Biological Conservation 159 (2013) 16–23

Contents lists available at SciVerse ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Effects of habitat fragmentation on plant reproductive success and population viability at the landscape and habitat scale

Belinda J. Newman[a,b,*], Philip Ladd[b], Mark Brundrett[c], Kingsley W. Dixon[a,d]

[a] Kings Park and Botanic Garden, The Botanic Gardens and Parks Authority, West Perth, WA 6005, Australia
[b] Terrestrial Ecology Research Group, School of Environmental Science, Murdoch University, Murdoch 6150, Australia
[c] Department of Environment and Conservation, Kensington, Australia
[d] School of Plant Biology, The University of Western Australia, Nedlands 6009, Australia

ARTICLE INFO

Article history:
Received 2 April 2012
Received in revised form 2 October 2012
Accepted 12 October 2012
Available online 20 January 2013

Keywords:
Fragmentation
Orchid
Pollination
Population viability
Urban

ABSTRACT

Habitat fragmentation can significantly affect plant reproductive success and ultimately population viability, but little is known about the magnitude, direction or time scale of these impacts on plant–pollinator mutualisms. In this study, four species of terrestrial orchid with specialist and generalist pollination syndromes were used to investigate the effects of fragmentation on capsule set in urban bushland remnants. Supplementary pollination showed pollination limitation, but not resource limitation, occurs across all species. Habitat and landscape scale fragmentation predictor variables were used to build parsimonious models that explained capsule set data collected over 2 years. We found the sexually deceptive species, *Caladenia arenicola*, to be sensitive to interactions between landscape (perimeter to area ratio) and habitat scale (bare ground cover and population size) predictor variables. The effect of perimeter to area ratio was heavily tempered by the significant negative influence of bare ground cover, where values of over 40% bare ground cover resulted in reproductive failure. We found that generalist pollinated species had significant interactions at the habitat scale including significant positive interactions between capsule set and population size and litter cover. Our results suggest the effects of habitat fragmentation at the landscape and habitat scale are important drivers of population viability. Our results suggest population viability will depend on the sensitivity of the pollination syndrome and the pollinator involved. This study highlights the need for research into reproductive success across multiple spatial scales to improve and inform conservation efforts.

1. Introduction

Habitat fragmentation is considered to be one of the greatest causes of biodiversity loss and the increasing urbanisation of ecosystems has played a key role in ongoing species extinctions globally (Goddard et al., 2010). Human impacts on landscapes usually result in fragmentation and isolation of ecosystems (Saunders et al., 1991), and disrupt biological processes, contributing to the decline of plant populations (Hobbs and Yates, 2003). Urbanised landscapes can be extensively transformed, as can agricultural landscapes, but the degree and intensity of the modification can differ (Kupfer et al., 2006). Simplistic views of habitat fragments as biological islands in a hostile matrix are no longer considered realistic (Hobbs and Hopkins, 1990; Kupfer et al., 2006), with the permeability and patch dynamics of a fragmented system contingent on the hostility of the matrix (Zipperer et al., 2000), particularly in an urban setting. The ability of plants or animals to survive in urban landscapes will depend on their life histories and their capacity to adapt to the challenges of urbanisation, with more generalist species typically having a higher resilience to fragmentation (Winfree et al., 2011).

Habitat fragmentation results in changes to the physical and functional interactions within an ecosystem – such as plant–pollinator mutualisms (Jennerston, 1988; Aizen and Feinsinger, 1994; Murren, 2002; Ashworth et al., 2004; Tscharntke and Brandl, 2004; Dixon, 2009). Impacts of fragmentation on the plant–pollinator mutualism can be deleterious (Aizen and Feinsinger, 1994; Cunningham, 2000a,b), especially for invertebrates (Cheptou and Avendano, 2006; Winfree et al., 2011) and may also be so for birds (Pauw and Louw, 2012). Pollination limitation has also been strongly linked to habitat fragmentation (Rathcke and Jules, 1993; Gonzalez-varo et al., 2009; Nayak and Davidar, 2010; Pauw and Bond, 2011), the effects of which become further exacerbated by the compounding spatial and temporal nature of fragmentation (Steffan-Dewenter and Tscharntke, 1999; Pauw, 2007).

Few studies have linked findings on plant reproductive success to specific aspects of habitat fragmentation (Aguilar et al., 2008; Eckert et al., 2010), particularly at differing spatial scales and

---

[*] Corresponding author. Address: Fraser Ave., West Perth, WA 6005, Australia. Tel.: +61 8 9480 3614; fax: +61 8 9322 5064.
E-mail address: Belinda.Newman@bgpa.wa.gov.au (B.J. Newman).

0006-3207/$ - see front matter © 2012 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.biocon.2012.10.009

across multiple interacting environmental variables. An increase in the spatial distance between plant populations and reduced pollinator habitat, in turn leads to reduced pollinator visitation and increased genetic isolation of plant populations (Jennerston, 1988; Donaldson et al., 2002; Ward and Johnson, 2005; Llorens et al., 2012). Other pressures on habitat fragments include increased edge effects to a potentially hostile urban matrix, which can prevent or hamper pollinator movement between fragments (Hopkins and Webb, 1984; Ricketts, 2001). Increased weed invasion (Saunders et al., 1991; King and Buckney, 2001), loss of species diversity and structure (Watson, 2002; Tscharntke and Brandl, 2004) and an increase in disturbances such as fire (Saunders et al., 1991; Sabatino et al., 2010), rubbish dumping and proliferation of internal paths (Stenhouse, 2004) can all alter aspects of the mutualism or even collapse sections of a pollination web (Pauw, 2007).

Patch dynamics can be highly influenced by the matrix in which they occur with some studies finding that a ‘softened’ matrix, such as suburban gardens (see Goulson et al., 2002 on *Bombus terrestris*), or agricultural matrices (Ricketts, 2001; Klein et al., 2003), can benefit some pollinators. An agricultural landscape can provide niches that can be exploited by a higher diversity of invertebrate pollinators than a purely urban matrix can support (Winfree et al., 2006). Conversely, other studies have found the agricultural matrix to greatly inhibit pollinator movement and pollination success in remaining fragments, particularly when fragment connectivity is limited (Krewenka et al., 2011; Llorens et al., 2012). However, the degree of matrix permeability becomes irrelevant if the fragments are no longer able to support part or all of the mutualism in question.

Many studies suggest that susceptibility to habitat fragmentation is a function of the degree of dependence and specialisation on their pollinator mutualism (Bond, 1994; Ashworth et al., 2004; Aguilar et al., 2006; Pauw and Bond, 2011). Bond (1994) states that predictions of extinction risk are based on the probability of the mutualism failing, the importance of seeds in the species’ demography and the degree of reproductive dependence on the mutualism. Thus a plant relying on a single species of pollinator may be at greater risk of extinction than a generalist pollinated species that is buffered against potential pollinator losses in a fragmented landscape (Bond, 1994; Waser et al., 1996). Typically, plant–pollinator mutualisms have a compensatory mechanism in cases of specialisation, such as vegetative reproduction compensating for declines in pollen availability (Bond, 1994).

The prevalence of Western Australian terrestrial orchids in urban bushland fragments and the range of pollination syndromes they employ, from specialist, single pollen vectors to generalist guild pollination (Brundrett, 2007), provides an ideal opportunity to examine how habitat fragmentation influences capsule set in an urban context. While it has been shown that some orchids can overcome the absence of an obligate pollinator through clonality (Pauw and Bond, 2011), the majority of the Western Australian terrestrial orchid flora are not clonal (Dixon, 1991). Obligate seeders are particularly prevalent in the sexually deceptive species (Dixon, 1991) and are reliant on seed rain for recruitment (Bond, 1994; Swarts and Dixon, 2009), placing them at greater risk of reproductive failure, and hence eventual extirpation in fragmented habitats (Swarts and Dixon, 2009; Gaskett, 2011; Pauw and Bond, 2011). There is currently a paucity of data defining the thresholds of susceptibility to reduced plant pollination capacity and the environmental factors that can most strongly influence long-term population viability of orchids in the urban context.

In this study we test the hypothesis that habitat fragmentation has a significant effect on plant reproductive success and population viability by using four species of terrestrial orchid as model species. Based on this hypothesis, we make three predictions on the effects of fragmentation on population viability. (i) There will be significant pollination limitation occurring across species, (ii) capsule set across species is predicted to decline with increasing isolation, fragment size and increased internal disturbance, and (iii) specialist pollinated species will show greater sensitivity to fragmentation predictor variables than generalist species. We aim to identify the habitat and landscape scale parameters that may be driving population viability, by investigating the relationships of these predictor variables with capsule set in four species of terrestrial orchid common to Western Australian urban reserves.

2. Methods

2.1. Study sites

The study was conducted on the Swan Coastal Plain of Perth, Western Australia in the southwest Australian biodiversity hotspot (South-West Australian Floristic Region (SWAFR); Myers et al., 2000; Hopper and Gioia, 2004). *Banksia* woodland is the characteristic vegetation type of the Swan Coastal Plain (Beard, 1989). An estimated 80% of the original *Banksia* woodlands have been cleared for urban land use and the remaining urban fragments are under increasing pressure from surrounding activities (Beard, 1989; Hopper and Burbidge, 1989; Crosti et al., 2007).

We selected eleven urban bushland fragments within a 530 km^2 study area on the Swan Coastal Plain (Fig. 1). All sites were between 4 ha and 300 ha in size with a 50 km distance between the northernmost and southernmost sites. Sites were chosen to represent indicative reserve sizes, shapes and internal characteristics. To eliminate the effects of soil type on capsule set response, sites were restricted to locations of matched soil types (Spearwood association) and matched vegetation types (*Banksia attenuata*/*menziesii* – *Eucalyptus gomphocephala* woodlands). Sites were also chosen on the basis that they contained populations of the chosen orchid species totalling at least five plants.

2.2. Study species

Orchid species were included in this study on the basis of abundance and distribution across the eleven study sites. All species are common and widespread on the Swan Coastal Plain and represent both food and sexually deceptive pollination syndromes (Table 1). The four species selected were *Caladenia arenicola* Hopper and A.P. Brown (sexual deception), *Caladenia flava* R.br subsp. *flava* (food deception), *Diuris magnifica* D.L. Jones (food deception), and *Pterostylis sanguinea* D.L. Jones and M.A. Clements (fungus gnats of uncertain attraction).

2.3. Capsule set

Capsule set is used as the main dependent variable in this study, and serves as a proxy for population viability, on the basis that it represents the recruitment potential for the next generation. The total number of flowers sampled at the sites was the ‘trials’, and the number of capsules that formed were the ‘successes’ for each species. Capsule set was collected for a total of 1402 flowers comprising 656 *D. magnifica*, 289 *C. flava* subsp. *flava*, 170 *C. arenicola*, and 292 *P. sanguinea*. The boundaries of a population were defined with a buffer radius of 40 m within which no other plant of the same species was found. Orchid populations of each of the four species in this study were located in the eleven study sites and revisited in two consecutive years, where possible. An additional ten plants of each species were hand pollinated at the eleven sites. All hand pollination involved out-crossing with donors and recipients at least 30 m from each other.

Orchid plants were tagged prior to flowers opening (in June for *P. sanguinea* and September for the other species) and assessed at