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ORIGINAL ARTICLE

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The impact of habitat fragmentation on the interaction between *Centaurium erythraea* (Gentianaceae) and its specialized seed predator *Stenoptilia zophodactylus* (Pterophoridae, Lepidoptera)

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Abstract Habitat fragmentation can affect plant population characteristics and plant traits, which in turn can change biotic interactions, such as plant–insect interactions. Because of this, habitat fragmentation can affect reproductive success and survival of both the plant and seed predators, especially when the predator is rare and specialized. This study focuses on the level of fruit predation in *Centaurium erythraea* by its specific seed predator, the plume moth *Stenoptilia zophodactylus*, in a fragmented coastal dune landscape. To investigate the consequences of habitat fragmentation, we assessed the effect of population and plant characteristics of 25 *C. erythraea* populations on fruit predation by *S. zophodactylus*. Although the distribution of this specialized predator is poorly documented, our results show that *S. zophodactylus* occurred frequently in most of the studied *C. erythraea* populations. We found a strong correlation between the spatial isolation of the host plant and the level of fruit predation, with low predation in isolated populations, most likely due to the limited dispersion capacity of the plume moth. *C. erythraea* individuals experienced a higher risk of fruit predation when showing a large floral display size, presumably because they are more attractive. However, at fruit level, the risk of predation decreases with increasing floral display at individual plant level, representing a sort of dilution effect. Our findings indicate that maintaining and restoring large, dense and rather connected populations of *C. erythraea* will be beneficial for the sustainable conservation of the rare specialist seed predator *S. zophodactylus*, without increasing the predation pressure on the host plant.

Keywords Biotic interaction · Habitat fragmentation · Fruit predation · *Centaurium erythraea* · *Stenoptilia zophodactylus*

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Introduction

Due to habitat fragmentation, many plant populations experience a reduction in their habitat, population size and density, as well as an increase in spatial isolation between populations (Saunders et al. 1991; Dauber et al. 2010). In the short term, these changes in population characteristics can have far-reaching consequences on plant survival and reproduction. During the last few decades, this was demonstrated empirically by a number of studies, which generally revealed that small and isolated populations risk reduced reproduction and recruitment (Kery et al. 2000; Jacquemyn et al. 2001; Brys et al. 2003, 2004; Kery and Matthies 2004).

Besides its direct impact on the process of reproduction and recruitment, habitat fragmentation may also have indirect effects on the reproductive output and survival of plants. One of these indirect effects is the impact on biotic interactions between plants, herbivores, predators and/or pathogens (Elzinga et al. 2005). The ecology and evolution of herbivores, predators and pathogens can indeed be influenced by several population and individual characteristics of the host plant. But conversely, herbivores, predators and pathogens may also affect individual plant vigor and population dynamics. Therefore, effects of habitat fragmentation on ecology and evolution of herbivores, predators and pathogens can have indirect effects on the reproductive outcome and population dynamics of their host plants (Ouborg and Biere 2003).

From the plant's perspective, it may be expected that when a population becomes more isolated and reduced in size, this may offer some advantages. Individuals in those populations may be exposed to a lower number of herbivores, predators or pathogens, and thus likely experience lower risks in terms of plant damage at an individual plant level (Zabel and Tscharntke 1998; Kery et al. 2001; Colling and Matthies 2004; Elzinga et al. 2005).

When a potentially positive effect occurs for plant populations, this might work negatively for their herbivores and seed predators, which is especially true for rare and specialized herbivores and/or seed predators. Because of their higher trophic level, the negative effects of habitat fragmentation on these specialized herbivores and/or seed predators become even more detrimental (Tscharntke and Brandl 2004; Elzinga et al. 2005; Piessens et al. 2009). Steffan-Dewenter and Tscharntke (2000) indeed documented that the diversity of specialized butterflies in fragmented calcareous grasslands declined significantly faster than the diversity of their host plants. In addition, the diversity of specialized mono- and oligophagous butterfly species decreased more rapidly than the diversity of generalistic oligo- and polyphagous butterfly species.

In this study, we examine the impact of population and plant characteristics of *Centaurium erythraea* at the level of fruit predation by its specific seed predator *Stenoptilia zophodactylus* in a fragmented coastal dune area along the western Belgian coast. The plume moth *S. zophodactylus* is a very rare and poorly known specialized seed predator of *C. erythraea*. Preliminary research pointed out that this moth occurs in some populations of *C. erythraea* along the Flemish coast, and that it can cause extensive damage at the level of fruit production. Additionally, previous work on the process of reproduction within a large number of natural *C. erythraea* populations in the same area revealed that the consequences of habitat fragmentation, such as decreasing population size and increasing isolation, had only limited effects on total seed production in this species (Brys et al. 2011). Habitat fragmentation may thus be detrimental to the plume moth, but may offer some advantages to the plant, at least in terms of total reproductive output, as it may escape predation risks.

To obtain more insight into the degree of fruit predation and the consequences of plant- and population characteristics on the interaction between *C. erythraea* and its specialized seed predator *S. zophodactylus*, we studied 25 fragmented *C. erythraea* populations along the Belgian coast. We examined (1) whether there is an influence of fruit and seed predation by the larvae of *S. zophodactylus* on the net seed set of *C. erythraea* and (2) whether the presence of *S. zophodactylus* is determined by plant and population characteristics of *C. erythraea*.

Methods

Study species

Centaurium erythraea Rafn. (Gentianaceae) is a rosette-forming biennial/winter-annual plant, which occurs mainly in open, often transient habitats, such as grasslands or early-successional stages of forest colonization, forest clearings and open woods. *C. erythraea* has a distribution range that expands from western and southern Europe to Southwest Asia and North Africa (Lambinon et al. 1998). From July until September, this herb produces one or more stems, with, on each stem, a dense cyme that carries numerous pink hermaphroditic flowers (Ubsdell 1979; Fig. 1a). *C. erythraea* is self-compatible and, in the absence of pollinators or potential partners, constant levels of total seed production are guaranteed by reproductive assurance through autonomous selfing (Brys and Jacquemyn 2011, 2012; Brys et al. 2011). Flowers of *C. erythraea* do not produce any nectar and are therefore visited mostly by pollen-gathering pollinators. Most common pollinators of this herb are hoverflies (Syrphidae), but some bees (Apidae), small flies (Empididae–Muscidae), moths and butterflies (Lepidoptera) are also documented as sporadic visitors (Müller 1883; Knuth 1909; Ubsdell 1979; Van Rossum 2009; Brys and Jacquemyn 2011, 2012).

The plume moth *Stenoptilia zophodactylus* (Duponchel 1840) (Pterophoridae, Lepidoptera; Fig. 1b) has a Palaearctic, Afrotropical and Oriental distribution (Alipanah and Gielis 2010; Gielis 1993). Despite its wide distribution range, the species is rare in Belgium. It is reported only fragmentarily at some locations in Antwerp and East and West Flanders. This plume moth can be observed from June until September, often in two or more overlapping broods. *S. zophodactylus* is found most often in grasslands on sandy soils but, in the field, its presence is often hard to detect (Gielis 1993). *S. zophodactylus* is an oligophagous and specialized plume moth on some members of the Gentianaceae, including *C. erythraea* (Gielis 2006). Larvae first feed on basal leaves, but later on they feed on flowers and fruits (Gielis and Muus 2011; Fig. 1c–d). In *C. erythraea* plants infected by *S. zophodactylus* larvae, total seed production can be reduced markedly (up to 50 % of the fruits can be destroyed per plant, E.D.C. and R.B., personal observation).

Study site

From July until August 2009, we studied a total of 25 fragmented *C. erythraea* populations in a highly fragmented dune area at the western part of the Belgian coast, within the Nature Reserve Ter Yde (close to Oostduinkerke; coordinates: 51°08′05″N 02°41′33″E) (Fig. 2). All populations were located in fragmented calcareous dune grasslands surrounded by a matrix of

Fig. 1 **a** Habitus of the hostplant, *Centaurium erythraea*. **b** The plume moth *Stenoptilia zophodactylus*; **c–d** Predation marks on *Centaurium erythraea* caused by *Stenoptilia zophodactylus*

dense and species poor scrub vegetation that was dominated mainly by *Hippophae rhamnoides*, *Salix repens*, *Ligustrum vulgare* and *Sambucus nigra*.

Population and plant characteristics of *C. erythraea*

We assessed the size of each *C. erythraea* population studied by counting the total number of flowering individuals. The spatial isolation of each population was determined as the mean distance between a population and its three nearest *C. erythraea* populations. In each population, we selected randomly 15 flowering plants (when possible) and recorded their height and the total number of flowers produced. To obtain a measure of local plant density, we determined the average distance of each of these focal plants to the three nearest conspecific flowering *C. erythraea* plants.

Occurrence of *S. zophodactylus*

In August, we visited all focal plants again and determined the number of fruits predated by *S. zophodactylus*. Predation of fruits can be recognized easily by the presence of a little hole in the pericarp and/or the occurrence of a remains of a larva or (partially) digested seeds in a fruit capsule (Fig. 1c–d). Once a larva infects a fruit, it consumes all the developing seeds before leaving this fruit and attacking another one (E.D.C. and R.B., personal observation). Total fruit predation per plant could thus be determined easily and proportional fruit predation at a flower basis was calculated as the ratio between the number of predated fruits and the total number of mature fruits.

Statistical analyses

Based on the hierarchical structure of our data, with plants within populations and fruits within plants, we used a generalized linear mixed model (GLMM) to test for the effects of population size, spatial population isolation, local plant density and floral display size (i.e., number of flowers per plant; fixed factors) on the proportional fruit predation per flower and on the absolute number of fruits that was predated per plant (dependent factors). To incorporate random population effects, and to avoid pseudo replication, we added population as a random categorical variable in each of the models (Littell et al. 2002).

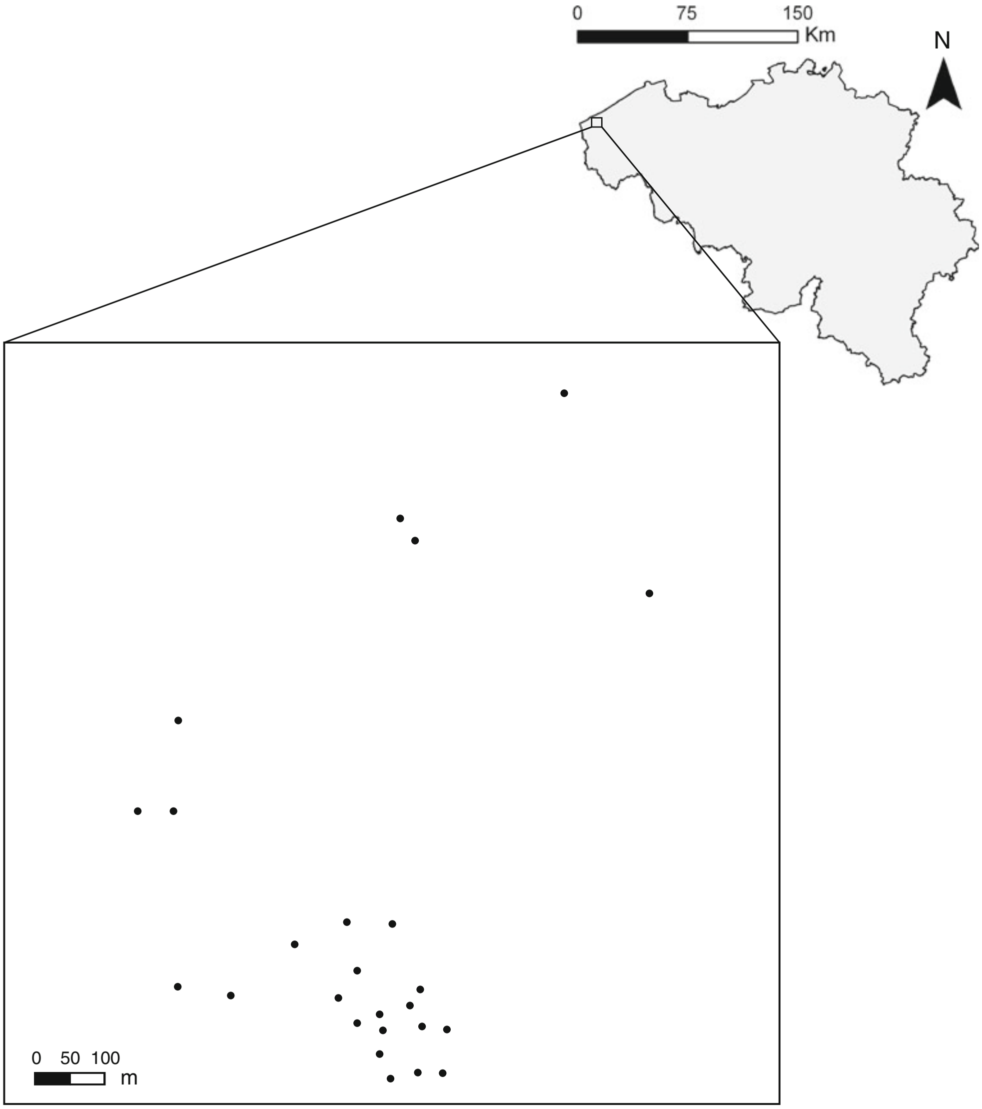

Fig. 2 Map of the study area indicating the locations of the study site (Nature Reserve Ter Yde) in Belgium, with the exact location of the populations of *Centaurium erythraea* ($n = 25$)

All analyses were carried out with the statistical software package SAS 9.2 (SAS Institute 2010). The GLIMMIX procedure with log link function was used for dependent variables with Poisson distributions (Littell et al. 2002). All analyses were conducted using a backward elimination procedure to obtain the final model, and the significance of terms in combination with F values was used as a criterion for model selection. The Kenward–Rogers approximation was applied to determine appropriate denominator degrees of freedom (Littell et al. 2002).

Results

Population and plant characteristics of *C. erythraea*

The *C. erythraea* populations studied varied greatly in size, ranging from 14 up to 1,264 flowering individuals (mean population size = 132 flowering individuals). The average distance between a population and the three nearest conspecific populations was 81 m and ranged from 28 up to 271 m. Population size and spatial population isolation appeared to be significantly correlated ($F_{1,20} = 18.04$; $P \leq 0.001$).

Plant height ranged from 3.5 to 49 cm throughout the different populations, with a mean height of 17.1 cm. Flowering *C. erythraea* plants produced on average 24.6 flowers per plant, but this number varied strongly over the different populations, ranging from 4 up to 178 flowers per plant. Since plant height showed a strong correlation with the number of flowers produced per plant ($F_{1,362} = 250.66$; $P \leq 0.001$), and because the number of flowers per plant is assumed to be the characteristic that is most relevant when dealing with the attraction of seed predators, we used floral display size in the further analyses and omitted plant height. Mean local distance among flowering plants was 39.2 cm and ranged from 2.3 up to 299.3 cm.

Predation by *S. zophodactylus*

Within the studied *C. erythraea* populations, *S. zophodactylus* predated on average 10.27 % of the fruits per plant, ranging from zero infection up to 52.22 % of fruits predated per plant. The probability that a fruit was predated was affected negatively both by the spatial isolation of the populations (Table 1; Fig. 3a) and by the total number of flowers produced per plant (Table 1; Fig. 3b). There was no significant effect of population size and local isolation of flowering plants within the populations on the probability that a fruit was predated (Table 1). On average, 1.48 fruits were predated per plant, ranging from 0 up to 26 predated fruits per plant. Total fruit predation per plant is related significantly with the spatial population isolation (Table 1; Fig. 4a) and the number of flowers produced per plant (Table 1; Fig. 4b). Again, there was no significant effect of population size and local plant density (Table 1).

Discussion

Although knowledge about the distribution and occurrence of the specialist moth *S. zophodactylus* is very limited and observations of this seed predator are very sparse, our data clearly demonstrate that *S. zophodactylus* is present in nearly all the *C. erythraea* populations in the study area. Up to 88 % of the populations showed signs of *S. zophodactylus* infection, and eight (32 %) of the populations were exposed to intense fruit predation by the moth (more than 25 % of the plants were predated). More interestingly, our data further revealed that both the absolute and proportional fruit predation rates were related significantly with the spatial configuration of the host plant populations. Although biological data on *S. zophodactylus* are very scarce, especially regarding the dispersal capacity of this species, our findings suggest that this moth is not capable of

Table 1 Generalized linear mixed model (GLMM) analyses of the effects of population size, mean spatial isolation of populations, local isolation of flowering plants and the number of flowers per plant on the level of fruit predation in *Centaurium erythraea*

Variable	SE	Parameter estimate	*df*	*F*	*P*
Proportional fruit predation ($n = 226$)					
Population size	0.881	−0.092	1, 17.64	0.01	0.9178
Mean spatial isolation of populations	0.005	−0.023	1, 23.25	21.12	0.0001*
Local density of flowering plants	0.058	−0.103	1, 359	3.16	0.0764
Number of flowers per plant	0.056	−0.391	1, 361	48.48	<0.0001*
Total fruit predation per plant ($n = 226$)					
Population size	0.778	−0.006	1, 19.75	0.00	0.9938
Mean spatial isolation of populations	0.005	−0.021	1, 32.11	19.62	0.0001*
Local isolation of flowering plants	0.154	−0.008	1, 351	0.00	0.9598
Number of flowers per plant	0.139	1.218	1, 352	77.21	<0.0001*

Presented models were obtained by backward selection, using the significance of terms and the *F* values of the model as the criterion for model selection

* $P < 0.001$

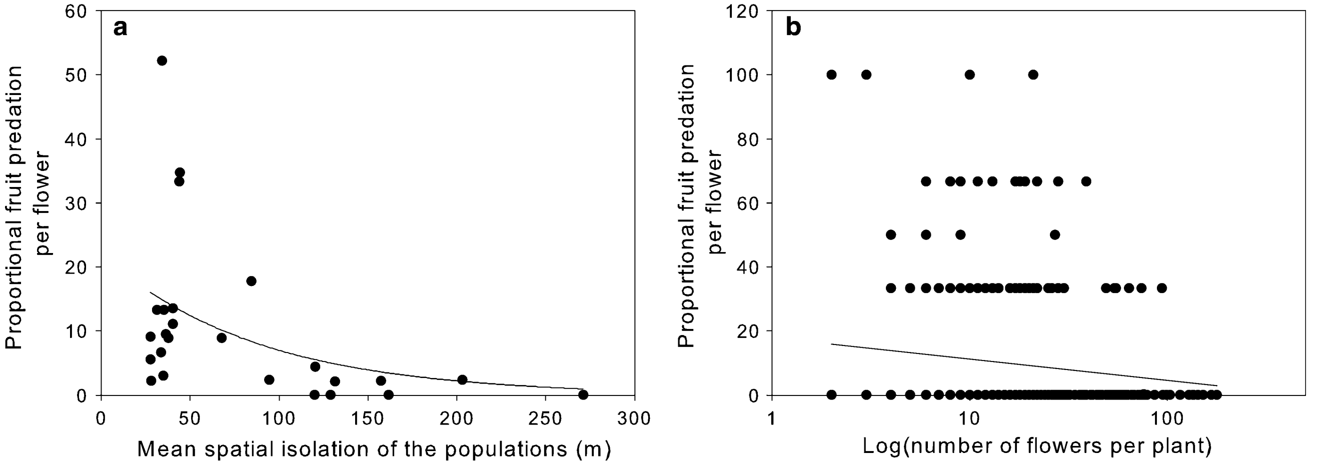

Fig. 3 Relationship between the proportional fruit predation per flower and **a** mean spatial isolation of populations, and **b** the number of flowers per plant in the studied populations of *Centaurium erythraea*. See Table 1 for statistical details

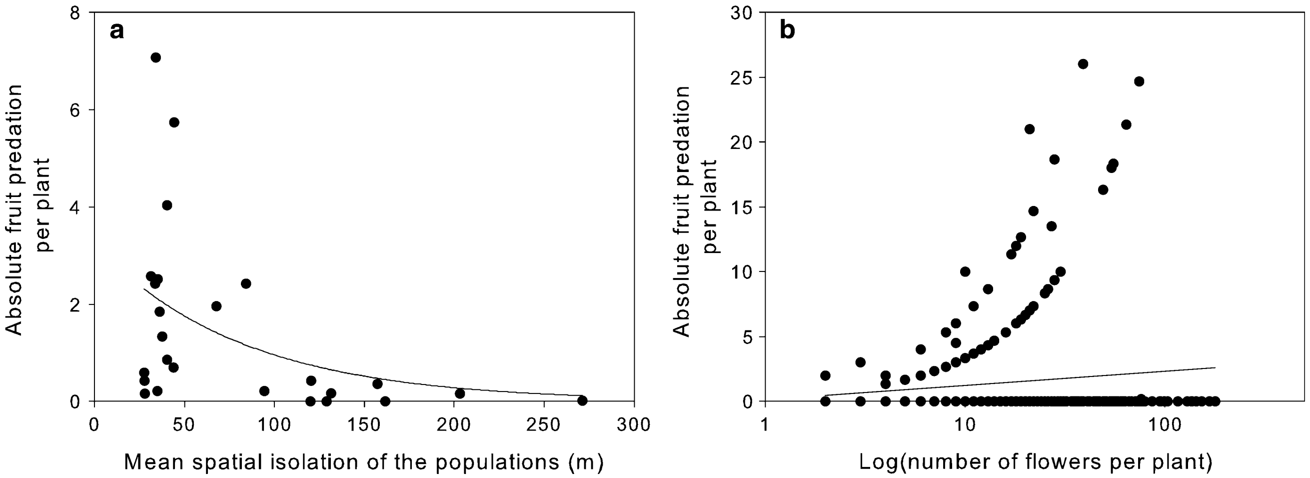

Fig. 4 Relationship between the absolute fruit predation per plant and **a** mean spatial isolation of populations, and **b** the number of flowers per plant in the studied populations of *Centaurium erythraea*. See Table 1 for statistical details

dispersing over long distances and experiences difficulties in finding and/or reaching small and isolated *C. erythraea* populations. These observations are in agreement with results found by Menéndez and Thomas (2000) for the plume moth *Wheeleria spilodactylus*, a specialized fruit predator of *Marrubium vulgare*, (with c. 2 cm, the species has a similar wingspan as *S. zophodactylus*). In their study on the metapopulation structure of this plume moth, they also found that this species is relatively sedentary, with an average dispersion capacity of 7 ± 20 m (max. 116 m) for males and 9 ± 23 m (max. 101 m) for females.

Our observations thus indicate that the consequences of habitat fragmentation, in this case an increased spatial isolation of host plant populations, may have a detrimental impact on the specialized *S. zophodactylus*. By analogy, Groom (2001) also documented that isolated subpopulations of *Clarkia concinna concinna* endure lower herbivory by various herbivores than non-isolated subpopulations. In contrast to these findings, Elzinga et al. (2005) reported that small and isolated populations of *Silene latifolia* however, experienced stronger levels of seed predation by *Hadena bicruris*, compared to larger and less isolated populations. They attributed these remarkable patterns to a decreasing level of parasitism by parasitoids on the predator in smaller and more isolated populations of their host plant, *S. latifolia*.

Across the populations studied in this work, fruit predation in *C. erythraea* is influenced strongly and positively by the number of flowers that a plant exposes. The more flowers a plant produces, the higher the number of fruits that are infected by the larvae. Similarly, Arvanitis et al. (2007) found that the intensity of predation by *Anthocharis cardamines* on its host plant *Cardamine pratensis*, is also determined significantly by the number of flowers developed per plant. By analogy, a similar positive relationship between fruit predation and floral display size was also found in *Primula veris* and its herbivorous plume moth *Amblyptilia punctidactyla* (Leimu et al. 2002, Kolb and Ehrlen 2010). Preference of female moths or butterflies to drop their eggs on plants with larger floral display sizes may have several causes. First, plants with a large number of flowers are more attractive and better visible to these predators (Courtney 1982; Kolb and Ehrlen 2010). By selecting plants that are also likely to be attractive to pollinators, a seed predator may enhance the probability that their larvae will have sufficient high-quality fruits available to feed on (Ehrlen et al. 2002; Kolb and Ehrlen 2010). Second, when larvae can feed on plants with a large floral display size, the possibility that they will need to move to another host plant because of a fruit or seed shortage is also significantly lower (Arvanitis et al. 2007). Finally, plants with a larger floral display size will also have open flowers for a longer period, as in many cases not all flowers open at the same time, which may increase the chance that they are found by ovipositing female butterflies (Courtney 1982).

However, at a flower or fruit level, the probability for predation decreases significantly with increasing floral display size, which can be explained as a sort of dilution effect. Even if large flowered plants have a larger total number of predated fruits, the proportion of unaffected fruits, and thus total net seed output, will still be higher compared to smaller plants with fewer flowers. In this context, Leimu et al. (2002) found very similar patterns of fruit predation of the plume moth *Amblyptilia punctidactyla* on its host plant *Primula veris*.

Since this study was conducted in one large coastal dune nature reserve (Ter Yde), in which the distribution (i.e., fragmentation) of the studied *C. erythraea* populations was rather small compared to the majority of coastal dune relicts overall, it can be expected that this specialized plume moth may experience much stronger difficulties in finding appropriate host plant populations once these populations become more isolated from each other. On the other hand, our results also illustrate that maintaining and restoring large and highly connected (pioneer) grassland patches, that are suitable for *C. erythraea*, may also offer promising possibilities for the maintenance of this rare and specialized seed predating plume moth.

Conclusion

Although hardly any data are available on the distribution and the behaviour of the rare *S. zophodactylus* overall, this study illustrates that this plume moth shows an apparently overlooked and surprisingly widespread distribution, not least in the studied area of Ter Yde. The predation level of the plume moth on *C. erythraea* is related negatively with the spatial isolation of the *C. erythraea* populations, both at fruit and individual level. The predation intensity at individual level increased with an increasing floral display of plants, although the predation intensity at fruit level decreased with an increasing floral display of plants. In other words, habitat fragmentation appears to affect the predation intensity of *S. zophodactylus* on *C. erythraea*.

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References

Alipanah H, Gielis C (2010) Notes on the tribes Platyptiliini and Exelastini from Iran (Lepidoptera: Pterophoridae). Shilap-Revista De Lepidopterologia 38(149):57–63

Arvanitis L, Wiklund C, Ehrlen J (2007) Butterfly seed predation: effects of landscape characteristics, plant ploidy level and population structure. Oecologia 152(2):275–285

Brys R, Jacquemyn H (2011) Variation in the functioning of autonomous self-pollination, pollinator services and floral traits in three *Centaurium* species. Ann Bot 107(6):917–925

Brys R, Jacquemyn H (2012) Effects of human-mediated pollinator impoverishment on floral traits and mating patterns in a short-lived herb: an experimental approach. Funct Ecol 26(1):189–197

Brys R, Jacquemyn H, Endels P, Hermy M, De Blust G (2003) The relationship between reproductive success and demographic structure in remnant populations of *Primula veris*. Acta Oecol Int J Ecol 24(5–6):247–253

Brys R, Jacquemyn H, Endels P, van Rossum F, Hermy M, Triest L, De Bruyn L, Blust GDE (2004) Reduced reproductive success in small populations of the self-incompatible *Primula vulgaris*. J Ecol 92(1):5–14

Brys R, De Crop E, Hoffmann M, Jacquemyn H (2011) Importance of autonomous selfing is inversely related to population size and pollinator availability in a monocarpic plant. Am J Bot 98(11):1834–1840

Colling G, Matthies D (2004) The effects of plant population size on the interactions between the endangered plant *Scorzonera humilis*, a specialised herbivore, and a phytopathogenic fungus. Oikos 105(1):71–78

Courtney SP (1982) Coevolution of pierid butterflies and their cruciferous foodplants.4. Crucifer apparency and *Anthocharis cardamines* (L.) oviposition. Oecologia 52(2):258–265

Dauber J, Biesmeijer JC, Gabriel D, Kunin WE, Lamborn E, Meyer B, Nielsen A, Potts SG, Roberts SPM, Sober V, Settele J, Steffan-Dewenter I, Stout JC, Teder T, Tscheulin T, Vivarelli D, Petanidou T (2010) Effects of patch size and density on flower visitation and seed set of wild plants: a pan-European approach. J Ecol 98(1):188–196

Ehrlen J, Kack S, Agren J (2002) Pollen limitation, seed predation and scape length in *Primula farinosa*. Oikos 97(1):45–51

Elzinga JA, Turin H, van Damme JMM, Biere A (2005) Plant population size and isolation affect herbivory of *Silene latifolia* by the specialist herbivore *Hadena bicruris* and parasitism of the herbivore by parasitoids. Oecologia 144(3):416–426

Gielis C (1993) Generic revision of the superfamily Pterophoroidea (Lepidoptera). Zoologische Verhandelingen 290:1–139

Gielis C (2006) Review of the Neotropical species of the family Pterophoridae, part I: Ochyroticinae, Deuterocopinae, Pterophorinae (Platyptiliini, Exelastini, Oxyptilini) (Lepidoptera). Zoologische Mededelingen Leiden 80–2(1):1–290

Gielis C, Muus TST (2011) Microlepidoptera.nl—De kleine vlinders van Nederland. http://www.microlepidoptera.nl/soorten/species.php?speciescode=420190&p=1 (accessed 23 January 2011)

Groom MJ (2001) Consequences of subpopulation isolation for pollination, herbivory, and population growth in *Clarkia concinna concinna* (Onagraceae). Biol Conserv 100(1):55–63

Jacquemyn H, Brys R, Hermy M (2001) Within and between plant variation in seed number, seed mass and germinability of *Primula elatior*: effect of population size. Plant Biol 3(5):561–568

Kery M, Matthies D (2004) Reduced fecundity in small populations of the rare plant *Gentianopsis ciliate* (Gentianaceae). Plant Biol 6(6):683–688

Kery M, Matthies D, Spillmann HH (2000) Reduced fecundity and offspring performance in small populations of the declining grassland plants *Primula veris* and *Gentiana lutea*. J Ecol 88(1):17–30

Kery M, Matthies D, Fischer M (2001) The effect of plant population size on the interactions between the rare plant *Gentiana cruciata* and its specialized herbivore *Maculinea rebeli*. J Ecol 89(3):418–427

Knuth P (1909) Handbook of flower pollination, vol 3. Clarendon, Oxford

Kolb A, Ehrlen J (2010) Environmental context drives seed predator-mediated selection on a floral display trait. Evol Ecol 24(2):433–445

Lambinon J, De Langhe J-E, Delvosalle L, Duvigneuad J (1998) Flora van België, Het Groothertogdom Luxemburg, Noord-Frankrijk en de aangrenzende gebieden (3e druk). Nationale Plantentuin van België, Meise

Leimu R, Syrjanen K, Ehrlen J, Lehtila K (2002) Pre-dispersal seed predation in *Primula veris*: among-population variation in damage intensity and selection on flower number. Oecologia 133(4):510–516

Littell RC, Stroup WW, Freund RJ (2002) SAS for linear models. SAS Institute, Cary

Menendez R, Thomas CD (2000) Metapopulation structure depends on spatial scale in the host-specific moth *Wheeleria spilodactylus* (Lepidoptera : Pterophoridae). J Anim Ecol 69(6):935–951

Müller H (1883) The fertilization of flowers by insects. Macmillan, London

Ouborg NJ, Biere A (2003) The relationship between plant–pathogen and plant–herbivore interactions and plant population persistence in a fragmented landscape. In: Brigham CA, Schwartz MW (eds) Population viability in plants. Springer, Berlin, pp 99–116

Piessens K, Adriaens D, Jacquemyn H, Honnay O (2009) Synergistic effects of an extreme weather event and habitat fragmentation on a specialised insect herbivore. Oecologia 159(1):117–126

SAS Institute (2010) The GLIMMIX procedure. http://www.supportsas.com/rnd/app/papers/glimmix.pdf (accessed 3 May 2010)

Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation—a review. Conserv Biol 5(1):18–32

Steffan-Dewenter I, Tscharntke T (2000) Butterfly community structure in fragmented habitats. Ecol Lett 3(5):449–456

Tscharntke T, Brandl R (2004) Plant–insect interactions in fragmented landscapes. Annu Rev Entomol 49:405–430

Ubsdell RAE (1979) Studies on variation and evolution in *Centaurium erythraea* Rafn and *C. littorale* (D. Turner) Gilmour in the British Isles, 3. Breeding systems, floral biology and general discussion. Watsonia 12:225–232

Van Rossum F (2009) Pollen dispersal and genetic variation in an early-successional forest herb in a peri-urban forest. Plant Biol 11(5):725–737

Zabel J, Tscharntke T (1998) Does fragmentation of *Urtica* habitats affect phytophagous and predatory insects differentially? Oecologia 116(3):419–425