

PART OF A SPECIAL ISSUE ON FUNCTIONAL–DEVELOPMENTAL PLANT CELL BIOLOGY

Dominant pollinators drive non-random community assembly and shared flower colour patterns in daisy communities

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Received: 26 January 2018 Returned for revision: 27 March 2018 Editorial decision: 7 June 2018 Accepted: 13 June 2018
Published electronically 10 July 2018

- **Background and Aims** As most plants rely on pollination for persistence in communities, pollination interactions should be important determinants of plant community assembly. Here, trait and phylogenetic null modelling approaches were combined with pollinator interaction networks to elucidate the processes structuring flower colour assembly patterns in Asteraceae communities in Namaqualand, South Africa.
- **Methods** Plant species were assigned to flower colour pattern categories (CPCs) that incorporate the complexity of the bulls-eye colour pattern, using pollinator vision models. Null models were used to assess whether daisy communities exhibit clustering (driven by filtering, facilitation or convergence) or overdispersion (driven by competitive exclusion or character displacement) of CPCs. Next, flower visitor networks were constructed for communities with non-random CPC assembly to confirm the functional role of pollinators in determining floral trait assembly.
- **Key Results** Plant species are unevenly distributed across CPCs, the majority of which are not phylogenetically conserved, suggesting that certain CPCs have a selective advantage. Clustering of CPCs in communities is more frequent than overdispersion, and this does not reflect non-random phylogenetic assembly. In most communities at least one CPC is overrepresented relative to null assemblages. Interaction networks show that each community has a single dominant pollinator that strongly interacts with the overrepresented CPC, suggesting a role for pollinator preferences in driving clustered assembly of CPCs within daisy communities.
- **Conclusion** This novel approach, which demonstrates non-random assembly of complex flower colour patterns and corroborates their functional association with particular pollinators, provides strong evidence that pollinators influence plant community assembly. Results suggest that in some community contexts the benefits of pollinator sharing outweigh the costs of heterospecific pollen transfer, generating clustered assembly. They also challenge the perception of generalized pollination in daisies, suggesting instead that complex daisy colour patterns represent a pollination syndrome trait linked to specific fly pollinators.

Keywords: Community assembly, bipartite interaction networks, convergence, facilitation, biogeography, Asteraceae, fly pollination, Namaqualand.

INTRODUCTION

Studies of plant community assembly usually consider interactions between plants and their abiotic environments, highlighting the importance of species filtering by abiotic environments (e.g. climate, soils – Kraft *et al.*, 2015) and competition for limited resources (light, water, nutrients – Tilman, 1994, 2004; Rees *et al.*, 2001) in structuring plant communities. However, seed set, and thus persistence of a species in a community, is dependent on successful pollinator-mediated fertilization in the vast majority of angiosperms (Ollerton *et al.*, 2011), and this is particularly true for annual species. Thus, pollinators represent a necessary resource for plant reproduction, and we would expect ecological sorting, and the evolution of particular suites of functional (pollination-linked) traits, to result from interactions between plants for the pollinator resource. In addition, the available pollinator fauna (i.e. the pollinator climate – Grant

and Grant, 1965) might impose strong filters on which plant species can successfully occur in communities. Because floral traits are largely shaped by pollinator-mediated selection, and less so by abiotic conditions (reviewed by Harder and Johnson, 2009), the importance of pollination interactions in plant community assembly should be evident in the way floral traits are arrayed across species within communities relative to the regional species pool (Sargent and Ackerly, 2008). A substantial body of work, focused on the structuring of flowering phenologies within communities in response to competition mediated through heterospecific pollen transfer, has provided mixed evidence for the importance of pollination in plant community assembly (e.g. Poole and Rathcke, 1979; Rabinowitz *et al.*, 1981; Rathcke, 1983; Armbruster, 1986; Moeller, 2004; Aizen and Vazquez, 2006). However, the assembly of floral traits that function in both pollinator attraction (e.g. colour

pattern, scent, reward type) and the efficiency of the pollination process (e.g. mechanical fit traits) has received less attention (but see Muchhala and Potts, 2007; McEwen and Vamosi, 2010; Heystek and Pauw, 2014; Muchhala *et al.*, 2014; Runquist *et al.*, 2016). These are traits that can influence both the pollination niche of a plant species, and its interactions with other plant species vying for the available pollinator resources.

Competition for pollinators is likely to lead to overdispersion of floral traits within communities (Fig. 1). This can occur through direct competition for pollinator visits where some flowers are more attractive to particular pollinators than others (Rathcke, 1983; Brown *et al.*, 2002; Mitchell *et al.*, 2009), or through indirect competition mediated by the fitness costs

of heterospecific pollen transfer (HPT) between plants that share pollinators (Waser, 1978; Cambell and Motten, 1985; Fishman and Wyatt, 1999; Mitchell *et al.*, 2009; Matsumoto *et al.*, 2010). Both competition pathways could lead to competitive exclusion of weaker competitors from communities, or alternatively, they could drive the evolution of character displacement and consequent divergence of pollination niches between community members (e.g. Muchhala and Potts, 2007; Morales and Traveset, 2008; Grossenbacher and Stanton, 2014). It is often difficult to discern whether competitive exclusion or character displacement is driving trait overdispersion, but if character displacement is occurring, trait overdispersion and shifts between pollinators is likely to

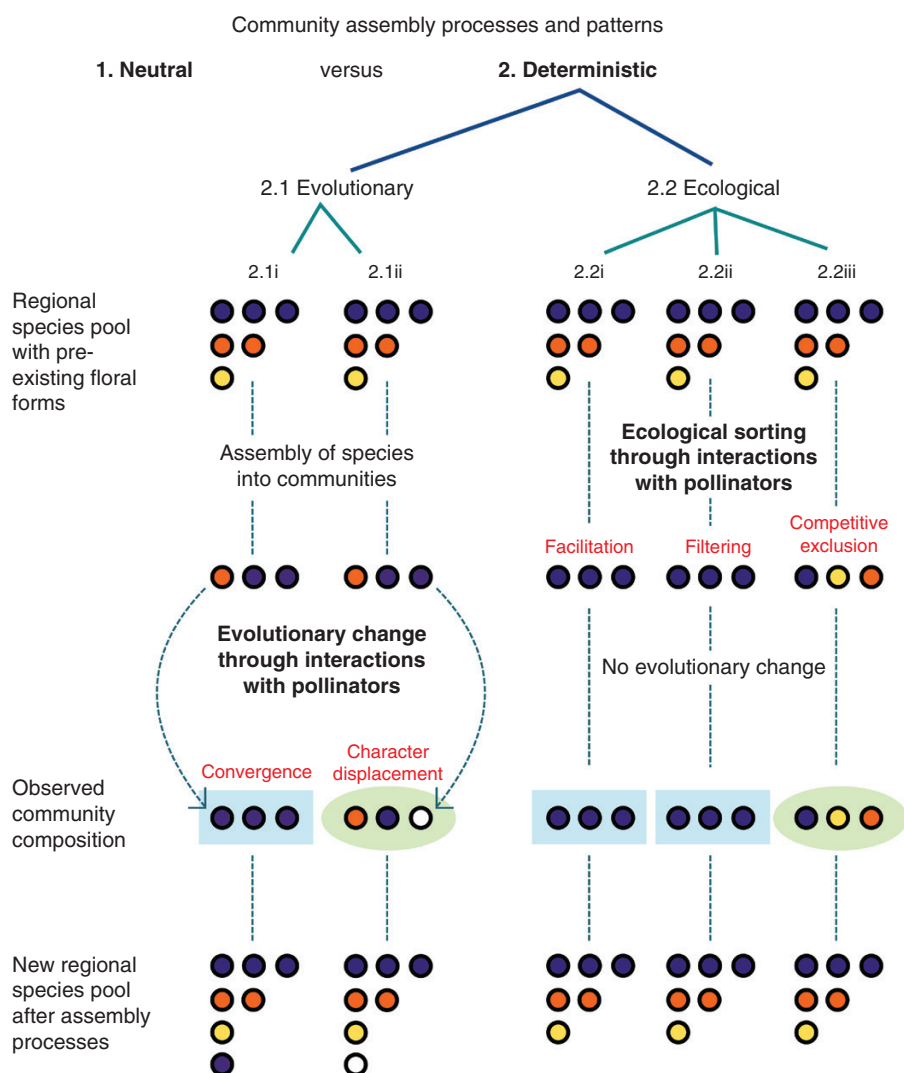


FIG. 1. The assembly of plant traits into communities from a regional pool occurs through either (1) random or (2) deterministic processes. Deterministic processes can either be (2.1) evolutionary, where traits evolve in response to selection within communities, or (2.2) ecological, where ecological sorting of species into communities depends on their pre-existing traits. If pollinators have visual preferences, then selection may favour certain flower colours over others, leading to convergent flower colour evolution and clustering of flower colour within a community (2.1i). Similarly, flower colours within a community may evolve to be different from one another if there are costs associated with pollinator sharing (2.1ii). Alternatively, pre-existing flower colours may be sorted into communities by ecological interactions (2.2). Plant species may facilitate the recruitment of other plant species with similar flower colours into a community if a pollinator species with strong preferences performs better with a varied resource base (2.2i). Strong pollinator preferences can also act as a filter to plant species that have a non-preferred flower colour (2.2ii). Competition between plant species for the available pollinator resources can lead to similar flower colours failing to recruit into a community, which leads to a variety of flower colours in the community. Thus, convergence, facilitation and filtering will lead to clustered trait assembly patterns, and character displacement and competitive exclusion will lead to trait overdispersion.

be more pronounced in sympatric populations than in allopatric populations (Coyne & Orr, 1989).

A clustered distribution of floral traits within communities could result when pollinator climates vary spatially across the landscape and the benefits of shared attraction outweigh the costs of HPT (Fig. 1). Clustering of floral traits, such as flower colour pattern, within communities relative to their distribution in the regional species pool also implies spatial structuring of traits across the region: where, for instance, the dominant flower colour pattern will vary between communities. Plant species might be excluded from communities if their pollinators are absent, in a process akin to environmental filtering. Trait clustering within communities could also be caused by contemporary facilitative interactions, where an increase in the number of plant species with the same floral phenotype increases pollinator visitation rates, either by providing a more prominent attraction signal (Ashton *et al.*, 1988) or by providing a more varied resource base (Ghazoul, 2006). Alternatively, selection imposed by spatially variable dominant pollinators can lead to evolutionary convergence of floral traits amongst community members. The limited previous work using null models to explore floral trait distributions within communities has mostly shown support for overdispersion in pollination traits (Muchhala and Potts, 2007; McEwen and Vamوسي, 2010; Heystek and Pauw, 2014; Muchhala *et al.*, 2014; Runquist *et al.*, 2016), but limited support has also been found for clustering of traits within communities (De Jager *et al.*, 2011; Runquist *et al.*, 2016).

In addition to producing distinctive patterns of floral trait distributions within communities, mechanisms of pollinator-mediated community assembly should also create clear signal in the structure of community plant–pollinator interaction networks. For example, if communities exhibit overdispersed assembly of floral phenotype, suggesting character displacement or competitive exclusion as probable structuring mechanisms, we would expect interaction networks to comprise multiple distinct modules, each representing subsets of plant and pollinator species interacting more strongly with each other than with other subsets in the network. In contrast, if community assembly models show clustering of floral traits, where filtering, facilitation or convergence is inferred, we expect interaction networks to be dominated by a single, or few, functional pollinator types that strongly interact with plants possessing the over-represented floral traits to form a single large module.

Here we assess pollinator-mediated assembly of daisy (Asteraceae) communities in the Namaqualand subregion of South Africa. This system is characterized by a narrow temporal flowering window, high densities of flowers, low incidence of selfing and the predominance of annual species, factors that are likely to increase reliance on seed-mediated reproductive assurance and the importance of pollination interactions (De Waal *et al.*, 2014). In addition, exceptionally high angiosperm diversity (~ 3800 angiosperm species, and > 400 species of Asteraceae, in ~ 55 000 km²; Snijman, 2013) provides a rich regional species pool, ideal for testing community assembly hypotheses. Every year in spring, mass flowering displays, dominated by daisies, carpet the Namaqualand landscape in swathes of colour. Our observations, and anecdotal reports, suggest that dominant daisy flower colours vary across the region with, for example, white colours dominating on the sandy coastal plain and orange predominating in the upland areas (e.g. Fig. 2). Recent work on other Mediterranean-type ecosystems has shown that flower colour mediates facilitative interactions, and that

both flower colour and scent structure plant–pollinator networks (Kantsa *et al.*, 2017). The daisy ‘flower’ is a compound inflorescence (the capitulum) with an outer ring of petal-like ray florets, which are frequently bi-coloured, surrounding an inner circle of disc florets. This capitulum arrangement produces a complex bulls-eye colour pattern, often comprising three distinctly coloured concentric rings. The open shape of the capitulum does not physically preclude visits from any insects, nor pollination by them, and daisies are thus widely considered to be pollination generalists (Fenster *et al.*, 2004). However, like other plants with apparently generalist floral phenotypes, daisy species may exploit only a subset of the available pollinator species within a community (e.g. Ellis and Johnson, 2009; de Jager and Ellis, 2014; de Waal *et al.*, 2015). One possibility is that distinct daisy colour patterns (i.e. different combinations of contrasting concentric colour rings) represent different floral syndromes, or traits associated with distinct groups of flower-visiting animals (Fenster *et al.*, 2004). In some cases flower colour, and the pattern of colour arrangement, has been shown to strongly influence both pollinator preference (Bradshaw and Schemske, 2003; Horth *et al.*, 2014) and pollinator constancy (Hill *et al.*, 1997), consequently influencing pollination success (Johnson and Dafni, 1998; Goodale *et al.*, 2014; Koski and Ashman, 2014, 2015). While some studies have considered how flower colours are assembled in communities (McEwen and Vamوسي, 2010; De Jager *et al.*, 2011; Muchhala *et al.*, 2014), none has investigated the assembly of more complex colour patterns. This perhaps reflects the difficulty of considering complex phenotypes such as the typical bulls-eye colour pattern of radiate daisy capitula (e.g. Fig. 3).

We first used an objective categorization scheme based on reflectance measurements from ray and disc florets to classify each species in the regional pool of Namaqualand daisies into a colour pattern category (hereafter CPC), providing a measure of pattern diversity. This was done based on raw reflectance spectra and accounting for the visual systems of the dominant pollinators in the system (bees and flies). We then built a genus-level phylogeny of the sampled species to assess phylogenetic signal of flower colour patterns and to determine whether communities exhibit significant phylogenetic structuring. Next we used null models to investigate how colour patterns are assembled in communities. We expected CPCs to be overdispersed in communities if pollinator-mediated competitive exclusion or character displacement structures communities (Fig. 1). Alternatively, if pollinator-mediated facilitation, filtering or convergence structure communities we expected that the majority of plant species should represent just a few CPCs within a community (i.e. clustering of CPCs), and that the dominant CPCs should vary between communities across the region. Next, we assembled multiple pollinator visitation networks to determine whether network structure conforms to expectations based on the processes identified by the community assembly models. Finally, to confirm the functional role of CPCs in determining the pollination niche, we assessed the influence of flower colour pattern on plant–pollinator interaction strengths in the visitation networks.

MATERIAL AND METHODS

Study system

Limited work on the pollination systems of Namaqualand daisies suggests pollinator abundances are low despite the extremely



FIG. 2. The semi-desert Namaqualand sub-region of the Succulent Karoo in South Africa transforms annually during a mass flowering display in the austral spring. The display is dominated by daisies, most of which are self-incompatible annuals that are reliant on pollinators for seed set and population persistence. The photos illustrate changes in dominant flower colours across communities. Photos by J.E.K. and A.G.E.

high densities of rewarding flowers (Struck, 1994). Flower visits are dominated by bees (Apoidea), flies (Bombyliidae, Tabanidae) and Hopliini beetles (Scarabaeidae), and pollinator assemblage composition varies at fine spatial scales (Struck, 1994; Ellis and Johnson, 2009). Further work has shown pollinator preferences for particular flower colour patterns that result in divergent selection on floral phenotype (Ellis and Johnson, 2010; de Jager and Ellis 2012, 2014; but see Ellis and Johnson, 2012).

Sampling

Plant community composition and flower spectral reflectance data. Plant species occurrence data and floral reflectance spectra were collected for all annual and perennial daisy species (and colour forms of polymorphic species) at 16 sites (0.5×0.5 km) in Namaqualand during the last week of August and first week of September 2007, and at four additional sites during in 2015 (Supplementary Data Table S1). Sites were located 2.8–282.8 km apart (mean \pm s.d. = 81.7 ± 55.3 km). Spectra were recorded indoors at a 45° angle to the floret surface using an OceanOptics USB4000 Spectrometer calibrated with a diffuse reflectance WS-2 white standard. Spectra were averaged over three measurements of flowers from different plants chosen at random at a site. To quantify flower colour pattern, which in daisies conforms

to a series of concentric circles, three points on the capitulum of each species were sampled (Fig. 3): (1) the outer ray floret (OR – Fig. 3A), (2) the inner ray floret (IR – Fig. 3B) and (3) the disc floret petals (D – Fig. 3C). It was not always possible to accurately measure reflectance of disc florets due to their small size and changeable orientation of disc floret corolla lobes. However, across species disc spectra always conformed to either a yellow or black coloration. Thus, to reduce the effects of disc measurement inaccuracy on our model results, the ‘D’ measure in all species was assigned either a yellow or a black spectrum.

Interaction networks

Flower visitor networks were constructed in August and September 2015 for two of the sampled community types that showed non-random assembly patterns. Networks were sampled in the same community types as represented by community 2 and community 7, but not at the exact localities, and in a different sampling year. Three 100×100 m sites were sampled within each of the two community types, to produce three networks in each community type. Flower visitors to all daisy species were recorded during 15-min observation periods in 100 m^2 plots at each site, resulting in 25 observation hours per site and 75 observation hours per community type. For each plot, the number of open flowers of

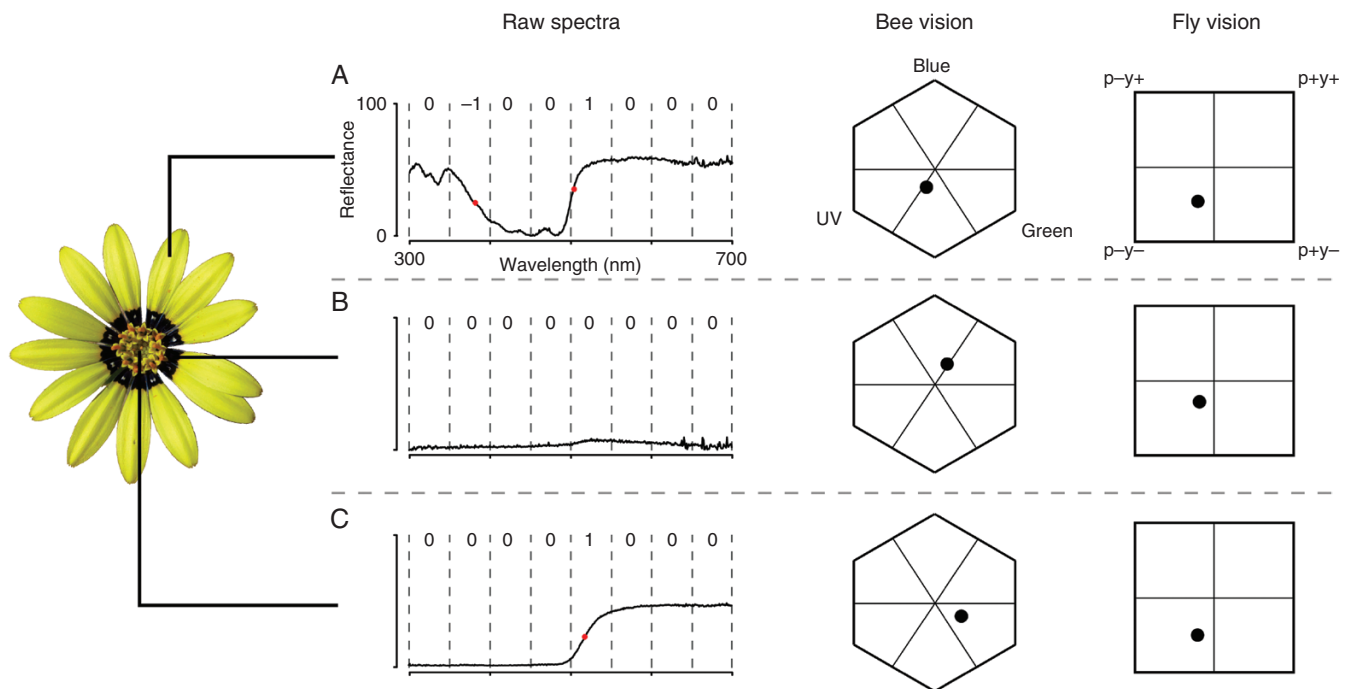


FIG. 3. Reflectance spectra were measured for three flower sections for each plant species: (A) the outer ray floret (OR); (B) the inner ray floret (IR); and the disc floret (D). To characterize overlapping reflectance curves between species and to group similar species into colour pattern categories (CPCs), inflection points were calculated for raw spectra (indicated as red dots on the curves). For each 50-nm interval, we determined whether an inflection point exceeding a change in reflectance of 10 % was absent (0) or present, and if present, whether it represented a change from concave to convex (–1) or the opposite (1). Each 50-nm interval was then treated as a separate variable in cluster analysis, and cluster analysis was performed for the three flower sections separately. Species with the same combination of OR, IR and D were grouped together in a phenotype. Plant species were also sorted into colour pattern groups based on bee and fly visual models respectively.

each plant species was recorded and the number of visits to each plant species from each insect species was noted. Insect visitors were caught, preserved and sorted to morphospecies.

Phylogeny inference

Our Namaqualand daisy communities incorporated 76 species from 27 genera. Sequence data were obtained from GenBank for representatives of each genus (Table S2) for two nuclear (ETS and ITS) and four plastid DNA regions (*matK*, *ndhF*, *rbcL* and the *trnL-trnF* region). Although some gene regions were lacking for some genera, most (22 of 27) were represented by four or five regions. We estimated a genus-level phylogeny using a rooted phylogenetic approach in the BEAST v. 1.8.3 software (Drummond et al., 2012). A detailed description of phylogeny estimation is given in the Supplementary Data.

Data analysis

Identifying flower colour pattern categories (CPCs). All analyses were performed in R (R Core Team, 2016). Sampled species/colour forms were classified into CPCs using three approaches. First, we followed the approach of Shrestha et al. (2014) to identify CPCs from raw reflectance spectra. We then incorporated visual models of bees (Chittka, 1992) and flies (Troje, 1993).

Raw reflectance spectra. The colour of each measured part of the capitula (OR, IR, D) was categorized by identifying inflection

points along raw reflectance spectra (i.e. points where the direction of the curvature of the spectrum changes), after lumping reflectance values into 1-nm bins (see Shrestha et al., 2014). Eight 50-nm windows across the UV/VIS spectrum (i.e. 300–700 nm) were examined for the presence of inflection points. Changes from a concave-downward to a concave-upward curve (i.e. decreasing reflectance) were scored as negative inflection points, while the opposite changes were scored as positive. Each 50-nm window was scored as having no inflection point (0), a negative inflection point (–1) or a positive inflection point (1) (see Fig. 3). These eight variables were then used to group raw reflectance spectra in a cluster analysis using Euclidean distances in the R ‘pvclust’ package (Suzuki and Shimodaira, 2015). Clustering was performed separately for reflectance spectra from the OR and IR sections of the capitulum, and plant species showing at least 90 % similarity were grouped together in a cluster. As D sections were assigned only to black or yellow, no clustering was necessary. Next, plant species belonging to the same combination of OR, IR and D clusters were grouped together as a CPC. Species lacking ray florets were all placed in a single CPC, as these were all found to have yellow disc florets.

Bee vision model. A separate group of CPCs were identified based on how they are perceived by honey-bees using Chittka’s (1992) honey-bee visual model. Because this model requires a background spectrum for contrast, we used a standard green spectrum as background for the OR reflectance spectra, the OR spectra as background for the IR spectra, and the IR spectra as background for the D spectra. The *x* and *y* coordinates of the

hexagon plot for each of the three flower sections were used to cluster species using Euclidean distances in ‘pvclust’ (Suzuki and Shimodaira, 2015). Plant species showing 70 % or greater similarity were grouped together, as we found that this threshold divided plant species into intuitive groups, while minimizing the number of groups that contained only a single species across the regional pool. We refer to the groupings as bee CPCs.

Fly vision model. To categorize the colour patterns according to fly visual perception, we used Troje’s (1993) fly visual model in the ‘pavo’ package (Maia et al., 2016). As in our bee vision analysis, we used standard green as background for the OR, the OR as background for the IR, and the IR as background for the D spectra. This fly vision model does not encompass gradients of colour, but packages colours into four discrete categories distinguishable by flies, to which we assigned each flower colour measurement. Plant species with the same combination of categories for the three floral sections were grouped into the same CPC phenotype, and we refer to these as fly CPCs.

Phylogenetic signal in CPCs and in community composition

To assess whether variation in colour pattern is significantly affected by common ancestry, we examined the correlation between evolutionary divergence (as measured by the branch lengths in our BEAST maximum clade credibility tree (Fig. S1) and colour pattern variation between daisy species in our sampled regional pool. A Brownian motion model of trait evolution was used to estimate the value of Pagel’s λ (Pagel, 1999) in the ‘phylosignal’ package (Keck et al., 2016). As the CPC phenotype is unordered and not continuous, we tested for phylogenetic signal in each CPC separately, treating each as a binary variable with species either belonging to it, or not. If colour pattern is a pollination syndrome trait, we would expect repeated evolution of colour pattern categories across the phylogeny; alternatively, if it is not under selection or is phylogenetically constrained we expect the categories to exhibit strong correlation with phylogenetic relatedness.

We also tested for phylogenetic structuring of plant community composition, because non-random assembly of CPCs in communities might reflect non-random phylogenetic composition of plant communities if CPCs are phylogenetically conserved. Here we used the ‘phylostruct’ function in the ‘picante’ package (Kembel et al., 2010) with Gotelli’s independent swap algorithm (Gotelli, 2000).

Community assembly patterns

Community assembly patterns were characterized in a step-wise manner. First, we performed 999 random assemblies of species into communities from the regional pool using Patefield’s (1981) r2d null model algorithm, keeping both row and column totals constant. For each of the randomly assembled communities, plant species were replaced by their CPC (this was repeated for categories derived from raw spectra, from bee visual space and from fly visual space). The polymorphic plant species (those exhibiting multiple CPCs that always occurred allopatrically) were randomly represented by one of their observed CPCs. A community-level CPC diversity metric was calculated

for each randomly assembled community to assess whether communities show overdispersion or clustering of CPCs. Community CPC diversity was quantified using a Hill number-adjusted Sørensen alpha diversity index (Jost, 2007), which incorporates the evenness of the distribution of plant species across CPCs. For example, if many plant species share a colour pattern, then the effective number of CPCs (i.e. CPC diversity) is lower. Observed CPC diversity was calculated for each of the 20 sampled communities separately, and then compared to null communities to test for departure of the metric from expectations under random assembly. Significantly lower observed CPC diversity within a community would indicate clustering, while significantly higher values indicate overdispersion.

We further examined whether assembly of species from the regional pool into local communities was non-random by computing a phenotype-level metric using z -scores to determine whether the observed number of plant species belonging to each CPC in each community differed from the random expectation. This phenotype-level metric explicitly tests for the pattern underlying CPC clustering at the community level, i.e. overrepresentation of individual CPCs within communities. As the test is sensitive to the presence of regionally rare CPCs within communities we adopted a conservative approach and only computed this metric for CPCs represented by ten or more taxa in the regional pool (eight of 28 raw CPCs, eight of 21 bee CPCs, five of eight fly CPCs). Thus, the test asks whether the regionally most common CPCs are overrepresented in local communities relative to the regional pool, as would be expected under assembly through facilitation or convergence driven by spatial variation in dominance of pollinators with different colour preferences.

Interaction network patterns

If community assembly patterns result from competitive exclusion or character displacement (i.e. colour patterns are overdispersed), we expect strongly modular networks, with evenly sized compartments centred on many different insect species. We explored this expectation in two ways. First, we calculated modularity for each network using the QuanBiMod algorithm (Dormann and Strauss, 2014), and compared observed values to 999 randomized values to assess significance. Next, we tested the expectation of an even spread of interactions across many insect visitor species using rank-abundance approaches from community ecology. Flower visiting species were first ranked, in descending order, on the basis of their interaction frequencies in order to produce rank–abundance (or rank–interaction frequency) curves for the overall networks for each community type. If interaction frequencies are evenly spread across pollinator species, then a broken-stick distribution (MacArthur, 1957) is expected, while a Zipf distribution (Zipf, 1949) (characterized by few elements that occur very frequently and many that occur rarely) is expected if interactions in networks are dominated by one (or few) pollinator species. We compared the fit of these two distributions to our data for the two community types separately using Akaike’s information criterion (AIC) values computed by the ‘radfit’ function in ‘vegan’.

If community assembly patterns result from filtering, facilitation or convergence (i.e. colour patterns are clustered), we

expect to find a single (or few) dominant pollinator(s) that strongly interacts with the dominant floral phenotypes. To test this we calculated the link temperature (see Junker et al., 2010) of the interaction between the dominant pollinator species and each plant species in each community. Link temperature ranges from -1 to 1 , where positive values indicate disproportionately favoured interactions and negative values indicate avoided interactions. We used ANOVA with a priori contrasts to assess whether the overrepresented CPCs (identified in the null model section) in these two communities are associated with high link temperatures to the dominant pollinator. This was done separately for the two communities, and separately for CPCs based on raw spectra, bee vision and fly vision.

RESULTS

Floral colour pattern categories (CPCs)

We recorded 76 daisy species from 27 genera at our 20 sites. Community plant species richness ranged from three to 25 (mean = 12.9). Plant species were assigned to 28 CPCs based on inflection points from raw reflectance spectra, and the number of CPCs in each community varied from two to 16 (mean = 8.8) (see Table S3). Eight species were polymorphic (based on raw spectra), i.e. comprised more than one CPC. Colour patterns varied in the number of plant species assigned to them (range = 1–11; mean = 3.21), and the five largest CPCs (each containing 4–8 genera) contained 51 % of plant species. Most plant species thus tend to belong to just a few CPCs. **Seven of the 28 CPCs (i.e. 25 %) exhibited significant phylogenetic signal (Table S4).**

Based on bee visual space, plant species were assigned to 21 CPCs, which again varied in the number of plant species they contained (range = 1–12; mean = 4.29), and the five most common bee CPCs contained 60 % of plant species. Each community harboured between two and 12 bee CPCs (mean = 7.7). Four (19 %) of the bee colour patterns exhibited phylogenetic conservedness. Only eight CPCs were identified based on fly vision (size range = 1–51 species; mean = 11.25), and two fly CPCs contained 71 % of the plant species. **The three most common fly colour patterns (37.5 %) exhibited significant conserved phylogenetic signal.**

Communities exhibited random phylogenetic assembly patterns ($P > 0.05$), and thus community assembly patterns are independent of phylogeny.

Community assembly patterns

In more than half of the communities, at least one CPC was overrepresented relative to its occurrence across the landscape as a whole (the phenotype-level metric in Table 1). This pattern held regardless of whether colour patterns were delineated using fly, bee or no visual model. Clustering was the most common assembly pattern detected using the CPC alpha diversity metric. Only two communities exhibited significant overdispersion for this metric (communities 17 and 19, Table 1), while eight communities exhibited significant clustering of colour pattern. However, in the majority of communities, we detected

no departure from random assembly for the three methods of pattern delineation for the alpha diversity metric.

Network patterns

Three interaction networks from three separate sites were constructed for each of the two examined community types. Community type 2 contained 19 daisy species, 109 insect morphospecies and 7811 interactions, while community type 7 contained 12 daisy species, 47 insect morphospecies and 3161 interactions. All six networks from both communities were less modular than expected by chance ($Q_{\text{mean}} = 0.26$; s.d. = 0.11; $z_{\text{mean}} = -4.50$; $P < 0.05$), thus providing support for neither character displacement nor competitive exclusion.

For community 2, interaction frequencies were unevenly distributed across pollinator species ($AIC_{\text{Zipf}} = 1101$, $AIC_{\text{broken-stick}} = 21\,600$). The bee fly *Megapalpus capensis* was responsible for 68 % of interactions in community type 2 (Fig. 4). For community type 7, interaction frequencies were also unevenly distributed across species ($AIC_{\text{Zipf}} = 323$, $AIC_{\text{broken-stick}} = 6217$) and a single horsefly (*Rhigioglossa* sp.) species contributed 57 % of interactions. Analysis of variance with a priori contrasts showed that overrepresented CPCs were significantly associated with high link temperatures to the dominant pollinators in both community types (Table 2; Fig. 4).

DISCUSSION

Our analysis demonstrates clustered assembly of flower colour patterns in Namaqualand daisy communities, confirming anecdotal observations that the dominant colour patterns in communities vary across the landscape. By drawing on additional insights from interaction networks, we provide direct evidence that spatially variable pollinator climates underlie this clustered assembly pattern.

Community assembly through filtering, ecological facilitation or evolutionary convergence

Sixteen of 20 sampled communities contained at least one regionally common CPC that was overrepresented within the community relative to the regional pool, and the community-level CPC diversity metric suggests clustering more frequently than overdispersion (although in most cases it suggests random assembly of colour pattern). This result is consistent with facilitation or evolutionary convergence driving coexistence of species with a shared colour pattern favoured by locally dominant pollinators, and suggests that competition for pollination is not a dominant process influencing daisy community assembly. Furthermore, while we have not incorporated relative density of individual plant species within each community, accounting for this would probably strengthen the pattern we discern, i.e. overrepresented colour groups within communities usually encompass the most common species in communities (Fig. 2).

Clustering of flower colour pattern within communities could arise through several mechanisms. First, we would expect clustering if colour pattern is strongly phylogenetically conserved

TABLE 1. The community structuring of complex flower colour patterns (categorized using raw spectra, bee vision and fly vision models) across 20 daisy communities from Namaqualand, South Africa

Community	Number of species	Raw spectra			Fly vision			Bee vision		
		<i>n</i>	Alpha diversity	Phenotype-level	<i>n</i>	Alpha diversity	Phenotype-level	<i>n</i>	Alpha diversity	Phenotype-level
1	9	6	C*	C	4			7		
2	13	11		C	4	C*	C	9		
3	15	9		C	5		C	10		
4	23	12	C	C	4	C	C	12		C
5	12	9		C	4		C	8		C
6	8	7			3	C*		6		
7	15	8	C	C	6	C*	C	8		C
8	8	7			4			7		
9	25	12	C*		6		C	9	C	
10	12	10			4		C	8		C
11	14	11		C	4		C	9		C
12	12	9		C	4			8		C
13	18	12		C	6		C	9	C	C
14	18	12		C	5		C	9		C
15	25	16		C	6		C	12		C
16	16	12			6			10		C
17	3	3	O		1		C	3	O	
18	5	4			3		C	4		
19	4	4	O		3			4	O	
20	3	2			2			2		
% clustered			20	55		20	65		10	50
% overdispersed			10	0		0	0		10	0

Non-random assembly of colour patterns (CPCs), detected using community- (CPC diversity) and phenotype-level metrics, is indicated for each community. ‘C’ indicates significant phenotypic clustering ($P < 0.05$); ‘O’ indicates significant phenotypic overdispersion; blank cells represent random assembly. Values that are nearly significant ($P < 0.07$) are also indicated (*). The number of species and CPCs (*n*) are indicated for each community. The last two rows provide the percentage of either clustered (C) or overdispersed (O) communities according to each measure.

and strong environmental filters (pollinators or other abiotic filters) result in frequent coexistence of related taxa with similar traits (i.e. phylogenetically clustered community assembly – Wolowski *et al.*, 2017). We can reject this possibility as we find no evidence for non-random community assembly in terms of phylogeny, and limited evidence for phylogenetic conservatism of colour pattern.

Second, abiotic filters could account for the clustering of flower colour. Indeed, several studies have demonstrated an influence of environmental factors, such as incident UV light, on the distribution of colour pattern. Koski and Ashman (2014), for example, showed a global latitudinal cline in the UV-bullseye pattern, where the bullseye is larger in regions closer to the Equator. Warren and Mackenzie (2001) showed that more pigmented floral forms have higher fitness under drought stress, which could lead to clustering of flower colours across rainfall gradients. While we cannot exclude this possibility, it seems unlikely that abiotic factors are the primary determinants of flower colour pattern in our system, as our sampling area was relatively small (maximum distance between two sites was 282.8 km) and does not span a large range of altitude, latitude or climatic variability. Also, many colour patterns spanned the whole sampling area, varying only in frequency between communities.

Third, pollinators can drive the clustering of flower colour pattern in communities through three distinct mechanisms: (1) ecological filtering might exclude colour patterns mismatched with local pollinator preferences, (2) positive facilitative pollinator-mediated plant–plant interactions would favour

recruitment into communities of colour patterns that are already present, and (3) selection by dominant pollinators could result in evolutionary convergence of species on preferred colour patterns. We interpret our results as indicating that the clustered distribution of colour pattern that we observe within communities relative to null assemblages is due to these mechanisms operating across a geographical mosaic of dominant pollinators, i.e. when dominant pollinators with varying colour preferences differ between communities. This interpretation is supported by visitation network data that demonstrate the existence of a geographical mosaic of dominant pollinators and a functional link between colour pattern and the dominant pollinators present in communities.

The bee fly *Megapalpus capensis* and the horsefly *Rhigioglossa* sp., respectively, were dominant in the two community types for which interaction networks were constructed. For both of these pollinators, interaction strengths were strongly influenced by floral CPC, suggesting that this trait may be under selection by pollinators. In both communities, the dominant pollinators interacted most strongly with colour patterns that were overrepresented in these communities. Although pollinator interaction frequency is not necessarily a proxy for pollinator effectiveness, it is probably an important determinant of pollinator efficiency in daisies where the open capitulum structure ensures that all visitors can remove and deposit pollen. Interestingly, the switch between two dominant pollinators across community types was a switch between two fly species, which would often be classified into the same functional group. *Megapalpus capensis* is known to choose flowers based on visual signals

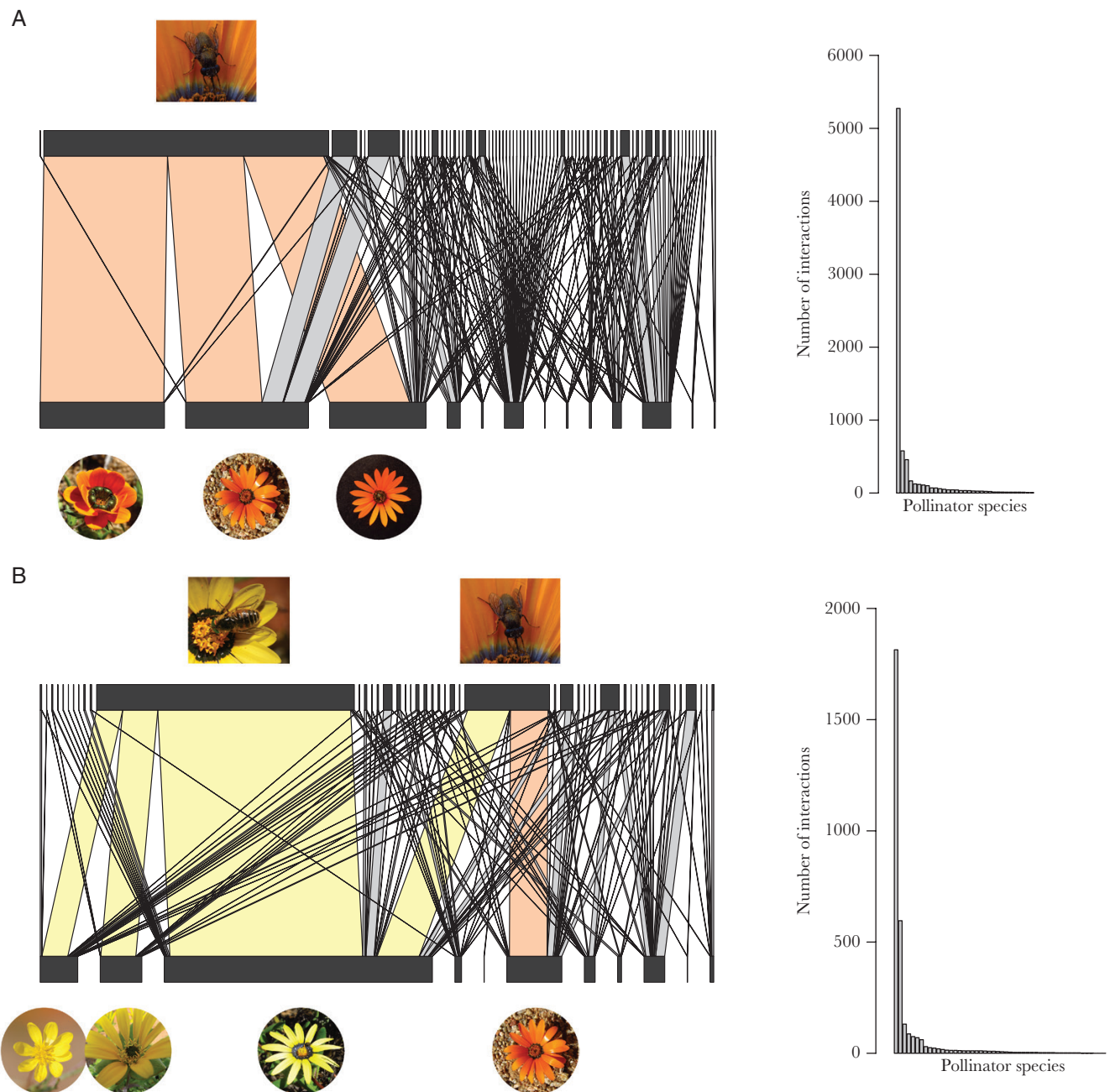


FIG. 4. Bipartite interaction webs for communities 2 (A) and 7 (B) that exhibited clustered assembly of flower colour. ANOVAs with a priori contrasts showed that the dominant pollinators interact significantly more frequently with overrepresented CPCs in both communities. In community 2 (A) a bombyliid fly, *Megapalpus capensis*, was responsible for 68 % of observed visits, and in community 7 (B) a tabanid fly, *Rhiogioglossa* sp., is dominant (57 % of visits). Graphs on the right indicate interaction frequencies for all pollinator species in these two communities (ranked by interaction frequency) illustrating the overriding dominance of a single pollinator in each community. Photos by J.E.K., A.G.E., N.G.B. and Bruce Anderson.

and to prefer orange flowers with black centres (De Jager and Ellis, 2012, 2013), but experimental evidence for colour preferences of other fly species in this region is unfortunately lacking. In particular, Troje's (1993) fly visual model might not fully capture the visual discrimination capabilities of the pollinators in this system. Fly vision, particularly the range of variation in colour perception between species, is not fully understood. Although colour vision has been shown for all fly species tested to date, it is unclear whether all species have categorical vision

(reviewed by Lunau, 2014), and different species might have different spectral tuning filters that can alter what flies see (Lunau and Knüttel, 1995). Recent work on bees has shown that caution should also be applied when interpreting bee colour vision models, as colour discrimination abilities of bees are potentially influenced by neural tuning (Avarguès-Weber and Giurfa, 2014), and can vary between bee species (García et al., 2017). Although colour discrimination modelling can be done using models of closely related species, ideally models should

TABLE 2. The effect of colour pattern categories (CPCs), delineated from raw spectra, bee vision and fly vision, on link temperature of the dominant pollinator species in two clustered communities; the effects of overrepresented colour pattern categories were tested with ANOVA with a priori contrasts. Effects significant at $P < 0.05$ are indicated in bold

		Community 2 <i>Megapalpus capensis</i>			Community 7 <i>Rhigioglossa</i> sp.		
		d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>
Colour pattern category	Raw spectra	9, 15	3.271	0.02	8, 15	3.634	0.02
	Bee vision	8, 16	3.64	0.01	7, 16	2.745	0.04
	Fly vision	3, 21	1.274	0.31	5, 18	1.403	0.27

always be verified with behavioural data (Garcia *et al.*, 2017), which did not fall within the scope of our study.

While our data suggest a strong influence of pollinators on colour pattern assembly, we cannot unequivocally separate the influence of the three possible mechanisms that could result in clustering of colour pattern within communities (Fig. 1). However, our results suggest that the clustering of flower colour patterns is, at least partly, driven by evolutionary convergence on pollinator-preferred patterns. Most daisy species belong to just a few colour pattern categories that have evolved repeatedly in several distantly related daisy lineages, a pattern probably resulting from convergence through pollinator-driven selection. Also, eight of our sampled plant species exhibited allopatric intraspecific CPC polymorphisms, again demonstrating the evolutionary lability of flower colour in these daisies. Flower colour patterns may thus represent independent pollinator syndromes generated by pollinator-driven convergence, where syndromes are specific to particular functional groups of pollinators, or even to specific pollinator species. Flower colour is frequently an important syndrome trait (Fenster *et al.*, 2004; but see Reverté *et al.*, 2016), which in some cases is associated with a single pollinating species, as in the case of the long proboscis fly, *Prosoeca longipennis*, that visits 17 plant species in South Africa, all of which exhibit matching long-tubed flowers and similarly coloured petals (Newman *et al.*, 2014). Similarly, our results suggest that the differential colour pattern preferences of *Rhigioglossa* sp. and *Megapalpus capensis* may be generating syndromes of floral traits in daisy species. Previous work has shown that fly pollinators have different innate colour preferences than bees (Shrestha *et al.*, 2014), and that bees also exhibit differential colour preferences (Dyer *et al.*, 2016).

Although we cannot unequivocally rule out filtering as a process, the presence of many different floral phenotypes in each community suggests that strong filters for single or just a few flower colour patterns are not present. This may indicate that most pollinator types are present in all communities, but that pollinator abundances vary strongly across the region. Evidence for filtering of plant species by pollinator availability exists in the invasion and agricultural literature (Blanche *et al.*, 2006), but has not been demonstrated extensively in natural systems (Sargent and Ackerly, 2008). In particular, filtering seems unlikely in systems where plants have easily accessible floral rewards, such as daisies, and are not in specialized mutualisms with just one or a few species of pollinators. However, certain flower colours could be filtered from communities if the available pollinators are unable to detect them. For instance, Bukovac *et al.* (2017) recently showed that flowers with single inflection

points between 420 and 480 nm are not easily detected by bees, and that these colours are rarely found in flowers.

While several studies have demonstrated facilitative pollination interactions in other floras (e.g. Tur *et al.*, 2016), the only existing study in Namaqualand daisy communities found no evidence for facilitation of visitation (De Waal *et al.*, 2015). Facilitation is most likely at low plant densities (Moeller, 2004; Ghazoul, 2006), while daisy flower densities in the Namaqualand spring mass flowering events are often very high (Fig. 2). However, it is possible that facilitation may promote infiltration of species into communities with colour patterns that are already present, as new immigrants to a community will always initially occur at lower densities (as argued by De Jager *et al.*, 2011).

Plant community assembly through competition for pollinator resources or character displacement

If competition for pollinators is an important mechanism structuring plant communities, we expect to detect both overdispersion of colour patterns within communities, and strongly modular interaction networks. Both of these patterns are consistent with pollinator niche divergence of community members. We found very little evidence of these patterns, as colour pattern overdispersion was only detected in two communities, and interaction webs were not significantly modular. In addition, both of the overdispersed communities were relatively species-poor, and contained regionally rare colour patterns that were overrepresented in these communities relative to the regional species pool, which may account for the overdispersed pattern.

In this sense our findings contrast with most previous studies of floral trait assembly, which show overdispersion patterns indicative of either character displacement or competitive exclusion (Muchhala and Potts, 2007; McEwen and Vamosi, 2010; Heystek and Pauw, 2014; Muchhala *et al.*, 2014), although one previous study has demonstrated clustering of flower colour within *Oxalis* communities (De Jager *et al.*, 2011). One possibility is that floral community trait assembly reflects a system-specific balance between the costs of heterospecific pollen transfer and the benefits of sharing pollinators. Tur *et al.* (2016), for example, showed that although south Andean plants share pollinators, the costs of HPT do not outweigh the benefits of facilitation, thus making clustered floral trait assembly likely. Because of the strong dominance of a single pollinator species in our daisy interaction networks, the benefits of exploiting the

dominant pollinator (i.e. high visitation rates) may well outweigh the HPT costs of sharing it with co-occurring plant species.

CONCLUSIONS

The clustered assembly of complex flower colour patterns we demonstrate adds to the accumulating evidence that pollinators are an important determinant of plant community assembly. Our novel approach, of combining a standard community trait and phylogenetic null modelling approach with insights from pollination interaction networks, goes beyond previous studies in providing direct evidence for the role of pollinators in driving floral trait assembly patterns. We show that pollinator-mediated assembly need not involve competitive interactions. Instead in some ecological contexts, such as when pollinator communities are dominated by one or few species as was the case here, the benefits of pollinator sharing might outweigh the costs of competition to generate a clustered assembly. In addition, our findings are particularly interesting given the prevailing perception of the generalized pollination systems of daisies, suggesting instead that daisy colour patterns represent a pollination syndrome trait linked not only to specific pollinator functional groups, but also to different species within a functional group (e.g. different species of fly).

SUPPLEMENTARY DATA

Supplementary data are available online at <https://academic.oup.com/aob> and consist of the following. **Table S1.** Species occurrences (presence/absence) for the 20 sampled sites. **Table S2.** GenBank accession numbers for the sequences of generic representatives used in the phylogenetic reconstruction. **Table S3.** Assignment of species to colour pattern categories using raw spectra, bee vision and fly vision. **Table S4.** Pagel's lambda and *P*-values are shown for the different CPCs based on raw spectra. **Figure S1.** BEAST maximum clade credibility tree based on analysis of combined nuclear and plastid DNA.

ACKNOWLEDGEMENTS

We thank Steve Johnson for use of the spectrophotometer. The project was made possible by funding from the South African National Research Foundation (to JEK: 95181 and 111281; and to AGE) and Stellenbosch University (to AGE).

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