

Short Communication

Orchid fruiting success is unrelated to surrounding floral resources in South Australian plant communities

Irene Martín-Forés^{1,*}, Samantha L. Bywaters¹, Ben Sparrow^{1,2} and Greg R. Guerín^{1,2}

¹Department of Ecology and Evolutionary Biology, School of Biological Sciences, The University of Adelaide, Adelaide, SA 5005, Australia, ²Terrestrial Ecosystem Research Network (TERN), The University of Adelaide, Adelaide, SA 5005, Australia

*Corresponding author. E-mail: irene.martin@adelaide.edu.au

Handling Editor: Da-Yong Zhang

Received: 27 February 2022, **First Decision:** 24 April 2022, **Accepted:** 12 June 2022, **Online Publication:** 31 July 2022

Abstract

To maintain recruitment in orchid populations in an ecosystem setting, we must understand how surrounding floral resources affect fruiting success. We studied fruiting success in two endemic Australian species, *Diuris pardina* and *Glossodia major*, in relation to surrounding floral resources. *Diuris pardina* has a visually deceptive pollination strategy via mimicry of pea flowers, attracting pollinators associated with co-flowering plants of *Pultenaea*. *Glossodia major* displays dummy anthers and has a more generalist pollination strategy. We expected fruiting success of both species to positively correlate to conspecific and heterospecific floral density because orchid pollination should be enhanced by the attraction of higher densities of native bees. We expected fruiting success of *D. pardina* to positively correlate with abundance of *Pultenaea* flowers. Surveying 18 plots in South Australia, we counted species, individuals and flowers of conspecifics and heterospecifics and returned to count flowers that set fruit. We conducted Pearson correlations between fruiting success and density of conspecific flowers, richness, abundance and Shannon index of surrounding floral resources and floral abundance of individual species. Fruiting success was correlated with conspecific floral density for *D. pardina* but not *G. major*. No relationship was found between fruiting success and heterospecific floral resources. Fruiting success of *D. pardina* was not correlated with abundance of *Pultenaea*; instead it was positively correlated with the invasive species *Lavandula stoechas*.

Keywords Australia, deceptive, endemic orchids, floral resources, fruiting success, pollination

澳大利亚南部植物群落中的兰花的结实成功率与周围花卉资源无关

摘要：为保证生态系统不断补充兰花的种群数量，了解兰花周围的花卉资源如何影响兰花的结实成功率是很有必要的。为此，本论文研究了澳大利亚的两种特有物种*Diuris pardina*和*Glossodia major*的结实成功率与其周围花卉资源之间的关系。*D. pardina*模仿豌豆花，通过视觉欺骗手段吸引*Pultenaea*共花植物的专化传粉者；*G. major*展现假花药，吸引泛化传粉者。因为吸引密度更高的本地蜜蜂可以促进兰花传粉，我们假设这两个物种的结实成功率与其周围同种花和异种花的密度呈正相关。我们还假设*D. pardina*的成功结实与其周围*Pultenaea*花的丰度呈正相关。我们调查了澳大利亚南部的18个地块，统计了同种花和异种花的物种数、个体数和花朵数，以及成功结实的花朵数。对结实成功率与同种花的密度、周围花卉资源的多度、丰度和香农指数以及单个物种的花卉丰度进行了Pearson相关分析，发现*D. pardina*的结实成

功率与周围同种花的密度相关，但*G. major*的结实成功率与周围同种花的密度无关，未发现结实成功率与异种花资源之间存在关联。*D. pardina*的结实成功率与*Pultenaea*的丰度无关，而与入侵物种法国薰衣草(*Lavandula stoechas*)呈正相关。

关键词：澳大利亚，欺骗性的，特有兰花，花资源，结实成功，授粉

INTRODUCTION

The orchid family includes over 27 000 species (Chase *et al.* 2015; Govaerts 2016), but their rapid decline over the past decades and threatened status in the IUCN Global Red List point to the need for urgent conservation measures (IUCN 2021; Wraith and Pickering 2018). Due to the complexity of their symbiotic interactions with other species and their dependence on specific association with pollinators (Hutchings 2010), orchids constitute a complicated group from conservationist and management perspectives (Martín-Forés *et al.* 2022; Reiter *et al.* 2016; Swarts and Dixon 2017). Therefore, to design successful conservation strategies for this plant family, we need to fully understand orchid reproduction and pollination deficits that might contribute to orchid decline (Fay 2018); for that, comprehensive orchid flowering and pollination data are of particular relevance, as they reflect the complexity and maintenance of underlying ecosystem interactions and allow study of the activity of key insect groups (Brundrett 2019).

Orchid reproduction depends on pollination success, normally by insects, although there are some orchid species that can undergo auto-pollination or asexual propagation by forming clonal populations (Roberts and Dixon 2008). Orchid pollination is often one sided and specialized, with the orchid relying more on its pollinator than the pollinator on the orchid (Joffard *et al.* 2019; Johnson and Steiner 2003; Roberts and Dixon 2008; Tremblay 1992). Orchid pollination can be based on nectar rewards or partial rewards (Shrestha *et al.* 2020), although one-third of orchid species have developed deceit strategies, including food and sexual deception, in which orchids mimic a reward (mimicry of floral features and production of a copy of the insect pheromone or even resembling insect forms, respectively; Jersáková *et al.* 2006; Roberts and Dixon 2008).

Australia is a diversity hotspot for nectarless plants with deceptive pollination strategies (Dafni and Bernhardt 1990; Herberstein *et al.* 2013). Endemic Australian species from the genus *Diuris* are an

example of orchid species resembling legumes and pollinated by a visually deceptive mechanism (i.e. via mimicry of orange and yellow peas flowers from the genus *Pultenaea*; Beardsell *et al.* 1986; Indsto 2009); therefore, they attract a suite of pollinators associated with co-flowering plants of similar appearance (Scaccabarozzi *et al.* 2018, 2019). Thus, floral mimicry such as the one displayed by *Diuris* is expected to be more effective with a higher ratio of model to mimic flowers (Anderson and Johnson 2006). Species from the genus *Glossodia* have a more generalist pollination strategy (Bates and Weber 1990; Beardsell *et al.* 1986; Faast 2010), and they display dummy anthers (Jersáková *et al.* 2006). Pollination success of *Diuris* and *Glossodia* rely upon communities of native bees, which vary in space and time according mainly to the local availability of floral resources (Bates and Weber 1990; Faast 2010). The ‘magnet species effect’ states that rewardless and deceptive orchids benefit from an abundance of neighbouring rewarding plants because they attract potential pollinators (Thompson 1978). Thus, fruiting success for these two genera (and especially for species whose specific pollinators have a large nectar component in their diet) is expected to be impacted by the surrounding vegetation, with pollinator activity typically enhanced by greater density and diversity of floral resources (of both, conspecifics and heterospecifics mimicked by the deceptive orchid; Faast 2010; Johnson *et al.* 2003).

The aim of this study was to explore how species composition and relative abundance of surrounding floral resources influenced reproductive success (i.e. fruiting success) of *Diuris pardina* Lindl. and *Glossodia major* R.Br. in South Australian orchids communities. These species are representative of orchid communities in the region and are frequent and locally abundant, making them suitable subjects for scoring fruiting success. Additionally, we chose these species because they have contrasting degrees of reproduction specialization (i.e. *D. pardina* is more specialist whereas *G. major* is more generalist), yet relatively little is known about their reproductive biology. For example, the specific pollinators and their effect on the reproduction of these species

are unknown to date. We tested the following hypotheses:

1. Fruiting success of both species is correlated with the density of conspecific flowers.
2. Diverse and abundant heterospecific floral resources increase orchid pollination by attracting higher densities of bees to the local patch. Fruiting success in orchid species is correlated with heterospecific floral abundance and diversity.
3. Pollination of *D. pardina* is increased by deceptive mimicry in the presence of *Pultenaea* flowers in the surrounding vegetation. Fruiting success of *D. pardina* is correlated with the abundance of *Pultenaea* flowers.

MATERIALS AND METHODS

Study area

Australia harbours a high diversity of endemic orchid species (approximately 1800 species, 95% endemic; Backhouse 2007; Wraith and Pickering 2019), with species from this family being over-represented among Australia's threatened species (Faast and Facelli 2007). The study was conducted in the Spring Gully Conservation Park, in the northern area of the Mount Lofty Ranges, South Australia. The area of study is a large (4 km²), unique vegetation remnant protected to conserve the only occurrence of *Eucalyptus macrorhyncha* F.Muell. ex Benth. in South Australia, embedded in an agricultural landscape. The Mount Lofty Ranges are considered a climatic refugium at the continental scale (Byrne 2008; Crisp *et al.* 2001; Guerin *et al.* 2016; Guerin and Lowe 2013). The area has a Mediterranean

climate. Mean annual precipitation ranges from 460 to 990 mm, whereas minimum and maximum annual mean temperatures range from 7.8 to 10.3 °C and from 18.1 to 21.7 °C, respectively (Harwood *et al.* 2016).

Data collection

To explore the effect of floral resources on fruiting success of two common orchid species, we related the proportion of recorded flowers that developed into fruits, to both the density of flowers and the abundance and diversity of floral resources in the plot. For this, we surveyed 18 plots 30 m × 30 m size, with a minimum distance of 100 m from each other, located at Spring Gully Conservation Park. In early-mid September 2020, during the peak flowering period, we counted the number of open flowers of the orchid species *D. pardina* Lindl. and *G. major* R.Br. (counting ~3000 individuals; Fig. 1). We returned to the same plots in late October to count the orchid flowers that had set fruit. Fruiting success was then expressed as the percentage of flowers that had set fruit.

To test the idea that fruiting success relates to the floral resources provided to pollinators in the surrounding vegetation at the time of flowering, we set up a floral transect in each plot to quantify the diversity and species composition of other floral resources available to insect pollinators. The transect consisted of a 1.8-m wide strip across the plot (54 m²); for all surrounding vegetation except for non-insect pollinated species such as grasses and sedges, we recorded floral abundance data per species. Hence, for each plant species, we recorded number of individuals

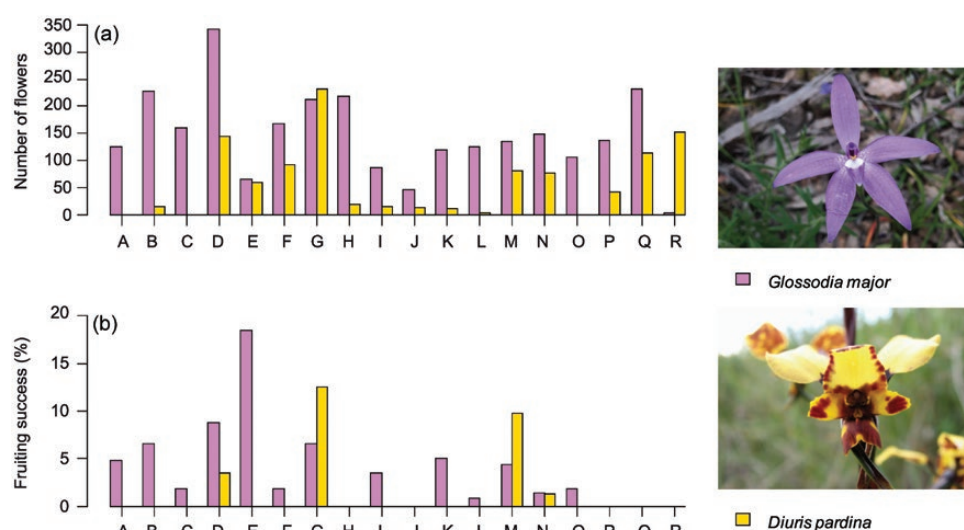


Figure 1: Number of flowers (a) and fruiting success (b) for *Diuris pardina* and *Glossodia major* in a set of 18 systematically surveyed 30 m × 30 m plots (labelled A through to R) in Spring Gully Conservation Park, South Australia.

and the number of open flowers. Flowers were either counted or, where necessary, estimated by counting the flowers on branchlets and multiplying by number of branchlets.

Data analyses

To determine the fruiting success, we calculated the proportion of recorded flowers that develop into fruit. We related the fruiting success of *D. pardina* and *G. major* to conspecific floral density (i.e. number of individuals and number of flowers) through Pearson correlations.

We also related the fruiting success of *D. pardina* and *G. major* to heterospecific floral density (i.e. number of individuals and number of flowers of other species in the surrounding vegetation), and to the overall species richness, abundance and Shannon diversity index of heterospecific floral resources in the plot through Pearson correlations.

Finally, we explored plant–plant relationships of surrounding floral resources affecting fruiting success by conducting pairwise correlations for *D. pardina* and *G. major* with the floral abundances of each of the recorded species (Supplementary Tables S1 and S2). For those species that we observed significant correlation coefficients (Supplementary Table S3), we conducted linear models between *D. pardina* and *G. major* fruiting success rates and the species abundance to check for the significance of the effect of that particular flowering species on enhanced pollination.

All statistical analysis and calculations were performed using R (R Core Team 2020) employing the package *corrplot* (Wei and Simko 2021).

RESULTS

Fruiting success in *D. pardina* and *G. major* was low (0%–18%). *Glossodia major* and *D. pardina* exceeded 5% of fruiting success only in five and two plots, respectively (Fig. 1). Fruiting success for *D. pardina* was especially low, with eleven plots showing flowers but not fruits (Fig. 1; Table 1). *Diuris pardina* fruiting success was correlated with conspecific floral density (i.e. number of individuals and number of flowers per plot; adjusted r -squared = 0.39, $P < 0.01$; Fig. 2), but there was no apparent trend between flowering and fruiting *G. major* individuals (adjusted r -squared = -0.05 , $P = 0.71$; Fig. 2).

Fruiting success for both species was not significantly correlated to overall heterospecific floral resources (i.e. number of flowers from all the species

present in the plot), nor to overall floral diversity in terms of both, species richness and Shannon diversity (Fig. 3).

Contrary to our predictions, fruiting success for *D. pardina* was not significantly correlated with the abundance of *Pultenaea largiflorens* (adjusted r -squared = 0.02, $P = 0.28$), although it was positively correlated with the abundance of *Lavandula stoechas* (adjusted r -squared = 0.23, $P < 0.05$). Fruiting success for *G. major* was significantly correlated to *Wurmbea dioica* flowers (adjusted r -squared = 0.24, $P < 0.05$), and marginally to *Drosera auriculata* (adjusted r -squared = 0.14, $P < 0.1$).

DISCUSSION

According to our results, fruiting success for *D. pardina* and *G. major* is mainly stochastic and not obviously controlled by heterospecific local floral resources and surrounding vegetation, contradicting *a priori* predictions. Fruiting plants of both species were often observed in clusters, which suggests chance encounters with pollinators that visited neighbouring plants. It is also possible that developing fruits could have been grazed by deer, kangaroos and euros, although grazing pressure on vegetation in the area and palatable plants in the plots was not high and many spent orchid flowers were observed during fruiting surveys, confirming that they had not been pollinated. Overall, the success rate of the studied species appeared to be low; however, for food deceptive orchids, it is common that the reproductive success rate does not reach 20% (Jacquemyn and Brys 2010). Fruiting success for *D. pardina* was positively associated with conspecific floral resources, whereas fruiting success for *G. major* cannot be predicted from conspecific flower density. Deceptive species which typically have low fruiting success, typically compensate this by displaying greater seed output per fruit than non-deceptive, nectar-rewarding orchids (Sunkoly *et al.* 2016). In this sense, populations of the species studied here might rely on a small number of individuals producing seed to replenish the population or even long-lived individuals that are rarely pollinated, contrary to other less abundant species, such as orchids from the genus *Thelymitra* for which developing fruits were observed more consistently in the vegetation.

Contrary to our expectation, fruiting success of *D. pardina* was not significantly correlated with

Table 1: Number of individuals, flowers and fruits of *Diuris pardina* and *Glossodia major* in each plot

Plot	Number of individuals		Number of flowers		Number of fruits		Fruiting success (%)		Richness	Shannon	Flower abundance
	<i>Diuris</i>	<i>Glossodia</i>	<i>Diuris</i>	<i>Glossodia</i>	<i>Diuris</i>	<i>Glossodia</i>	<i>Diuris</i>	<i>Glossodia</i>			
A	0	126	0	126	0	6	0	4.7	10	0.139	9121
B	4	227	15	227	0	15	0	6.6	9	0.351	3209
C	0	161	0	161	0	3	0	1.9	10	1.604	321
D	41	342	145	342	5	30	3.4	8.8	9	0.362	3335
E	17	65	61	65	0	12	0	18.5	8	0.984	702
F	29	168	93	168	0	3	0	1.8	6	0.276	7191
G	59	212	231	212	29	14	12.6	6.6	4	0.859	317
H	7	219	20	219	0	0	0	0	6	1.491	327
I	4	87	15	87	0	3	0	3.4	8	1.243	224
J	3	44	13	46	0	0	0	0	15	2.205	691
K	3	118	12	119	0	6	0	5.0	15	2.054	851
L	2	126	5	126	0	1	0	0.8	13	1.896	1232
M	25	136	82	136	8	6	9.76	4.4	12	1.051	1444
N	28	148	78	148	1	2	12.8	1.4	8	1.164	1285
O	0	106	0	106	0	2	0	1.9	9	0.289	3349
P	12	137	42	137	0	0	0	0	9	1.537	477
Q	35	231	114	231	0	0	0	0	11	0.763	10 528
R	41	4	152	4	0	0	0	0	7	0.814	1067

Species richness, Shannon diversity index and abundance of floral resources in each plot are also displayed.

the native pea it mimics, *P. largiflorens*, despite bees being observed visiting *P. largiflorens* individuals during sampling. This trend was also observed in Australia for *Diuris magnifica*, which did not increase its reproductive success associated with the presence of native pea plants but appeared to be influenced by another non-model plant (Scaccabarozzi *et al.* 2018, 2019). These findings might be related to the likelihood of the pollinators also feeding on a range of other species apart from the model plant. In addition, when relying on floral mimicry, the reproductive success of the deceptive orchid might be diminished with an increased ratio of deceptive orchid/model to mimic (Anderson and Johnson 2006). Unexpectedly, fruiting success of *D. pardina* was positively correlated with the abundance of *L. stoechas*, an introduced labiate woody species which strongly attracts honeybees (Kantsa *et al.* 2018). This might be related to the production of essential oils

by *L. stoechas*, and the fact that this aromatic plant is known to serve as hubs in plant–pollinator networks in other Mediterranean systems (Raguso 2020). The fact that *G. major* was positively correlated with the abundance of *W. dioica* might be due to the fact that male individuals of this dioecious lily attract certain species of Australian native bees, and, to a lesser extent, honeybees (Dyer *et al.* 2016; Vaughton and Ramsey 1998). Previous studies focussing on the pollination and fruiting success of the Australian orchid *Caladenia versicolor* also observed in their plots of study co-flowering plants of *W. dioica* and two species from the genus *Drosera* (Reiter *et al.* 2019).

Contrary to our expectations and to previous studies stating that the presence of neighbouring flowering plants played an essential role for maintaining pollinator visits in rewardless orchid communities (e.g. Sakata *et al.* 2014), orchid fruiting success for *D. pardina* and *G. major* was not

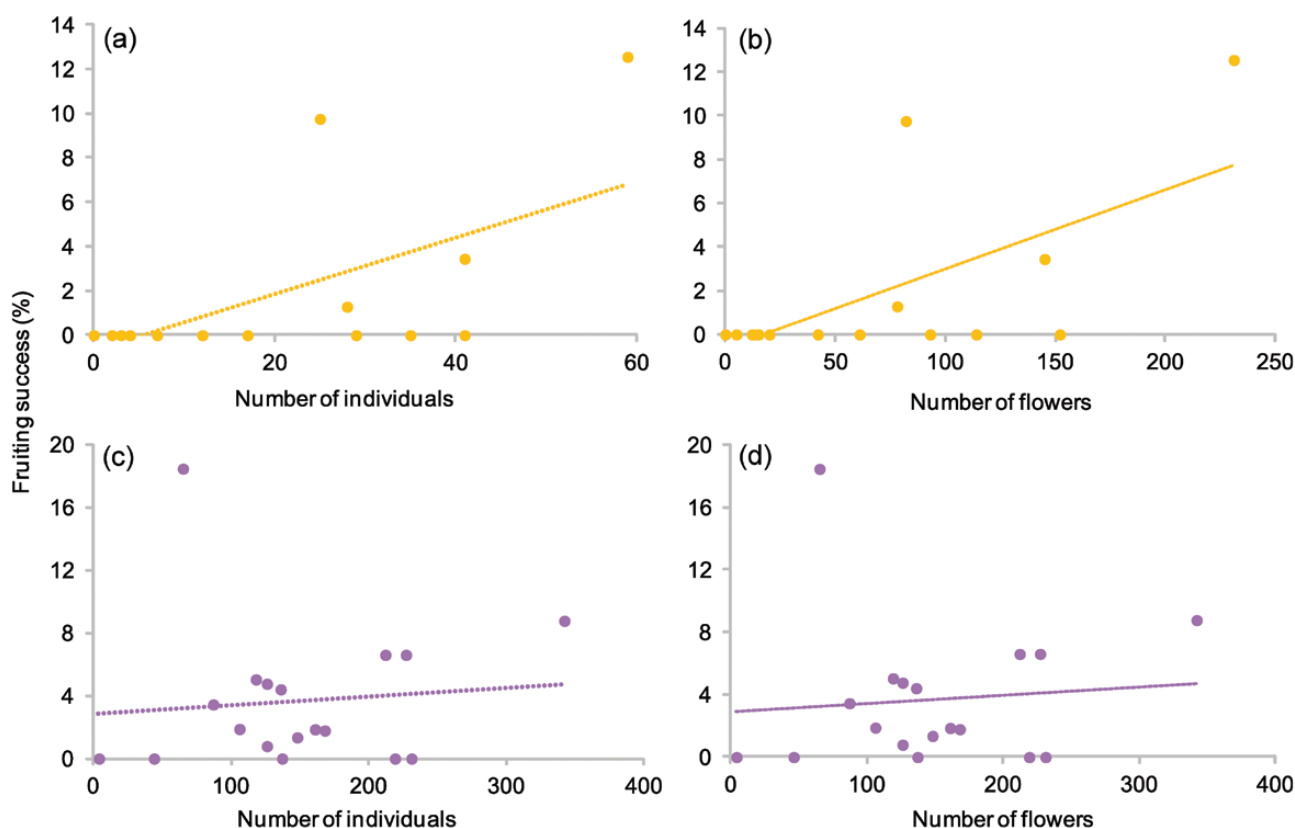


Figure 2: Correlation between fruiting success of *Diuris pardina* (gold) and *Glossodia major* (purple) with their own floral density in terms of number of individuals (respectively, **a** and **b**) and number of flowers per plot (**c** and **d**).

related to overall heterospecific floral resources in terms of species richness, abundance and Shannon diversity. This is surprising, as facilitated pollination enhanced by co-flowering surrounding vegetation through pollinator sharing and ‘the magnet effect’ has commonly been observed for deceptive orchids (Johnson *et al.* 2003; Juillet *et al.* 2007; Pellegrino *et al.* 2008). The lack of relationship between orchid fruiting success and heterospecific floral resources, could be related to divergent flowering phenologies (Internicola *et al.* 2008), or to contrasting pollination syndromes between the species of study and the surrounding vegetation recorded in the study. Previous literature suggested that the effect of the pollination syndrome displayed by the different surrounding species and the specificity of orchid species with their pollinators can play a key role in orchids reproduction success and subsequent orchid diversity within the targeted communities (Newman *et al.* 2013). In this sense, elucidating pollination syndromes of orchid species and the surrounding vegetation could shed light into this matter.

We would like to highlight that the results reported in this short communication are subjected to logistic limitations and therefore should be interpreted

conservatively. Ideally, fruiting success in orchids should be sampled across several years, as it can vary considerably from 1 year to another, and some orchid species can undergo masting events (Sakai 2002; Xiong *et al.* 2015). This was a single survey within one flowering season and not a longitudinal study. Sampling was deliberately located within the same geographic area (Spring Gully Conservation Park) and broad vegetation type (*E. macrorhyncha* woodlands) in elevated landscape positions to control for potentially confounding environmental and soil factors. Thus, the conclusions here should not be interpreted as a generalization, neither for South Australian orchid communities, nor across the full geographic range of these two species. In future, experimental designs encompassing several years of sampling and a wider range of vegetation systems, and in which surrounding co-flowering plants can be manipulated, may provide further clarity.

Further studies aiming to inform conservation practices should aim to control for the species’ pollination syndrome by including the specific pollinator for each species and its whole potential diet including co-flowering plants. Unfortunately, the existing literature does not cover the pollinators

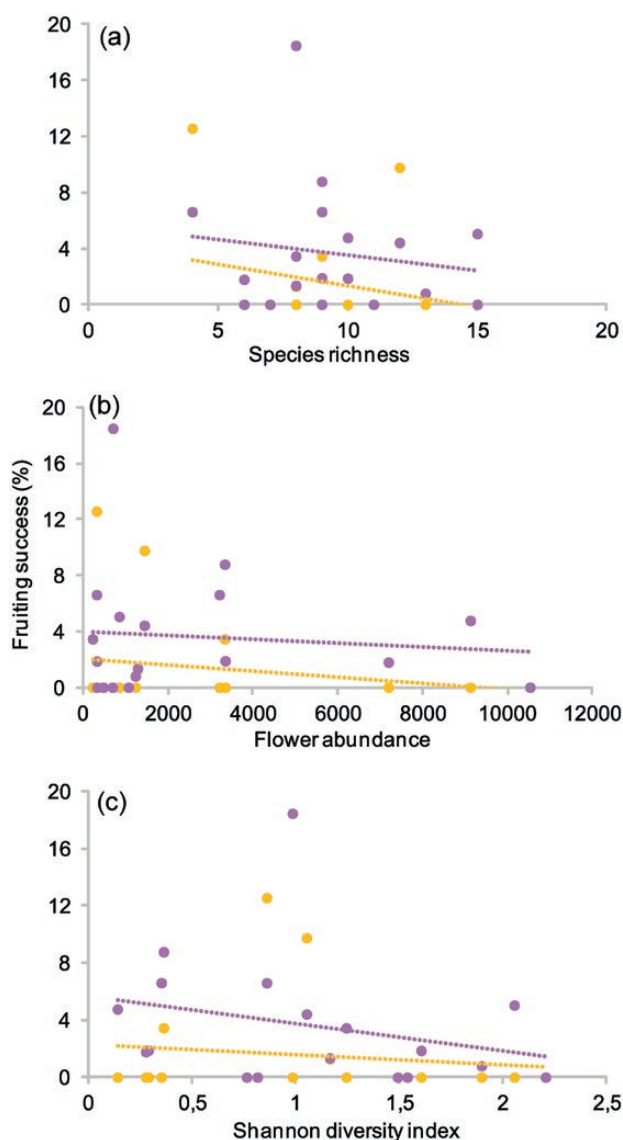


Figure 3: Correlation between fruiting success of *Diuris pardina* (gold) and *Glossodia major* (purple) and overall floral resources in terms of species richness (a), flower abundance (b) and Shannon diversity index (c) of the surrounding vegetation community.

for the species recorded in the present study; e.g. Kuiter (2016) presented the only pollinator data existing to date for *Glossodia*. Therefore, tackling this knowledge gap would be necessary as a preliminary step to be able to best inform management guidelines aiming to preserve orchid diversity. Finally, the unexpected positive association between the invasive species *L. stoechas* and the fruiting success of *D. pardina* deserves further studies targeting plant–plant interactions of *L. stoechas* within the community, which will help designing adaptive management strategies for the control of this weed. If it is proved that *L. stoechas* might be enhancing the

pollination regulating service for certain Australian orchid species, the eradication of this species should be ideally accompanied by the restoration of the pollination service it provides via planting bee-attracting native species.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Table S1: Number of counted individuals for each plant species within the surrounding vegetation in each of the sampled plots.

Table S2: Number of counted flowers for each plant species within the surrounding vegetation in each of the sampled plots.

Table S3: Pearson correlation coefficients between floral abundance in plant species of the surrounding vegetation and fruiting success of *Diuris pardina* and *Glossodia major*.

Funding

This work has been funded by the grant 327-2018—Australian Orchid Foundation—Climate and habitat condition controls on orchid populations—research outcomes associated with a citizen science program. Likewise, it has been possible thanks to the grant from the Department of Industry, Innovation and Science—Inspiring Australia, Citizen Science Grants—Wild Orchid Watch.

Acknowledgements

We thank the TERN Ecosystem Surveillance team, Rosalie Lawrence, Robert Lawrence, Penny McLachlan, Katie Irvine, Michael Starkey, Sally O'Neill, Candy Guerin and the South Australian Department for Environment and Water.

Conflict of interest statement. The authors declare that they have no conflict of interest.

Authors' Contributions

I.M.-F. and G.R.G. conceived the ideas; G.R.G. and S.L.B. collected the data; I.M.-F. analysed the data and drafted the paper. All authors reviewed the final version of the manuscript and approved its submission.

REFERENCES

- Anderson B, Johnson SD (2006) The effects of floral mimics and models on each others' fitness. *Proc R Soc B Biol Sci* **273**:969–974.
- Backhouse G (2007) Are our orchids safe down under? A national assessment of threatened orchids in Australia. *Lankesteriana* **7**:28–43.

- Bates RJ, Weber JZ (1990) *Orchids of South Australia*. Adelaide, Australia: The Flora and Fauna of South Australia Handbooks Committee.
- Beardsell DV, Clements MA, Hutchinson JF, *et al.* (1986) Pollination of *Diuris maculata* R. Br. (Orchidaceae) by floral mimicry of the native legumes *Daviesia* spp. and *Pultenaea scabra* R. Br. *Aust J Bot* **34**:165–173.
- Brundrett MC (2019) A comprehensive study of orchid seed production relative to pollination traits, plant density and climate in an urban reserve in Western Australia. *Diversity* **11**:123.
- Byrne M (2008) Evidence for multiple refugia at different time scales during Pleistocene climatic oscillations in southern Australia inferred from phylogeography. *Quat Sci Rev* **27**:2576–2585.
- Chase MW, Cameron KM, Freudenstein JV, *et al.* (2015) An updated classification of Orchidaceae. *Bot J Linn Soc* **177**:151–174.
- Crisp MD, Laffan S, Linder HP, *et al.* (2001) Endemism in the Australian flora. *J Biogeogr* **28**:183–198.
- Dafni A, Bernhardt P (1990) Pollination of terrestrial orchids of Southern Australia and the Mediterranean region. Systematics, ecological and evolutionary implications. *Evol Biol* **24**:193–252.
- Dyer AG, Howard SR, Garcia JE (2016) Through the eyes of a bee: seeing the world as a whole. *Anim Res* **5**:97–109.
- Faast R (2010) The reproductive ecology of two terrestrial orchids, *Caladenia rigida* and *Caladenia tentaculata*. *Ph.D. Thesis*. School of Earth and Environmental Sciences, University of Adelaide.
- Faast R, Facelli JM (2007) Investigation of processes leading to the decline of South Australia's *Caladenia* species. *Lankesteriana* **7**:269.
- Fay MF (2018) Orchid conservation: how can we meet the challenges in the twenty-first century? *Bot Stud* **59**:1–6.
- Govaerts R (2016) *World Checklist of Orchidaceae. Facilitated by the Royal Botanic Gardens, Kew*. <http://apps.kew.org/wcsp/> (4 November 2016, date last accessed).
- Guerin GR, Biffin E, Baruch Z, *et al.* (2016) Identifying centres of plant biodiversity in South Australia. *PLoS One* **11**:e0144779.
- Guerin GR, Lowe AJ (2013) Multi-species distribution modelling highlights the Adelaide Geosyncline, South Australia, as an important continental-scale arid-zone refugium. *Austral Ecol* **38**:427–435.
- Harwood T, Donohue R, Harman I, *et al.* (2016) 9s climatology for continental Australia 1976–2005: summary variables with elevation and radiative adjustment. In CSIRO (ed). *Data Collection*. Canberra, Australia, CSIRO.
- Herberstein ME, Baldwin HJ, Gaskett AC (2013) Deception down under: is Australia a hot spot for deception? *Behav Ecol* **25**:12–16.
- Hutchings MJ (2010) The population biology of the early spider orchid *Ophrys sphegodes* Mill. III. Demography over three decades. *J Ecol* **98**:867–878.
- Indsto JO (2009) Pollination ecology and molecular systematics of *Diuris* (Orchidaceae). *Master Thesis*. Institute for Conservation Biology and Law, Biological Sciences, University of Wollongong.
- Internicola AI, Bernasconi G, Gigord LD (2008) Should food-deceptive species flower before or after rewarding species? An experimental test of pollinator visitation behaviour under contrasting phenologies. *J Evol Biol* **21**:1358–1365.
- IUCN (2021) *The IUCN Red List of Threatened Species*. 2021-1. <http://www.iucnredlist.org/> (29 April 2021, date last accessed).
- Jacquemyn H, Brys R (2010) Temporal and spatial variation in flower and fruit production in a food-deceptive orchid: a five-year study. *Plant Biol* **12**:145–153.
- Jersáková J, Johnson SD, Kindlmann P (2006) Mechanisms and evolution of deceptive pollination in orchids. *Biol Rev* **81**:219–235.
- Joffard N, Messol F, Grenie M, *et al.* (2019) Effect of pollination strategy, phylogeny and distribution on pollination niches of Euro-Mediterranean orchids. *J Ecol* **107**:478–490.
- Johnson SD, Peter CI, Nilsson LA, *et al.* (2003) Pollination success in a deceptive orchid is enhanced by co-occurring rewarding magnet plants. *Ecology* **84**:2919–2927.
- Johnson SD, Steiner KE (2003) Specialized pollination systems in southern Africa. *S Afr J Sci* **99**:345–348.
- Juillet N, Gonzalez MA, Page PA, *et al.* (2007) Pollination of the European food-deceptive *Trautsteinera globosa* (Orchidaceae): the importance of nectar-producing neighbouring plants. *Plant Sys Evol* **265**:123–129.
- Kantsa A, Raguso RA, Dyer AG, *et al.* (2018) Disentangling the role of floral sensory stimuli in pollination networks. *Nat Commun* **9**:1–13.
- Kuiter RH (2016) *Orchid Pollinators of Victoria*. Seaford, Victoria, Australia, Aquatic Photographics.
- Martín-Forés I, Bywaters SL, Sparrow B, *et al.* (2022) Simultaneous effect of habitat remnancy, exotic species, and anthropogenic disturbance on orchid diversity in South Australia. *Conserv Sci Pract* **4**:e12652.
- Newman BJ, Ladd P, Brundrett M, *et al.* (2013) Effects of habitat fragmentation on plant reproductive success and population viability at the landscape and habitat scale. *Biol Conserv* **159**:16–23.
- Pellegrino G, Bellusi F, Musacchio A (2008) Double floral mimicry and the magnet species effect in dimorphic co-flowering species, the deceptive orchid *Dactylorhiza sambucina* and rewarding *Viola aethnensis*. *Preslia* **80**:411–422.
- R Core Team (2020) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/> (June 2021, date last accessed).
- Raguso RA (2020) Functions of essential oils and natural volatiles in plant-insect interactions. In Baser KHC, Buchbauer G (eds). *Handbook of Essential Oils: Science, Technology, and Applications*, 3rd edn. Boca Raton, US: CRC Press, 481–496.
- Reiter N, Bohman B, Batley M, *et al.* (2019) Pollination of an endangered *Caladenia* species (Orchidaceae) by nectar-foraging behaviour of a widespread species of colletid bee. *Bot J Linn Soc* **189**:83–98.

- Reiter N, Whitfield J, Pollard G, *et al.* (2016) Orchid re-introductions: an evaluation of success and ecological considerations using key comparative studies from Australia. *Plant Ecol* **217**:81–95.
- Roberts DL, Dixon KW (2008) Orchids. *Curr Biol* **18**: R325–R329.
- Sakai S (2002) General flowering in lowland mixed dipterocarp forests of South-east Asia. *Biol J Linn Soc* **75**: 233–247.
- Sakata Y, Sakaguchi S, Yamasaki M (2014) Does community-level floral abundance affect the pollination success of a rewardless orchid, *Calanthe reflexa* Maxim.? *Plant Spec Biol* **29**:159–168.
- Scaccabarozzi D, Cozzolino S, Dixon KW (2019) Pollination ecology and pollination evolutionary processes with relevance in ecosystem restoration – pollination biology of *Diuris*: testing for Batesian mimicry in southwestern Australia. *Ph.D. Thesis*. Curtin University.
- Scaccabarozzi D, Cozzolino S, Guzzetti L, *et al.* (2018) Masquerading as pea plants: behavioural and morphological evidence for mimicry of multiple models in an Australian orchid. *Ann Bot* **122**:1061–1073.
- Shrestha M, Dyer AG, Dorin A, *et al.* (2020) Rewardlessness in orchids: how frequent and how rewardless? *Plant Biol* **22**:555–561.
- Sonkoly J, Vojtkó AE, Tökölly J, *et al.* (2016) Higher seed number compensates for lower fruit set in deceptive orchids. *J Ecol* **104**:343–351.
- Swarts ND, Dixon KW (2017) *Conservation Methods for Terrestrial Orchids*. J. Ross Publishing, United States, pp. 240. ISBN: 978-160427-123-2.
- Thompson JD (1978) Effect of stand composition on insect visitation in two-species mixtures of *Hieracium*. *Am Midl Nat* **100**:431–440.
- Tremblay RL (1992) Trends in pollination biology of the Orchidaceae: evolution and systematics. *Can J Bot* **70**:642–650.
- Vaughton G, Ramsey M (1998) Floral display, pollinator visitation and reproductive success in the dioecious perennial herb *Wurmbea dioica* (Liliaceae). *Oecologia* **115**:93–101.
- Wei T, Simko V (2021) *corrplot: Visualization of a Correlation Matrix*. R Package Version 0.90. <https://github.com/taiyun/corrplot> (June 2021, date last accessed).
- Wraith J, Pickering C (2018) Quantifying anthropogenic threats to orchids using the IUCN Red List. *Ambio* **47**:307–317.
- Wraith J, Pickering C (2019) A continental scale analysis of threats to orchids. *Biol Conserv* **234**:7–17.
- Xiong YZ, Liu CQ, Huang SQ (2015) Mast fruiting in a hawkmoth-pollinated orchid *Habenaria glaucifolia*: an 8-year survey. *J Plant Ecol* **8**:136–141.