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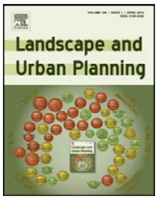

Sex in the city: Reproductive success of *Digitalis purpurea* in a gradient from urban to rural sites

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ABSTRACT

Urbanization of natural habitats is considered to have large impacts on local plant populations and their associated pollinator faunas, which are expected to cause changes in both plant-pollinator interactions and increased pollen limitation. This study investigated the effects of increasing intensity of urban land use on pollinator diversity, flower visitation rates and reproductive success in *Digitalis purpurea*. To this end, we set up experimental populations of *D. purpurea* in three urban–rural gradients and contrasted these against two large, natural populations. In the experimental populations we quantified the number of flower visits per 20 min and applied supplemental hand-pollinations to determine the impact of pollen limitation on fruit-level seed set. We found no impact of urbanization intensity on pollinator diversity at all locations studied, and also the number of flower visits did not differ significantly between urban and rural populations. Reproductive success appeared, however, pollen limited in all sites, even in the large and optimal reference populations. This led us to conclude that the pollen limitation was caused by a bet-hedging strategy of the species rather than by insufficient pollination.

1. Introduction

Habitat fragmentation through human activities is widely recognized as being one of the processes most impacting ecosystems (McKinney, 2006), negatively affecting biodiversity and possibly disrupting interactions between organisms (Steffan-Dewenter & Tscharntke, 2002). An extreme form of human activity is found in both the urban environment and in agricultural landscapes. Due to the increasing area of urbanization worldwide (United Nations, 2008), it is evident that the impact of urban land use on ecosystems is of great importance and merits study (Alberti, 2010). The impacts of urban environments on biodiversity are fairly well studied (for a review see McKinney, 2008). Much less work has been done on ecosystem processes so far (Alberti, 2010). One of these important ecosystem processes is the pollination of plants by insects.

Although the impact of agricultural land use on reproductive success of animal-pollinated plant species has already been studied on various occasions (e.g. Brys et al., 2004; Jacquemyn, Brys, & Hermy, 2002; Steffan-Dewenter & Tscharntke, 1999), the effects of urbanization received far less attention. Increasing urbanization may affect several aspects of both pollinator faunas and plant population characteristics that may affect plant–pollinator interactions and ultimately plant reproductive success.

Wild bees, which are the most important pollinating insects, can be expected to be strongly affected by increasing urbanization as the availability and nature of food resources and nesting sites in urban environments are likely to differ from that of rural areas. Since urban areas are characterized by a high amount of sealed surfaces, it is likely that soil nesting bees will have a harder time finding appropriate nesting sites in the city compared to the countryside. It is reasonable to expect that this may induce shifts in urban versus rural pollinator communities whereby cavity nesting species are favored over soil nesting species in urban areas (Cane, Minckley, Kervin, Roulston, & Williams, 2006; Matteson, Ascher, & Langellotto, 2008). In addition, also food resources are likely to differ between urban and rural habitats. For instance, ditch banks and field margins have proven to hold valuable forage resources for wild bees (including bumblebees) in agricultural areas, whereas such small-scale landscape elements are often missing in the city (Kells, Holland, & Goulson, 2001). Urban areas may, on the other hand, include large areas of public green spaces and private gardens, and most food resources for pollinators in the urban environment will come in the form of intentionally cultivated plants in gardens and parks. Urban gardens have indeed proven to hold a very diverse array of flowering plants (Thompson et al., 2003).

Differences in food and nesting resources between urban and rural environments could cause differences in abundance and

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diversity of pollinators which could in turn result in altered visitation rates to local plant populations and ultimately differences in reproductive success of these plant species. Only recently, studies on the consequences of urbanization on plant–pollinator interactions and plant reproductive success have begun to be published. For instance, Van Rossum (2010) showed that reproductive success of *Centaurea jacea* was higher in park populations than in semi-natural sites in Brussels, Belgium, indicating the potential of these parks as high quality habitats for plants and bees. Additionally, Osborne, Martin, Shortall, et al. (2008) recently reported a positive effect of gardens on the abundance of bumblebees caused by an increasing availability of nest sites in a nation-wide survey in the UK. This study showed bumblebee nest densities to be significantly higher in gardens than in other countryside habitats (mostly lacking linear features such as hedgerows). Reproductive success of *Glechoma hederaceae* and *Lotus corniculatus* was also found to be significantly higher in gardens than in arable farmland (Cussans et al., 2010), again suggesting the beneficial role of gardens which typically harbor high densities of flowering plants.

It can, on the other hand, be expected that such positive effects of urbanization on pollination and ultimately reproductive success of plant species may become smaller with increasing urbanization. For instance, a negative effect of the urban environment on pollination of *Crepis sancta* was found by Andrieu, Dornier, Rouifed, Schatz, and Cheptou (2009) in Montpellier, France, due to fewer pollinator visits and longer visit and search duration in small urban fragmented populations than in large populations in the countryside. Because population sizes differed strongly between the urban and rural sites in this study, it is, however, difficult to separate the effect of reduced pollinator attraction due to low population size from the effect the urban matrix exerts on pollinator communities. Reproductive success of these populations was previously found to be reduced in the small, fragmented urban populations compared to large, rural populations (Cheptou & Avendaño, 2006).

It is clear, that no clear-cut comparisons between reproductive success of plants from urban and rural environments have been made so far. This study aimed to study the effect of urbanization on female reproductive success of *Digitalis purpurea* (Purple foxglove, Scrophulariaceae) which is (mainly) reliant on bumblebees for successful pollination. To do so, we set up experimental plant populations of constant size in urban-rural gradients around three Belgian cities. This gradient consisted of three site types: countryside (CS), city edge (CE), and city center (CC). The overall hypothesis was that reproductive success of *D. purpurea* plants would be most depressed in the (dominantly agricultural) rural sites and in the heavily urbanized sites (city center) and would be highest in the moderately urbanized sites (city edge). This led to the following research questions: (1) Do flower visitors of *D. pupurea* differ in species composition between the different sites? (2) Do the city edge populations receive more pollinator visits than plants in city center and countryside populations? (3) Do plants in city center and countryside sites exhibit (stronger) pollen limitation of reproductive success than plants flowering in city edge sites?

2. Materials and methods

2.1. Study species

We chose *D. purpurea* as a model plant in this study, because it is an allogamous, bumblebee-pollinated plant (Sletvold, 2002) that can be frequently found both in urban and rural, disturbed environments in natural populations and in gardens as an ornamental. *D. purpurea* is a facultative biennial herb. Large populations can arise due to the persistent seed bank and abundant germination after soil disturbance (van Baalen, 1982). The species forms a basal rosette from which a large flowering stalk (1–2 m) emerges in the second year at the earliest (Grindeland, 2008). Plants flower from June to August with peak flowering in July (Percival & Morgan, 1965). Flowering is acropetal. The pink-to-purple, bell shaped flowers are protandrous, with the stigmas becoming receptive five days after the anthers dehisce. This leads to an inflorescence on which there are at a given time female phase flowers at the bottom, followed by neuters (due to pollen depletion) and male phase flowers above (Grindeland, 2008; Percival & Morgan, 1965). Flowers are self-compatible and capable of delayed selfing, but seed set is variable and rather low after autonomous self-pollination (Darwin, 1876; Grindeland, 2008). Its large flowers made it easy to manipulate the stigmas and stamens. Seed production can be very high, with more than a thousand seeds per fruit and 20 - 100 flowers per inflorescence (Grindeland, 2008). Seeds are dispersed passively ballistically (Grindeland, 2008). Most plants die after flowering (monocarpic) (Sletvold, 2002).

2.2. Study areas and experimental populations

We conducted the study in and around three Belgian cities: Ghent, Leuven, and Hasselt, which are located at least 40 km apart (see Fig. 1). In each city we chose a gradient from urban to rural environment, and selected three study sites over this gradient: 'city centre', 'city edge', and 'countryside' (see Fig. 1). We chose these sites after an inspection of satellite images and an on-site visit. We chose the city center sites so as to be as close as possible to the actual center of the city. We considered a site as a city edge site when it was located in the outskirts of the city and bordered land use that was typical for the countryside (such as meadows or agricultural fields). Countryside sites had to be farther away from the city center (at least 5 km) and had to be adjacent to land use that was characteristic for the given countryside location. The average distance between city center and city edge sites was 3 km and the average distance between city center and countryside sites was 12 km. We assessed the land use of the surrounding environment of the study site types using a land use map from 2003 (National Geographic Institute, Brussels, Belgium). We constructed buffers of a 1000 m radius around the study sites in ArcGIS 9 and calculated the percentage of area occupied by different land use classes in these buffers. Of particular interest were the land use classes sealed surfaces, agricultural fields and semi-natural areas in combination with gardens. Buildings and roads were classified as sealed surfaces. Agricultural fields consisted of wheat and maize fields. Orchards were also considered as agricultural land use as these are typically characterized by high levels of pesticide use, short periods of flowering, and a low tolerance for spontaneous plant growth. Semi-natural areas were defined as meadows, lawns and areas with ruderal plant species. The percentage of sealed surfaces was highest in city centers and declining toward the countryside (see Fig. 2, see also Table 2). Semi-natural areas and gardens showed an increase from the city center to the city edge and then dropped again due to the amount of agricultural land in the countryside.

In each of the study sites we constructed one experimental population of *D. purpurea* plants at the beginning of June 2009. We bought plants in six different nurseries and mixed them to ensure genetic diversity. Each population consisted of 18 plants in pots (7.5 L, 21 cm in diameter) filled with commercial potting soil. On average 16 (minimum 15, maximum 18) plants per population flowered and produced fruits. All experimental populations were set up in school yards on regularly mown lawns except for two that were located on bare soil. Populations of the countryside site type were set up at the edge of the village and adjacent to land use that was typical of the location. For the countryside around Ghent this was a mix of pastures, wheat and maize fields. This was also the