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The role of biotic interactions in plant
reproductive performance

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers which are referred to in the text by their Roman numerals.

- I. **Dauber, J., Biesmeijer, J. C., Gabriel, D., Kunin, W. E., Lamborn, E. Meyer, B., Nielsen, A., Potts, S. G., Roberts, S. P. M. Söber, V., Settele, J., Steffan-Dewenter, I., Stout, J. C., 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. *Journal of Ecology* **98**: 188–196.
- II. **Söber, V., Moora, M. & Teder, T.** Florivores decrease pollinator visitation rate in a self-incompatible plant. *Basic and Applied Ecology* (in press).
- III. **Söber, V., Teder, T. & Moora, M. 2009.** Contrasting effects of plant population size on florivory and pollination. *Basic and Applied Ecology* **10**: 737–744.
- IV. **Moora, M., Söber, V. & Zobel, M. 2003.** Responses of a rare (*Viola elatior*) and a common (*Viola mirabilis*) congeneric species to different management conditions in grassland – is different light competition ability responsible for different abundances? *Acta Oecologica* **24**: 169–174.

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The author contributed to designing the experiments (III, IV), data collection (I, IV), analysing the results (IV), and was responsible for designing the experiment (II), data collection (II, III), analysis and writing the papers (II, III).

I. INTRODUCTION

Recruitment success is considered to be largely determined during two stages of the plant life cycle: reproduction (including flowering) and seedling establishment (Fig. 1, e.g., Grubb 1977). Biotic interactions that occur during these stages may affect the survival and reproduction of individual plants, thus affecting the recruitment of plant populations and communities. The nature of these biotic interactions ranges from mutualistic (e. g. pollination) to antagonistic (e. g. florivory, competition). Furthermore, these different biotic interactions may interfere with each other, thereby producing complex patterns of direct and indirect effects on plant reproductive performance (Strauss & Irwin 2004). Historically, however, most studies on plant-animal interactions have focused on single interactions in isolation, which may not provide an adequate understanding of the effects of interfering biotic interactions on plant reproduction (Bronstein *et al.* 2003).

Rapid human-induced landscape and habitat changes make it necessary to study the effect of biotic interactions on the reproduction of flowering plants in landscape and habitat contexts. In fragmented landscapes, the recruitment of plant populations can be reduced as a result of small population size, edge effects, isolation and changes in management (Eriksson & Ehrlén 1992, Turnbull *et al.* 2000, Ehrlén & Eriksson 2000, Myers & Harms 2009). A change in land-use can affect plant populations directly, e.g., when habitats are destroyed, or indirectly, by altering interactions with other organisms (Cunningham 2000, Lennartsson 2002, Tylianakis *et al.* 2008). However, population- and individual-level consequences for plant performance may be difficult to predict since landscape changes affect different organisms and the strength of their interactions in different ways. The responses of the partners that interact with plants to habitat alterations depend on characteristics such as life-history traits, the degree of specialization/dependence and dispersal ability. Therefore, effective conservation of plants in rapidly changing landscapes could be aided by deeper insight into the role of interactions between biotic interactions on the reproduction of flowering plants.

Furthermore, the nature of the responses of plant partners to land-use changes may determine the long-term perspectives of the plant species, (in a given habitat fragment, or even throughout its distributional range). For example, world-wide decline in pollinator diversity and abundance may lead to insufficient pollination of animal-dependent wild plant populations thus reducing further floral resources for pollinators (Potts *et al.* 2010). Pollinators may then decline further so that even plants that are less sensitive to pollinator diversity also suffer. Thus, such spiralling events could lead to the rarity of a range of plants and pollinators. Although the simultaneous action of different biotic interactions and their potential to interfere has gained more attention recently (Herrera *et al.* 2002, Gómez 2005, Sánchez-Lafuente 2007, McCall 2008), the net effect of different plant-animal interactions on plant performance

as dependent on plant population attributes has rarely been addressed. The few known studies examining the net effect of different interactions on seed set in response to plant population size have found no uniform pattern (Steffan-Dewenter *et al.* 2001, Colling & Matthies 2004, Ågren *et al.* 2008, Kolb 2008). More studies on different combinations of biotic interactions and species are therefore needed to draw broader generalizations.

All animals which interact with flowers may affect seed production. Among these, pollinators greatly enhance reproduction in the majority of plant species (80%; Ashman *et al.* 2004), and are essential for obligate outcrossing animal-pollinated plants (Aguilar *et al.* 2006). The effect of pollinator availability on plant reproductive success has mostly been studied in relation to two types of factors. First, floral traits: larger flowers and inflorescences commonly attract higher numbers of pollinators than small or single flowers (Stanton & Preston 1988, Ohashi & Yahara 2002, Mitchell *et al.* 2004). Second, population and landscape attributes: several studies have demonstrated a relationship between plant population size or isolation and fitness. Insufficient pollination may be a major cause of reproductive failure in flowering plants inhabiting fragmented habitats (Aguilar *et al.* 2006) because habitat degradation can affect plant and pollinator populations, which in turn may affect pollinator visitation frequency, seed set and plant fitness. Apart from population size (number of flowers or flowering plants) and isolation (distance between habitat fragments; Klinkhamer & De Jong 1990, Ågren 1996, Jennersten & Nilsson 1993, Bosch & Waser 1999, Leimu *et al.* 2006), population density can importantly influence pollination (Sih & Baltus 1987, Kunin 1997). Since plant density may not be uniform throughout a patchily-distributed population, different density values may be obtained when considering different spatial scales. Moreover, different aspects of pollination (e.g., pollinator visitation in relation to floral herbivory) may respond to density differently and at different spatial scales (Mustajärvi *et al.* 2001). Thus, in order to understand how plants, and, hence, plant reproductive output, respond to habitat fragmentation it is important to consider density effects at all potentially important spatial scales (Gunton & Kunin 2007).

Various organisms affect floral display or reward levels and thus alter flower attractiveness to pollinators, and, thereby, plant reproductive success. Florivores (flower-feeding herbivores) are an example of organisms that, in addition to their direct consumption of reproductive tissues (Krupnick & Weis 1999), may influence plant reproductive success by various indirect means, such as altering plant-pollinator interactions. In terms of flower and inflorescence attributes, florivores may decrease pollinator availability indirectly by decreasing display size (Lohman *et al.* 1996, Ashman *et al.* 2004), and reward levels (Krupnick *et al.* 1999), as well as by changing floral morphology (Sánchez-Lafuente 2007, McCall 2008) and floral volatile composition (Theis *et al.* 2007, Zangerl & Berenbaum 2009). While the potential of florivores to indirectly influence plant performance is widely recognized, corresponding empirical evidence is still

relatively scarce (McCall & Irwin 2006). Furthermore, the intensity of floral antagonism may, like floral mutualism, also be related to flower attractiveness, reward levels, host plant population size and structure.

Pollinators and florivores affect the amount of seeds that enters the recruitment stage. However, because of possible limitations at the recruitment stage, population growth rate or density might not respond to changes in seed production. Successful recruitment also requires suitable microsites for germination and early development (Grubb 1977). Microsites, often created by small-scale disturbances such as grazing or mowing, may limit germination and seedling establishment in many wild plant species in different plant communities (Zobel *et al.* 2000, Rünk *et al.* 2004, Sletvold & Rydgren 2007, Hellström *et al.* 2009, Mendoza *et al.* 2009). Even if microsites are not scarce, germination and seedling establishment may be limited by biotic interactions occurring at this sensitive phase of the life cycle. For instance, in addition to herbivory, the success of seedling establishment depends on the ability to compete with neighbouring plants (e.g., Herrera & Laterra 2009). Theoretically, direct competition between plants may have population-level consequences in terms of population size and density as well as the spatial structure of plant aggregations (patchiness). Thus, low competition ability may affect plant abundance at local and regional scale, causing rarity (Rabinowitz *et al.* 1984). Yet, whether rare plant species systematically differ from common species in their competitive ability/tolerance is unknown because most ecological studies investigate common species (Kunin & Gaston 1993). Current evidence is insufficient because the number of studies comparing the competitive responses of rare and common plant species is too low to make reliable generalizations (Bevill & Louda 1999, Murray *et al.* 2002).

The objectives of this doctoral thesis were to explore the effects of the three above-described biotic interactions – pollination, florivory and among-plant competition – on the performance of flowering plants, also relating these effects to the spatial structure of plant populations.

First, I studied the effects of spatial structure in plant populations on pollinator availability and seed set. More precisely, I explored pollinator availability and seed set in relation to host plant population size and density (**I**, **III**).

Second, I explored the direct and indirect effects of florivory on pollinator availability and host plant performance at the individual plant and population levels (**II**, **III**).

Third, I studied the effect of among-plant competition on germination and seedling establishment (**IV**).

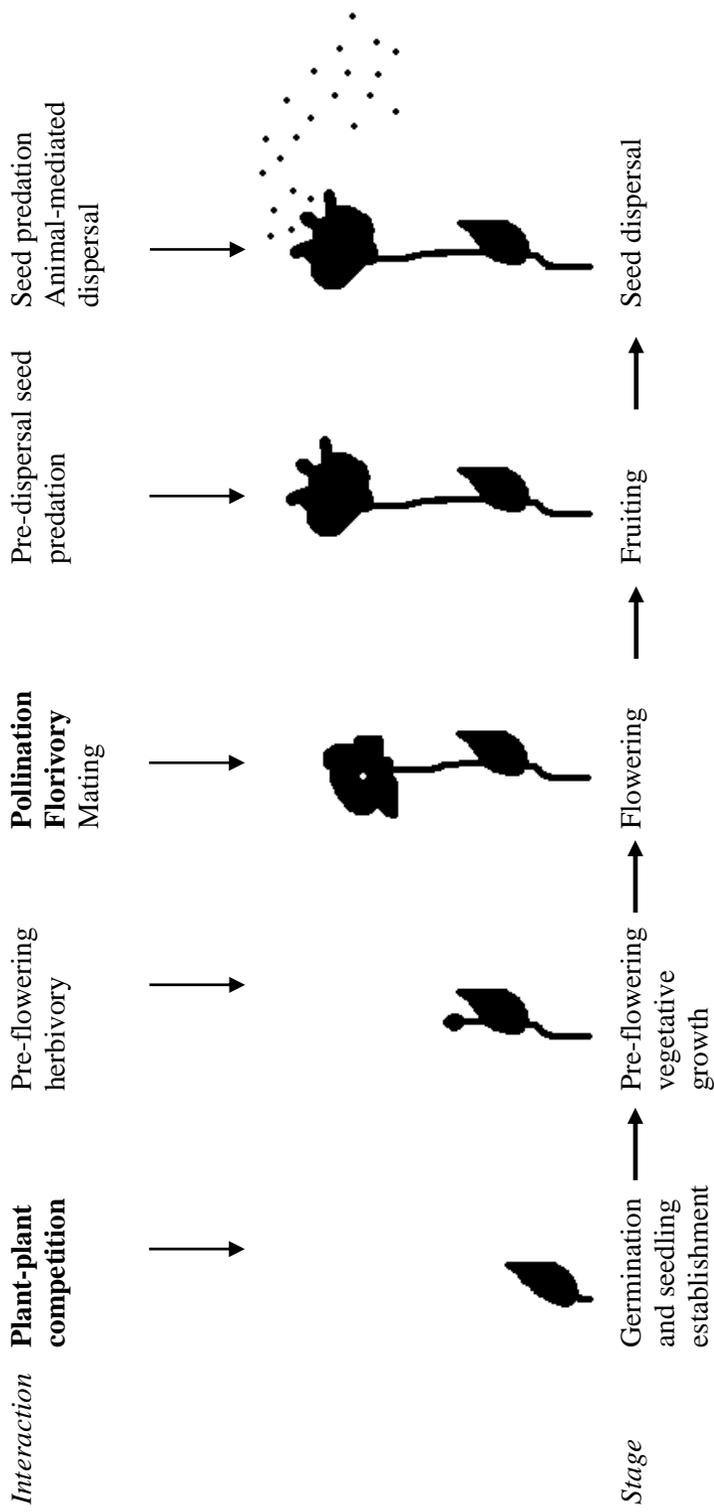


FIGURE 1. Major biotic interactions affecting flowering plant fitness at different stages of the life cycle. The current thesis focuses on the interactions in bold.

2. MATERIALS AND METHODS

2.1. Study systems

To gain a broad understanding of the effects of population structure on flower visitation and seed set, these factors were explored at the pan-European level (I). Natural populations of ten wild insect-pollinated plant species in five European countries from four bioclimatic zones (Table 1 in I) were used. These species were selected because they grow in semi-natural or remnant landscapes.

The model system used in studies II and III allowed me to investigate the combined effects of pollination and florivory at different organizational levels: the flower, plant and population levels. This tripartite system consisted of *Verbascum nigrum* L. (Scrophulariaceae), its specialized herbivore, the weevil *Cionus nigritarsis* Reitter (Coleoptera, Curculionidae), and its generalist pollinators, bumblebees (*Bombus spp.*, Hymenoptera, Apidae).

V. nigrum is a mono- to oligocarpic, perennial herb occupying open disturbed habitats (Reier 2007) where it forms relatively discrete populations of varying size. It is an insect-pollinated self-incompatible species that does not reproduce vegetatively. *V. nigrum* is the principal host of a specialist florivore, the weevil *Cionus nigritarsis*. The females of this beetle oviposit in developing flower buds. As the larvae develop in the buds, they consume the floral tissues, primarily the anthers. Older larvae move around the inflorescence consuming the anthers and causing some damage to petals. While some damaged buds abort, many succeed in blooming, though mostly without functional anthers (Fig. 1 in III).

The model system used in IV consisted of two phylogenetically close, flowering plant species with similar habitat preferences: *Viola elatior* Fr., a rare species in Estonia, and its common congener *V. mirabilis* L. Both grow on mesic calcareous soils in wooded meadows and mixed forests.

2.2. Experimental design and sampling

To study the effects of population structure on flower visitation and seed set, study I was conducted in 6–8 natural populations from each of the ten insect-pollinated plant species, i.e., altogether 74 populations (Table 1 in I), in 2006. In these populations, the effects of area and density of populations and patches (defined as continuous aggregations of the respective plant species) on flower visitation and seed set were investigated at the pan-European level by measuring pollinator visitation rate and seed set in each focal species.

To study the direct and indirect effects of florivory on plant reproductive performance, studies II (2009) and III (2006) were conducted in 2 and 21 *V. nigrum* populations, respectively. These populations were located in gravel pits,

within a radius of 70 km in eastern Estonia. Study **II** focused on measuring pollinator visitation rates in relation to florivore damage at the flower and plant levels, combining experimental approaches with observations in natural populations. Study **III** measured pollinator visitation rates in relation to plant population size and florivore damage at the population level.

Pollinator observations were carried out similarly in all cases (**I**, **II**, **III**). Within each population, patches of flowering plants were selected. The patch was defined as a continuous aggregation of the respective plant species. For each patch, the number of flowering plants in it and its area were measured. In each patch, pollinator activity was observed *either* once for 30 min during the peak flowering period (**II**, **III**), *or* three to six times during the flowering season for the observations of flower visitation rates during 15 minutes (**I**). Pollinator visitation rate per patch was measured as the average number of visits per plant per unit time (**II**, **III**) or as the total number of visits per number of flowers during an observation period of 15 minutes (**I**).

To measure seed set, up to 40 flowering plants per population were collected (**I**, **III**). To assess pollen limitation in relation to population spatial structure (**I**), two flowers on each plant were selected randomly. One of the flowers was hand-crossed (as a measure of potential maximum seed set) and the other was left untreated to be accessed by pollinators. Mature fruits were harvested and seeds were counted. The ratio of seed set in hand-crossed flowers to open-pollinated flowers was used to measure pollen limitation (**I**). To assess seed set in relation to plant population size (**III**), all seeds from all fruits of collected individuals were weighed. Because of the high number of produced fruits and seeds, it was not feasible to count all seeds, thus, standardized seed set was estimated to account for the total seed number produced per individual.

To assess the natural intensity of florivory at the plant level, the abundance of florivores was measured in 30 plants from 2 *V. nigrum* populations as the proportion of damaged flowers per plant (**II**). To assess the natural intensity of florivory at the population level, up to fifty randomly chosen flowering plants in 21 *V. nigrum* populations were examined for the presence or absence of *C. nigratarsis* larvae during the peak of florivore abundance (**III**). The intensity of florivory was estimated as the proportion of damaged plants in the population.

To evaluate the direct (i.e., consumption of flowers) and indirect (i.e., effect on pollinator visitation rate) effects of florivory on plant reproductive performance, a manipulative experiment with 132 pre-grown *V. nigrum* plants with four different levels of experimentally inflicted damage (ranging from 0–75% of flowers damaged) was performed (**II**).

To study the effect of among plant competition on the germination and seedling establishment of plant species with contrasting regional abundances, study **IV** (1999–2000) was conducted using 10 microcosms. The microcosms were patches of natural grassland community vegetation maintained at the University of Tartu experimental garden for the duration of the experiment. A factorial experiment was performed where competition intensity was

manipulated by clipping/not clipping the aboveground vegetation of two plant species with contrasting regional abundances (one rare and one abundant species of the genus *Viola*). The number of germinated and established seedlings of target plants was counted for two years.

2.3. Statistical methods

Linear mixed models were used to analyze the effects of population size, density and the intensity of florivores on pollinator visitation rate and seed set (**I**, **II**, **III**), as well as to test for the effect of competition on the germination and establishment of the two study species (**IV**). Linear mixed models were also used to test for the effects of the intensity of florivory on pollinator visitation rate at the plant and flower levels in both natural populations and experimental patches (**II**). To visualize all direct and indirect effects of population size on seed set, path analysis was performed using structural equation modelling (**III**).

3. RESULTS AND DISCUSSION

3.1. Biotic interactions related to seed availability

3.1.1. Pollination and florivory

Biotic interactions occurring at the flowering stage, such as pollination and florivory, can strongly affect seed availability. Florivores, for example, can reduce seed production considerably both directly and indirectly. In *V. nigrum*, one direct effect of florivores is the consumption of pollen by the weevil larvae of *C. nigratarsis*. Natural levels of florivory varied greatly at both plant and population levels, ranging from 0% of open flowers per plant or 10% of flowering plants per population up to almost 100% of damage at both levels (p. 5 in **II**, Fig. 1 in **III**). Furthermore, average seed set in highly damaged *V. nigrum* populations was smaller by an order of magnitude compared to less damaged populations (p. 742 in **III**).

Furthermore, florivory can affect plant reproduction indirectly by influencing pollinator preferences. The weevil larvae of *C. nigratarsis* also initiate an indirect effect by altering the behaviour of pollinators (*Bombus spp.*) at the flower, plant and population levels. Naturally or experimentally damaged flowers were almost never visited (p. 9 in **II**). In natural populations of *V. nigrum*, pollinator visitation rates were negatively related to levels of natural florivory (Table 1 & Fig. 2 in **II**). Plants and flowers that sustained more damage by the florivore received fewer visits from the pollinators compared to the less damaged plants and flowers (Fig. 2 in **II**). The results of the simulated florivory experiment confirmed the natural pattern (Fig. 3 in **II**). The observed declines in pollinator availability to *V. nigrum* plants can be explained by pollinator behaviour. Florivores alter the appearance of flowers by consuming pollen (Fig. 1 in **II**) and, therefore, decrease flower attractiveness for pollinators. Pollinators, in turn, respond by visiting damaged flowers and plants less frequently.

Although there are situations where direct and indirect effects may be of comparable strength (Schmitz *et al.* 2000), indirect interactions are usually weaker (Halaj & Wise 2001). In accordance with this general pattern, in both the natural *V. nigrum* populations and in the experiment of simulated florivory, the indirect effect of florivory on plant performance (decrease in pollinator availability) was smaller in magnitude than the direct effect (Fig. 2 & Fig. 3 in **II**). Nevertheless, the magnitude of the indirect effect of florivory was proportional to the magnitude of the direct effect (i.e., proportion of floral display damaged; Fig. 2 & Fig. 3 in **II**). Therefore, higher direct damage in *V. nigrum* is compounded by higher indirect damage for the plant because for every flower actually damaged, several could remain unused (Krupnick *et al.*

1999). For self-incompatible plants like *V. nigrum*, this may result in complete seed production failure.

Large variation in damage intensity within and among populations may have ecological and evolutionary consequences for plant reproduction. It would be interesting to investigate whether *V. nigrum* plants defend themselves against florivory and thereby reduce the effects of both direct and indirect damage. Many plant species can tolerate herbivory by producing compensatory growth after injury or postponing reproduction (Lennartsson *et al.* 1998, Huhta *et al.* 2009). Furthermore, there is some evidence that another group of herbivores associated with plant reproductive organs, seed predators, may influence flowering phenology (the timing, synchrony and duration of flowering; Parachnowitsch & Caruso 2008, Atlan *et al.* 2010). Florivory may also affect pollinator availability by influencing flowering phenology (Ehrlén & Münzbergová 2009), yet corresponding experimental evidence is still extremely scarce.

Some characteristics of the flowering phenology of self-incompatible *V. nigrum* might be associated with florivore damage. First, a pilot study showed that most plants in five natural populations started flowering within a few days of one another (unpublished data), possibly indicating synchronization of flowering, which can potentially reduce damage by satiating florivores (Janzen 1971, Augspurger 1981). Second, among these plants, those that sustained higher florivore damage flowered for significantly shorter time periods compared to less damaged plants (unpublished data). The mechanism behind the observed pattern (adaptive or mechanistic) remains to be experimentally investigated. Whether plants reduce flower production rate, existent flowers bloom faster, or whether the observed pattern arises from mechanical damage alone is currently unclear. Irrespective of the exact mechanism, the resulting shorter flowering duration may lead to lower seed set per plant due to the shorter time period available for pollination to occur. Moreover, a common garden experiment in the absence of florivores revealed considerable variation in life history strategies: about 2/3 of >400 plants grown from seeds collected from 6 separate natural populations exhibited annual and monocarpic life history whereas about 1/3 were biennial or even pluriennial. Furthermore, some biennial and pluriennial plants reproduced only once whereas others set seed every year (unpublished data). Whether the observed variation in these life-history traits is related to the “historical” intensity of florivory or other biotic interactions in the populations of origin is currently unknown.

3.1.2. The effects of plant population structure on pollination and florivory

Plant-insect interactions may reflect changes in host plant population structure, but they do not change in a uniform way. For instance, the intensity of florivory by specialist *C. nigritarsis* clearly increased, whereas pollinator visitation rate by generalist *Bombus spp.* decreased with *V. nigrum* population size (Fig. 1 in **III**). Thus, the levels of florivory and pollination responded to the increase in host population size in a contrasting manner, illustrating the importance of the degree of specialization in the process (Root 1973, Tscharnke *et al.* 2002, Münzbergová 2006). The observed decline in pollinator visits with plant population size in *V. nigrum* likely results from the negative association between florivory and pollinator visitation at the flower, plant and population levels (Fig. 2 & Fig. 3 in **II**, Fig. 4 in **III**) rather than from increasing plant population size directly. Thus, separate investigation of the biotic interactions in which a plant is involved may result in misleading conclusions on the effect of these interactions on plant reproduction because of the potential for interference between simultaneous interactions. Furthermore, the result stresses the need for correlative analyses to assess the strength of interactions in natural populations. As shown, these are no less important than manipulative studies that can reveal causal relationships.

Interactions with insects that are important for plant sexual reproduction may also depend on aspects of plant population structure other than size, such as density, for example. Whereas neither pollinator visitation rate nor seed set depended on population density or on the abundance of co-flowering species in *V. nigrum* in Estonia (unpublished data), the pan-European study of 10 wild plant species pollinated by insects showed that, in small populations, pollinators tend to visit larger and denser patches more often (Table 3 & Fig. 1 in **I**) and plants tend to produce more seeds there (Table 4 & Fig. 2 in **I**) compared to smaller and sparser patches. In large populations, however, no such effect was observed. This result is in concordance with the general finding that, in fragmented landscapes, plant seed set is related to the characteristics of patchy distribution of flowers within populations (Kery *et al.* 2000, Wolf & Harrison 2001, Kirchner *et al.* 2005).

The results presented here highlight the fact that community processes that indirectly affect species population dynamics may occur at different organizational levels. In particular, pollinators may respond to florivore damage not only at the flower and plant levels (Krupnick *et al.* 1999, **II**) but also at higher organizational levels. More precisely, pollinators visited entire populations where most of the plants sustained high damage less frequently (Fig. 2 in **III**). Thus, a multiscale approach based on individual fitness responses to different scale-related parameters of plant-insect interactions is clearly required (Gunton & Kunin 2007). Nevertheless, although average seed production in *V. nigrum* populations was strongly negatively affected by the

intensity of florivory, seed production did not depend on population size (Fig. 3 in **II**). The realized indirect effect of florivory on seed production at the population level is unlikely to be large in the studied populations of *V. nigrum* because they are not pollen-limited (Table 5 in **I**). Yet, the effect of florivory on pollinator visitation may potentially produce population-level consequences for host plant demography in pollen-limited plants or pollinator-limited environments. The recruitment of seed-limited plants compared to microsite-limited plants is generally expected to be more influenced by herbivores such as flower antagonists (Andersen 1989, Louda & Potvin 1995, Maron & Simms 1997).

3.2. Biotic interactions at seedling establishment: the effect of among-plant competition

Sexual reproduction and, hence, recruitment in plant populations is affected by biotic interactions related to seedling establishment, in addition to the previously discussed interactions affecting seed availability. Thus, the effects of biotic interactions on plant sexual reproduction may not only interfere (when they occur at the same time) but also accumulate throughout the individuals' lifetime. Moreover, individual-level fitness effects scale up to population-level consequences for host plant demography. For instance, the local and regional abundance of flowering plants (spatial patchiness) may be affected by competitive interactions among plants at the stages of germination and seedling establishment, in addition to the constraining effects of florivory and pollinator limitation. The results of Study **IV** support this possibility: the number of established seedlings of the rare *Viola elatior* increased strongly compared to its abundant congener *V. mirabilis* in response to relaxed plant-plant competition in the seed sowing experiment (Fig. 1 & Table 1 in **IV**).

Furthermore, *V. elatior* seems to be a weak competitor during later life (Moora & Jõgar 2006). So far, rare plant species have shown to be worse (Walck *et al.* 1999, **IV**), better (Rabinowitz *et al.* 1984), or roughly equal competitors (Rünk *et al.* 2004) compared to common species, and the number of studies is not yet sufficient to draw broader generalizations. Nevertheless, competitive ability is one of the traits related to biotic interactions that seem to be associated with rarity in many plant species (Murray *et al.* 2002, Lloyd *et al.* 2002). Moreover, pollinator availability depends greatly on local plant abundance (e.g., **I** and **III**). Not surprisingly, therefore, rare plants tend to be self-compatible more frequently and, if self-incompatible, have longer-living and larger flowers than common species (Kunin & Shmida 1997). It would also be interesting to know whether traits related to competitive ability differ systematically between rare and abundant plant species. In conclusion, the *Viola* result (**IV**) is an example of a potential mechanism by which biotic interactions related to both seedling establishment and seed limitation together drive plant population and community dynamics: pollinator availability is indirectly

affected by plant-plant interactions at the early stages of the plant life cycle when competitive interactions among plants affect the spatial aggregations of flowering plants. Studies exploring the entire life cycle and across different population densities are required to understand long-term population consequences of among-plant competition-, herbivore- and pollinator-mediated variation in seed set, ideally over multiple generations (Price et al. 2008).

3.3. Conclusions

The work reported in this thesis demonstrates potential mechanisms by which direct and indirect effects of biotic interactions on plant reproduction may extend into plant population and community dynamics. The overall outcome of different biotic interactions on plant reproductive performance likely depends on the simultaneity of these interactions because of their potential for interference. The outcome also depends on plant population structure, e.g., size and density, because this may affect the strength of interactions. Therefore, predicting the response of plant reproductive performance to rapidly changing landscapes requires analyses of major biotic interactions together with population structure.

SUMMARY

Recruitment success is largely determined during two stages of the plant life cycle: reproduction (including flowering) and seedling establishment. Biotic interactions that occur during these stages may affect the survival and reproduction of individual plants, thus affecting the recruitment of plant populations and communities. Furthermore, different biotic interactions may interfere with each other, thereby producing complex patterns of direct and indirect effects on plant reproductive performance. Historically, however, most studies on plant-animal interactions have focused on single interactions in isolation, which may not provide an adequate understanding of the effects of interfering biotic interactions on the reproduction of flowering plants. Moreover, changes in land-use may result in changes to population attributes (e.g., size) that in turn affect plant performance by altering co-acting biotic interactions. However, the net effect of different plant-animal interactions on plant performance in relation to plant population attributes has rarely been addressed.

Flower mutualists and antagonists, such as pollinators and florivores, influence seed set. In addition to biotic interactions at the flowering stage, which directly determine the amount of seeds entering the stage of dispersal, competitive ability at the seedling stage may affect seed production in a population or community by affecting local and regional plant abundance, and potentially causing rarity. Yet, whether rare plant species differ systematically from common species in their competitive ability is not well known because the number of studies that have compared the competitive responses of rare and common plant species at the seedling stage is too low to make reliable generalizations.

The aim of the work reported in this thesis was to contribute to filling the aforementioned gaps in our knowledge. The direct effect of florivores on plant reproduction was documented at the flower, plant, and population levels. The indirect effect of florivores at the flower and plant levels was investigated both in experimental and natural systems; the same effect at the population level was documented in natural populations. Additionally, the direct and indirect effects of host plant population attributes on plant reproduction were studied. More precisely, the direct and indirect (through pollination and florivory) effects of host plant population size on plant reproduction were investigated. The effect of plant population size and density, both within and between populations, on pollination and seed production was also studied. Finally, the effect of plant-plant competition on seedling establishment was investigated experimentally in two congeneric species with contrasting abundances. Three model systems were used to answer these questions: 1) the natural tripartite system of obligate outcrossing *Verbascum nigrum* (Scrophulariaceae), its specialized herbivore, the weevil *Cionus nigritarsis* (Coleoptera, Curculionidae), and its generalist pollinators, bumblebees (*Bombus spp.*, Hymenoptera, Apidae), in Estonia; 2)

natural populations of ten insect-pollinated plant species in semi-natural or remnant fragmented habitats in five European countries from four bioclimatic zones; 3) two *Viola* species: *V. elatior*, a rare species in Estonia, and its common congener *V. mirabilis*, in experimental patches of mesic calcareous grassland.

The results presented in this thesis show that the indirect effects of the florivorous insect larvae on plant reproduction can be considerable at the flower, plant and population levels. First, plants and flowers that sustained more damage by the weevil *C. nigritarsis* received fewer visits by bumblebee pollinators compared to less damaged plants and flowers. Furthermore, the magnitude of the indirect effect of florivory (decrease in pollinator availability) was proportional to the magnitude of the direct effect (i.e., proportion of floral display damaged). Therefore, higher direct damage may also mean higher indirect damage for plants. Second, in natural populations of *V. nigrum*, pollinator visitation rates were negatively related to levels of natural florivory.

The levels of florivory and pollination responded to an increase in host population size in contrasting ways, illustrating the importance of the degree of specialization in the process: the intensity of florivory by the specialist *C. nigritarsis* clearly increased, whereas the visitation rate by the generalist pollinator *Bombus spp.* decreased with *V. nigrum* population size. The observed decline in pollinator visits with plant population size likely results from the negative association between florivory and pollinator visitation at the flower, plant and population levels. Although average seed production in *V. nigrum* populations was strongly negatively affected by the intensity of florivory, seed production did not depend on population size, probably because *V. nigrum* is not pollen-limited. Nevertheless, the effect of florivory on pollinator visitation may potentially produce population-level consequences for host plant demography in pollen-limited plants or pollinator-limited environments.

The pan-European study of 10 wild plant species showed that pollinators tend to visit larger and denser patches more often and that plants tend to produce more seed in these compared to smaller and sparser patches, but only in small populations. This result shows that interactions with insects that are important in plant sexual reproduction may depend on different aspects of population structure.

Recruitment of flowering plants may be affected by competitive interactions among plants at the seedling establishment phases, in addition to the interactions affecting seed production. The number of established seedlings increased more strongly in response to relaxed plant-plant competition in the rare *V. elatior* compared to its abundant congener *V. mirabilis*. Thus, low competitive ability at the seedling stage may explain the low abundance of *V. elatior*. Low abundance, in turn, may decrease seed production in a population due to both the smaller number of plants and their lower attractiveness to pollinators. Therefore, this result illustrates a possible mechanism by which the effects of biotic interactions on plant sexual reproduction may not only cause

immediate interference (in the case of simultaneous occurrence) but may also accumulate throughout the plant life cycle.

The work reported in this thesis demonstrates potential mechanisms by which direct and indirect effects of biotic interactions on plant reproduction may extend into plant population and community dynamics. The overall outcome of different biotic interactions on plant reproductive performance likely depends on the simultaneity of these interactions because of their potential for interference. The outcome also depends on plant population structure, e.g., size and density, because this may affect the strength of interactions. Therefore, predicting the response of plant reproductive performance to rapidly changing landscapes requires analyses of major biotic interactions together with population structure.

SUMMARY IN ESTONIAN

Biootiliste vastasmõjude roll taimede paljunemisedukuses

Taimepopulatsioonide ja -koosluste taastootmist mõjutab enim see, mis toimub kahes õistaimede elutsükli faasis – paljunemisel (sh õitsemisel) ja idandite püsijäämisel. Organismidevahelised vastasmõjud, mis toimuvad nende kahe faasi vältel, mõjutavad taimeisendite elumust ja paljunemist populatsioonides ja kooslustes ja seega nende taastootmist. Erinevad organismidevahelised vastasmõjud võivad ka modifitseerida üksteise toimimist, moodustades keerukaid mustreid otsestest ja kaudsetest mõjudest taime paljunemisedukusele. Sellele vaatamata on enamik varasemaid uurimusi taimede ja loomade vahelistest vastasmõjudest keskendunud vaid ühele vastasmõjule korraga. Selline lähenemine aga ei võimalda mõista organismidevaheliste vastasmõjude koostoimet õistaimede paljunemisele. Pealegi võivad maakasutuse muutused mõjutada populatsiooniomadusi (nt -suurust), sellega omakorda biootilisi vastasmõjusid ja selle kaudu ka taimede paljunemist. Selliseid mitme vastasmõju koostoimet uurivaid töid, mis võtaksid arvesse ka taimede populatsiooni-suurust või muid populatsiooniomadusi, on aga vähe.

Seemnetoodangut mõjutavad õitel elavad või õisi külastavad antagonistlikud või mutualistlikud organismid, nt tolmeldajad ja herbivoorid. Lisaks õitsemise faasis toimuvatele organismidevahelistele vastasmõjudele, mis otseselt määravad levivate seemnete hulga populatsioonis või koosluses, võivad seemnete hulka mõjutada ka idandifaasis toimuvad konkurentsisuhted taimede vahel. Viimased võivad mõjutada taimede ohtrust idandite erineva ellujäämise kaudu nii lokaalses kui ka regionaalses skaalas ja võivad nii olla mõne liigi puhul ka harulduse põhjuseks. Siiski pole teada, kas haruldaste taimeliikide konkurentsivõime idandifaasis erineb süstemaatiliselt tavaliste taimede omast, sest nende konkurentsivõimet võrdlevate tööde hulk on üldistuste tegemiseks liiga väike.

Käesoleva doktoritöö eesmärgiks oli panustada eelmainitud lünkade täitmisse meie teadmistes. Dokumenteeriti õitsemisfaasis toimuva florivooria (õitest toitumise) otsest mõju taime paljunemisele õie, taime ja populatsiooni tasemel. Samuti uuriti nii loodusliku kui ka simuleeritud florivooria kaudset mõju õie ja taime tasemel; loodusliku florivooria kaudset mõju dokumenteeriti ka populatsiooni tasemel. Lisaks uuriti taimepopulatsiooni struktuuri otsest ja kaudset mõju taimeisendite paljunemisele. Täpsemalt uuriti populatsiooni-suuruse otseseid ja kaudseid mõjusid taimede seemnetoodangule. Kaudne mõju toimus läbi florivooria määra ja tolmeldamise sageduse muutumise. Muuhulgas uuriti õitsevate taimede laigu suuruse (pindala) ja tiheduse mõju tolmeldamise sagedusele nii populatsioonisiselt kui ka populatsioonidevaheliselt. Idandifaasis uuriti katseliselt taimedevahelise konkurentsi mõju idandite püsijäämisele kahel looduses äärmiselt erineva ohtrusega esineval sama perekonna liigil. Käesolevas töös esitatud tulemused saadi kasutades kolme erinevat mudelsüsteemi: 1) Eesti looduses esinev kolmest osapooltest koosnev süsteem

obligaatselt võõrtolmlevast mustast vägiheinast (*Verbascum nigrum*, *Scrophulariaceae*), kes moodustab erineva suurusega distinktseid populatsioone, temale spetsialiseerunud florivoorist *Cionus nigratarsis* (*Coleoptera*, *Curculionidae*) ja generalistidest tolmeldajatest (kimalased, *Bombus spp.*, *Hymenoptera*, *Apidae*); 2) kümne putuktolmleva taimeliigi looduslikud populatsioonid pool-looduslikes või jäänukkooslustes viiest Euroopa riigist, kokku neljast biokliimaatilisest tsoonist; 3) kaks ühte perekonda kuuluvat sarnase ökoloogiaga, kuid äärmiselt erineva ohtrusega liiki, nimelt Eestis haruldane kõrge kannike *Viola elatior* ja tavaline imekannike *V. mirabilis* (*Violaceae*) lubjarikkal niidul.

Käesolevas doktoritöös esitatud tulemuste kohaselt võib florivoorsete putukavastsete kaudne mõju taimede paljunemisele nii õie, taime kui ka populatsiooni tasemel olla märkimisväärselt suur. Nimelt külastasid kimalastest tolmeldajad kärsaka *C. nigratarsis* vastsete poolt enam kahjustatud taimi ja õisi harvem kui vähem kahjustatud taimi ja õisi. Samas oli florivooride kaudse mõju suurus (õite külastamise sageduse vähenemine) võrdeline otsese mõju suurusega (kahjustatud õite osakaaluga). Seega kaasneb suurema otsese mõjuga taime jaoks ka suurem kaudne mõju. Musta vägiheina looduslikes asurkondades ilmnes, et keskmine õite külastamise sagedus korreleerus keskmise florivooria-kahjustuse määraga negatiivselt ka populatsiooni tasemel.

Tolmeldamise ja florivooria intensiivsus reageeris peremeestaimede populatsioonisuuruse muutusele vastupidiselt: populatsioonisuuruse kasvades spetsialistidest (s.o. põhiliselt mustal vägiheinal toituvate) kärsakavastsete õitekahjustamise määr suurenes, kuid generalistidest (s.o. paljudel taimeliikidel toituda võivate) kimalaste visiitide sagedus õitsevatele taimedele kahanes. See tulemus näitab spetsialistidest ja generalistidest taimepartnerite erinevat reaktsiooni peremeestaimede populatsioonisuuruse muutusele. Käesoleval juhul võib tolmeldamissageduse kahanemist populatsioonisuuruse kasvades seletada õiekahjustuse määra ja tolmeldamissageduse vahelise negatiivse seosega nii õie, taime kui ka populatsiooni tasemel. Vaatamata sellele, et florivooria intensiivsus mõjutas keskmist seemnetoodangut musta vägiheina populatsioonides tugevasti negatiivselt, ei sõltunud seemnetoodang populatsioonisuurusest, ilmselt seetõttu, et ei tolmeldajate ega ka õietolmu nappust ei olnud. Küll aga võib florivooria selline mõju tolmeldamissagedusele mõjutada populatsioonitasemel toimuvaid demograafilisi protsesse õietolmu- või tolmeldajate puuduses taimede puhul.

Taimede paiknemine ruumis ei ole enamasti ühtlane, nii võib populatsioonis esineda erineva suurusega hõredama ja tihedama taimede paigutusega alasid ehk laike. Kümne loodusliku taimeliigiga tehtud üle-euroopalisest uurimusest nähtus, et väikestes taimepopulatsioonides kaldusid tolmeldajad suuremaid ja tihedamaid õitsevate taimede laike külastama sagedamini, ning sellega kaasnes ka suurem seemnetoodang neis laikudes võrreldes väiksemate ja hõredamate laikudega. Suuremates populatsioonides sellist seost ei leitud. Sellest tulemusest nähtub, et taimede sugulise paljunemise jaoks vajalikud interaktsioonid

putukatega võivad sõltuda peremeestaime populatsiooni ruumilise struktuuri erinevatest aspektidest.

Taimepopulatsioonide ja -koosluste taastootmine võib lisaks seemnetoodangut mõjutavatele biotilistele vastasmõjudele sõltuda ka taimedevahelistest konkurentsuhettest idandite kasvamise faasis. Võrreldes tavalise liigi, imekannikesega, suurenes konkurentsivabades tingimustes kasvama jäänud haruldase kõrge kannikese idandite hulk oluliselt rohkem. Seega võib väikest konkurentsitaluvust idandifaasis pidada kõrge kannikese madala ohtruse põhjuseks, see aga võib omakorda kahandada seemnetoodangut populatsioonis, seda nii väiksema taimede arvu tõttu kui ka nende väheste taimede väiksema atraktiivsuse tõttu tolmeldajatele. Seega näitlikustab antud tulemus võimalikku mehhanismi, kuidas erinevate organismidevaheliste vastasmõjude toime taimede paljunemisele võib akumuldeeruda läbi erinevate elutsükli faaside, lisaks eelmainitud vastasmõjude üksteist modifitseerivale mõjule ka nende samaaegse toimimise puhul.

Käesolevas väitekirjas esitatud tulemused näitavad võimalikke mehhanisme, kuidas nii otsesed kui ka kaudsed taimede paljunemist mõjutavad organismidevahelised vastasmõjud kombineeruvad ja laienevad taimede populatsiooni- ja kooslusedünaamikaks. Erinevate biotilistele vastasmõjude summaarne toime taimede paljunemisedukusele sõltub nende vastasmõjude samaaegsusest, sest vastasmõjud modifitseerivad üksteise toimet. Summaarne toime sõltub ka taimepopulatsiooni struktuurist (nt tihedusest ja suurusest), sest see mõjutab vastasmõjude tugevust. Seetõttu on taimede paljunemise seost maastike muutustega võimalik prognoosida ainult juhul, kui koos populatsioonistruktuuriga võetakse arvesse kõiki taime jaoks olulisi vastasmõjusid elupaiga-kaaslastega.

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PUBLICATIONS

CURRICULUM VITAE

I. General

Name: Virve Sõber
Date and place of birth: 16.09.1976 Tartu
Citizenship: Estonian
Language skills: English, Estonian, Russian, Spanish
Address: Department of Botany, Institute of Ecology and Earth Sciences, University of Tartu, 40 Lai St., 51005 Tartu, Estonia
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Current position: University of Tartu, Institute of Ecology and Earth Sciences, PhD student

II. Education

1994 Hugo Treffner Gymnasium
2004 University of Tartu, Estonia (B. Sc in botany and ecology)
2006 University of Tartu, Estonia (M. Sc. in plant ecology and ecophysiology)
2006–present University of Tartu, Institute of Ecology and Earth Sciences (PhD student in plant ecology and ecophysiology)

III. Scientific and research activity

Research interests:

pollination, herbivory and competition; the combined effect of biotic interactions on plant reproduction.

Publications:

Sõber, V., Moora, M. & Teder, T. Florivores decrease pollinator visitation rate in a self-incompatible plant. *Basic and Applied Ecology* (in press).
Dauber, J., Biesmeijer, J. C., Gabriel, D., Kunin, W. E., Lamborn, E. Meyer, B., Nielsen, A., Potts, S. G., Roberts, S. P. M. Sõber, V., Settele, J., Steffan-Dewenter, I., Stout, J. C., 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. *Journal of Ecology* 98: 188–196.

- Söber, V., Teder, T. & Moora, M. 2009. Contrasting effects of plant population size on florivory and pollination. *Basic and Applied Ecology* 10: 737–744.
- Moora, M., Söber, V. & Zobel, M. 2003. Responses of a rare (*Viola elatior*) and a common (*Viola mirabilis*) congeneric species to different management conditions in grassland – is different light competition ability responsible for different abundances? *Acta Oecologica* 24: 169–174.

Conference presentations:

- Söber, V., Teder, T., Moora, M. How does population size affect positive and negative insect-plant interactions and the seed set of two congeneric plant species with contrasting breeding systems? The Annual Meeting of the Scandinavian Association for Pollination Ecologists, Galö, Sweden, 20–22 October 2006.
- Söber, V., Teder, T., Moora, M. The combined effect of a positive and a negative plant-insect interaction on seed set. The Annual Meeting of the European Society for Evolutionary Biology, Uppsala, Sweden, 20–25 August 2007.
- Söber, V., Teder, T., Moora, M. Florivores decrease flowering duration. The EURECO-GFOE 2008, a joint meeting of the European Ecological Federation, and the Ecological Society of Germany, Austria and Switzerland. Leipzig, Germany, 15–19 September 2008.
- Söber, V., Teder, T., Moora, M. Florivores decrease pollinator visitation and flowering duration. The Annual Meeting of the European Society for Evolutionary Biology, Torino, Italy, 24–29 August 2009.

Scholarships:

- 2000 Estonian Students' Fund USA, undergraduate student scholarship
- 2002 United Estonian Central Council, undergraduate student scholarship
- 2006 Doctoral School of Ecology and Environmental Sciences, graduate student scholarship
- 2007 Kristjan Jaak's scholarship
- 2007 Doctoral School of Ecology and Environmental Sciences, graduate student scholarship

Other professional activities:

Member of the Estonian Seminatural Community Conservation Association.

CURRICULUM VITAE

I. Üldandmed

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II. Haridus

1994 Hugo Treffneri Gümnaasium, Tartu
2004 Tartu Ülikool, Eesti (B. Sc. botaanika ja ökoloogia erialal)
2006 Tartu Ülikool, Eesti (M. Sc. taimeökoloogia ja ökofüsioloogia erialal)
2006– Tartu Ülikool, Ökoloogia ja Maateaduste Instituut (doktorant taimeökoloogia ja ökofüsioloogia erialal)

III. Teadustegevus

Peamised uurimisvaldkonnad:

Biootilised interaktsioonid: tolmeldamine, herbivooria ja konkurents. Biootiliste interaktsioonide koosmõju taimede paljunemisele.

Publikatsioonide loetelu:

Sõber, V., Moora, M. & Teder, T. Florivores decrease pollinator visitation rate in a self-incompatible plant. *Basic and Applied Ecology* (in press).
Dauber, J., Biesmeijer, J. C., Gabriel, D., Kunin, W. E., Lamborn, E. Meyer, B., Nielsen, A., Potts, S. G., Roberts, S. P. M. Sõber, V., Settele, J., Steffan-Dewenter, I., Stout, J. C., 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. *Journal of Ecology* 98: 188–196.
Sõber, V., Teder, T. & Moora, M. 2009. Contrasting effects of plant population size on florivory and pollination. *Basic and Applied Ecology* 10: 737–744.

Moora, M., Sõber, V. & Zobel, M. 2003. Responses of a rare (*Viola elatior*) and a common (*Viola mirabilis*) congeneric species to different management conditions in grassland – is different light competition ability responsible for different abundances? *Acta Oecologica* 24: 169–174.

Konverentsiettekanded:

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Sõber, V., Teder, T., Moora, M. Florivores decrease flowering duration. The EURECO-GFOE 2008, a joint meeting of the European Ecological Federation, and the Ecological Society of Germany, Austria and Switzerland. Leipzig, Saksamaa, 15.–19. sept. 2008.

Sõber, V., Teder, T., Moora, M. Florivores decrease pollinator visitation and flowering duration. The Annual Meeting of the European Society for Evolutionary Biology, Torino, Itaalia, 24.–29. aug. 2009.

Saadud stipendiumid:

2000 Eesti Üliõpilaste Toetusfondi õppestipendium

2002 Ühendatud Eesti Kesknõukogu õppestipendium

2006 Ökoloogia Keskkonnateaduste doktorikooli teadustöö stipendium

2007 Kristjan Jaagu välislähetuse stipendium

2007 Ökoloogia Keskkonnateaduste doktorikooli teadustöö stipendium

Liikmelisus erialastes organisatsioonides:

Pärandkoosluste Kaitse Ühingu liige alates 1998. a.

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