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Competition for pollinators between invasive and native plants: Effects of spatial scale of investigation (note)[1]

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Abstract: In this study we show that spatial scale of investigation affects the estimated strength of competition for pollinators between an invasive and a native plant species. The effect of the invasive herb *Oxalis pes-caprae* on pollinator visits to the native herb *Diplotaxis erucoides* was studied when the invader was (1) totally present, (2) present on a large scale (of hectares) but absent on a small scale (of square metres), and (3) totally absent. No difference in number of pollinator visits to *D. erucoides* was found between treatment 1 and 3, *i.e.*, between total presence and total absence of the invader. However, when the invader was removed in the small scale while still remaining in the large scale, a higher number of visits to the native was recorded. Our study thus shows the importance of incorporating multiple spatial scales to allow for investigation of hierarchical effects on competition for pollinators, and it suggests that small-scale studies of effects of invasive plants on pollinator visitation might risk overstating negative effects of the invader.
Keywords: competition, *Diplotaxis erucoides*, invasive plants, *Oxalis pes-caprae*, pollination, spatial scale.

Résumé : Dans cette étude, nous montrons que l'échelle spatiale étudiée a un effet sur la force estimée de la compétition pour les pollinisateurs entre une espèce de plante envahissante et une espèce indigène. L'effet de l'herbe envahissante *Oxalis pes-caprae* sur les visites de pollinisateurs à l'herbe indigène *Diplotaxis erucoides* a été étudié dans trois situations : (1) l'envahisseur était présent partout, (2) l'envahisseur était présent à grande échelle (hectares) mais absent à petite échelle (mètres carrés) et (3) l'envahisseur était totalement absent. Aucune différence n'a été trouvée dans le nombre de visites de pollinisateurs à *D. erucoides* entre les traitements 1 et 3, c'est-à-dire, entre la présence partout et l'absence totale de l'envahisseur. Cependant, lorsque l'envahisseur a été retiré à petite échelle tout en demeurant présent à grande échelle, un nombre plus élevé de visites à la plante indigène a été noté. Notre étude démontre ainsi l'importance d'incorporer des échelles spatiales multiples qui tiennent compte des effets hiérarchiques sur la compétition pour les pollinisateurs et suggère que les études à petite échelle des effets des plantes envahissantes sur la visite de pollinisateurs risquent de surestimer les effets négatifs de l'envahisseur.
Mots-clés : compétition, *Diplotaxis erucoides*, échelle spatiale, *Oxalis pes-caprae*, plantes envahissantes, pollinisation.

Nomenclature: Fauna Europaea, 2004; Tutin *et al*., 2001.

Introduction

That ecological patterns observed in nature may change with the spatial scale of observation has been common knowledge for over a decade (Levin, 1992; Tilman & Kareiva, 1997), but the topic remains an active area of research. Only a few field studies have explicitly considered the spatial scale of observation when examining pollination interactions (Steffan-Dewenter *et al*., 2002; Veddeler, Klein & Tscharntke, 2006). Plant–plant interactions mediated by pollinators can be either facilitative (*e.g*., Schemske, 1988) or competitive (*e.g*., Campbell, 1985; Caruso, 2000), and the direction and intensity of the interaction may change with population density, population size, and relative abundance (Ratchke, 1983; Feldman, Morris & Wilson, 2004; Moeller, 2004). In this study we show that the direction and intensity of the interaction can also depend on the spatial scale of the investigation.

The effect of invasive species on ecological interactions is of increasing concern in invasion biology (Mitchell *et al*., 2006; Traveset & Richardson, 2006; White *et al*., 2006), and because these studies commonly compare invaded and non-invaded systems, the choice of spatial scale is of vital concern. If the distance between uninvaded and invaded areas is less than pollinators' feeding range there is a risk that the invasive species will affect the "non-invaded" area. Effects may include changes in pollinator population sizes by removal or addition of critical resources to the system (Bjerknes *et al*., 2007) or by functioning as a pollinator magnet that attracts pollinators from areas in the neighbourhood. The latter can lead to hierarchical effects where groups of plants compete for pollinators. Plants may benefit from growing in the same area as a very attractive species if abundance of pollinators is much higher than in areas without this species and the net effect is an increase in pollinator visits to the co-flowering plants. However, long

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distances between invaded and non-invaded areas may on the other hand prevent a satisfactory comparison due to large differences in abiotic or biotic factors. Chittka and Schürkens (2001) elegantly circumvented this problem by making observations of pollinator visits before and after experimental introduction of an alien species in pure stands of the native species. We performed a similar before and after study by taking advantage of the light-sensitive mechanisms that cause the invasive *Oxalis pes-caprae* to close its flowers in early afternoon to investigate its effect on pollinator visitation to the native *Diplotaxis erucoides* at multiple spatial scales.

Methods

Diplotaxis erucoides (Brassicaceae) is a common annual in the Mediterranean basin. It bears numerous white flowers and requires cross-pollination to set seed (Kunin, 1992). *Oxalis pes-caprae* (Oxalidaceae) is a bulbous herb originating from South Africa (Peirce, 1997) and a very aggressive invader throughout the Mediterranean area. It has relatively large, bright yellow flowers that are light-sensitive, opening in full sun and closing during very cloudy days. The 2 species share habitat and flowering period (late autumn to late spring). The study took place in Mallorca, Spain, close to the University of the Balearic Islands in a 3.2-ha area where *O. pes-caprae* grew in high abundance. The observations were performed in a 200-m^2 abandoned field in the centre of the area, where *D. erucoides* and *O. pes-caprae* grew intermingled. The flowers of *O. pes-caprae* opened around 10 am and started to close after 1 pm, and most were fully closed after 2 pm even during very sunny days. Individuals in deep shade opened and closed later, but since the field site and the surroundings were dominated by open places, the occurrence of such individuals was very low and around 95% of all *O. pes-caprae* flowers in the 3.2-ha area were closed after 2 pm.

We observed pollinator visits to *D. erucoides* and *O. pes-caprae* in 24 haphazardly chosen 2- × 2-m plots within the abandoned field. We made all observations between 10 am and 4 pm during sunny and calm days between March 30th and April 12th, 2006. Each plot was observed 3 times over the course of 1 day: (1) when *O. pes-caprae* flowers were abundant inside and outside the plot (presence of the invasive); (2) when *O. pes-caprae* had been removed within the plot (small-scale absence, large-scale presence of the invasive); and (3) when > 95% of the *O. pes-caprae* flowers had closed in the area (absence of the invasive). Immediately after observation of treatment 1, *O. pes-caprae* flowers, but no vegetative parts, were removed within the plot and within a 50-cm-wide strip around the plot by hand-cutting. The observation of treatment 2 began 15 min after the cutting of flowers to avoid disturbance effects on pollinator visitation. Thus, treatments 1 and 2 were made for plot number 1, and then treatment 1 and 2 were made for plot number 2, and so on. Treatment 3, on the other hand, was always performed in the afternoon, between 2 and 4 pm, since a prerequisite for this treatment was that *O. pes-caprae* flowers had closed. During treatment 1, pollinator visits were recorded for both plant species with the purpose of comparing the visitor community and overlap in visitor species among the 2 plant species.

Pollinator visits to *D. erucoides* and *O. pes-caprae* were recorded during 15-min censuses, and for practical reasons only relatively large (> 3 mm) pollinators were recorded. Tiny flies, beetles, or thrips were thus not considered, but these kinds of small pollinators were seldom observed to visit the species. The same pollinator sometimes visited several flowers in the plot; visits to all flowers in the plot were recorded. Thus, the response variable was number of visits per plot per 15 minutes. After censuses were finished, we caught the pollinators by sweep-netting for identification. To check for disturbance effects of flower cutting, a control experiment was performed in 10 plots, where the investigator moved around as if cutting flowers but without actually cutting them. Pollinator visitation to the plot was monitored 15 min afterwards. We found no effect of disturbance ($F = 1.10$, $P = 0.32$, df = 2).

Visitation data were analyzed by a randomized block ANOVA with plot as a random factor and treatment as a fixed factor. This blocked design is of advantage since treatments are always compared within the same plot and factors like flower densities of *D. erucoides* and presence of other flowering species are thereby automatically accounted for. Data fulfilled the requirements of ANOVA by showing no significant deviations from homogeneity of the variances (Levene's test) and having normally distributed residuals. The data were analyzed with the statistical package STATISTICA v 6.0. (Statsoft Inc., Tulsa, USA).

To assess if the 3 treatments were really comparable, that is, the activity of pollinators did not decline from the period of treatment 1 and 2 (10 to 12 am) to the period of treatment 3 (2 to 4 pm), we carried out complementary insect censuses during March 1st to 4th, 2008. Visits to 18 flowering species, including *D. erucoides*, in the neighbourhood of the abandoned field (in the field margins and up to 600 m away from the field) were censused during 5-min periods on 1- × 1-m plots, and the number of visits observed was recorded. Each plant species was observed both in the morning and in the afternoon; a total of 55 observations were made in each of these periods, *i.e.*, 55 paired observations with respect to each plant species. Visitation rate per flower was calculated by dividing the number of visits observed in each census by the number of flowers observed. The difference in visitation rate between the 2 time periods was analyzed for all pollinators, and also separately for *Apis mellifera* and *Eucera* sp. (the 2 most common pollinators), using the Wilcoxon matched pair test, which accounts for paired observations.

Results

Diplotaxis erucoides and *O. pes-caprae* shared 70% of their pollinator species (Table I). The majority of visits to *O. pes-caprae* were made by *Apis mellifera* (87%), followed by *Eucera* sp. (8%); these 2 pollinators also made more than half of the visits to the native *D. erucoides* (66%). Presence of *O. pes-caprae* flowers had a significant effect on the total number of pollinator visits to *D. erucoides* ($F = 13.6$, $P < 0.001$, df = 2, 46), which was higher for treatment 2 (small-scale absence, large-scale presence of the invader) than for treatment 1 (presence of the invader) or treatment 3 (absence of the invader) (Figure 1).

The complementary censuses showed that there was no difference in visitation rate of all pollinators between the morning (10 to 12 am) and afternoon (2 to 4 pm) censuses ($Z = 0.53$, $P = 0.59$, $n = 55$) or of *Apis mellifera* ($Z = 0.66$, $P = 0.51$, $n = 55$). However, there was a difference in the visitation rate of *Eucera* sp. ($Z = 3.41$, $P < 0.006$, $n = 55$), which was higher in the afternoon than in the morning (afternoon visitation rate: 0.006 ± 0.003 [mean ± SE]; morning visitation rate: 0.03 ± 0.006).

Discussion

Invasive plants have been found to negatively impact pollinator visitation to native plants at the local scale, within the range of a few metres (Grabas & Laverty, 1999; Brown, Randall & Graham, 2002; Totland *et al*., 2006). Our study confirms these findings, as the native *D. erucoides* received more pollinator visits when flowers of the invasive *O. pes-caprae* were removed within plots of 2- × 2-m. However, when we compared total presence to total absence of the invasive we did not find evidence for an impact on pollinator visitation. Our interpretation is that when *O. pes-caprae* is open it attracts pollinators to the area, but when plants of both species are adjacent to each other pollinators prefer to visit the invader and the 2 processes counterbalance each other. If such hierarchical effects are common in plant–plant interactions for pollinators, small-scale studies of showy invasive plants may overstate negative effects. It is, however, important to note that we only measured visitation and not reproduction success and that our study was conducted at only 1 location, and thus its generality has to be interpreted with some caution.

TABLE I. Pollinator species visiting *Diplotaxis erucoides* and *Oxalis pes-caprae* during 72 and 24 observation periods (15 min), respectively. Note that the total number of visits is not comparable across species, since observations were made on different numbers of flowers, being more frequent on *D. erucoides*.

Insect species	Visits to *Diplotaxis* (% of total)	Visits to *Oxalis* (% of total)
Andrena sp.1	24	0.5
Andrena sp.2	3	-
Anthophora sp.1	0.3	0.3
Anthophora sp.2	5	2
Apis mellifera	21	87
Pieris brassicae	-	0.7
Eristalis tenax	1	1.3
Eucera sp.	45	8
Melecta sp.	-	0.3
Polistes gallicus	0.6	0.3
Total number of visits	1148	407

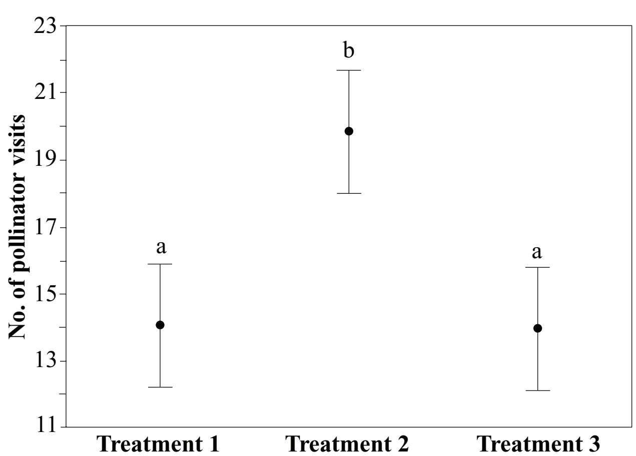

FIGURE 1. Effect of presence of *Oxalis pes-caprae* on frequency of pollinator visits to *Diplotaxis erucoides* observed during 15-min periods. Treatment 1 = presence of *Oxalis*; Treatment 2 = small-scale absence, large-scale presence of *Oxalis*; Treatment 3 = absence of *Oxalis*. Different letters above the bars indicate significant differences among treatments according to Tukey's HSD test ($P < 0.001$, $n = 24$ for each treatment). Vertical bars denote 0.95 confidence intervals around least square means.

The impact of invasive plant species on pollination of native species has seldom been studied at multiple spatial scales, with the exception of Nielsen, Heimes, and Kollmann (2008), who investigated pollinator visits to a target species at 0, 10, 30, and 60–100 m from the invasive *Heracleum mantegazzianum* and found visitation to be higher closer to the invasive. Moreover, in most studies where the distance between invaded and non-invaded areas has been greater than just a few metres, it has ranged between 50 and 250 m (Aigner, 2004; Moragues & Traveset, 2005; Larson, Royer & Royer, 2006; Nielsen, Heimes & Kollmann, 2008), which is probably less than the feeding range of most pollinators, at least for bees and bumblebees (Osborne *et al*., 1999; Greenleaf *et al*., 2007). Thus, in these studies the area that is classified as non-invaded could potentially be affected by the invader. Exceptions are the studies by Lopezaraiza-Mikel *et al*. (2007) and Ghazoul (2004), where distances between areas ranged between 225 and 1045 m, and 5 and 10 km, respectively. There is often a trade-off, however, between including flying distances such as these and comparing areas that are similar enough in biotic and abiotic factors.

Our experimental design, where treatment 3 was always performed in the afternoon when all flowers of *O. pes-caprae* were closed, is unlikely to be responsible for the lower insect visitation because there were no differences in total pollinator visits between the morning and afternoon censuses. One species (*Eucera* sp.) even appeared to be more common in the afternoon. It is however possible that diurnal patterns in floral reward caused our result, but, *D. erucoides* is mostly pollen producing and the abundant presence of flowers in the area makes it unlikely that most flowers would be devoid of pollen in the afternoon.

Our study indicates the importance of scale in studies of plant–plant competition for pollinators, but more studies are needed to confirm if scale dependency is a general phenomenon in pollination interactions. Although our study only provides a "snap-shot" of the competition for pollinators between plant species, we believe that it points to the importance and challenge of considering multiple spatial scales in field studies of species interactions.

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Literature cited

Aigner, P. A., 2004. Ecological and genetic effects on demographic processes: Pollination, clonality and seed production in *Dithyrea maritima*. Biological Conservation, 116: 27–34.

Bjerknes, A.-L., Ø. Totland, S. J. Hegland & A. Nielsen, 2007. Do alien plant invasions really affect pollination success in native plant species? Biological Conservation, 138: 1–12.

Brown, B. J., J. M. Randall & S. A. Graham, 2002. Competition for pollination between an invasive species (*Purple loosestrife*) and a native congener. Ecology, 83: 2328–2336.

Campbell, D. R., 1985. Pollinator sharing and seed set of *Stellaria pubescens*: Competition for pollination. Ecology, 66: 544–553.

Caruso, C. M., 2000. Competition for pollination influences selection on floral traits of *Ipomopsis aggregata*. Evolution, 54: 1546–1557.

Chittka, L. & S. Schürkens, 2001. Successful invasion of a floral market. Nature, 411: 653.

Fauna Europaea, 2004. Fauna Europaea version 1.1. [Online] URL: http://faunaeur.org

Feldman, T. S., W. F. Morris & W. G. Wilson, 2004. When can two plant species facilitate each other's pollination? Oikos, 105: 197–207.

Ghazoul, J., 2004. Alien abduction: Disruption of native plant–pollinator interactions by invasive species. Biotropica, 36: 156–164.

Greenleaf, S. S., N. M. Williams, R. Winfree & C. Kremen, 2007. Bee foraging ranges and their relationship to body size. Oecologia, 153: 589–595.

Johnson, S. D., C. I. Peter, L. A. Nilsson & J. Ågren, 2003. Not cited in article. Pollination success in a deceptive orchid is enhanced by co-occurring rewarding magnet plants. Ecology, 84: 2919–2927.

Kunin, W. E., 1992. Density and reproductive success in wild populations of *Diplotaxis erucoides* (Brassicaceae). Oecologia, 91: 129–133.

Larson, D. L., R. A. Royer & M. R. Royer, 2006. Insect visitation and pollen deposition in an invaded prairie plant community. Biological Conservation, 130: 148–159.

Levin, S. A., 1992. The problem of pattern and scale in ecology. Ecology, 73: 1943–1967.

Lopezaraiza-Mikel, M. E., R. B. Hayes, M. R. Whalley & J. Memmott, 2007. The impact of an alien plant on native plant–pollinator network: An experimental approach. Ecology Letters, 10: 539–550.

Mitchell, C. E., A. A. Agrawal, J. D. Bever, G. S. Gilbert, R. A. Hufbauer, J. N. Klironomos, J. L. Maron, W. F. Morris, I. M. Parker, A. G. Power, E. W. Seabloom, M. E. Torchin & D. P. Vázquez, 2006. Biotic interactions and plant invasions. Ecology Letters, 9: 726–740.

Moeller, D. A., 2004. Facilitative interactions among plants via shared pollinators. Ecology, 85: 3289–3301.

Moragues, E. & A. Traveset, 2005. Effect of *Carpobrotus* spp. on the pollination success of native plant species of the Balearic Islands. Biological Conservation, 122: 611–619.

Nielsen, C., C. Heimes & J. Kollmann, 2008. Little evidence for negative effects of an invasive alien plant on pollinator services. Biological Invasions, DOI 10.1007/s10530-007-9210-1.

Osborne, J. L., S. J. Clarke, R. J. Morris, I. H. Williams, J. R. Riley, A. D. Smith, D. R. Reynolds & A. S. Edwards, 1999. A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. Journal of Applied Ecology, 36: 519–533.

Peirce, J. R., 1997. The biology of Australian weeds. 31. *Oxalis pes-caprae* L. Plant Protection Quarterly, 12: 110–119.

Ratchke, B., 1983. Competition and facilitation among plants for pollination. Pages 305–329 *in* L. Real (ed.). Pollination Biology. Academic Press, London.

Schemske, B., 1988. Interactions for pollination among co-flowering shrubs. Ecology, 69: 446–457.

Steffan-Dewenter, I., U. Münzenberg, C. Bürger, C. Thies & T. Tscharntke, 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology, 83: 1421–1432.

Tilman, D. & P. Kareiva, 1997. Spatial Ecology. Princeton University Press, Princeton, New Jersey.

Totland, Ø., A. Nielsen, A.-L. Bjerknes & M. Ohlson, 2006. Effects of exotic plant and habitat disturbance on pollinator visitation and reproduction in a boreal forest herb. American Journal of Botany, 93: 868–873.

Traveset, A. & D. M. Richardson, 2006. Biological invasions as disruptors of plant reproductive mutualisms. Trends in Ecology and Evolution, 21: 208–216.

Tutin, T. G., V. H. Heywood, N. A. Burges, D. H. Valentine, S. M. Walters & D. A. Webb (eds.), 2001. Flora Europaea. Cambridge University Press, Cambridge.

Veddeler, D., A.-M. Klein & T. Tscharntke, 2006. Contrasting responses of bee communities to coffee flowering at different spatial scales. Oikos, 112: 594–601.

White, E. M., J. C. Wilson & A. R. Clarke, 2006. Biotic indirect effects: A neglected concept in invasion biology. Diversity and Distributions, 12: 443–455.