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Variation in the reproductive success of a narrow endemic plant: Effects of geographical distribution, abiotic conditions and pollinator community composition

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Abstract

Geographic variation in reproductive output determines plant distribution. In this study, we investigate the geographic structure and the factors affecting reproductive success throughout the life cycle of the near-threatened crucifer *Erysimum popovii* across its entire distribution range. We worked in 21 populations, in which we measured fruit set, seed set, seed weight, seed germination in the laboratory, germination time, seedling emergence in the field, seedling survival and fecundity. We also sampled the pollinator assemblages visiting *E. popovii* at each site, as well as some population characteristics (population size and density, flower density of *E. popovii* and other co-occurring species, and rainfall). Germination success in the laboratory was very high (range: 0.56–0.98), but seedling emergence in the field was low (0.005–0.32). Beefly visitation rate was positively related to seedling emergence, whereas visitation rate by ants, beetles and other minor pollinator groups was negatively related to fruit set and positively related to germination time. Populations in sites with high density of co-occurring flowers produced fewer fruits. Most variables related to reproductive output varied widely across populations, but this variation did not show a clear regional structure. The low seedling survival may constitute a bottleneck for the recruitment of this species. Overall, less than 0.2% of the ovules produced developed into reproductive individuals. Our results suggest a metapopulation structure for *E. popovii*.

Zusammenfassung

Geographische Variabilität beim Reproduktionsergebnis bestimmt die Verteilung von Pflanzen. Hier untersuchen wir die geographische Struktur und die den Reproduktionserfolg bestimmenden Faktoren im Lebenszyklus des potentiell gefährdeten Kreuzblüters *Erysimum popovii* in seinem gesamten Verbreitungsgebiet. Wir untersuchten 21 Populationen und maßen Fruchtansatz, Samenansatz, Samengewicht, Keimung im Labor, Keimungszeit, Auflaufen der Keimlinge im Freiland, Überleben der Keimlinge und Fekundität. Wir erfassten auch die Bestäubergemeinschaften von *Erysimum popovii* an jedem Standort sowie einige Populationsparameter (Populationsgröße und -dichte, Blütendichte von *Erysimum popovii* und vergesellschafteten Arten und den Niederschlag). Der Keimungserfolg im Labor war sehr hoch (0.56 bis 0.98) aber im Freiland erschienen nur wenige Keimlinge (0.005 bis 0.32). Die Besuchshäufigkeit durch Wollschweber war positiv mit dem Keimungserfolg verbunden,

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während Besuche von Ameisen, Käfern und anderen weniger bedeutenden Bestäubergruppen negativ mit dem Fruchtansatz und positiv mit der Keimungszeit verbunden waren. Populationen an Standorten mit einer hohen Dichte von vergesellschafteten Blüten produzierten weniger Früchte. Die meisten den Reproduktionserfolg kennzeichnenden Variablen variierten stark von Population zu Population, aber diese Variation zeigte kein klares regionales Muster. Die geringe Überlebensrate der Keimlinge könnte einen Flaschenhals für die Rekrutierung von Nachkommen bei dieser Art darstellen. Insgesamt entwickelten sich weniger als 0.2% der Samenanlagen in ein reproduktives Individuum. Unsere Ergebnisse legen für *Erysimum popovii* eine Metapopulationsstruktur nahe.

Keywords: *Erysimum popovii*; Fitness; Fruit set; Germination; Germination time; Reproduction; Seed set; Seedling; Seed weight

Introduction

The study of factors determining plant reproduction is crucial to understand species distribution. Most studies addressing this issue focus on demographic analyses, and include various phases of the plant's life cycle such as fruit set, seed production and seed germination (e.g. Menges 1991; Colas, Olivieri, & Riba 2001; Rebollo, Perez-Camacho, Garcia-de, Benayas, & Gomez-Sal 2001; Metz et al. 2010). Overall, limitation of reproduction in pre-dispersal phases (fruit set and seed production) may be determined by different factors such as the genetic constitution of the mother plant, pollen limitation (Knight et al. 2005; Aizen & Harder 2007; Fernández, Bosch, Nieto-Ariza, & Gómez 2012), ovule abortion (Stephenson 1981), resource limitation (Bloom, Chapin, & Mooney 1985), and predation (Grieg 1993). Fruit set has often been found to be low in many plants (Ayre & Whelan 1989), supporting the view that flowers represent a reservoir of ovules that can be used when resources are plentiful, thus providing an adaptive response to stochastic environments. Instead, under sub-optimal conditions, plants may save resources by discarding flowers or fruits at the beginning of their development (Ayre & Whelan 1989). In addition to fruit set, final seed yield, may also be limited by low seed set within fruits (ratio of ripe seeds to ovules). Limitation of reproduction in the post-dispersal phase (seed germination) has commonly been linked to plant population size (Menges 1991), density of conspecific and heterospecific plants, abiotic conditions such as precipitation regime (Venable 2007), and seed quality (Winn 1985; Burke & Grime 1996). Two of the most widely used estimators of seed quality are seed weight and germination time. Seed weight affects many processes of the reproductive cycle, including seed germination (Naylor 1993), dormancy period (Stamp 1990; Fenner & Thompson 2004), resistance to competition (Houssard & Escarré 1991; Turnbull, Coomes, Hector, & Rees 2004), seed dispersal (Fenner & Thompson 2004), and seedling growth and recruitment (Coomes & Grubb 2003). Germination time, on the other hand, may be especially determinant in annual and herbaceous plant species at the community level via competitive dominance of the early germinating individuals. Very short delays in emergence time can be amplified in the long term, with strong effects on final biomass and reproductive output (Weiner & Thomas 1986).

Therefore, different life cycle phases are affected by different extrinsic biotic and abiotic factors, which in addition, may vary spatially at different scales (Anderson & Johnson 2008; Nattero, Sérsic, & Cocucci 2011). That is, the relative contribution of the different phases of the life cycle to the plant's reproductive output may vary spatially depending on the locally prevailing biotic interactions and abiotic conditions (Stevens, Bunker, Schnitzer, & Carson 2004; Kim & Donohue 2011). Pollinator abundance, composition and diversity have often been related to plant reproductive success (Steffan-Dewenter et al. 2001; Cosacov, Naretto, & Cocucci 2008; González-Varo, Arroyo, & Aparicio 2009; Gómez, Abdelaziz, Lorite, Muñoz-Pajares, & Perfectti 2010). Pollen limitation is often associated with low pollinator abundance (Cosacov et al. 2008; González-Varo et al. 2009; Gómez et al. 2010), and different pollinator species usually differ in pollinating effectiveness and may thus have different effects on plant fitness (Klein, Steffan-Dewenter, Buchori, & Tscharntke 2002; Gómez, Bosch, Perfectti, Fernández, & Abdelaziz 2007; Perfectti, Gómez, & Bosch 2009). Additionally, some habitat characteristics such as plant population size, habitat fragmentation, co-occurring flower composition, and altitude can influence plant reproduction either directly or indirectly via their effect on biotic interactions (González-Varo et al. 2009; Kim & Donohue 2011). Understanding how these biotic and abiotic variables affect different phases of the reproductive cycle is essential to interpret the reproduction dynamics, geographical structure and conservation status of a plant species (Colas et al. 2001; Metz et al. 2010).

In this study, we explore the geographic variation of reproductive success and recruitment, as well as their relationship with local pollinator assemblages and abiotic conditions in *Erysimum popovii*, a narrow endemic Brassicaceae species. Our objectives are: (1) to study the different phases of the reproductive cycle and evaluate their relative contribution to recruitment; (2) to analyze the geographic structure of the reproductive output across the entire distribution range of the species; (3) to measure the effect of pollinator diversity, abundance and composition on the various phases of the reproductive cycle; and (4) to measure the effect of *E.*