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RESEARCH ARTICLE

Bird and insect pollinators differ in specialization and potential pollination services along disturbance and resource gradients

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Abstract

Combined studies of the communities and interaction networks of bird and insect pollinators are rare, especially along environmental gradients. Here, we determined how disturbance by fire and variation in sugar resources shape pollinator communities and interactions between plants and their pollinating insects and birds. We recorded insect and bird visits to 21 *Protea* species across 21 study sites and for 2 years in Fynbos ecosystems in the Western Cape, South Africa. We recorded morphological traits of all pollinator species (41 insect and nine bird species). For each site, we obtained estimates of the time since the last fire (range: 2–25 calendar years) and the *Protea* nectar sugar amount per hectare (range: 74–62 000 g/ha). We tested how post-fire age and sugar amount influence the total interaction frequency, species richness and functional diversity of pollinator communities, as well as pollinator specialization (the effective number of plant partners) and potential pollination services (pollination service index) of insects and birds. We found little variation in the total interaction frequency, species richness and functional diversity of insect and bird pollinator communities, but insect species richness increased with post-fire age. Pollinator specialization and potential pollination services of insects and birds varied differently along the environmental gradients. Bird pollinators visited fewer *Protea* species at sites with high sugar amount, while there was no such trend for insects. Potential pollination services of insect pollinators to *Protea* species decreased with increasing post-fire age and resource amounts, whereas potential pollination services of birds remained constant along the environmental gradients. Despite little changes in pollinator communities, our analyses reveal that insect and bird pollinators differ in their specialization on *Protea* species and show distinct responses to disturbance and resource gradients. Our comparative study of bird and insect pollinators demonstrates that birds may be able to provide more stable pollination services than insects.

KEYWORDS
Cape Floristic Region, community composition, plant–animal interactions, pollination networks, pollinator specialization

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INTRODUCTION

Interacting species shape and organize the structure of ecological communities and networks (Bascompte & Jordano, 2013). Numerous ecological theories have been developed to uncover and describe the processes that alter communities of interacting species and the structure of interaction networks (Cadotte et al., 2013; Cody & Diamond, 1975; Marjakangas et al., 2021). However, community and network structures have mostly been analysed separately (Blüthgen et al., 2006; Trøjelsgaard & Olesen, 2016), despite the evidence that processes at the community and interaction levels are known to influence each other (Ponisio et al., 2019). Furthermore, ecological communities and interaction networks are usually composed of species from different taxonomic groups that may respond differently to environmental variation (Aronson et al., 2016; Dehling & Stouffer, 2018). This particularly applies to pollination which is provided by both insects and birds on many plant taxa, especially in the Southern hemisphere (Krauss et al., 2017). It is therefore necessary to analyse variation in pollinator communities and plant–pollinator networks across animal taxa.

Ecological communities are formed by immigrating and persisting species that can cope with local environmental conditions, and community ecologists strive to understand and predict how ecological communities assemble in response to environmental variation (Cadotte et al., 2013; Marjakangas et al., 2021). A key process for immigration is dispersal (Pilosof et al., 2017), while the persistence of species in a community is related to species sorting along environmental gradients (Soininen, 2014). For example, the temperature can filter species and interactions in hummingbird communities along an elevational gradient (Lessard et al., 2016). Analysing how functional traits and the functional diversity of ecological communities change along environmental gradients can yield additional insights into how ecological communities assemble and function (Gagic et al., 2015; Peña et al., 2023).

Trait matching between animal pollinators and their plant partners is a key factor that shapes species interactions and network structure (Zhang et al., 2013). Interaction is more likely if animal and plant traits align morphologically, such as the corolla and proboscis length of plants and insects (Stang et al., 2009). Moreover, the likelihood of an interaction depends on the abundance of co-occurring species (Bartomeus et al., 2016) and the competition between co-occurring species for resources (Ford & Paton, 1982). An important property of ecological networks emerging from these processes is the degree of specialization of animals on plant species (Blüthgen et al., 2007). For example, most pollinators visit only a subset of co-flowering plant species, and plants therefore interact only with a certain range of pollinators (Johnson & Steiner, 2000). Specialization in plant–pollinator networks varies at small and large spatial scales (Fründ et al., 2013; Schleuning et al., 2012). Importantly, the degree of pollinator specialization on plants can also influence the quality of pollination service provided to plants (Brosi & Briggs, 2013; Schleuning et al., 2015).

Two important environmental factors that may shape variation in pollinator communities and plant–pollinator networks are disturbance and plant resource availability (Bosc & Pauw, 2020; Burkle et al., 2016). Disturbance by fire plays a key role in fire-prone ecosystems (Keeley, 2012; Kraaij & van Wilgen, 2014; Ponisio et al., 2016) by shaping plant and animal community succession (Nimmo et al., 2019). For instance, LaManna et al. (2021) found that post-fire age influenced pollinator and flowering plant community composition at both local and regional scales in temperate coniferous forests. In another example, different functional groups of butterflies responded differently to post-fire age, probably because of differences in foraging strategies (Topp et al., 2022).

The provision of plant-based resources is another key factor in shaping variation in pollinator communities and plant–pollinator interactions (Heinrich, 1975; Nicolson, 2011). In particular, the availability of nectar affects flower visitations and pollinator community composition (Geerts et al., 2020; Schmid et al., 2015b). Generally, sites with increasing resource availability are expected to host more pollinator species (Mnisi et al., 2021). However, different species of pollinators may respond differently to resource availability; for example, large pollinators such as birds may only establish after a threshold of resource availability is reached (Schmid et al., 2015b). Variations in resource availability can also lead to changes in pollinator specialization on plants (Tinoco et al., 2017). Generally, ecological theory predicts an increase in resource specialization with decreasing resource availability due to stronger competitive interactions among consumer species (Pimm et al., 1985). Accordingly, the potential pollination service provided by hummingbirds to plants decreases with increasing resource availability because of a reduction in intraspecific pollen flow (Tinoco et al., 2017). While post-fire age and the number of available resources are key factors shaping pollinator communities and plant–pollinator interactions in fire-prone ecosystems (Adedoja et al., 2019; Ponisio et al., 2016), the effects of these two factors on pollinator communities and plant–pollinator interactions have rarely been studied together.

To determine the interplay of disturbance by fire and plant-based resources on plant–pollinator interactions, we investigated *Protea* species (Proteaceae) and their bird and insect pollinators. *Protea* is the dominant plant genus in fynbos, a fire-prone South African biome characterized by winter rainfall and pronounced summer drought (van Wilgen, 1982). Proteas supply copious amounts of nectar sugar that starts to build up in a community after the fire (Nottebrock et al., 2017). Moreover, insects and birds are both important pollinators of proteas (Collins & Rebelo, 1987; Hargreaves et al., 2004; Schmid et al., 2015a) so proteas are an ideal system to study the responses of different groups of pollinators to environmental variation.

Our main objective was to compare the responses of bird and insect pollinators to post-fire age and resource availability by studying pollinator communities and the interactions between plants and pollinators at 21 study sites. Specifically, we tested whether (1) time since fire plays a more important role in shaping the diversity of insect and bird pollinator communities than resource availability. Additionally, we tested whether (2) specialization and pollination services of insects and birds responded differentially to post-fire age and resource availability.

MATERIALS AND METHODS

Study system and sites

The study region is located in the Western Cape, South Africa, within the Fynbos biome (Goldblatt, 1978). Fynbos vegetation is fire-adapted and overstorey *Protea* species often make up most of the above-ground biomass (van Wilgen, 1982). Most *Protea* species do not survive fire and only recruit after the fire, leading to even-aged plant communities (Schurr et al., 2012). The 21 study sites (120 × 120 m, mean pair-wise distance 8530 m, minimum pair-wise distance 300 m) were selected across an area of 4738 km^2. Sites were chosen to cover a broad range of overstorey *Protea* species richness (2–8 species per site), and plant densities (ca. 79–127 000 individuals per site) and were located at different elevations (37–1461 m). We visited each site on 4 days in two consecutive years during the austral winter and early spring (late April to mid-September 2017 and 2018) to cover the main blooming periods of the 21 overstorey *Protea* species found on these sites (Rebelo, 2001). During that time of the year, *Protea* nectar is the main energy source for both insect and bird pollinators in the study area (Rebelo, 2001). We avoided rainy and windy days, as such conditions significantly reduce pollinator activity (Lee & Barnard, 2015). One study site was only observed in 2017 because the site burned later the same year.

Post-fire age and sugar resource amounts

For each site, we collected the date of the last fire by consulting landowners, the CapeNature Fire Database (http://bgis.sanbi.org/Projects/Detail/168), and satellite imagery (NASA FIRMS and Worldview application). We verified these post-fire ages by aging *Protea* plants by counting the number of yearly growth increments along the main growing stem (Bond et al., 1995; Treurnicht et al., 2016). Post-fire age was used as a proxy for the disturbance history of a site.

To obtain the site-level sugar amount as a measure of resource availability, we followed the approach of Nottebrock et al. (2017). We combined data on sugar amounts per flower head, detailed individual-based maps of all overstorey *Protea* species on the 21 study sites and data-based predictions of flower head numbers per individual. First, we calculated the species-mean amount of sugar per flower head by determining the sugar concentration (w/w) of an open flower head with refractometers and then multiplied the measured sugar concentration (transformed into weight per volume) by the nectar volume of the same flower head, extracted by centrifugation (data from Nottebrock et al., 2017 and our additional data). Second, individual-based maps were obtained with a differential GPS (Trimble GeoXH) noting the species identity and size of each individual (from the stem base to the tip of the plant in the stem's main growing direction). Mapping data were updated where necessary (e.g., newly constructed trails or firebreaks) in the field following the initial mapping of Nottebrock et al. (2017) and Schmid et al. (2015a, 2015b), or were newly recorded in 2017 and 2018 for the four newly established study sites. Third, we predicted the number of open flower heads for each mapped individual for a specific observation day using a generalized linear mixed-effect model assuming a Poisson error distribution. This model included empirical data on plant size and the additional species-level plant traits of length to first branching and resprouting ability, plus crossed random effects of the study site, *Protea* species and an observation-level random effect (following Nottebrock et al., 2017). In addition, the model controlled for the flowering phenology of *Protea* species by including the squared time difference between the observation day and the peak flowering date of the respective *Protea* species in the Western Cape (Nottebrock et al., 2017). We fitted this model to 7287 observations of the number of flower heads and used the fitted model to predict the number of open flower heads for all mapped plant individuals on each site (1-ha plot) and observation day. To estimate the sugar amount per plant, we multiplied the predicted number of flower heads per plant with the species-mean sugar amount per flower head. Finally, we summed these predictions across all protea individuals to obtain site-level sugar amounts for each of the four observation days and calculated the mean sugar amount per ha (log-transformed prior to the analyses).

Pollinator observations

To quantify pollinator interactions on *Protea* flower heads, we selected a maximum of 12 focal plants (or the maximum of flowering plants available) that were representative of all *Protea* species flowering on that day on the study site. We preferentially selected plants that had two open flower heads next to each other. We set up 12 time-lapse cameras to film the selected flower heads between 9:00 am and 4:00 pm to record pollinating birds. The resulting videos were standardized to 4 h of observation time, and all interactions were noted. In total, we reviewed 6420 h of video footage on 1605 flower heads.

Insect pollinator observations began immediately after setting up the time-lapse cameras, working on the same focal plants. Two observers simultaneously monitored one of each of the two focal flower heads per focal plant for 15 min. All insects we observed probing the flower head were identified and documented. We captured undetermined individuals with an aspirator for subsequent identification and trait measurements. We identified all insects to the species level or to the next possible taxonomic level. We compiled a total of 401 observation hours at the 1605 flower heads. We restricted interaction data to arriving pollinators that were moving into a flower head to reach the florets and came into contact with the reproductive organs. For compiling the interaction networks between *Protea* and animal species, observation data were pooled across the four observation days of each site. We compiled a combined network of bird–plant and insect–plant interactions (Figure 1) and assigned an interaction frequency of 0 to potential links between species pairs that co-occurred on a site but were never observed to interact. All interaction data are available from the Dryad Digital Repository (Neu et al., 2022).

Pollinator traits

For all recorded animal pollinators, we measured functional traits affecting food intake (mouth part and beak length), mobility (wing length) and metabolic requirements (body mass) (Table S2). We measured all insect morphological traits on a maximum of five specimens per morphospecies (on individuals from our reference collection). Bird pollinator traits were measured on a minimum of two male and two female museum specimens (Iziko South African Museum in Cape Town, South Africa; Senckenberg Naturmuseum Frankfurt, Germany). All measurements were taken to the nearest 0.001 mm.

For insect pollinators, we chose different methods for measuring mouth part length. For Hymenoptera, we cut off the head and measured the completely extended glossa from the prementum. In Coleoptera, we measured the length from the tip of the mouth parts to the base of the antennae. In Lepidoptera, we measured the extracted and unrolled proboscis. In Diptera, we measured the length from the lowest part of the head to the tip of the extended labella. For all bird pollinators, we measured beak length as a straight-line distance from the commissural point of the upper and lower beak to the tip of the closed beak. Further, we measured the wing length of insects as the maximum forewing length, except for Coleoptera where we measured the maximum hindwing length. In bird pollinators, we measured the distance from the carpal joint to the longest primary, following Eck et al. (2011). Finally, we measured species-level insect pollinator mean body mass as the accumulated dry body mass for all collected specimens (accurate to 0.001 g) divided by the number of specimens. Bird's mean body mass was obtained from the literature (Dunning, 2007).

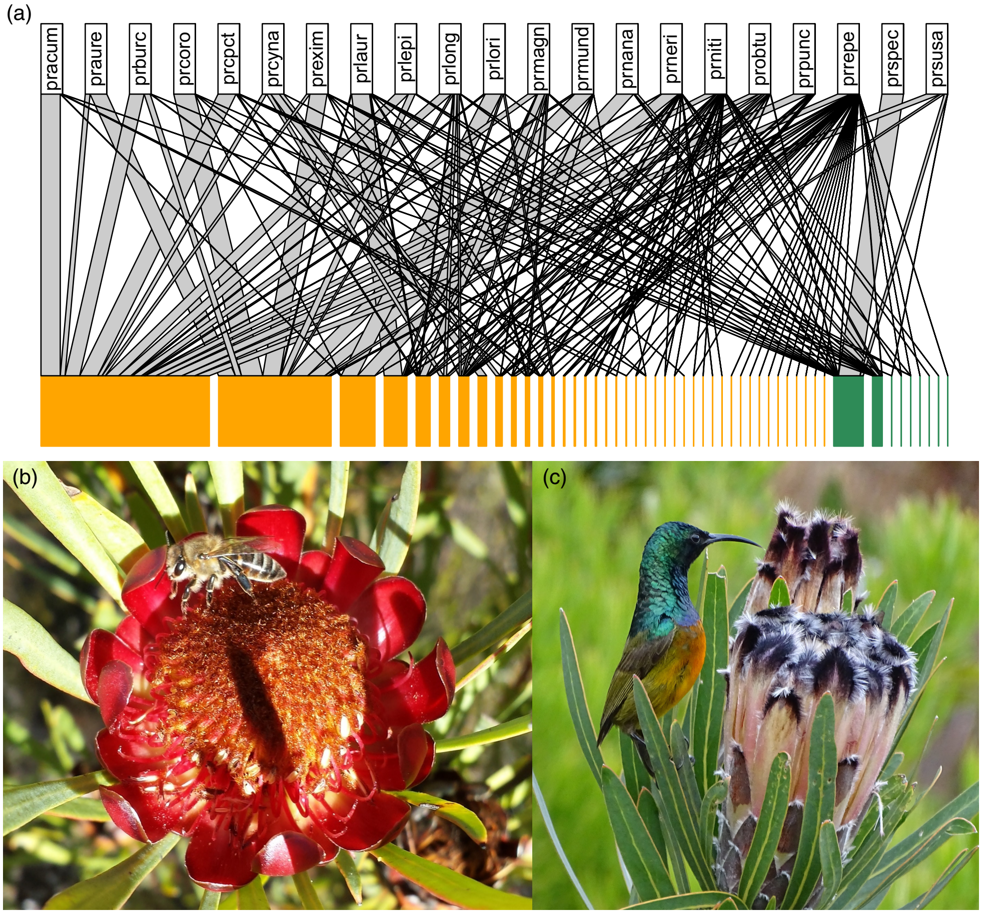

FIGURE 1 (a) Interaction network based on observations of plant–pollinator interactions on protea flower heads from 21 study sites in the Western Cape, South Africa. The lower bars represent insect (orange) and bird (green) species and the upper bars represent *Protea* species (species codes, see Table S3). Upper bars are standardized in size to represent 100% of pollinator visits to the respective *Protea* species. The width of the lower bars indicates the relative number of observed interactions for each pollinator species and the link width indicates the relative interaction frequency between the respective *Protea* and its pollinator species. (b) Cape honeybee (*Apis mellifera capensis*, the second-most frequent insect species) visiting *Protea acuminata*. (c) Orange-breasted sunbird (*Anthobaphes violacea*, the most frequent bird species) visiting *Protea lepidocarpodendron*; picture copyrights by the authors.

Species richness and functional diversity of pollinators

We calculated measures of the total interaction frequency, species richness and functional diversity separately for insect and bird pollinator communities at each site. To calculate the total interaction frequency, used as a surrogate for pollinator abundance, we summed the frequency of all pollinator observations per site for insects and birds, respectively. Further, we calculated species richness as the number of insect and bird pollinator species observed on a site across the four observation days. As a distance-based measure of functional diversity, we calculated functional dispersion for insect and bird pollinators, respectively, based on a principal coordinates analysis of log-transformed measures of mouth part/beak length, wing length and body mass. Functional dispersion was quantified as the unweighted mean distance of the species present in a community relative to the community centroid (Laliberté & Legendre, 2010). In addition, we calculated community-weighted means (CWM) of the individual traits weighted by the total number of observations per species on a site (Lavorel et al., 2008). Because CWMs of body mass and mouth part length (insects: $n = 21$, $r = 0.932$, $p < 0.05$; birds: $n = 21$, $r = 0.958$, $p < 0.05$), as well as of body mass and wing length (insects: $n = 21$, $r = 0.975$, $p < 0.05$; birds:

$n = 21$, $r = 0.995$, $p < 0.05$) were closely correlated, we restricted the analysis of CWM to body mass. Measures of functional diversity were computed with the function *dbFD* in the *R* (version 4.1.0; R Core Team, 2021) package *FD* (version 1.0.12; Laliberté et al., 2014).

Pollinator specialization and potential pollination service

We calculated measures of (1) pollinator specialization and (2) potential pollination service for each pollinator species on each site from the site-specific plant–pollinator networks. Pollinator specialization on specific *Protea* species was estimated as the relative number of plant partners, given by the effective number of plant partners divided by the total number of flowering *Protea* species on a site across all observation days. The number of effective plant partners corresponds to Shannon's diversity index of the interaction frequencies of pollinators across plants, raised by the power of *e*. The metric was calculated from the interaction frequencies of each pollinator species on each plant species. We used the standardized version of the effective number of plant partners to control for differences in *Protea* richness across sites; the standardized metric ranges between 0 and 1.

The potential pollination service provided by a pollinator to *Protea* plants was estimated by the pollination service index (PSI) as a proxy for the degree of conspecific pollen transfer provided by the pollinators to the plants (Dormann, 2011). PSI was defined as:

$$\mathrm{PSI}_j = \sum_{i=1}^{N} \left(p_{ij} \bullet p_{ji}^{\beta} \right)$$

where p_{ij} is the dependence of any plant species i on visits from a pollinator j, defined as the observed interactions between a pollinator species and a plant species divided by the total number of interactions of each plant species. The exponent β was set to 1 assuming that pollen is deposited proportional to the frequency of visits to different plants (Dormann, 2011). Low values of PSI correspond to generalized species with low frequencies, whereas large values correspond to specialized pollinators with a high frequency. PSI values range between 0 and 1. PSI quantifies the potential for conspecific pollen transfer based on the relative frequencies of plant–pollinator interactions, but it does not take into account per-capita differences in pollen transfer and differences in pollination quality (Schupp et al., 2017).

We calculated both metrics (the relative number of plant partners, PSI) in *R* (version 4.1.0; R Core Team, 2021) with the package *bipartite* (version 2.16; Dormann, 2011).

Statistical analyses

We conducted analyses for pollinator communities, pollinator specialization on plants and potential pollination services in combined models of insect and bird pollinators. Specifically, we tested the effects of post-fire age and resource availability and their interaction terms with the pollinator group on the respective metrics. The only exception was the CWMs of body mass that were tested in separate models for insects and birds, given the large size differences between insects and birds.

For all models except for CWM body mass, we started with a full model which included animal class, post-fire age, resource availability, as well as the interaction terms between animal class and the two other predictors. If interaction terms were non-significant (i.e., if insects and birds did not differ in their response), they were removed from the final models that still contained all main effects. Analyses of community metrics included site identity as a random term, whereas analyses of pollinator specialization and potential pollination service included both animal class and site identity as random terms. Total interaction frequency and species richness were log-transformed prior to the analyses. PSI and the relative number of plant partners were logit-transformed prior to the statistical analyses using the *car* package (version 3.1-0; Fox et al., 2022). Analyses of pollinator specialization and potential pollination services of insects and birds were weighted by the square-root of the total interaction frequency of each pollinator species to down weight the importance of rarely observed species.

RESULTS

In total, we recorded 2411 interaction events of 41 insect pollinator species (max = 15, median = 6 insect species per site) and nine bird pollinator species (max = 6, median = 2 bird species per site) (Figure 1, Table S2). The most frequent insect species was the beetle *Chirodica chalcoptera chalcoptera* with 684 observations on 14 sites, followed by the Cape honeybee *Apis mellifera capensi*s with 652 observations on 20 sites. Most insect species were rare, as we recorded 29 of the 41 species fewer than 10 times. The most frequently encountered bird species were the Orange-breasted sunbird (*Anthobaphes violacea*) with 444 observations on 18 sites, followed by the Cape sugarbird (*Promerops cafer*) with 182 observations on 16 sites. We recorded five bird species fewer than 10 times. Most *Protea* species were observed to interact with both insect and bird pollinators (Figure 1).

Across sites, post-fire age ranged from 2 to 25 years (median = 16.42 years) and the predicted mean sugar amount varied between 73.5 and 62268.3 g/ha (median = 4119.8 g/ha) (Table S1). Post-fire age and sugar amount (log-transformed) were negatively correlated (df = 19, $r = -0.61$, $p < 0.05$).

Pollinator communities

Overall, the total interaction frequency, species richness and functional dispersion were larger for insects than for bird pollinators (Table 1A–C) despite the shorter observation times for insects than for birds. Post-fire age explained more variation in pollinator communities (Figure 2a,c, Table 1B) than resource availability (Figure 2b,d), but effects were generally weak at the community level. Total interaction frequency showed no associations with post-fire age and resource availability for both insect and bird pollinators (Table 1A). Species richness of insects increased with post-fire age, while bird richness did not show such a trend (Figure 2a, Table 1B). Functional diversity measures (functional dispersion, and community-weighted means of body mass) were unaffected by post-fire age and resource availability (Figure 2, Tables 1C and 2A,B) although the community-weighted mean of insect body mass tended to increase with post-fire age (Table 2B).

Pollinator specialization and potential pollination services

Variations in pollinator specialization differed between insects and birds. Generally, birds tended to use a larger portion of the available *Protea* species than insects, but this difference varied along the gradient in resource

TABLE 1 Model summaries of the associations of post-fire age (years since the last fire) and resource availability (sugar amount per ha) with total interaction frequency (A), species richness (B) and functional dispersion (C).

Fixed effects	Estimate	Std. error	*t*-Value	*p*-Value
(A) Total interaction frequency				
Intercept	3.822	0.274	13.967	<0.001
Class (birds)	−1.138	0.322	−3.537	0.002
Post-fire age	0.482	0.282	1.711	0.104
Log sugar amount per ha	0.368	0.282	1.309	0.207
(B) Species richness				
Intercept	1.861	0.101	18.506	<0.001
Class (birds)	−1.146	0.101	−11.334	<0.001
Post-fire age	0.271	0.122	2.222	0.035
Log sugar amount per ha	0.117	0.111	1.062	0.302
Post-fire age × class (birds)	−0.218	0.102	−2.127	0.047
(C) Functional dispersion				
Intercept	1.353	0.071	18.989	<0.001
Class (birds)	−0.204	0.103	−1.983	0.058
Post-fire age	−0.050	0.078	−0.636	0.532
Log sugar amount per ha	−0.034	0.076	−0.445	0.661

Note: Shown are the main effects of animal class (birds), post-fire age and resource availability, as well as significant interaction terms of post-fire age and resource availability with animal class. Post-fire age and resource availability were scaled prior to the analyses so that estimates are directly comparable. Given are model estimates along with their standard error, *t*-value and *p*-value, as well as the variance explained by the random effect of the site. The number of observations = 42. The model equation of the full model in R followed this form, exemplified for species richness: lmer(log(nbsp) ~ post-fire age*class + log(sugar amount per ha)*class + (1|site), data). (A) Random effect site ($n = 21$, var = 0.486). (B) Random effect site ($n = 21$, var = 0.105). (C) Random effect site ($n = 21$, var = 0.0215).

availability. The relative number of plant partners decreased with increasing resource availability for birds, but not so for insects (Figure 3, Table 3). That is, insect pollinators visited a similar proportion of the flowering *Protea* species present on a site, independent of post-fire age and resource availability (Figure 3a, Table 3A). In contrast, bird pollinators specialized on fewer *Protea* species as sugar amounts increased (Figure 3b, Table 3A).

Potential pollination services also varied differently between insects and birds along the gradients of post-fire age and resource availability. Generally, birds showed higher potential pollinator service values than insects, albeit this difference could be due to different observation times for insect and bird pollinators. Independent of these sampling differences, potential pollination service values of insects decreased with post-fire age, as well as with increasing resource availability (Figure 4, Table 3B). In contrast, potential pollination service values of birds remained constant along the respective gradients (Figure 4, Table 3B).

DISCUSSION

Here, we examined how pollinator communities and plant–pollinator interactions vary in response to disturbance by fire and resource availability. Despite the pronounced environmental differences between our study sites, we found little between-site variation in communities of insect and bird pollinators. However, specialization and potential pollination services of insects and birds varied differentially along the environmental gradients.

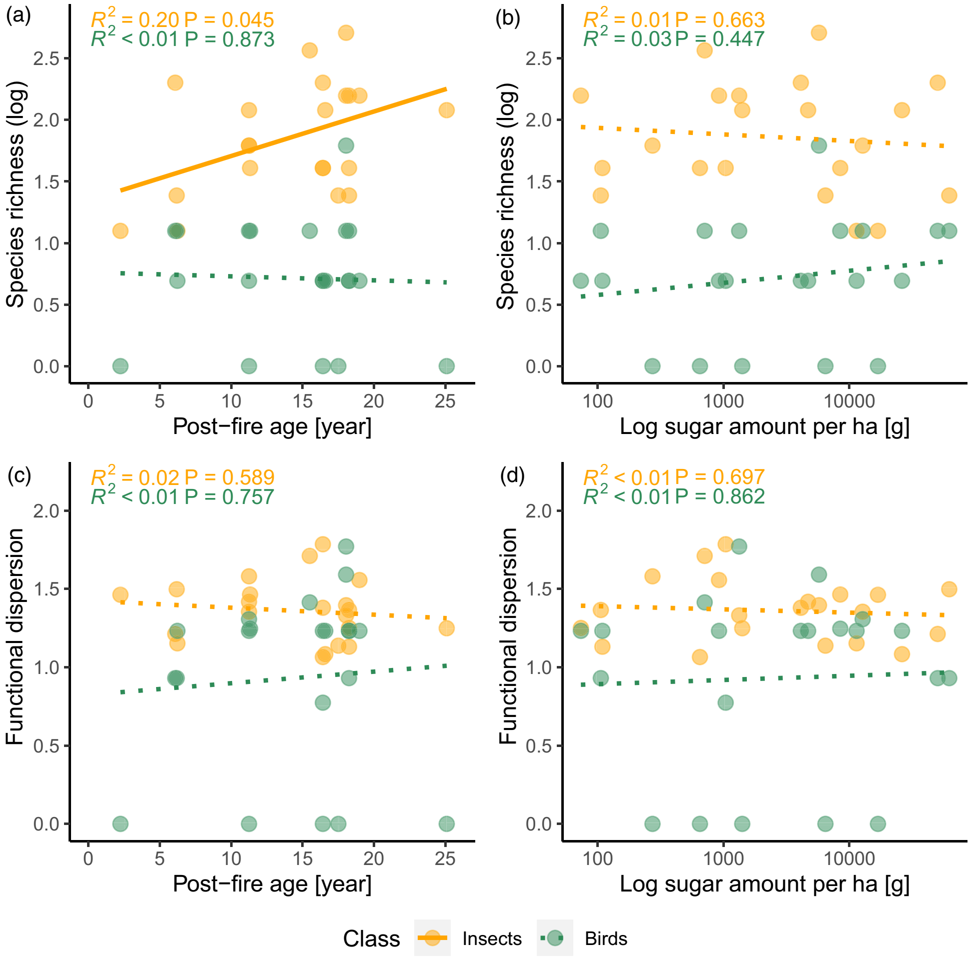

FIGURE 2 Effects of post-fire age (a, c) and resource availability (b, d) on species richness (a, b) and functional dispersion (FDis) (c, d) of pollinators in South African Fynbos. Trends are shown separately for insect (orange) and bird (green) pollinators. See Tables 1 and 2 for sample sizes and statistics. Linear fits show trends in the original data, fitted separately for insect and bird pollinators. Partial effects of the respective predictors are shown in Table 1. Given are conditional r^2 values and p-values of the respective associations.

TABLE 2 Model summaries of the associations of post-fire age (years since the last fire) and resource availability (sugar amount per ha) with community-weighted mean measures of insect (A) and bird (B) body mass.

Fixed effects	Estimate	Std. error	*t*-Value	*p*-Value
(A) CWM insect body mass				
Intercept	−2.423	0.075	−32.366	<0.001
Post-fire age	0.197	0.096	2.044	0.056
Resource availability	0.097	0.096	1.002	0.330
(B) CWM bird body mass				
Intercept	1.189	0.045	26.188	<0.001
Post-fire age	−0.045	0.058	−0.767	0.453
Resource availability	−0.036	0.058	−0.620	0.543

Note: Results are based on linear models testing these associations with post-fire age and resource availability separately for insect and bird pollinators. Post-fire age and resource availability were scaled prior to the analyses so that estimates are directly comparable. Given are model estimates along with their standard error, *t*-value and *p*-value. Number of observations = 21 in both models.

While insect specialization was decoupled from resource availability, birds visited proportionally fewer *Protea* species with increasing sugar amount per site. Potential pollination services of birds were less context-dependent than those of insects which showed a decrease in potential pollination services with increasing post-fire age and resource amount. Therefore, our comparative study reveals how insect and bird pollinators differ in the potential pollination services that they provide to plants in different environmental contexts.

Pollinator communities of insect and bird pollinators

Insect and bird pollinator communities varied little along the studied environmental gradients. However, insect species richness was positively related to the post-fire age. This relationship was mostly driven by the low insect richness at most of the sites <15 years of age (Figure 2a). The increase in insect pollinator richness is in line with other Mediterranean-type ecosystems, where post-fire age is one of the main drivers of bee species richness (Potts et al., 2003). In addition, mature post-fire habitats show a larger number of pollinator species in comparison to recently burnt sites (Potts et al., 2006). A rapid increase in habitat complexity may explain the relatively quick recovery of insect communities after the fire in Fynbos (Hope et al., 2012; Procheş & Cowling, 2006).

Bird pollinator community richness also quickly recovered after the fire (Figure 3a). While no bird pollinators were recorded at the youngest site, all sites with an age of more than 5 years had similar bird species richness. In previous studies, Chalmandrier et al. (2013) observed that nectarivorous bird species avoid recently burned Fynbos, but the abundance of nectar-feeding birds quickly recovered after the fire (Geerts et al., 2012). Our findings suggest that both insect and bird pollinator communities quickly recover after the fire in this fire-prone ecosystem although the effects of post-fire age appear to be stronger for insects than for bird pollinators. Future comparative studies should aim to include more recently burned study sites to compare insect and bird community dynamics shortly after the fire.

We found no relationships between resource availability with pollinator interaction frequency and species richness for both insects and bird pollinators. In contrast, a previous study in Fynbos found that the abundance of bird pollinators increases with plant resource availability (Schmid et al., 2015b). In another Mediterranean-type ecosystem, bee diversity is closely linked to nectar resource diversity (Potts et al., 2003). A possible explanation for the lack of response to resource availability at the community level may be those insect and bird pollinator communities were dominated by generalist species such as the Cape honeybee and Orange-breasted sunbird. These species may find sufficient resources even if resource availability is low. While species such as the Cape sugarbird show an increase in population abundance with increasing resource availability, Orange-breasted sunbirds can already be present at sites with few resources (Schmid et al., 2015b). In comparison to previous work, our abundance measure based on the total interaction frequencies across all bird and insect species may have been too coarse to detect changes in individual population sizes.

The functional diversity of insect and bird pollinators did not change along the studied environmental gradients. This suggests that different types of insect and bird pollinators responded similarly to disturbance and resource availability. As we recorded a wide range of trait values for insects (e.g., mean body mass ranged between 0.6564 g for *Trichostetha fascicularis* and 0.0002 g for Tephritidae sp. 1) and birds (e.g., mean body mass ranged between 133.00 g for Red-winged starlings and 7.85 g for Southern double-collared sunbirds), species with very different morphological traits responded similarly to the high environmental variability in this ecosystem.

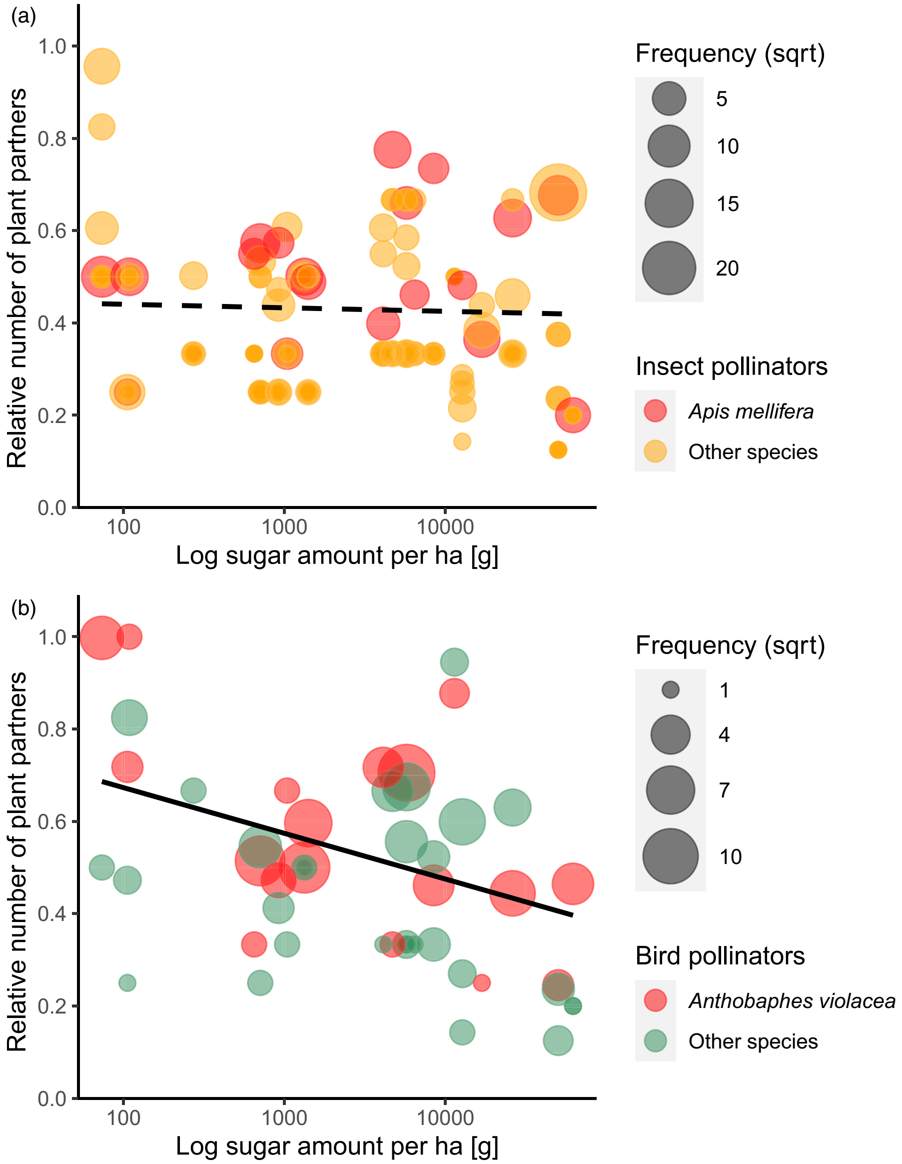

FIGURE 3 The effect of resource availability on the relative number of plant partners for insect (a) and bird pollinators (b) at 21 study sites in South African Fynbos. Red points indicate the pattern for the most frequent insect (Cape honeybee) and bird (Orange-breasted sunbird) species, respectively; orange points indicate all other insect species and green points all other bird species. Trend lines correspond to the trends across all insect and bird species, respectively, in the original data. Size of points corresponds to the square root of the total interaction frequency of each species at each site. See Table 3A for the combined models of insect and bird pollinators and the respective partial effects.

This interesting finding implies that different types of pollinators coexist in Fynbos and may contribute complementarily to the pollination of *Protea*. In our study, we focused entirely on morphological traits, whereas other types of traits may be more important for shaping species' responses to environmental variation. This particularly applies to the response to the disturbance that may be independent of pollinators' dependence on plant resources. Previous studies have shown that ecological traits, such as diet breadth, nest location or sociality are related to insect response to disturbance (Carrié et al., 2017). In addition, the dispersal ability of species may determine habitat colonization after the fire, especially for birds (Brotons et al., 2005). Future work could try to collect such additional trait data for bird and insect pollinators and test whether disturbance leads to

TABLE 3 Model summaries of the associations of post-fire age (years since the last fire) and resource availability (sugar amount per ha) on the relative number of plant partners (A), and the pollinator service index (PSI) (B).

Fixed effects	Estimate	Std. error	*t*-Value	*p*-Value
(A) Relative number of plant partners (logit-transformed)				
Intercept	−0.411	0.137	−2.992	0.006
Class (birds)	0.442	0.191	2.317	0.029
Post-fire age	−0.051	0.130	−0.393	0.699
Resource availability	−0.050	0.140	−0.357	0.725
Resource availability × class (birds)	−0.467	0.109	−4.301	<0.001
(B) Pollinator service index (logit-transformed)				
Intercept	−1.912	0.233	−8.201	<0.001
Class (birds)	0.923	0.450	2.052	0.047
Post-fire age	−0.491	0.175	−2.812	0.010
Resource availability	−0.386	0.180	−2.140	0.044
Post-fire age × class (birds)	0.643	0.252	2.554	0.011
Resource availability × class (birds)	0.571	0.244	2.339	0.021

Note: The relative number of plant partners and PSI values range between 0 and 1 and were logit-transformed prior to the analyses. Results are based on linear mixed-effect models accounting for random variation among sites and pollinator species. Post-fire age and resource availability were scaled prior to the analyses so that estimates are directly comparable. Given are model estimates along with their standard error, *t*-value and *p*-value, as well as the variance explained by random effects. The number of observations = 197 in both models. (A) Random effects: pollinator species ($n = 50$, var = 0.077), site ($n = 21$, var = 0.205). (B) Random effects: Pollinator species ($n = 50$, var = 0.652), site ($n = 21$, var = 0.206).

systematic shifts in pollinator communities mediated by these additional niche dimensions.

Pollinator specialization and potential pollination services

We found divergent trends in the specialization of insect and bird pollinators with changing resource availability. For bird pollinators, specialization increased with increasing resource availability because bird pollinators used a smaller proportion of the available *Protea* species with increasing resource amounts. Insect pollinators used a similar proportion of the available *Protea* species across the entire resource availability gradient. This suggests that bird pollinators tend to use all available resources at the lowest resource amounts (Cohen & Shmida, 1993), but were able to specialize in specific resources when total resource amounts increased. In contrast to theoretical expectations (Pimm et al., 1985), high metabolic demands of nectarivorous birds (Brown et al., 1978; Montgomerie & Gass, 1981) may explain this niche expansion towards more *Protea* species at low resource amounts (Schmid et al., 2016). At sites with high resource amounts, large bird population sizes may further lead to an increase in resource competition between bird pollinators (Schmid et al., 2015b). Bird pollinators have been shown to strongly compete for resources between each other (Ford & Paton, 1982; Krauss et al., 2017), especially for plants providing highly rewarding resources (Mac Nally & Timewell, 2005). Other studies found that birds are also competitively superior over insect pollinators (Carpenter, 1979; Kodric-Brown & Brown, 1979). However, it has also been shown that honeybees can decrease nectar amounts and flower visits of nectarivorous bird species through exploitative or interference competition, in particular in areas beyond their native range (Paton, 1993). Within the

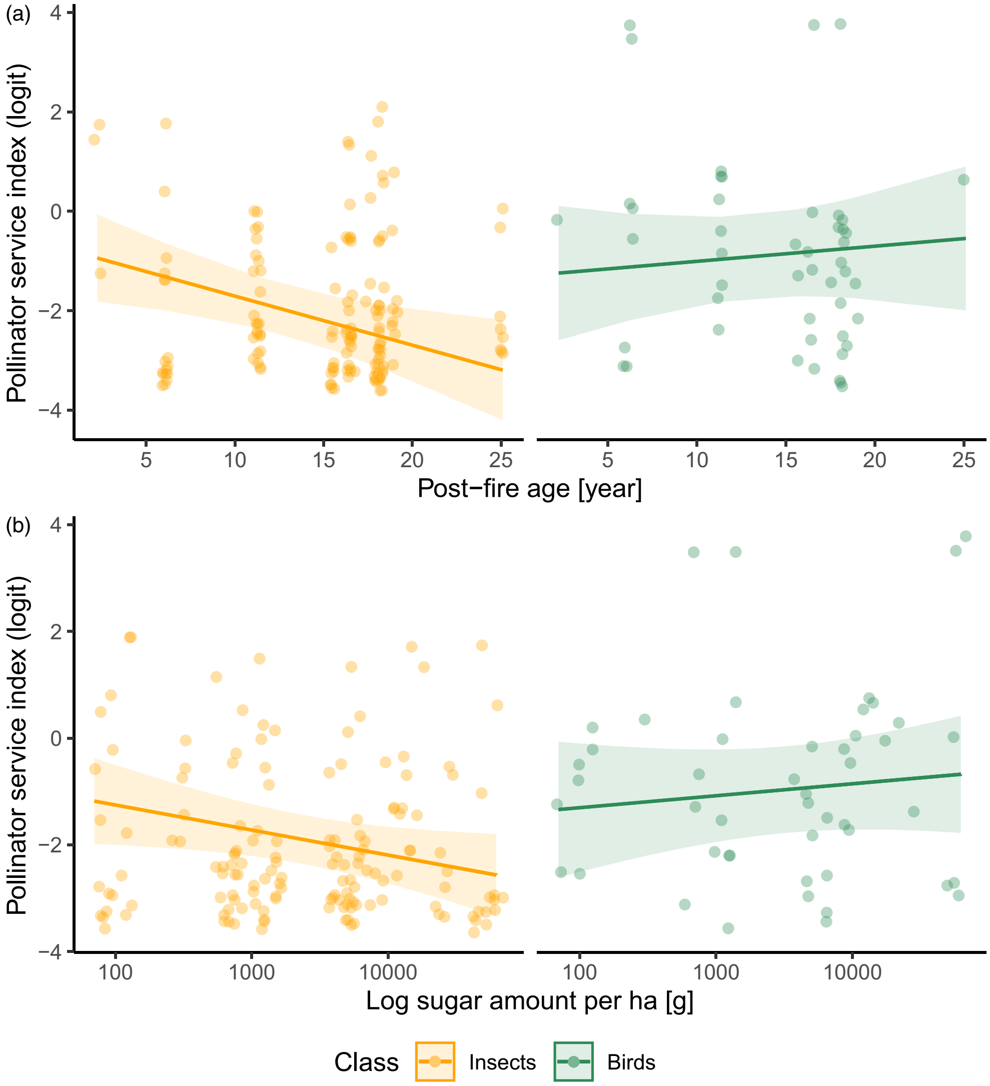

FIGURE 4 Relationship between pollinator service index (PSI) and post-fire age (a) and resource availability (b), shown separately for insect (orange) and bird (green) pollinators. Plots represent partial residual plots based on the partial effects as shown in the statistical model (Table 3B). The shaded areas represent the 95% confidence interval of the fitted values. Dots represent PSI values of a pollinator species at a site ($n = 21$ sites in total). PSI values were logit-transformed prior to the analyses.

native range of the Cape honeybee in South Africa, Geerts and Pauw (2011) found no decrease in protea nectar amounts and only weak and inconsistent effects of Cape honeybees on nectar-feeding birds.

In contrast to birds, the specialization of insect pollinators was similar across the entire resource availability gradient. One reason for this is that insect pollinators cannot forage on all *Protea* species due to morphological barriers that exclude insects from certain *Protea* species (Schmid et al., 2015a). For example, the functional group of bearded proteas (e.g., *Protea coronata* and *Protea speciosa*) is inaccessible to many insect pollinators because of the closed structure of their inflorescences that does not allow most insects to reach the nectaries (Rebelo et al., 1984). Another reason could be the competitive exclusion of insects from plant species, due to competitive or predatory interactions with bird pollinators (Carpenter, 1979; Kodric-Brown & Brown, 1979). This is supported by experimental studies that found a competitive release in insect pollinators in response to bird exclusions (Hargreaves et al., 2004). Despite these limitations in resource use, many insects visited a large number of the available *Protea* species (on average insect species visited almost 50% of the available *Protea* species, Figure 3a). This suggests that *Protea* species are a key resource for many insect pollinators that are similarly exploited across the studied disturbance and resource gradients.

We found that the potential pollination services of insects were more variable than those of birds along the studied gradients. An increase in post-fire age resulted in a reduction in the potential pollination services of insects as derived from the calculation of the PSI. This could be the consequence of the increasing number of insect pollinator species with post-fire age, rendering individual insect pollinator species less important for pollination. This is in line with a study from another Mediterranean-type ecosystem, where the pollination service was reduced on the oldest sites because more insect pollinators shared the available resources (Potts et al., 2006). In addition, we found that the potential pollination services of insects tended to decrease with increasing resource amounts. This directly relates to our finding that insects, unlike birds, did not specialize in specific protea species when resources became more abundant (Figure 3a). Although our analyses did not control for per-capita differences in pollen transfer, this suggests that conspecific pollen transfer by insects was reduced at high resource amounts.

Despite these changes in the roles of insect pollinators, bird pollinators contributed similarly to protea pollination across the disturbance and resource gradients. Because bird pollinators specialized on fewer *Protea* species at high resource amounts (Figure 3b), this suggests that they were potentially able to transfer high amounts of conspecific pollen independent of the environmental context. A previous study found that per-plant visitation rates of Cape sugarbirds and Orange-breasted sunbirds decreased at high site-level sugar densities, suggesting an increase in plant competition for bird pollinators (Schmid et al., 2015b). Moreover, individual Cape sugarbirds showed high levels of flower constancy (Schmid et al., 2016) which should increase conspecific pollen transfer (Chittka et al., 1999). Although studies have shown that visitation frequencies and pollination quality may be unrelated in hummingbirds (Cárdenas-Calle et al., 2021; Watts et al., 2012), other studies from the Fynbos biome strongly suggest that birds are indeed reliable pollinators of proteas. The compact and protandrous protea florets mainly burst open by the strong force of probing bird pollinators (Collins & Rebelo, 1987), which explains why experimental studies found that birds are better pollinators than insects for many *Protea* species (Hargreaves et al., 2004; Schmid et al., 2015a). Moreover, individual birds are able to carry a substantially greater load of conspecific pollen than insects (Collins & Rebelo, 1987). Accordingly, many *Protea* species have specialized in bird pollination in this biome (Hargreaves et al., 2004; Pauw & Johnson, 2018).

Outlook

In Fynbos, rising temperatures during the southern winter will likely increase the severity and frequency of fires (Wilson et al., 2015) and lead to changes in plant community composition and associated animal communities (van Wilgen et al., 2010). Shorter fire intervals can lead to the local extinction of slow-maturing non-sprouting proteas (van Wilgen, 1982), which could trigger a collapse in pollinator communities dependent on proteas. To avoid such a collapse of interacting plant and animal communities, future fire intervals should not drop below 14 years (Geerts, 2021), whereas fire intervals have already decreased to 6–9 years in some Fynbos areas (Southey, 2009). Given these future projections of environmental change, we expect that the differences in the potential pollination services provided by birds and insects to *Protea* species may further increase. According to our findings, increased fire frequencies may affect the richness of insect pollinators more than those of bird pollinators. In addition, the reliability of potential pollination services provided by birds suggests that the relative importance of bird pollination for proteas may further increase in more unstable future environments. Therefore, we conclude that bird-pollinated proteas may be less likely to suffer from the disrupted plant–pollinator interactions compared to protea species that primarily rely on insect pollinators.

AUTHOR CONTRIBUTIONS

Alexander Neu: Conceptualization (lead); data curation (lead); formal analysis (lead); investigation (lead); methodology (lead); validation (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Huw Cooksley:** Conceptualization (equal); data curation (supporting); formal analysis (supporting); investigation (supporting); methodology (supporting); validation (supporting); visualization (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Karen J. Esler:** Conceptualization (supporting); investigation (supporting); methodology (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Anton Pauw:** Conceptualization (supporting); investigation (supporting); methodology (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Francois Roets:** Conceptualization (supporting); investigation (supporting); methodology (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Frank M. Schurr:** Conceptualization (equal); formal analysis (supporting); funding acquisition (equal); investigation (supporting); methodology (supporting); project administration (equal); resources (equal); software (equal); supervision (supporting); validation (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Matthias Schleuning:** Conceptualization (equal); formal analysis (supporting); funding acquisition (lead); investigation (supporting); methodology (supporting); project administration (lead); resources (lead); software (lead); supervision (lead); validation (supporting); visualization (supporting); writing – original draft (supporting); writing – review and editing (supporting).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available at Dryad Digital Repository: https://doi.org/10.5061/dryad.nvx0k6dwm (Neu et al., 2022).

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SUPPORTING INFORMATION

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