997; Levine et al., 2017; Losapio et al., 2019). Competition for resources, for example, frequently co-occurs with apparent competition through predators (Gurevitch et al., 2000; Nottebrock, Schmid, Treurnicht, et al., 2017) and pollinator-mediated interactions (Mustajärvi et al., 2001; Palladini & Maron, 2013; Nottebrock, Schmid, Mayer, et al., 2017). However, the combined effects of plant–plant and animal-mediated interactions on long-term fecundity of individuals have rarely been quantified in natural communities of long-lived plants.

A way to reduce complexity when analysing interactions between multiple species is to move from a species-based to a trait-based description of the community (Kissling et al., 2012; McGill et al., 2006). Functional traits, as proposed by Violle et al. (2007), are traits that indirectly affect the fitness of a plant and underlie performance traits which directly measure different fitness components (growth, survival and reproduction). Functional traits of neighbours, therefore, describe species' life histories and rates of resource acquisition (Adler et al., 2014; Collins et al., 2016; Qiu et al., 2022; Rüger et al., 2018; Wright et al., 2004), as well as the resources they provide for mutual pollinators and seed predators (Gardarin et al., 2018; Lavorel et al., 2013). Hence, functional traits are also related to competition for resources and animal-mediated interactions between plants (Funk & Wolf, 2016; Kraft et al., 2015; Kunstler et al., 2016; Morales-Castilla et al., 2015; Nottebrock, Schmid, Mayer, et al., 2017; Nottebrock, Schmid, Treurnicht, et al., 2017).

Interactions between plants are limited in spatial extent, and the effect of these interactions on a plant's fitness, thus, depends on the composition of the plant's spatial neighbourhood. It has been shown that the size and density of con- and heterospecific neighbours, and hence also the amount of resources that these neighbours acquire, affect competition (Bonser & Reader, 1995; Lamonica et al., 2020; Nottebrock et al., 2013; Nottebrock, Schmid, Treurnicht, et al., 2017). In the same way, animal-mediated interactions are related to the amount of resources that the neighbourhood provides for mediating pollinators or predators (Bell & Clark, 2016; Bogdziewicz et al., 2018; Carvalheiro et al., 2014; Garzon-Lopez et al., 2015; Nottebrock, Schmid, Mayer, et al., 2017; Nottebrock, Schmid, Treurnicht, et al., 2017; Seifan et al., 2014).

Interactions, furthermore, vary with the size and age of neighbours and changes in the functional structure of the neighbourhood over time (Armas & Pugnaire, 2009; Callaway & Walker, 1997; CaraDonna et al., 2021;Goldberg et al., 2001; Schiffers & Tielbörger, 2006). It is therefore not sufficient to study neighbourhood effects at only one point in time. To understand the total effects on fitness, neighbourhood effects need to be integrated over the lifetime of a plant. While lifetime effects of biotic interactions on fitness components have been assessed for annual plants (Goldberg et al., 2001; Schiffers & Tielbörger, 2006), it is far more difficult to do so for perennial plants. In most communities of perennial plants, one cannot disentangle the importance of time, space, and functional composition because spatial and functional structure change over time. To assess temporal changes of interactions, not only plant performance at different times needs to be measured, but also the spatial and functional structure of the interacting community at these times. In communities of long-lived plants, this typically requires prohibitive investment of time and labour.

Fire-driven *Protea* shrub communities provide a system in which functional and spatial variability are uncoupled from age and in which fitness components can be assessed retrospectively. *Protea* communities are predominantly even-aged with low adult mortality between fires (Le Maitre, 1992; Le Maitre & Midgley, 1992). The spatial and functional composition of communities is, thus, largely constant during inter-fire intervals. Furthermore, the even-aged nature of *Protea* communities means that age-related changes at the individual level happen simultaneously in the entire community and thus reinforce each other in their effect on biotic interactions and plant fitness. Moreover, the high beta-diversity among *Protea* communities (Cowling & Lamont, 1998) offers the possibility to study communities with different spatial and functional structures at different post-fire stand ages. Previous studies in the system have shown that the lifetime fecundity of Proteas is influenced by inter-fire intervals (Treurnicht et al., 2016) and by plant–plant as well as pollinator- and seed predator-mediated interactions (Nottebrock et al., 2013; Nottebrock, Schmid, Mayer, et al., 2017; Nottebrock, Schmid, Treurnicht, et al., 2017). Temporal variation in biotic interactions, which has not been looked at yet and is the subject of this study, in interaction with ongoing changes in fire frequency (Forsyth & van Wilgen, 2008; Wilson et al., 2015) could therefore have important implications for community dynamics. Furthermore, plant–plant and animal-mediated interactions in *Protea* communities have been shown to take place on different spatial scales. While the spatial scale on which apparent competition through seed predators takes place only seems to be a bit larger than that for competition (Nottebrock, Schmid, Treurnicht, et al., 2017), the scale on which more mobile pollinators act is bigger (Nottebrock, Schmid, Mayer, et al., 2017; Schmid, Nottebrock, Esler, Pagel, Pauw, et al., 2016). Neighbourhood effects of floral resources on pollination are competitive between species, but facilitative within species (Nottebrock, Schmid, Mayer, et al., 2017). Since monospecific stands are common in *Protea* communities, these facilitative effects dominate pollinator-mediated interactions at the neighbourhood scale (see Nottebrock, Schmid, Mayer, et al., 2017). Moreover, Proteas store their seeds in cones in the canopy that can be aged (Bond et al., 1995). Hence, Proteas are ideally suited to study the temporal dynamics of plant–plant and animal-mediated interaction effects on the fecundity of long-lived plants.

Based on individual-level maps of 19 plant communities, age-stratified data of fecundity components from individuals of 20 species, trait data from the same species and a neighbourhood model fitted to these data, we test the following hypotheses: (i) plant–plant and animal-mediated interactions affect three fecundity components (cone production, seed set, seed survival) during post-disturbance recovery (H1), (ii) the spatial scale of interactions increases from plant–plant over predator-mediated to pollinator-mediated interactions (H2), (iii) functional traits shape the effect of neighbouring plants, with traits related to resource uptake influencing competitive effects on cone production and traits determining resources availability for pollinators and seed predators influencing neighbourhood effects on seed set and seed survival, respectively (H3), (iv) the total neighbourhood of plants has a negative effect on cone production and seed survival and a facilitative effect on seed set and the strength of these effects increases with stand age (H4) and (v) temporal changes in the strength of individual interactions causes net neighbourhood effects on cumulative reproductive output to vary in strength during post-disturbance recovery and potentially to switch between facilitation and competition (H5).

2 | MATERIALS AND METHODS

2.1 | Study system and species

We study biotic interactions between shrubs of the genus *Protea* (see the previous section) in 19 plant communities in the South African Fynbos. Proteas frequently dominate the over-storey of Fynbos plant communities (Le Maitre & Midgley, 1992; Schurr et al., 2012). *Protea* is a species-rich genus and a particularly high beta-diversity arises from a high turnover in species occurrence between sites (Cowling & Lamont, 1998). Across all sites, we included 20 *Protea* species (Table S5) with an average of 4.4 species occurring per site. Fynbos communities are fire-driven with average fire return intervals of about 10 to 13 years, although fire return intervals can also be longer than 20 years (Van Wilgen et al., 2010). Most Fynbos *Protea* species (including all of our study species) are serotinous: they store their seeds in cones for many years and hence form a canopy seed bank, but no soil seed bank (Bond, 1985). Cones open and release their seeds after a fire, and recruitment occurs shortly thereafter (Bond et al., 1984). Fire usually kills the adult plants of nonsprouting species ($n = 17$), whereas resprouting species ($n = 3$) follow a different life history strategy and frequently survive fire (Treurnicht et al., 2016) by regrowing from above- or below-ground meristems. There is a clear trade-off between fire survival and reproduction: per capita, resprouters produce fewer seeds and post-fire recruits than nonsprouters (Treurnicht et al., 2016). On the other hand, adult resprouting plants reproduce sooner after fire than nonsprouters (Van Wilgen & Forsyth, 1992), and are thus favoured by short fire return intervals.

The studied *Protea* species are pollinated by birds and insects (Coetzee & Giliomee, 1985; Rebelo, 1987; Schmid et al., 2015; Whitehead et al., 1987). The most common pollinators are the Cape Sugarbird (*Promerops cafer*) and the Orange-breasted Sunbird (*Anthobaphes violacea*) (Rebelo et al., 1984; Schmid, Nottebrock, Esler, Pagel, Pauw, et al., 2016), as well as species of different beetle families (Coetzee & Giliomee, 1985; Whitehead et al., 1987). Bird and beetle pollinators feed on nectar and/or pollen (Rebelo, 1987; Whitehead et al., 1987), and Sugarbirds have additionally been shown to feed on insects that are found in the inflorescences (Mostert et al., 1980). Pre-dispersal seed predation of *Protea* species occurs mainly through endophagous larvae of beetle, moth and butterfly species, that are found in the inflorescences and infructescences of Proteas (Coetzee & Giliomee, 1987; Wright & Samways, 1999). Larvae feed on seeds and/or the involucral receptacle, which causes seeds to die (Coetzee & Giliomee, 1987). Adults of beetle predators may feed on pollen, nectar or foliage or use the inflorescences as shelter (Coetzee & Giliomee, 1987).

2.2 | Individual-level maps of plant communities

Every over-storey nonsprouting *Protea* individual taller than 0.3 m and every resprouting *Protea* was mapped on the 19 study sites. The study sites have an extent of 200 × 200 m, which exceeds the size of bird pollinator territories (Calf et al., 2003; Nottebrock, Schmid, Mayer, et al., 2017; Schmid, Nottebrock, Esler, Pagel, Pauw, et al., 2016). Seventeen sites were mapped in 2011–2012 and another two sites were mapped in 2017–2018. Further details on the mapping procedure can be found in Schmid, Nottebrock, Esler, Pagel, Pauw, et al. (2016) and Nottebrock, Schmid, Mayer, et al. (2017). The mapping resulted in a total of 107,197 individuals of 20 *Protea* species (Table S5), with 17 to 46,807 individuals per species (Table S4) and 83 to 37,253 individuals of 3 to 8 species per site (Tables S3 and S4). Post-fire stand age was obtained from ageing of the plants (Bond et al., 1995; Treurnicht et al., 2016), information provided by landowners, the CapeNature Fires database and freely available satellite imagery (NASA FIRMS application and NASA Worldview application). Post-fire stand ages of the study sites ranged from 2.5 to 27 years (Table S3).

2.3 | Age-stratified data of fecundity components of focal plants

Age-stratified data of cone production were collected for 497 focal plants growing within the 120 × 120 m large core zones of the study sites, thus avoiding edge effects. Focal plants were a priori chosen from community maps to cover the functional and spatial variation of neighbourhoods in a community. Closed and open cones and scars of abscised cones were counted on each focal plant to obtain the total number of cones produced in each reproductive period of the plant. This resulted in 6107 observations of cone counts on the 497 focal plants. By counting growth increments above and below a cone, the rate as well as the time of cone production can be determined by the position of the cone on the plant (Bond, 1985; Treurnicht et al., 2016). We calculated cone production at the plant level as the rate of produced cones per year. Occasionally, there can be more than one reproductive period per year. Therefore, the number of counted cones was multiplied by the number of reproductive periods per year to obtain the rate of cone production per year at each reproductive period.

For each cone-bearing focal plant, a single closed cone was harvested from each reproductive period, to measure seed set and seed survival. This resulted in an average number of 3.5 (min = 1, max = 13) harvested cones per plant (excluding plants for which no cones could be harvested). And an average number of 68.9 (min = 23, max = 195) harvested cones per site. Cones were cross-sectioned at the seed stratum, and viable seed number and predation proportion were determined (Nottebrock, Schmid, Mayer, et al., 2017; Treurnicht et al., 2016). A proportional seed set was then calculated for 1167 cones on 349 focal plants as the counts of viable seeds divided by the maximum potential seed set. The potential seed set is calculated as the number of seeds that potentially fit in a cone corrected for the proportion of the cone that was consumed by seed predators.

$$\text{Potential seedset}_i = \frac{\text{cone area}_i}{\text{seed area}_s} * \left(1 - \text{predation proportion}_i\right) \quad (1)$$

where i denotes the cone for which the seed set was measured and s denotes the species to which the cone belongs to. Seed area is the mean cross-sectional area of a seed of a given species and cone area is the area of the involucral receptacle.

Seed survival was measured as the proportion of the cone that was not consumed by seed predators $\left(1 - \text{predation proportion}_i\right)$ for 1309 cones on 377 plants. The number of focal plants varies between cone production, seed set and seed survival because seed set and survival rate could not be calculated in all cases due to plants not having reproduced or missing data (e.g. open or abscised cones, complete predation, missing data for cone area).

2.4 | Species-level functional traits

To assess how functional traits shape neighbourhood effects (H3), we included in our analysis a set of species-level functional traits, which are either linked to resource uptake by plants or to resource availability for pollinators and seed predators (Table 1). For six continuous functional traits, we calculated species-level median trait values from measurements obtained from the Fynbase database (Schurr et al., 2007), which is part of the TRY database (Kattge et al., 2020).

Specific leaf area (SLA; in m^2 kg^{-1}), leaf nitrogen concentration (leaf N; in % mass) and wood density (in g cm^{-3}) were measured following Pérez-Harguindeguy et al. (2013). To measure SLA and leaf N, 3–5 fully expanded and undamaged one-year-old leaves per sampled plant were collected from the outer canopy. They were stored in a sealed plastic bag in the field and measured on a flatbed scanner in the lab on the same day. ImageJ was used to calculated one-sided projected surface area. Leaves were then dried at 70°C to constant mass and weighed. To calculate leaf N, dried leaves were ground to a fine powder and total nitrogen was obtained by elemental analysis (vario EL cube elemental analyser, Elementar Analysensysteme GmbH, Germany). Wood density was measured on 3–5 cm large samples of one-year-old wood. From the undamaged samples, the bark was removed and subsequently the volume of the samples was measured with the water-displacement method (Pérez-Harguindeguy et al., 2013). Samples were then dried at 70°C to constant mass and weighed. To obtain cone dry mass (in g), closed cones were oven dried at 70°C to constant mass and then weighed using precision scales. Similarly, fertile seeds were oven-dried at 70° to constant mass and population-pooled samples were weighed using precision scales to calculate population-mean seed dry mass (in mg). We counted the pollen load per pollen presenter with a flow cytometer (BD FACSMelody™ Cell Sorter), and used the Invitrogen™ LIVE/DEAD® BacLight™ Bacterial Viability and Counting Kit (L34856). For staining, we added 10 μl SYTOX™ Green Nucleic Acid Stain to 1988 μl PBS (phosphate-buffered saline) pollen suspension. After 15 min incubation, we added 2 μl beads (corresponding to 200,000 beads). Pollen per pollen presenter was then calculated by dividing pollen count per sample by the ratio of counted beads and the initial 200,000 beads. From all individual- or population-level trait values we calculated species-level median trait values. Pollen per inflorescence was then calculated as the product of species' average pollen counts per pollen presenter and species average number of florets per inflorescence. Values for the number of florets per inflorescence for each species were taken from the literature (Collins & Rebelo, 1987; Horn, 1962; Wiens et al., 1983) and own additional data. All species-level trait values were log-transformed before entering the analysis.

TABLE 1 Summary of expected influence of neighbour traits on neighbour effects on three fecundity components of a focal plant. Traits are linked to resource competition, apparent competition through seed predators or pollination and should therefore affect fecundity components differently. The last column shows how we expect neighbour effects on the fecundity components to change with an increasing trait value (↑: positive effect; ↓: negative effect) based on the literature

Neighbour trait	Interaction type	Fecundity component	Expected change of neighbour effects with increasing neighbour trait value
SLA	Plant–plant	Cone production	↑ competitive effect becomes less strong with increasing SLA (Kunstler et al., 2016)
Leaf N	Plant–plant	Cone production	↑ competitive effect becomes less strong with increasing leaf N (Funk & Wolf, 2016)
Wood density	Plant–plant	Cone production	↓ competitive effect becomes stronger with high wood density (Kunstler et al., 2016)
Size of reproductive organ (Cone dry mass)	Pollinator-mediated	Seed set	↑ ↓pollinators respond positively to the size of the reproductive organ which can lead to competition or facilitation between plants (Ghazoul, 2005)
	Seed predator-mediated	Seed survival	↑ woody structures increase defence (Le Maitre & Midgley, 1992)
Seed dry mass	Plant–plant	Cone production	↓ competitive effect increases with seed mass (Goldberg & Landa, 1991)
	Seed predator-mediated	Seed survival	↓ higher seed crop of neighbouring plants increases predation rate and reduces seed survival on focal plants (Nottebrock, Schmid, Treurnicht, et al., 2017)
Pollen per inflorescence	Pollinator mediated	Seed set	↑↓ increases in floral resources for pollinators can lead to competition or facilitation between plants (Ghazoul, 2005)
Resprouting ability	Plant–plant	Cone production	↓ early on adult resprouters are more competitive than juvenile nonsprouters (Bond & Midgley, 2001)
	Pollinator-mediated	Seed set	↑ ↓ shortly after fire: adult resprouters reproduce earlier than nonsprouters (Van Wilgen & Forsyth, 1992), increased resource availability can lead to facilitation or competition for pollinators (Ghazoul, 2005)
	Seed predator-mediated	Seed survival	↓ shortly after fire: adult resprouters reproduce earlier than nonsprouters (Van Wilgen & Forsyth, 1992), which attracts seed predators (Nottebrock, Schmid, Treurnicht, et al., 2017)
Conspecificity	Plant–plant	Cone production	↓ there is stronger intra- than interspecific competition between Proteas (Nottebrock, Schmid, Treurnicht, et al., 2017)
	Pollinator-mediated	Seed set	↑ having conspecific neighbours increases chance of conspecific pollen transfer (Mitchell et al., 2009; Nottebrock, Schmid, Mayer, et al., 2017)

2.5 | Statistical models

With neighbourhood models, we aim to quantify how plant–plant and animal-mediated interactions in the communities affect three fecundity components (cone production, seed set, seed survival) and on which spatial scale those interactions take place (H1–H3). Therefore, we formulated a linear mixed effects model for each of the three fecundity components.

Before entering the analysis, the rate of cone production was log(x + 1)-transformed and the proportions of seed set and seed survival were logit-transformed. To circumvent proportions of 0 and 1, which would lead to infinite values after logit-transformation, the minimum of the smallest difference to 0 or 1 was added to numerator and denominator in the logit-transformation (Warton & Hui, 2011). Pearson's correlation coefficients revealed that response variables are only weakly correlated or uncorrelated (cone production and seed set: −0.032; cone production and seed survival: 0.037; seed set and seed survival: 0.26).

As explanatory variables, we used post-fire stand age (*pfa*) of the study site, a neighbourhood index of plant density (*NI.dens*) and average neighbour trait values (*ANTVs*) of eight traits calculated for each focal plant, and the age of cones at the time of observation. *NI.dens* and *ANTVs* were calculated by weighing neighbours *i* or their trait values according to their distance d_i to the focal plant with a Gaussian kernel (Equations 2 and 3).

$$NI.dens = \sum_{i=1}^{N_{\text{neighbours}}} e^{-d_i^2 * \left(-\frac{\log(0.5)}{\alpha^2}\right)}, \tag{2}$$

$$NI.trait = \sum_{i=1}^{N_{\text{neighbours}}} \text{trait value}_i * e^{-d_i^2 * \left(-\frac{\log(0.5)}{\alpha^2}\right)}, \tag{3}$$

where α is the distance at which the effect of a neighbour is halved. As neighbours *i* we considered all mapped *Protea* individuals in a radius of 40 m around the focal plant. *ANTV*s for each focal plant and trait were then calculated as:

$$ANTV = \frac{NI.trait}{NI.dens}. \tag{4}$$

*ANTV*s were calculated for the log-transformed continuous trait values and for resprouting ability and conspecificity (Table 1). Resprouting ability and conspecificity are binary traits that take a value of 1 when the neighbour is a resprouter or conspecific and a value of 0 when it is a nonsprouter or heterospecific. The *ANTV*s of resprouting ability and conspecificity, therefore, correspond to the proportion of the *NI.dens* that is contributed by resprouters and conspecifics, respectively.

To test for temporal changes in trait-dependent neighbourhood effects, the models included an interaction between post-fire stand age (*pfa)* and *NI.dens*, and *ANTV*s affect the response variable via interactions with *NI.dens* and also via three-way interactions with *NI.dens* and *pfa*. Cone age was added as explanatory variable to account for observation errors (cone production model) and biological processes dependent on cone age (seed decay in the seed set model and predation after first year in the seed survival model). Cone age and *ANTV*s of continuous traits were scaled and centred around their mean, post-fire stand age was scaled and centred around 13 years (the average post-fire stand age at which cones were produced), neighbourhood density was scaled, but not centred. The models also included random intercepts of focal plant, species and site, as well as random slopes of species and site for the *pfa* effect. Thus, the general structure of the models (in notation of the LME4 R package [Bates et al., 2015]) is:

$$\begin{aligned} y \sim\ & cone\ age + pfa + NI.dens + NI.dens{:}\,pfa \\ & + \sum\nolimits_{m=1}^{M} \left(NI.dens{:}\,ANTV_m + NI.dens{:}\,ANTV_m{:}\,pfa\right) \\ & + (1|species + site + focalplant) + (pfa|species + site), \end{aligned} \tag{5}$$

where M is the number of traits included in the model.

Models were fitted in a two-level approach (Nottebrock, Schmid, Treurnicht, et al., 2017) where we used one dimensional optimisation (optimise function in R, R Core Team, 2019) to find the scaling parameter α which minimises the negative log likelihood of the linear mixed effects models fitted with the LMERTEST R package (Kuznetsova et al., 2017) in R version 3.6.2 (R Core Team, 2019). In doing so, we allowed α to take values between 0 and 40 m.

2.6 | Model evaluation

To test whether neighbours have an effect on the fecundity components (H1), we also fitted local models that only included the effects of post-fire stand age and cone age and the same random effects as the neighbourhood models, but neither density nor *ANTV*s of the neighbourhood. Local models were then compared to the full neighbourhood models with a likelihood ratio test (Table S1). Marginal and conditional R^2 values were calculated with the r.squaredGLMM-function of the MUMIN R package (Barton, 2020) for the full neighbourhood models. The marginal R^2 is the proportion of the total variance explained by the fixed effects and the conditional R^2 is the proportion of the total variance explained by the fixed and random effects (Johnson, 2014; Nakagawa et al., 2017; Nakagawa & Schielzeth, 2013). To test for differences in spatial scale between interactions types (H2), we computed 95% confidence intervals of the α parameters of the full neighbourhood models based on their likelihood-profile (Venzon & Moolgavkar, 1988; Table S1). The question whether traits shape neighbourhood effects (H3), was answered by comparing full neighbourhood models to models only containing neighbourhood density with likelihood ratio tests (Table S1).

2.7 | Relative effects of the total neighbourhood on fecundity components and the cumulative reproductive output

To estimate changes in strength and direction of the different interactions types in the communities over time (H4), we predicted the relative effect of the total neighbourhood on cone production, seed set and seed survival for each focal plant for which we had measurements of all three fecundity components (Table S1). Relative neighbourhood effects were calculated as the predictions of full models considering the neighbourhood divided by the respective predictions without considering the neighbourhood (i.e. setting neighbourhood plant density to zero). Predictions were made for effects on newly produced cones (i.e. setting cone age to a value of 1) at post-fire stand ages from 3 to 17 years.

To test for changes in neighbourhood effects on the cumulative reproductive output (H5), we calculated a plant's cumulative reproductive output as a measure of total fecundity up to a certain post-fire age (Table S1). We calculated the cumulative reproductive output of each focal plant *f* at each post-fire age *T* as the product of yearly predicted cone production, seed set and seed survival summed over all previous ages *t*.

$$\text{Cumulative reproductive output}_{f,T} = \sum_{t=3}^{T} \text{cones}_{f,t} * \text{seed set}_{f,t} * \text{seed survival}_{f,t}. \tag{6}$$

Note that predictions of seed set and seed survival include cone age ($T - t$) as explanatory variable to account for ongoing seed decay and predation after the year in which a seed was produced. The relative effect of the neighbourhood on the cumulative reproductive output was again calculated as the percentage of the cumulative reproductive output predicted with neighbourhood effects divided by the cumulative reproductive output predicted without neighbourhood effects.

3 | RESULTS

3.1 | Neighbourhood effects on fecundity components

We hypothesised that fecundity components of Proteas are influenced by interactions with their con- and heterospecific neighbourhood (H1). We could confirm this hypothesis by comparing our full neighbourhood models to local models that did not contain neighbourhood effects (cones: $\chi^2_{18df} = 82.8, p < 0.001$; seed set: $\chi^2_{18df} = 30.3, p = 0.035$; seed survival: $\chi^2_{18df} = 32.1, p = 0.022$). The marginal and conditional R^2-values of the full neighbourhood models were relatively high for cone production (marginal R^2 =0.52/conditional R^2 =0.79), and lower for seed set (0.07/0.31) and seed survival (0.06/0.37).

3.2 | Spatial scale of different interaction types

Neighbourhood interactions affecting the three fecundity components take place on different spatial scales (Figure 1, Figure S1). In accordance with our second hypothesis (H2), the scale of the interaction increases from plant–plant interactions on cone production (scaling parameter α = 0.8 m, 95% confidence interval: 0.7–1.0 m) over predator-mediated interactions on seed survival (α = 5.8 m, 3.9–8.3 m) to pollinator-mediated interactions on seed set (α = 30.1 m, 12.6–40 m).

3.3 | Temporal changes in trait effects on interactions

We could confirm that functional traits of the neighbours shape neighbourhood effects (H3) by comparing full models that included average neighbour trait values (*ANTVs*) to models only containing neighbour density (cones: $\chi^2_{16df} = 64.6, p < 0.001$; seed set: $\chi^2_{16df} = 28.1, p = 0.03$; seed survival: $\chi^2_{16df} = 29.2, p = 0.02$). Furthermore, we found that different traits are informative for the neighbourhood effects on the three fecundity components (Figure 2, Table S2). As hypothesised these traits are linked to the interaction type acting on the respective fecundity component (Table 1, Figure 2).

Cone production was best explained by neighbour density and SLA (Figure 2a). The per capita effect of a neighbour is negative at an average post-fire stand age and becomes less competitive with increasing SLA. The positive effect of SLA, furthermore, increases with post-fire stand age.

Neighbourhood effects on seed set are related to neighbour density, resprouting ability and whether the neighbour is a conspecific (Figure 2b). At an average post-fire stand age of 13 years, heterospecific nonsprouters have a negative effect, which is attenuated or even reversed for conspecific and resprouting neighbours. However, these effects of conspecificity and resprouting do not significantly change over time. Although only marginally significant, the per capita effect of an average neighbour seems to become more competitive over time (p = 0.06; Figure S2b). Competition on seed set therefore increases over time, but the change in competition strength is independent of the proportions of conspecific and resprouting neighbours.

Seed survival is mainly influenced by pollen amount per inflorescence and cone dry mass of the neighbours (Figure 2c). Pollen amount increases the apparent competition, whereas a high cone dry mass causes more facilitative effects. There is no significant change in neighbour trait effects on seed survival over time.

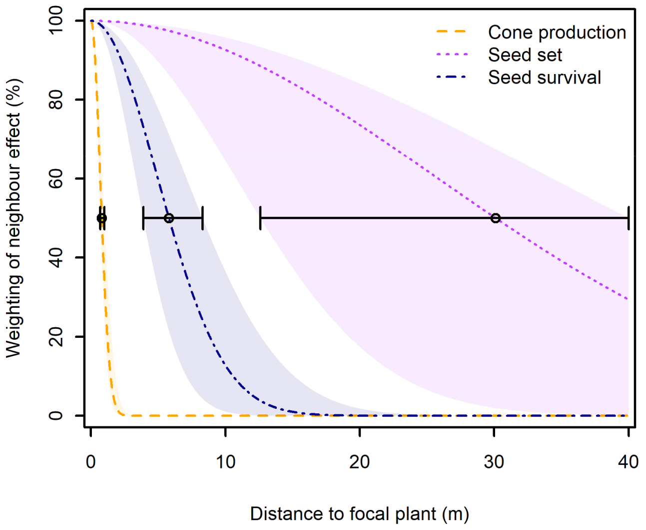

FIGURE 1 Estimated spatial kernels for the neighbour effects on three fecundity components (cone production (orange), seed set (purple), seed survival (blue)) in *Protea* communities, showing a decrease of neighbour influence with distance from the focal plant. Circles indicate the distances at which 50% of the neighbour effect is left, bars are their 95% confidence intervals. Shaded areas are the 95% confidence intervals of the neighbour effect at distances from 0 to 40 m. The absolute strength and sign of the neighbour effect depend on the neighbour species and the post-fire stand age (see Figure 2).

3.4 | Relative effects of neighbourhood interactions on fecundity components

Neighbourhood effects on fecundity vary throughout post-disturbance recovery of the community (Figure 3). The neighbourhood effects on cone production and seed set tend to change from more facilitative to more competitive effects as post-fire stand age increases. However, focal plants vary substantially in the experienced neighbourhood effect (Figure 3). As hypothesised (H4), most focal plants experience a competitive effect on cone production which gets more negative over time (Figure 3a). Contrary to our hypothesis, there is a competitive effect on seed set of most focal plants for a post-fire stand age of more than 5 years that gets more negative over time (Figure 3b). At younger post-fire stand ages the majority of focal plants experiences a facilitative effect of the neighbourhood on seed set. The neighbourhood effect on seed survival is slightly negative and seems to be stable throughout post-disturbance recovery for most (middle 50%) of the focal plants (Figure 3c).

3.5 | Effects of neighbourhood interactions on cumulative reproductive output

The integrative effect of the total neighbourhood on cumulative reproductive output can cause switches between facilitation and competition during post-disturbance recovery (H5). At young post-fire stand ages a small majority (51%) of focal plants experienced positive effects. However, relative effects of the total neighbourhood become increasingly negative over time and are competitive for most focal plants (70%) at older post-fire stand ages (Figure 3d).

4 | DISCUSSION

This study yields new insights into spatial, temporal and functional determinants of biotic interactions and fecundity in communities of long-lived plants. We found that biotic interactions affect three major fecundity components (H1) and that the spatial scale of biotic interactions increases from plant–plant over predator-mediated to pollinator-mediated interactions (H2, Figure 1). We also could confirm that the interactions are shaped by functional traits of the neighbouring plants (H3). Specifically, cone production is affected by plant traits related to resource acquisition, whereas seed set and seed survival are influenced by traits determining resource availability for pollinators and seed predators, respectively or increased chances of intraspecific pollen transfer (Figure 2). H4 was only partially confirmed. As hypothesised, we found that the neighbourhood has a negative effect on cone production of most focal plants that gets stronger with post-fire stand age (Figure 3a). However, contrary to H4 we found an increasingly negative effect on seed set (Figure 3b). As expected, there was a negative effect of the neighbourhood on seed survival of most focal plants. However, this effect was independent of post-fire stand age (Figure 3c). Furthermore, we found an increasingly competitive effect on cumulative reproductive output of most focal plants, with a small majority of plants experiencing facilitation at young post-fire stand ages. Therefore, we could also confirm switches between facilitation and competition during post-disturbance recovery (H5). In the following, we discuss which mechanisms caused this variation in biotic interactions and how this variation may impact community dynamics.

4.1 | Traits shape biotic interactions and plant fecundity

Both neighbour trait effects and spatial scales of interaction corroborate that different interaction types are acting on the three fecundity components. They strongly suggest that lifetime fecundity of Proteas is influenced by the effects of plant–plant interactions on cone production, of pollinator-mediated interactions on seed set and of predator-mediated interactions on seed survival (with the amount of variation explained by traits being larger for plant–plant than for animal-mediated interactions). Assessing interaction effects on only one fecundity component might thus miss important determinants of the total neighbourhood effect on reproduction (Laughlin et al., 2020).

The estimated trait effects on plant–plant interactions (Figure 2a) match expectations from the literature (Table 1). As expected (Kunstler et al., 2016), neighbour plants with higher SLA had reduced competitive (or even facilitative) effects on cone production at an intermediate post-fire stand age (Figure 2a). Moreover, the positive effects of neighbour SLA on interactions increased over time (Figure 2a), indicating that differences in competitive effects between species become larger over time. We also find a tendency for SLA increasing competition at young post-fire stand ages (Figure S2a). This is in line with a shift in effects of focal plant SLA on relative growth rate that has been reported previously (Gibert et al., 2016; Iida et al., 2014).

At an average post-fire stand age and with increasing time since the last fire resprouters, having lower investment in reproduction than nonsprouters (Treurnicht et al., 2016), reduce competition for pollinators (Figure 2b). However, although the trait-age interaction is not significant, we can see a tendency of resprouters having a competitive effect shortly after fire (Figure S2b). This coincides with resprouters having more inflorescences early on (Table 1, Van Wilgen & Forsyth, 1992). Not surprisingly, conspecific neighbours had a positive effect on seed set (Figure 2b, Table 1). The increasingly positive effect of conspecifics might not only be due to proportional effects, but can further be increased by pollinators preferring abundant plant species (Schmid, Nottebrock, Esler, Pagel, Böhning-Gaese, et al., 2016). In addition, some of our findings suggest that other animal species might mediate neighbourhood effects on different fecundity components at the same time. An example could be the scarab beetle *Genuchus hottentotus*, which feeds (at different life stages) on both seeds and pollen and acts as both seed predator and pollinator (Coetzee & Giliomee, 1985, 1987). This cannot only cause the negative effect of neighbour pollen amount on seed survival, but might also explain the marginally positive effect of neighbour seed dry mass on seed set (Figure 2b,c). As expected, seed survival increased with the average cone dry mass of the neighbours (Figure 2c, Table 1). This indicates that both attraction of and defence from seed predators in the neighbourhood play a role for seed survival and are not independent of neighbour trait effects on pollination (Herrera et al., 2002).

Although functional traits are often weak predictors of demographic rates in long-lived plants (Yang et al., 2018), they can still be useful to infer interaction direction and strength (Morales-Castilla et al., 2015). This is especially valuable when assessing interactions in multi-species (meta-)communities, where a trait-based description of interactions reduces complexity (Kissling et al., 2012; McGill et al., 2006). Clearly, traits not only shape interactions but trait

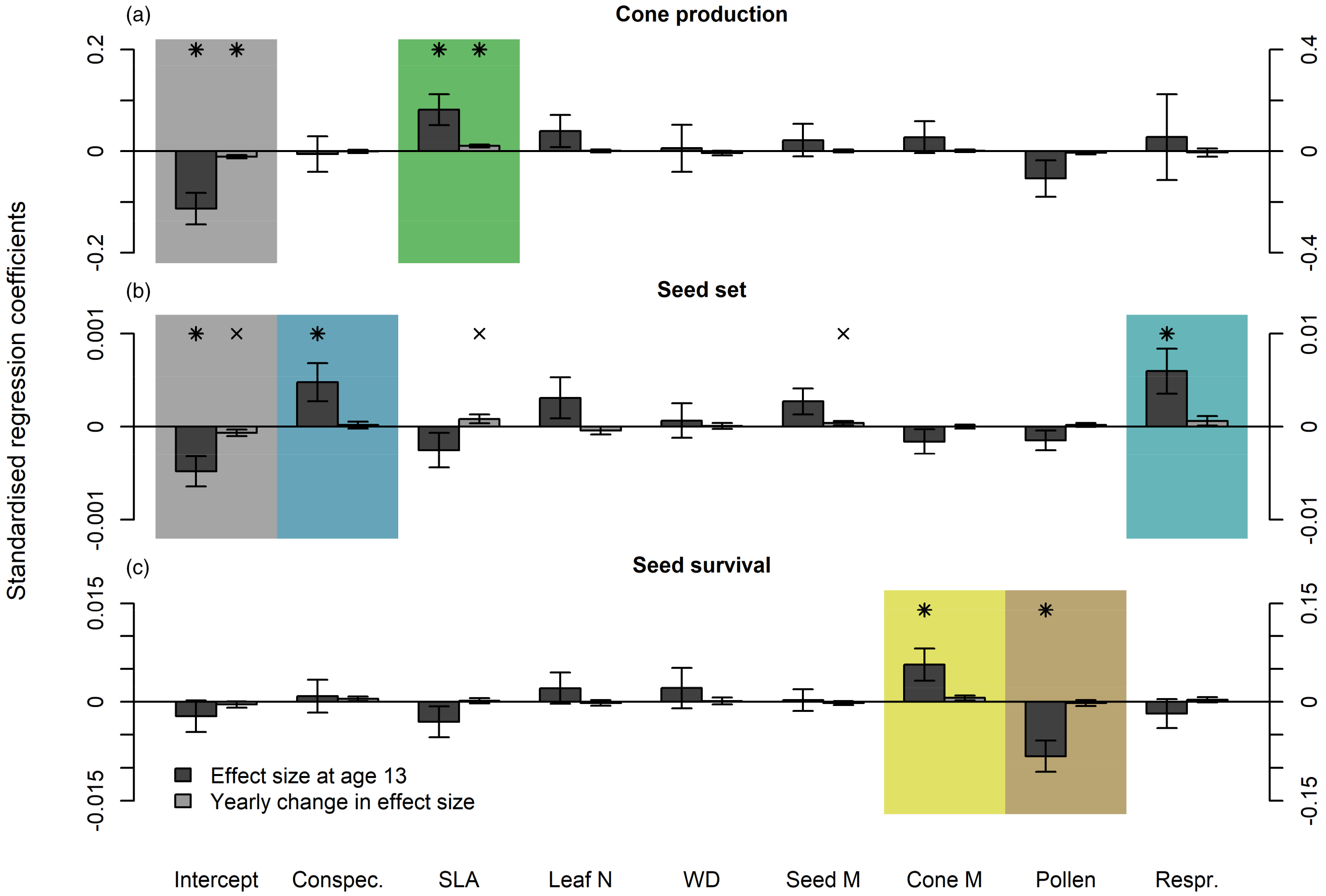

FIGURE 2 Effects of neighbour plant functional traits on cone production (a), seed set (b) and seed survival (c). The bars and whiskers indicate standardised regression coefficients and associated standard errors. Dark bars show trait effects at an average post-fire stand age of 13 years. Light bars show the yearly change in effect sizes. Traits that have at least one significant effect (trait effect at age 13 and/or yearly change in trait effect) on the respective fecundity component are coloured. Significant effects ($p < 0.05$) are marked with an asterisk, crosses denote marginally significant effects ($0.05 < p < 0.1$). Significance levels have been computed with the Satterthwaite method using the lmer function of the LMERTEST R package (Kuznetsova et al., 2017). The intercept represents the per capita effect of a heterospecific, nonsprouting neighbour at 0 m distance with other trait values set to their mean. SLA (specific leaf area), leaf N (leaf nitrogen content), WD (wood density), Seed M (seed dry mass), Cone M (cone dry mass) and Pollen (pollen per inflorescence) are the effects of the standardised log-transformed traits, Respr. (resprouter) and Conspec. (conspecific) correspond to the effects of one resprouting/ one conspecific neighbour. Note that the effect of resprouting is plotted on the right *y*-axis.

variation is also a result of ecological and evolutionary processes (Cariveau et al., 2004). Our finding that there are changes in strength of interaction types and shifts in trait effects over time, suggests that there is not a single optimal trait combination, which should promote functional diversity (and in fact, our system has a remarkably high functional diversity, Cramer et al., 2014).

4.2 | Biotic interaction effects change through time

With increasing post-fire stand age, biotic interaction effects on cone production and seed set become more competitive (Figure 3a,b). As discussed in the previous section, neighbourhood effects on the three different fecundity components are explained best by functional traits that can be related to resource acquisition and resource availability for pollinators and seed predators (Table 1, Figure 2). The intensification of competitive effects on cone production and seed set with post-fire stand age (Figure 3a,b) can therefore be attributed to an increase of neighbourhood biomass and changes in the ratio of resources for pollinators and pollinator abundance (Bonser & Reader, 1995; Nottebrock, Schmid, Mayer, et al., 2017; Nottebrock, Schmid, Treurnicht, et al., 2017; Schmid, Nottebrock, Esler, Pagel, Pauw, et al., 2016). However, despite the general trend, all interaction types also have facilitative effects on some focal plants at all post-fire stand ages.

A considerable proportion of focal plants experienced facilitative neighbourhood effects on cone production especially at young post-fire stand ages (Figure 3a). This suggests that there are facilitative processes between Proteas which do not get outweighed by resource competition from these neighbours. Facilitation between Proteas could occur through the mobilisation of soil nutrients. Proteas can grow cluster roots that facilitate the uptake of phosphorous through the release of root exudates and an increased surface area (Cramer et al., 2014; Lamont, 1982).

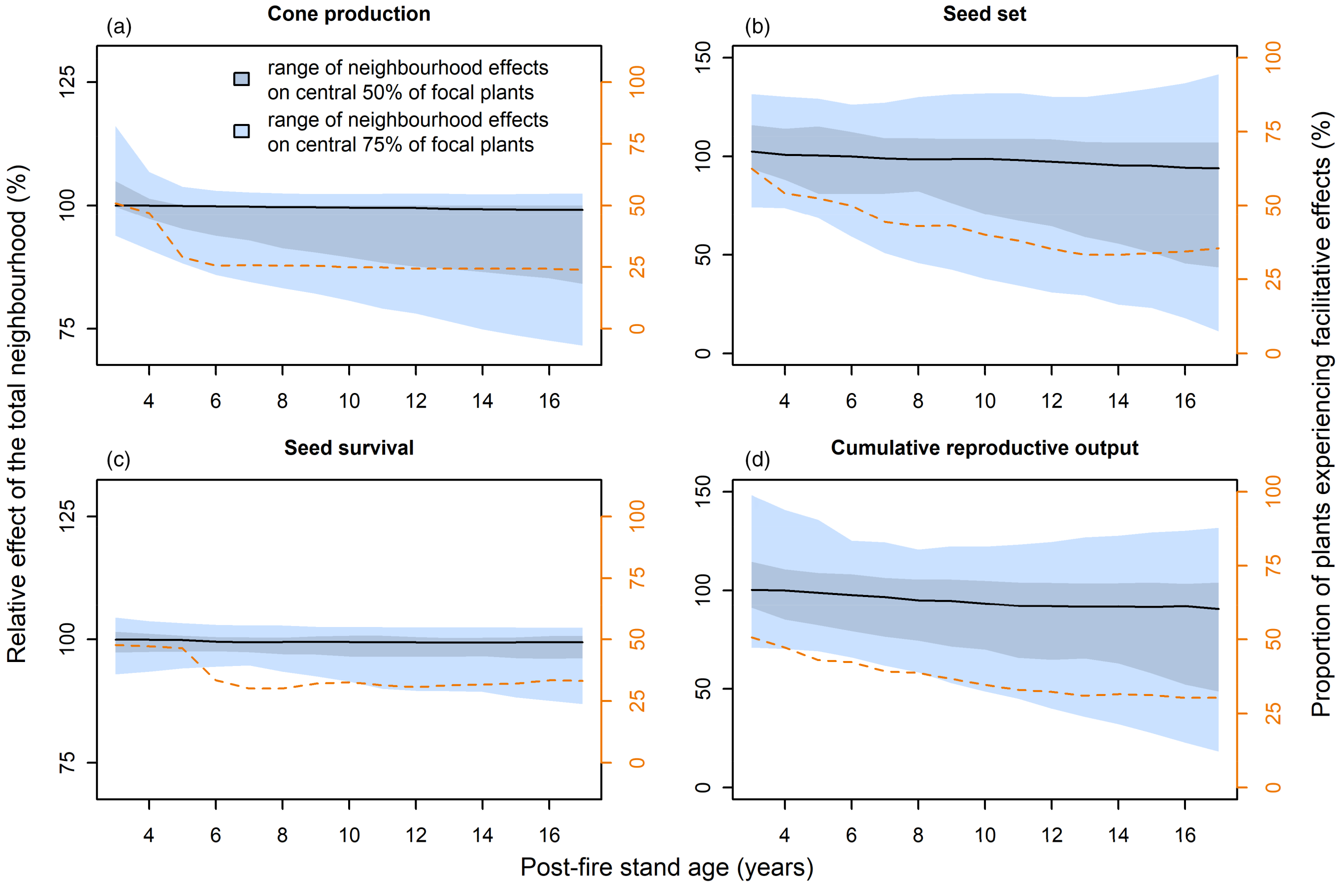

FIGURE 3 Neighbourhood effects vary between focal individuals and with time since fire disturbance. The figures show predicted relative neighbourhood effects on the 349 focal plants for which we had data on all three fecundity components. Predictions were made for post-fire stand ages from 3 to 17 years for the three fecundity components in the year of cone production (a–c) and the cumulative effect of the neighbourhood on all three fecundity components up to the specific post-fire stand age, including seed decay and predation after the first year (d). Values greater than 100% indicate a facilitative effect of the neighbourhood, values smaller than 100% indicate a negative effect of the neighbourhood. The solid black lines are the medians of the individual-level effects. Light blue areas represent neighbourhood effects on the central 75% of focal plants, dark blue areas the effects on the central 50% of focal plants. Relative neighbourhood effects are plotted on the left *y*-axis. Note that effects on cone production and seed survival are plotted on a different scale than the effects on seed set and cumulative reproductive output. The orange dashed lines show the proportion of focal plants experiencing a facilitative effect and are plotted on the right *y*-axis.

A study by Muler et al. (2014) has shown that Proteaceae that form cluster roots have a higher leaf phosphorous content when grown with a conspecific than when grown with a heterospecific without cluster roots.

The finding that with increasing time since fire more plants experience negative effects on seed set (Figure 3b) is likely driven by intensifying competition for pollinators. This is the case when pollinator abundance increases more slowly than floral resources. In our system this is likely due to the territorial behaviour of key pollinators (Nottebrock, Schmid, Mayer, et al., 2017; Schmid, Nottebrock, Esler, Pagel, Pauw, et al., 2016). Cape sugarbirds increase their breeding success by defending larger territories with a higher amount of floral resources (Calf et al., 2003). This will, however, intensify competition for pollinators when floral resources increase (Schmid, Nottebrock, Esler, Pagel, Pauw, et al., 2016). Neighbourhood effects on seed set varied considerably more between focal plants than neighbourhood effects on the other fecundity components (Figure 3). The functional and spatial structure of neighbourhoods thus seem to predominantly affect plant fecundity via pollinator-mediated interactions.

Unlike the other fecundity components, neighbourhood effects on seed survival remained constant over time (Figure 3c). Nonetheless, our results support that the neighbourhood affects predation (Nottebrock, Schmid, Treurnicht, et al., 2017). The signficant effects of neighbour traits indicate that variation in predator-mediated interactions can be attributed to differences in defence against and attraction of seed predators between species (Figure 2c, Table 1). Contrary to systems, where reproductive synchrony evolved to reduce predation in mast years (Zwolak et al., 2022), we find constant levels of predation throughout. This suggests that seed predator abundance, changes proportionally to the food resources provided by the plant community.

Year-to-year variation in the effect of biotic interactions on yearly fecundity has also frequently been assessed for mast seeding trees (Bell & Clark, 2016; Bogdziewicz et al., 2018). We showed how temporal changes in interactions related to plant age can be studied in even-aged communities of non-masting long-lived species and how those temporal changes affect lifetime fecundity. In doing so, our performance measures are closer to lifetime fecundity than what more time-constrained studies of masting can typically achieve.

4.3 | Implications for community dynamics

By integrating yearly neighbourhood effects on different fecundity components to the neighbourhood effect on lifetime fecundity up to a given post-fire stand age, we could combine information on temporal and spatial variability of different interaction types. The shift from more facilitative to more competitive effects with increasing time since fire (Figure 3d) indicates that a shortening of fire return intervals due to climate change (Forsyth & van Wilgen, 2008) will not only affect lifetime fitness of individuals but might also change the dynamics of *Protea* communities. Trait-dependent neighbourhood effects should therefore modify how much certain species suffer or benefit from changes in fire frequency. This could, for example, shape how much resprouters, which flower earlier (Van Wilgen & Forsyth, 1992) and survive fires more frequently than nonsprouters (Pagel et al., 2020; Treurnicht et al., 2016), actually benefit from shortening fire intervals (Enright et al., 2014).

To fully assess time-dependent biotic interaction effects on community dynamics, one would have to combine the relative neighbourhood effects quantified here with measures of absolute reproductive output and other demographic processes such as seedling establishment and serotiny. Furthermore, it should be considered how traits affect density-independent fecundity (Adler et al., 2014) and the response of plants to interactions (Funk & Wolf, 2016; Kunstler et al., 2016). Neighbourhood models such as these ones can also be included in a multi-species version of the data-driven population model of Pagel et al. (2020). We show that neighbourhood effects and variations in fire return intervals cause substantial variation in lifetime fecundity between individuals (Figure 3d). It will be exciting to examine to what extent this individual-level variation contributes to species coexistence in this biodiversity hotspot (see Clark, 2010).

5 | CONCLUSIONS

This study shows how biotic interactions vary with space, time and functional composition of neighbourhoods, and how these multiple interaction effects can be integrated to quantify neighbourhood effects on lifetime fecundity throughout the lifetime of a plant. This is an important step towards forecasting individual plant fitness and community dynamics under climate-driven changes in fire frequency (Wilson et al., 2015). More generally, the presented framework should help to quantify the impact of changing biotic and abiotic contexts on plant individuals and communities.

AUTHOR CONTRIBUTIONS

Hanna E. Walter, Jörn Pagel, Matthias Schleuning and Frank M. Schurr conceived the idea; Huw Cooksley and Alexander Neu collected the data; Hanna E. Walter, Jörn Pagel and Frank M. Schurr analysed the data; Hanna E. Walter led the writing of the manuscript and wrote the first full draft of the manuscript. All authors commented on the manuscript and contributed to the final version.

ACKNOWLEDGEMENTS

We thank our field and lab assistants for helping with data collection, especially Sarah de Gruchy, Madelein de Klerk, Liezel Knight, Michael Leach, Marisa Noordergraaf, Hannah Oliphant, Mujaahid Philander, Rouxlyn Roux, Adrian D.A. Simmers, Barbara Seele, Megan Smith, Martina Treurnicht and Esmarie Vivier. We are thankful for the assistance and advice to Carsten Buchmann, Karen J. Esler, Janette Hutton, Francois Roets and Mathias Templin. We thank the private landowners from Flower Valley Conservation Trust (Gansbaai), Grootbos Private Nature Reserve (Gansbaai), and Heuningklip Farm (Kleinmond), the City of Cape Town and their reserve managers at Helderberg Nature Reserve, and the Western Cape Nature Conservation Board, their nature reserve managers and collaborators at Ceres Mountain Fynbos (Ceres), Fernkloof (Overberg), Hottentots-Holland (Grabouw), Limietberg (Paarl), Mont Rochelle (Franschhoek) and Riviersonderend Nature Reserve (Overberg) for their support and for granting us access to their farms and nature reserves. The fieldwork was conducted under CapeNature permits 0028-AAA008-00262 and 0056-AAA008-00070. We acknowledge the use of imagery from the NASA FIRMS application (https://firms.modaps.eosdis.nasa.gov/) operated by the NASA/Goddard Space Flight Center Earth Science Data and Information System (ESDIS) project and the NASA Worldview application (https://worldview.earthdata.nasa.gov), part of the NASA Earth Observing System Data and Information System (EOSDIS). We also acknowledge the use of the CapeNature Fires database operated by the Western Cape Nature Conservation Board (WCNCB). This research was funded by the German Research Foundation (DFG) project ProteaNet (grant numbers SCHL 1934/1-3 and SCHU 2259/3-3) and the German Academic Scholarship Foundation (Studienstiftung des Deutschen Volkes).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.14018.

DATA AVAILABILITY STATEMENT

Trait raw data were taken from the Fynbase database which is part of the TRY Plant Trait database: https://www.try-db.org/de/Datasets.php. The data used are archived on Dryad: https://doi.org/10.5061/dryad.cfxpnvx8p (Cooksley et al., 2022). Note, however, that conservation regulations and agreements with landowners do not permit us to publish the precise locations of individuals due to poaching concerns. Precise relative positions of individuals on each study site have been provided, which enables repeatability of our analysis, and precise locations can be made available upon request to the author.

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How to cite this article: Walter, H. E., Pagel, J., Cooksley, H., Neu, A., Schleuning, M., & Schurr, F. M. (2023). Effects of biotic interactions on plant fecundity depend on spatial and functional structure of communities and time since disturbance. *Journal of Ecology*, *111*, 110–124. https://doi.org/10.1111/1365-2745.14018