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Department of Botany, Institute of Ecology and Earth Sciences, Faculty of Science and Technology, University of Tartu, Estonia

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LIST OF ORIGINAL PUBLICATIONS

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II Aavik, T., Carmona, C. P., Träger, S., **Kaldra, M.**, Reinula, I., Conti, E., Keller, B., Helm, A., Hiiesalu, I., Hool, K., Kaisel, M., Oja, T., Lotman, S., & Pärtel, M. (2020). Landscape context and plant population size affect morph frequencies in heterostylous *Primula veris* – results of a nationwide citizen-science campaign. Journal of Ecology, 108, 6, 2169–2183. https://doi.org/10.1111/1365-2745.13488

III Aavik, T., Reitalu, T., **Kivastik, M.**, Reinula, I., Träger, S., Uuemaa, E., Barberis, M., Biere, A., Castro, S., Cousins, S.A.O., Csecserits, A., Dariotis, E., Fišer, Ž., Grzejszczak, G., Huu, C.N., Hool, K., Jacquemyn, H., Julien, M., Klisz, M., Kmoch, A., Krigas, N., Lengyel, A., Lenhard, M., Moges, D.M., Münzbergová, Z., Niinemets, Ü., Odé, B., Pánková, H., Pärtel, M., Pätsch, R., Petanidou, T., Plue, J., Puchałka, R., Rienks, F., Samartza, I., Sheard, J.K., Stojanova, B., Töpper, J.P., Tsoktouridis, G., Uzunov, S., Zobel, M. (2025). A pan-European citizen science study shows population size, climate and land use are related to biased morph ratios in the heterostylous plant *Primula veris*. Journal of Ecology, 00, 1–19. https://doi.org/10.1111/1365-2745.14477

IV **Kaldra, M.**, Träger, S., Reinula, I., Keller, B., Conti, E. and Aavik, T. (2023). Skewed morph ratios lead to lower genetic diversity of the heterostylous *Primula veris* in fragmented grasslands. Plant Biology, 25, 703–714. https://doi.org/10.1111/plb.13531

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Author's contribution to the publications (was responsible for ***, contributed substantially **, contributed*):

	Original idea	Study design	Data collection	Analysis and interpretation	Manuscript writing
I	***	***	***	**	***
II	*	**	**	**	**
III	**	**	**	**	**
IV	**	*	*	***	***

GLOSSARY

Term	Definition
Heterostyly	Genetic floral polymorphism with morphologically distinct mating types (morphs) differing reciprocally in the stigma and anther height within a flower. Based on the number of types in a plant species, it can be divided into distyly and tristyly.
Distyly	The presence of two morphologically different mating types (morphs).
Tristyly	The presence of three morphologically different mating types (morphs).
Homostyly	Flowers have the stigma and anthers at the same position within a flower. Depending on the position of reproductive organs, high and low homostyly can be distinguished.
Isoplethy	An equal frequency of each morph.
Morph ratio bias/ skewed morph ratio	Deviation of morph frequencies from equal.
Absolute morph ratio deviation	A measure indicating unequal frequency of morphs. It does not consider which morph is more prevalent. For distylous plants, it usually varies from 0 (equal balance) to 1 (absence of one morph type).
Directional morph ratio deviation	A measure indicating unequal frequency of morphs, which also considers the type of the morph the balance is skewed towards. For distylous plants, it can vary from –1 (presence of only one morph) ...0 (equal morph frequency) …+1 (only the other morph is present). It can also be measured differently, with 0.5 indicating an equal balance and lower/higher values showing towards which morph the balance is skewed to.
Self-compatibility	The ability to set seed from self-pollination.
Self-incompatibility	Physiological mechanisms preventing seed set from self-pollination.
Intra-morph	Within the same morph (e.g., intra-morph compatibility).
Inter-morph	Between different morphs (e.g., inter-morph compatibility).
S-locus	Also known as “supergene”, a chromosomal region consisting of several tightly linked genes controlling different aspects of heterostyly.

1. INTRODUCTION

Recent land-use changes have resulted in unprecedented habitat loss and fragmentation, which is, next to climate change, one of the main threats to biodiversity and ecosystem functioning (Haddad et al., 2015; IPBES, 2019). Semi-natural grasslands – biodiversity hotspots of Europe (Habel et al., 2013; Wilson et al., 2012) – are particularly affected by this process, having lost a significant proportion of their area and connectivity during the last century (Cousins et al., 2015; Dengler et al., 2020; Jiang et al., 2013). Habitat loss and fragmentation influence plant diversity mainly through a decline in size and reduced connectivity between remaining fragments. This can lead to lower reproductive output (Cranmer et al., 2012; Mendes et al., 2022) and impoverished genetic diversity (Leimu et al., 2010). However, the relative vulnerability of different species to the loss and isolation of habitats strongly depends on life history traits, such as the mating system, pollination and seed dispersal vectors and distance, and life span of the species (Aguilar et al., 2008; Marini et al., 2012; Moser et al., 2015). In particular, animal-pollinated plant species are considered more susceptible than clonally reproducing, selfing or anemophilous species capable of self-pollination (Aguilar et al., 2008) because the latter do not depend on pollinators for reproduction. The majority (up to 90%) of flowering plants are animal-pollinated (Tong et al., 2023). Recent studies show drastic losses in insect diversity and abundance, particularly in human-altered landscapes (Hallmann et al., 2017; Powney et al., 2019), which severely threaten the reproductive success of those plants and may even lead to the disappearance of species relying on animal-pollination (Biesmeijer et al., 2006).

Many plant species have evolved specific floral traits to ensure cross-pollination by animals and to prevent self-pollination, such as heterostyly. Heterostyly is a plant floral polymorphism characterised by two or three morphologically distinct floral morphs, each having reciprocal positioning of sexual organs within the flower (Figure 1). It has evolved independently across 28 plant families and is especially representative of the Primulaceae (Naiki, 2012). Distylous species have two morphs – long-styled morph (L-morph or pin) and short-styled morph (S-morph or thrum; Figure 1a). The morphs are named after the positioning of the style inside the flower. In the S-morph, the style is short and positioned lower in the corolla tube, while anthers are located at a higher position. The style of L-morphs is long, and the anthers are placed lower inside the corolla. Tristyly is characterised by the presence of a third floral form – the mid-styled morph (M-morph), with the style in the middle and anthers located both at lower and higher positions relative to the style (Figure 1b).

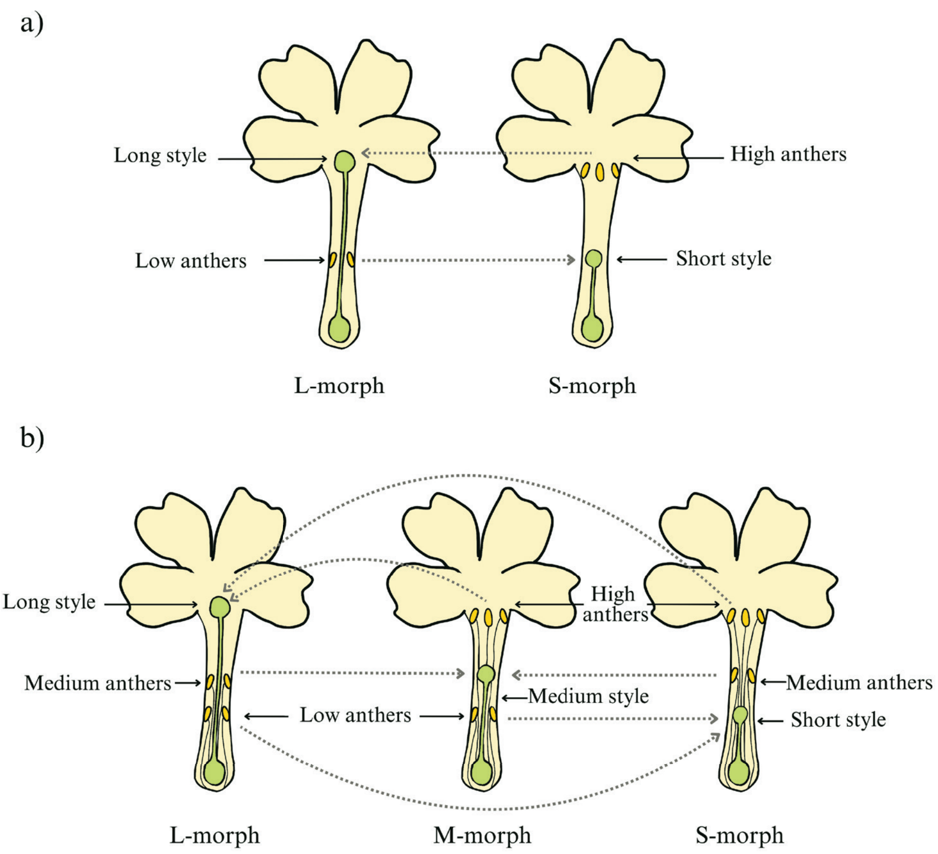

Figure 1. A scheme of heterostylous plants representing the morphologies and compatibilities between different morphs for a) distylous plants (two morphs based on *Primula* sp.) and b) tristylous plants (three morphs based on *Oxalis* sp.) (**I**). The dashed line represents the direction of compatible pollination, leading to successful fertilisation.

The reciprocal spatial arrangement of sexual organs is called herkogamy, and its purpose is to promote cross-fertilisation between individuals of different floral morph types and to avoid selfing and inbreeding (Darwin, 1862). Besides herkogamy, the morphs also differ from each other by the size and abundance of pollen grains. Generally, S-morphs produce larger pollen grains but in smaller amounts, while L-morphs produce more pollen of smaller size (Ornduff, 1980). Pollinators promote disassortative pollination, through which the pollen is positioned onto different parts of the pollinator's body and transferred to the matching morph type's stigma (Keller et al., 2014; Trevizan et al., 2021; Webb & Lloyd, 1986). The reciprocal arrangement of sexual organs is accompanied by a heteromorphic incompatibility system, which prevents pollen from the same morph type from germinating. Depending on the specific species, intra-morph pollination can result in non-existent or low seed production (Wedderburn & Richards, 1990). The degree of self-incompatibility can vary depending on the plant species, population, and individual, as well as different morph types within the same species (Shao et al., 2019; Wedderburn & Richards, 1990; Zietsman et al., 2008). However, negative frequency-dependent selection and disassortative pollination should ensure the equal frequency of each morph in a population, also known as isoplethy. Traits related to heterostyly, such as the length of the style and stamens, self-incompatibility and pollen size, are determined by several tightly linked genes located in the *S*-locus (also known as *S* supergene), which is a chromosomal region present only in the hemizygous S-morph haplotype and absent in the L-morph (Huu et al., 2016; Li et al., 2016).

Although heterostyly is traditionally characterised by incompatibility within the same morph type, there are many exceptions. Disruption in equal morph frequencies leads to fewer mating opportunities, in which case the relative differences in within-morph and self-incompatibility may have a stronger impact on population survival. Wedderburn and Richards (1990) studied the within-morph incompatibility of 52 *Primula* species. They demonstrated considerable self-incompatibility variation in this genus, ranging from a complete within-morph incFompatibility to illegitimate pollination (within the same morph), yielding as much seed as legitimate crosses. For *Primula veris*, one of the main model species in studies of heterostyly, legitimate crosses are expected to yield seeds with 75.4% success, while the L-morphs show a higher intra-morph compatibility (14.7%) than S-morphs (0.6%). Such variations of within-morph compatibility between different morphs may result in reproductive advantages for partly self-compatible morphs, especially in fragmented habitats, where more self-compatible morphs have higher mating opportunities. Studies on fragmented *P. veris* populations have found that in populations where the morph balance was skewed toward L-morphs, the seed set was higher (Van Rossum et al., 2006) compared to the populations skewed towards S-morphs. These populations were also characterised by lower inbreeding (Van Rossum & Triest, 2006b), possibly indicating how L-morph bias in small and fragmented populations may buffer the negative effects of reduced availability of legitimate mates (Van Rossum et al., 2006; Van Rossum & Triest, 2006b). However, although partial compatibility between L-morphs may be temporarily advantageous in fragmented conditions, continuously higher biparental inbreeding may eventually lead to inbreeding depression and lower population's genetic diversity and survival probability in the long term (Van Rossum & Triest, 2007).

Due to their dependence on pollinators and other heterostyly-specific traits, such as disassortative mating, optimal morph frequencies and self-incompatibility, loss in the area and connectivity of habitats may pose several threats to heterostylous species (Figure 2). This process reduces plant population sizes but also negatively affects the abundance and diversity of pollinators and their movement (Matsumura & Washitani, 2000; Van Rossum et al., 2015; Waites & Ågren, 2004). Reduced population sizes lead to unbalanced morph ratios (Endels et al., 2002; Kéry et al., 2003), which means that there is a lower availability of suitable mates, essentially lowering the effective population size (N_e). With a skewed morph balance and a growing distance of legitimate mating partners, the seed set is significantly lower, lowering the population's reproductive output (Brys &

Jacquemyn, 2010; Ishihama et al., 2006). The scarcity of mates can also favour more selfing, which may eventually lead to inbreeding depression and reduced genetic diversity (Meeus et al., 2012; Van Rossum et al., 2006). This can reduce the adaptability of populations to environmental change, making such populations more vulnerable to extinction (Leimu et al., 2010). These different factors can occur simultaneously, further amplifying each other's negative effects. Furthermore, plant-pollinator interactions may be affected by shifts in climatic conditions. For example, changes in precipitation may disrupt the phenological compatibility between plants and pollinators, alter foraging patterns, affect pollen quality and dilute nectar (Lawson & Rands, 2019).

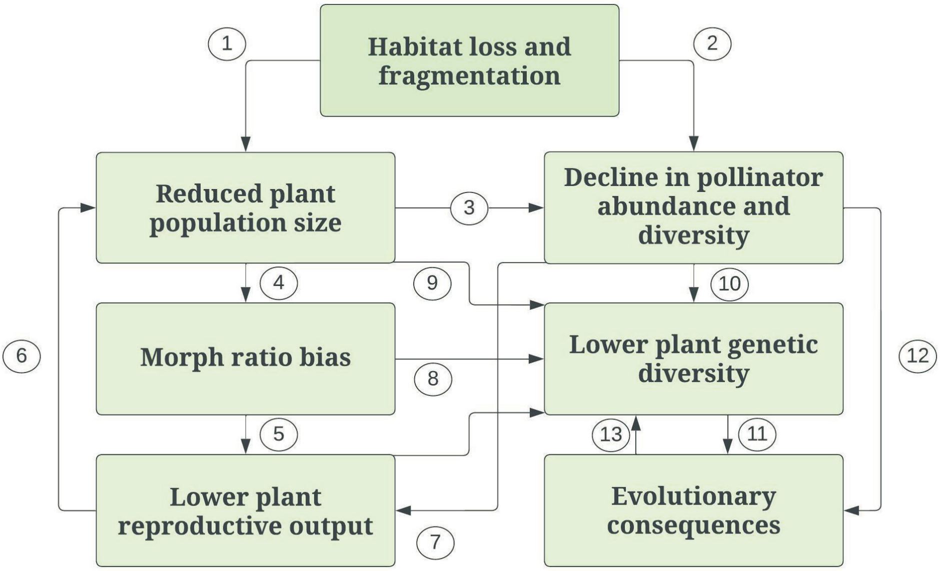

Figure 2. Potential consequences of habitat loss and fragmentation for heterostylous plant species (**I**). The main direct consequence of habitat loss and fragmentation is a reduction in population size (1). Since heterostylous plants depend on animal pollination, their reproductive success is directly affected by the availability and diversity of pollinators, which can be reduced due to habitat fragmentation (2). Smaller plant populations also support fewer pollinators (3). Reduced population size may lead to skewed morph ratios and fewer suitable mates for reproduction (4). This imbalance in morph ratios leads to lower reproductive output through a reduction in seed production (5), leading to smaller population sizes (6). Pollinator abundance and diversity directly affect the reproductive output of heterostylous populations by reducing pollen dispersal (7). Morph ratio bias and smaller population size can cause more (biparental) inbreeding and thus negatively affect the genetic diversity of populations (8, 9). With fewer pollinators, there is less movement among individuals inside and between populations and thus less gene flow, directly affecting genetic diversity (10). Populations with lower genetic diversity have lower adaptive evolutionary potential to respond to environmental change (11). A decline in pollinators can shift the mating system by evolving towards self-compatibility and homostyly or, alternatively, by becoming more visible and attractive to pollinators (12). Evolution to self-compatibility can lead to more inbreeding and reduced genetic diversity (13).

Lower likelihood of obtaining legitimate pollen, decreasing pollinator availability (Aguilar et al., 2008; Millard et al., 2021; Rodrigues et al., 2022; Xiao et al., 2016) accompanying loss in the area and connectivity of habitats and phenological mismatches between plants and pollinators favour plants with mixed mating system and self-pollination ability. The shift from outcrossing to selfing is considered one of the most common transitions in angiosperms (Cutter, 2019) and is becoming increasingly likely with further human-induced habitat loss (Harder & Aizen, 2010). Both habitat loss and isolation, as well as lower abundance of pollinators, can interact and further intensify the selection pressure on plants towards being more self-compatible and less dependent on pollinators. In heterostylous plants, it encompasses evolving towards being more self-compatible and replacing heterostylous flowers with homostylous ones (Barrett, 2019). The mutations in the *S*-locus have been associated with the breakdown of heterostyly (Kappel et al., 2017). In contrast to heterostylous flowers, homostylous flowers have the anthers and stigma at the same height, which can disrupt legitimate pollination and may lead to higher selfing rates (Brys & Jacquemyn, 2020; de Vos, Wüest, et al., 2014). However, there is still too little evidence to be sure whether these are evolutionary changes driven by habitat fragmentation or whether the loss of herkogamy reflects phenotypic plasticity (Jacquemyn et al., 2012). Although being self-compatible may be advantageous in fragmented habitats, homostylous plant populations show higher selfing rates and significantly reduced genetic diversity compared to heterostylous populations (Mora-Carrera et al., 2023; Shao et al., 2019; Yuan et al., 2017). Recent advances in molecular studies help us gain insight into the genetic consequences, not visible to the eye but detrimental to the well-being and sustainability of these species. With low genetic diversity, these plant populations are characterised by decreased adaptive potential (de Vos, Hughes, et al., 2014; Wang et al., 2021) and are therefore more vulnerable to different environmental changes, which, in turn, reduces their long-term viability (Leimu et al., 2010).

The studies on heterostyly date back to Darwin, who was the first to figure out the purpose of such floral polymorphism and he already uncovered that the different flower forms existed in equal numbers (Darwin, 1862, 1877). He influenced many further studies on heterostyly, and since then, heterostylous plants have been used as model systems in molecular and evolutionary studies not only because of the unique mating system relying on pollinators but also because of the interesting genetic background of the *S* supergene governing the trait complex expressed in heterostylous species (Li et al., 2016; Potente et al., 2022). Although heterostyly has been an interesting study system for biologists for a long time, there are still various gaps in the knowledge of the short- and long-term maintenance and functioning of heterostyly mating systems (Barrett, 2019). Some of these gaps include a better understanding of intra-morph compatibilities and the consequences of intra-morph crosses on the fitness of heterostylous plants. Many studies on heterostylous species indicate the connection between the population size and morph frequencies, but the generality of the trend has not been explored. There are still just a few studies on how the morph ratio bias may affect genetic diversity, and more studies on different heterostylous species are needed to understand the consequences and get better insight into the long-term sustainability of populations. Some studies have reported the breakdown of heterostyly in response to the scarcity of mates and lack of pollinators (e.g., Barmentlo et al., 2018; Mora-Carrera et al., 2023), but we do not know how widespread the phenomenon is and whether it can be expected for all heterostylous species. Finally, the role of pollinators in the context of habitat loss is understudied. Furthermore, unprecedented landscape changes in combination with expected shifts in climate make it even more important to understand the consequences of these processes on the functioning of heterostyly and uncover ways to support and maintain the short- and long-term viability of heterostylous plants.

The main objective of this thesis is to enhance our knowledge of the response of heterostylous plant species to factors of land use and climate change. This understanding improves our insights into the 'most complex marriage' arrangement of plants (Barrett, 2019) but also helps to guide towards better-informed conservation choices for heterostylous plants, but also for other species strongly relying on animal-pollination. To enhance the understanding of the main patterns and processes of heterostyly in an era of global change, I carried out several studies on heterostyly ranging from local and regional to a pan-European scale. For this, I used different methodological approaches: a literature review with a meta-analysis (**I**), a citizen science approach (**II, III**) and a combination of a field- and genetic study (**IV**).

The specific aims of the thesis were to:

1) get an overview of the different consequences of habitat loss and fragmentation on heterostylous species (**I**),
2) identify whether different heterostylous species respond to the decrease in population size in the same way (**I**);
3) uncover which landscape, environmental and climatic factors may affect morph frequencies (**II, III**);
4) get an understanding of how the disruption in morph balance affects the genetic diversity of heterostylous populations (**IV**);
5) determine whether there are any differences between morphs by how they are affected by the decrease in population size and whether there are different genetic patterns between morphs (**II–IV**);
6) identify possible evolutionary changes by studying homostylous phenotypes of *P. veris* (**III**).

Finally, the results from this thesis will provide guidance on how to better protect and manage heterostylous species and, through that, other animal-pollinated species as well.

2. METHODS

2.1. Study species

The studies in papers **II–IV** focused on *Primula veris* L. (Primulaceae), being one of the main model species in heterostyly research (Figure 3). *P. veris* is a distylous perennial plant that grows mainly in open habitats but can also be found in semi-open forests and other open and semi-open habitats similar to grasslands, such as road verges and forest edges.

Figure 3. The study species *Primula veris* is one of the most well-explored heterostylous species and is often used as a model system in heterostyly research (**I**). The different floral morphs are visibly recognised by looking inside the flower. The L-morph (stigma visible) is on the upper right, and the S-morph (anthers visible) is on the lower right photo.

The reproduction of *P. veris* depends on pollinators, but it is also capable of moderate vegetative reproduction (Tamm, 1972). The main pollinator groups of *P. veris* are *Hymenoptera* (bumblebees), *Lepidoptera* (butterflies), *Diptera* (bee flies) and *Coleoptera* (beetles) (Brys & Jacquemyn, 2009). The average pollen dispersal distance is around 2 meters, but seed dispersal is quite low, with an average of only 12 cm (Richards & Ibrahim, 1978). The life span of *P. veris* is relatively long, with an average longevity of around 50 years (Ehrlén & Lehtilä, 2002). The first observations on the heterostyly of *P. veris* were made already centuries ago (Gilmartin, 2015), but Charles Darwin was the first to suggest the significance of heterostyly in the reproduction of *P. veris* (Darwin, 1862). Besides the species being heterostylous, *P. veris* was chosen as our study species due to its reliability on pollinators (**II–IV**) and extensive background in molecular and evolutionary studies, including an available sequenced genome (Nowak et al., 2015) for genetic studies (**IV**). It is also an easily recognisable and well-known species, making it perfect for the citizen science approach (**II–III**). There were no focal species in paper **I**, which covered case studies on different heterostylous species worldwide with appropriate data availability.

2.2. Data collection

2.2.1. Literature search

For the review in paper **I**, I conducted a keyword search on the Web of Science to get an overview of the scientific literature on the effects of the loss in the area and connectivity of habitats, and habitat fragmentation on heterostylous species. We used combinations of keywords such as “heterostyly”, “distyly”, “tristyly”, “heteromorphic incompatibility”, “fragmentation”, “population size”, “habitat loss”, “connectivity”, “morph ratio”, and “morph bias”. As of October 21, 2024, my search yielded a total of 149 unique articles. I used the PRISMA protocol (Page et al., 2021) to identify suitable studies, which excluded 88 studies and resulted in 61 articles relevant to our study question.

2.2.2. Citizen science approach

To gather wide-scale data on heterostyly patterns of *P. veris* across Estonia (**II**) in 2019 (Figure 4b) and Europe (**III**) in 2021–2022 (Figure 4a), we conducted a citizen science study. Citizen science is the general public's engagement in scientific research, where obtaining large-scale observational data is often not possible with traditional methods (Vohland et al., 2021). Citizen science has been an increasingly recognised and widely used method, especially in ecological and environmental studies (Bonney et al., 2009; Fraisl et al., 2022). We developed a web platform where participants could get instructions and insert their observations (nurmenukk.ee or cowslip.science). Participants were asked to observe, if possible, at least 100 randomly selected individuals of *P. veris* and determine their morph type. In the pan-European study, the participants had to assess the population size of *P. veris* in three categories (small: some plants, up to 100 individuals; medium: about 100–200 individuals; large: more than 200 to thousands). Additionally, they were asked to share the location information of the population, which we could later use to add relevant environmental, landscape, and climatic data to the set of explanatory variables. Participants could also upload photos of the observation site and of observed flowers, which helped validate the data. All received observations were carefully checked and filtered according to the following criteria: (1) observations of the wrong species, (2) observations with less than 10 individuals observed, (3) unrealistic observations (for example, 1000 S-morphs and 0 L-morphs), (4) selecting only one observation if there were many entries located closer than 100 meters from each other.

In the pan-European study (paper **III**), we asked people to keep their eyes open for any homostylous *P. veris* plants (anthers and stigma at the same height). If encountered, the participants were encouraged to collect leaf material and send it to us for further genotyping. Homostylous phenotypes were genetically analysed and compared to S- and L-morph samples collected from the same populations at the University of Potsdam. The samples were genotyped by amplifying a gene CYP734A50 in the *S*-locus, which is present only in S-morphs. This allowed us to determine whether homostyly was caused by mutations in this genomic region (originating from S-morphs) or not.

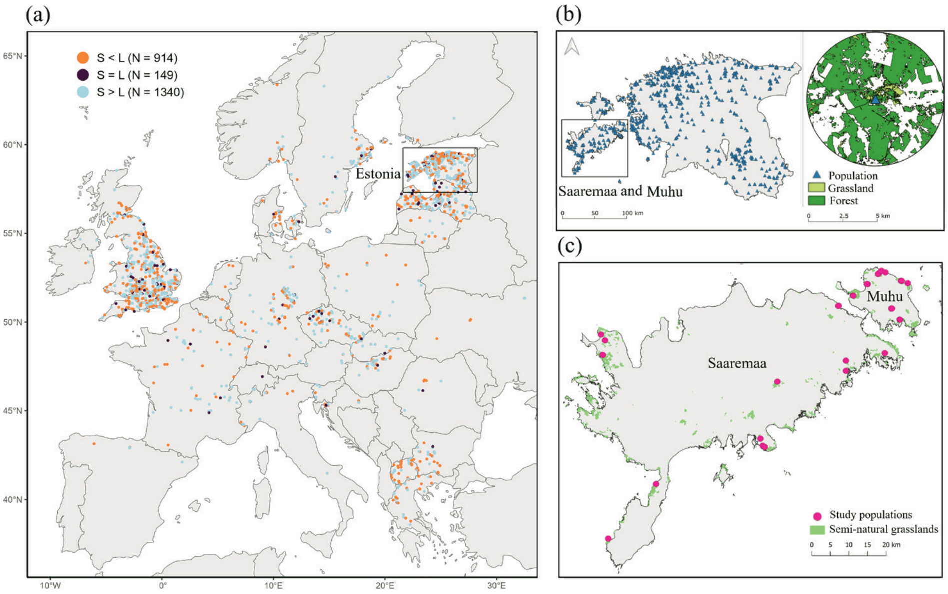

Figure 4. Locations of the study populations of *Primula veris* examined in this thesis (a) within the frames of the citizen science campaign 'Looking for Cowslips' in 2021 and 2022 in Europe, (b) within the frames of the citizen science campaign '*Eesti otsib nurmenukke'* in 2019 in Estonia, and (c) for the collection of genetic samples on Saaremaa and Muhu, Estonia. Only populations associated with geographic coordinates retained after quality filtering are depicted in (a) and (b). In (a) 'S < L' denotes populations where long-styled L-morphs were more abundant than short-styled S-morphs, while 'S > L' depicts populations where S-morphs were more frequent than L-morphs. 'S = L' stands for populations where S- and L-morphs had equal frequency. (b) includes an illustration of the buffer approach used for assessing the landscape characteristics (proportion of semi-natural grasslands and woody elements) in the surroundings of the study populations, and (c) includes the current distribution of semi-natural grasslands (light green).

To analyse the potential impact of land-use, climatic and environmental variables on morph ratios, we extracted different parameters from open-source global databases for those observations, which had GPS coordinates. We used the following datasets: the Estonian Environmental Agency for assessing the area covered by semi-natural grasslands, WorldClim for climatic data (Fick & Hijmans, 2017), ESA WorldCover for land use data (Zanaga et al., 2021), the database of Statistics Estonia (https://www.stat.ee/) and Global Human Settlement population grid for human population density data (Schiavina, 2022), AW3D30 for elevation data (Takaku et al., 2020), SoilGrid for obtaining information on soil variables (Hengl et al., 2017). We used Topographic Wetness Index as an indicator of soil moisture (Kopecký et al., 2021). Study **II** included the bedrock type assessed from the Map of Bedrock (Geological Survey of Estonia 1999, modified by Estonian Land Board in 2019). To take into account both local and large-scale effects of land cover and human population density, we generated buffer zones with different radiuses around the observation site and assessed the following variables for each buffer (radiuses from 100–5000 meters): the proportion of semi-natural grasslands, woody elements (**II, III**), built-up areas and croplands, and measures of landscape diversity (**III**). In both studies, we also assessed human population density to consider the potential impact of other anthropogenic factors on morph frequencies. In study **III**, we extracted information on a wide range of different bioclimatic variables from the global WorldClim 2 dataset, providing long-term averages for the 1970–2000 time period (Fick & Hijmans, 2017).

2.2.3. Collection of genetic data

Study sites of paper **IV** were located in Estonia on Saaremaa and Muhu islands on historically widespread semi-natural alvar grasslands (Figure 4c). These grasslands have degraded extensively because of decreased traditional management by grazing, leaving the remaining grasslands small and isolated from each other, thus making them a suitable study system for studying the effects of habitat loss and fragmentation on the species living there (Helm & Toussaint, 2020). Leaf samples of *P. veris* were collected from 30 populations occurring in open (18) and overgrown (12) grasslands of Saaremaa and Muhu islands. From each population, 1–3 leaves from up to 20 individuals, if possible, were collected with at least one meter between sampled individuals to avoid collecting samples of potentially genetically identical individuals. A total of 571 samples were collected and used for further analysis. To obtain population-level information about the morph ratios within each study grassland, at least one hundred random individuals, if possible, were visually inspected for their floral morph type. We used 2619 neutral single-nucleotide polymorphisms (SNPs) from previously generated restriction site-associated DNA sequencing (RAD-seq) data (Reinula et al., 2021) in the same study populations from Saaremaa and Muhu to calculate observed and unbiased expected heterozygosity (H_O and uH_E, respectively) and the percentage of polymorphic loci (%P). These measures of genetic diversity were calculated using GenAlex 6.503 for each study population of *P. veris*. The inbreeding coefficient (F_{IS}) within study populations and measures of pairwise genetic differentiation (F_{ST}) between populations were calculated using genepop v1.0.5. in R 3.6.1.

2.2.4. Assessing morph balance

To assess the influence of different landscape and climatic factors on morph ratios, we calculated two different types of indices that would take into account (a) the overall morph ratio balance and (b) the dominance of one morph over the other, i.e., directional deviation. Even though the core idea of assessing deviations of morph frequencies from balance is the same, different studies have applied distinct approaches for calculating these indices. My thesis also applied different approaches as our studies evolved and their specific aims developed. For example, in the citizen science campaigns (**II, III**), we were specifically interested in what factors favour one morph over the other, thus directional deviation measures were applied.

In papers **I** and **IV**, we assessed the morph ratios by calculating the absolute value of the difference in the number of individuals of the long- and short-styled morphs divided by the total number of flowering individuals (L-S/L+S), which ranges from 0 to 1. The directional deviation was assessed without calculating the absolute value. Negative values of directional deviation would indicate an excess of S-morphs (with the value of –1 suggesting the presence of only S-morphs), and positive values show an excess of L-morphs (with the value of 1 indicating the presence of only L-morphs). As paper **I** also included studies of tristylous species, a morph evenness index had to be used instead, which indicates how equally the different morphs are distributed in a population.

Traditionally used indices for assessing morph frequency deviations do not usually take into account the population size from which the deviation was calculated. For example, when a population with 50 individuals has 30 S-morphs observed and a second population with 500 individuals has 300 S-morphs observed, both populations have the same proportion of S-morphs and the same deviation index. The probability that such a proportion could be observed is much lower for the larger population than for the smaller one. In paper **II**, we calculated an index that also takes into account the population size by estimating the distance ($SES_{S\text{-morphs}}$) between the observed number of S-morphs in a population and the number of S-morphs expected in a balanced population. With the former example of populations with 500 individuals and 50 individuals, the $SES_{S\text{-morphs}}$ value for the bigger population would be larger, better reflecting the influence of morph deviation from equal balance. We also estimated the absolute deviation (SES_{ABS}) for each population. In addition, to compare the main findings of this study to previous research, we assessed the proportion of S-morphs ($DEV_{S\text{-morphs}}$) and deviation from an even morph frequency (DEV_{ABS}) as used in (Kéry et al., 2003).

In paper **III**, we used the proportion of S-morphs calculated as S/(S + L), where S and L are counts of S- and L-morphs, respectively (later referred to as

Sprop), and the general deviation of morphs from an even morph frequency that is isoplethy calculated as $|(S/(S + L)) – 0.5|$ (later referred to as ABSdev).

2.3. Data analysis

As the result of literature search done in study **I**, I found 28 case studies that had recorded both population size and morph frequencies. Of these, 20 were on distylous species, and eight were on tristylous species. Three studies had multiple recordings through different years, which were treated as separate observations in the analysis, giving us a total of 34 data points to include in the analysis. We used Fisher's z-transformed correlation coefficients to compare the correlations reported in different studies. The correlation coefficients and sample sizes were extracted from published texts. In studies where Pearson's correlation coefficient (r) was not reported, we either calculated it from other published statistics or from the raw data available in tables or figures. When population size was reported as a categorical variable, we used Spearman's rank correlation analysis and further transformed Spearman's rho to Pearson's. We fitted two random-effects meta-analysis models on the data of (1) distylous plants and (2) tristylous plants. The identity of a case study was included as a random factor in the models to account for dependent effect sizes arising from multiple correlation coefficients within the same study. Fisher's z was back-transformed to Pearson's r after the analysis for better interpretation.

In paper **II**, we used directional ($SES_{S\text{-morphs}}$ and $DEV_{S\text{-morphs}}$) and absolute deviation (SES_{ABS} and DEV_{ABS}) as response variables. Because landscape variables in different radiuses were highly correlated, we chose a 100 m buffer for the area covered by semi-natural grasslands and woody elements as an indicator of habitat availability at the local scale and a 5000 m buffer as an indicator of habitat availability at the landscape scale. Since a considerable proportion of populations presented a zero area of either variable, we transformed these variables into binary ones, indicating either the presence or absence of these elements in the 100 m buffer radius. We fitted linear models where we included log-transformed human population density as a cubic polynomial, and population size (large/small) and the other landscape variables as covariates (grassland and woody element presence at 100 m radius, proportional cover of grasslands and woody elements at 5000 m radius, and bedrock type). We also included all two-way interactions between the human population density and both population size and landscape variables. We used the MuMIn package (Barton, 2018) to generate subsets of the 'global' model and ranked them using the Akaike Information Criterion (AICc). Then, for each of the four response variables, we estimated the relative importance of each predictor. For each response variable, we estimated an averaged model based on AICc, including models within 6 AICc points from the best-ranked model. To explore the effect of important predictors, we created partial regression plots for predictors with a significant ($p < 0.05$) effect on the averaged model.

In paper **III**, i.e., pan-European study, we used the proportion of S-morphs (Sprop) and the general deviation of morphs from an even morph frequency (ABSdev) as response variables. Because many climatic variables were correlated with each other, we included only such variables whose intercorrelations did not exceed 0.6, resulting in the following parameters: mean temperature of the warmest quarter, precipitation seasonality, precipitation in the warmest quarter, and average yearly wind speed. To take into account the environmental conditions during the flowering of the study species, *P. veris*, we also assessed the impact of the average temperature, average solar radiation and precipitation in March, April and May. We first chose the best radius for landscape variables by creating general linear models of the response variables in relation to explanatory variables in each buffer radius. The radius with the lowest AIC value was chosen for further analysis. From four landscape configuration measures (edge density, patch density, mean shape index, and mean patch size), the two least correlated were kept for further analysis (mean shape index and patch density). Local land use parameters included in the next step of the analysis were human population density, land cover (proportion of cropland, built-up areas, woody elements and grasslands), elevation, soil organic carbon, pH and soil moisture, resulting in 18 numerical explanatory variables, in addition to categorical estimates of the population size of *P. veris* (<100 – small population size, 100–200 – medium and >200 – large population). For both response variables, we implemented a general linear mixed model (GLMM) with observation year (2021 or 2022) as a random factor and applied spatial autocorrelation structure. For both response variables, we used a backward selection of the 19 fixed explanatory variables by excluding the variables with the lowest explanatory power (based on the *p*-value) until only significant ($p < 0.05$) variables were included in the final models.

In paper **IV**, we used linear regression models to test whether morph ratios were more skewed in smaller populations and to see which factors influenced the genetic diversity of these populations. Explanatory variables included morph ratio bias (both absolute and directional deviation), population size, habitat succession (open or overgrown), and region (Saaremaa or Muhu). The genetic diversity indices (H_O, uH_E and %P) and inbreeding coefficient (F_{IS}) were treated as response variables. To further analyse the effects of population-level morph ratio bias, population size, habitat succession and region on the genetic diversity of S- and L-morphs separately, we used linear mixed-effects models with the population as a random variable to take into account the fact that the genetic indices for S-morphs and L-morphs were calculated from the same population. A paired-samples t-test was used to examine whether the genetic differentiation (F_{ST}) between the two morphs differed significantly. Multivariate generalised linear mixed models were used to test the effect of morph type, region and geographic distance on the genetic differentiation of populations. In this model, genetic differentiation (F_{ST}) was used as a dependent variable, and the morph type (S or L), geographical distance (isolation by distance), region, and their interactions were used as explanatory variables.

3. RESULTS

3.1. The frequencies of S- and L-morphs

The citizen science campaign carried out in 2019 in Estonia resulted in a total of 1680 observations and data from 225 797 individual flowers (**II**). After carefully filtering samples, 740 observations were included in the final analysis. The final dataset included 62 526 S-morphs and 54 002 L-morphs. Hence, there were nearly 15% more S-morphs compared to L-morphs. The pan-European campaign in 2021 and 2022 received data from 32 countries, resulting in 5269 observations, 3 475 observations in 2021 and 1794 in 2022 (**III**). Data from 28 countries qualified for further analysis (there were some wrong GPS entries and empty data forms which were removed), and after the filtering process, 3014 observations were retained for analysis of morph ratio bias, which included 179 796 S-morphs and 164 961 L-morphs. In this study, the number of S-morphs was about 9% higher compared to the number of L-morphs. Among these, 2403 observations had GPS coordinates, which were used for further analysis with different landscape and climatic analyses. The study carried out on Estonian alvars from 30 populations (**IV**) recorded in total 1210 S-morphs and 941 L-morphs, i.e., the number of S-morphs was nearly 28% higher than the number of L-morphs. Thus, all three studies reported more S-morphs than L-morphs.

3.2. The effect of plant population size on morph ratios

All studies in my thesis show a relationship between plant population size and morph ratio: a decrease in population size is related to a stronger deviation of morph frequencies from equal (i.e., isoplethy). First, this trend was observed in the meta-analysis, which included 28 studies on different heterostylous species, both distylous and tristylous plants (**I**). The random-effects meta-analysis showed a significant negative correlation between population size and morph ratio bias in distylous plant species ($r = -0.57$; 95% *CI* [–0.71, –0.39]; $p < 0.001$; Figure 5). Similarly, smaller populations of tristylous species had lower evenness of different flower morphs ($r = 0.54$; 95% *CI* [0.26, 0.74]; $p < 0.001$; Figure 6).

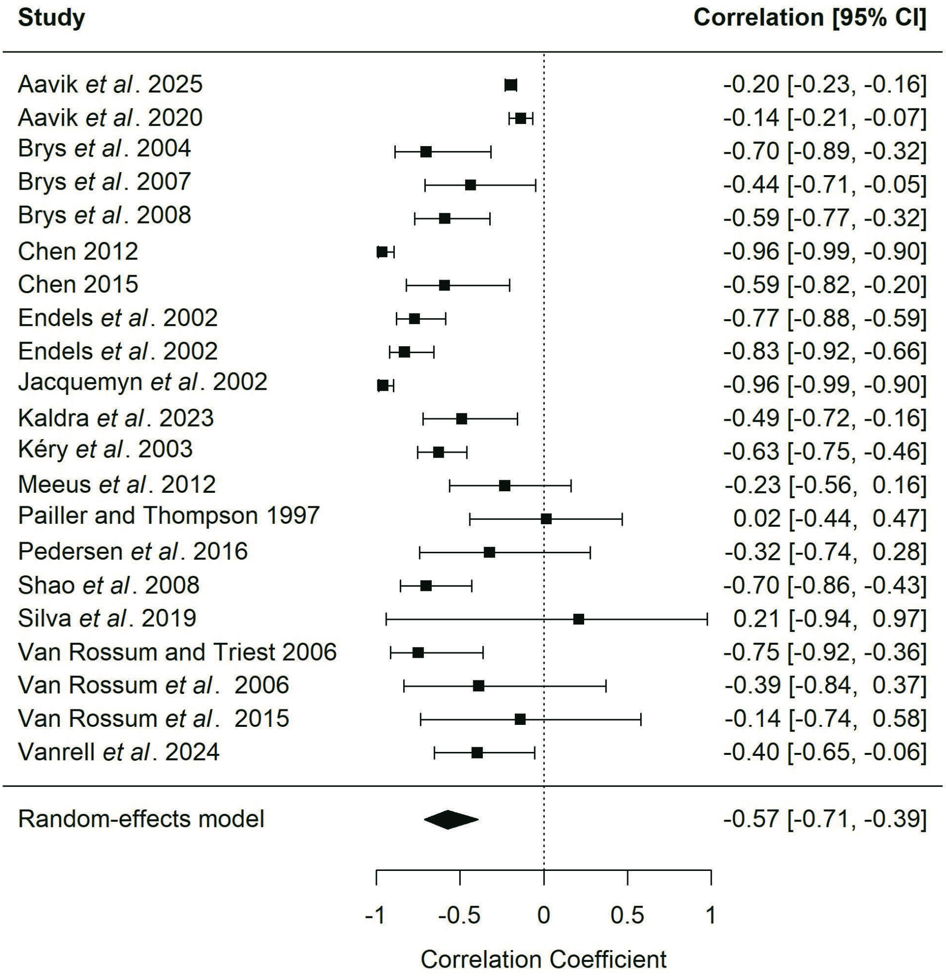

Figure 5. The results of the meta-analysis about the relationship between plant population size and morph ratio bias in distylous plant species (**I**). The study by Endels *et al.* 2002 encompassed distyly recordings from two different years, which were treated as separate observations in the analysis. Pearson correlation coefficients with 95% confidence intervals are shown. The diamond represents the mean correlation coefficient estimated from the model.

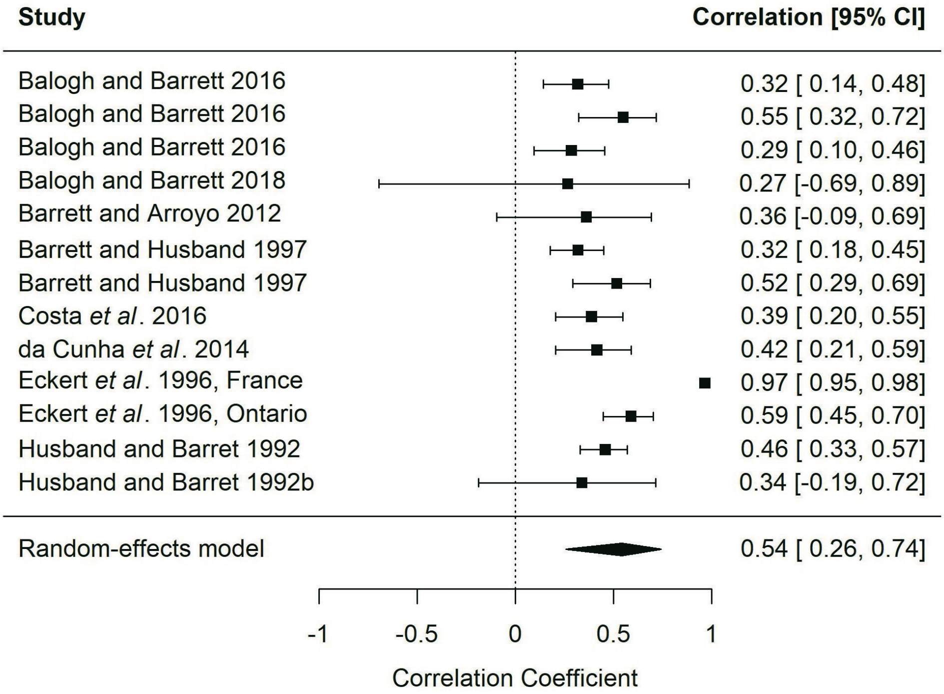

Figure 6. The results of the meta-analysis about the relationship between plant population size and morph evenness in tristylous plant species (**I**). The studies by Balogh and Barrett (2016) and Barrett and Husband (1997) had multiple recordings from different years, which were treated as separate observations in the analysis. Pearson correlation coefficients with 95% confidence intervals are shown. The diamond represents the mean correlation coefficient estimated from the model.

The same trend was also observed for the three other studies: the population size had a significant effect on DEV_{ABS} ($p = 0.005$), with more deviated morph balance in smaller populations. However, the effect disappeared in models with the standardised estimate of absolute deviation (i.e., SES_{ABS}) as a response variable (**II**). The population size significantly affected the absolute deviation, with the highest deviation found in small populations and the lowest in large populations (paper **III**). Furthermore, there were significant differences between the small and large populations and between the medium and large populations ($p < 0.001$; Figure 7). Lastly, in paper **IV**, the absolute morph bias was negatively related to population size, with less deviated values in large populations ($p = 0.003$).

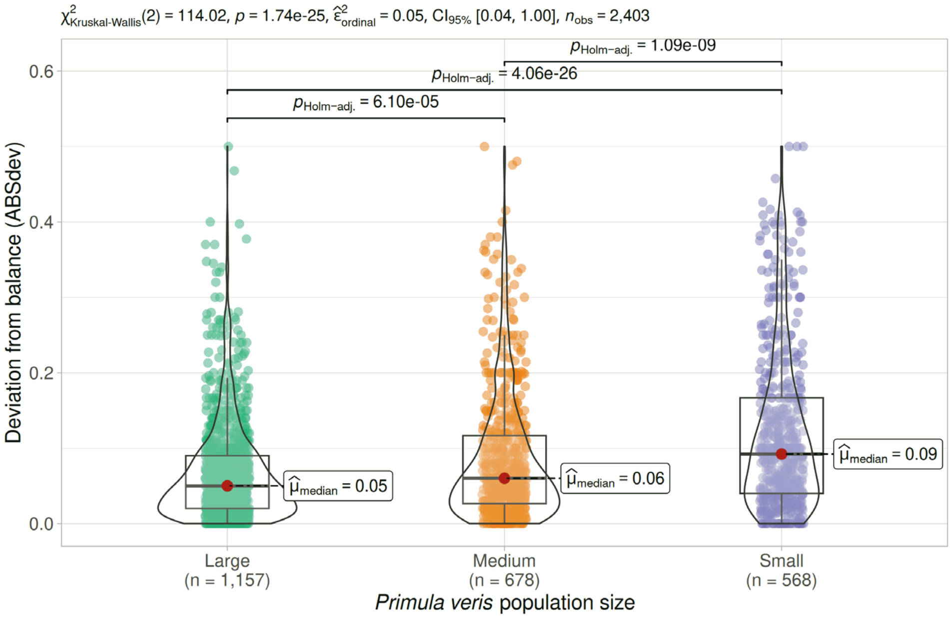

Figure 7. Effect of population size, that is the categorical estimate of population size (small: <100 individuals; medium: 100–200 individuals; large: >200 individuals) on absolute deviation from even morph frequency (ABSdev) in *Primula veris* populations recorded in the frame of the pan-European citizen science campaign ‘Looking for Cowslips’ (**III**). The graph represents the results of the Kruskal–Wallis test; adjusted *p*-values for pairwise comparisons have been estimated based on Dunn’s pairwise test (Dinno, 2015).

3.3. The effect of landscape and environmental variables on morph frequencies

In both citizen science studies (**II, III**), we observed a significant effect of the presence of grasslands on morph deviations as well as on the proportion of S-morphs, although with opposite effects (Table 1). Two morph deviation indices about the absolute morph deviation in paper **II** (SES_{ABS} and DEV_{ABS}), i.e., citizen science study carried out in Estonia, were significantly correlated with each other ($r = 0.86$; $p < 0.001$). Hence, the models using these indices as a response variable revealed similar results. The interaction between the presence of semi-natural grasslands within 100 m of the population and human population density affected the morph deviation from an equal balance ($p < 0.001$; Figure 8), with the balance being more deviated in grasslands allocated in regions with higher human population density. The same trend was observed in the models with directional morph deviation indices ($SES_{S\text{-morphs}}$ and $DEV_{S\text{-morphs}}$) as response variables, which were significantly correlated with each other ($r = 0.922$; $p < 0.001$). The directional deviation in favour of S-morphs was higher with semi-natural grasslands at the observation site or within 100 m of those study populations located in regions with higher human population density ($p < 0.001$).

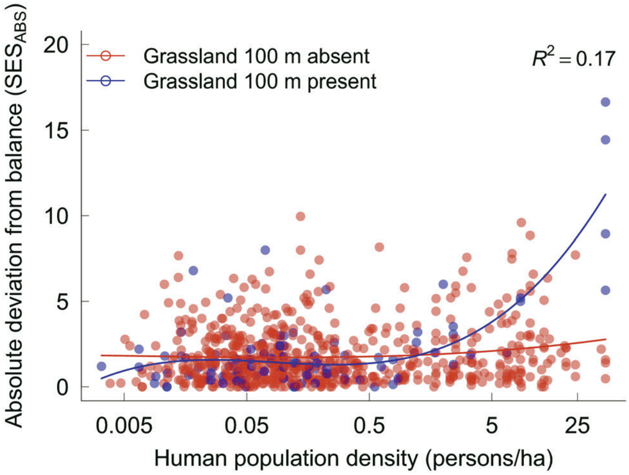

Figure 8. The effect of the interaction of human population density and the presence of semi-natural grasslands at the study population or in the closest proximity (within the buffer with a radius of 100 m) on absolute morph frequencies in the populations of *Primula veris* in Estonia recorded in the frames of the citizen science campaign (**II**). R^2 represents the explained variance in the dataset according to the averaged (using AICc) predictions of the selected models.

In paper **III**, we found that the higher proportion of grasslands was associated with a reduced proportion of S-morphs ($p = 0.003$; Figure 9c). The proportion of S-morphs also decreased with the higher proportion of woodland habitats ($p = 0.007$; Figure 9a). The proportion of S-morphs increased with the higher proportion of built-up areas (p = 0.003; Figure 9b), the higher precipitation of the warmest quarter (p = 0.002; Figure 9d) and higher mean shape index (p = 0.017; Table 1).

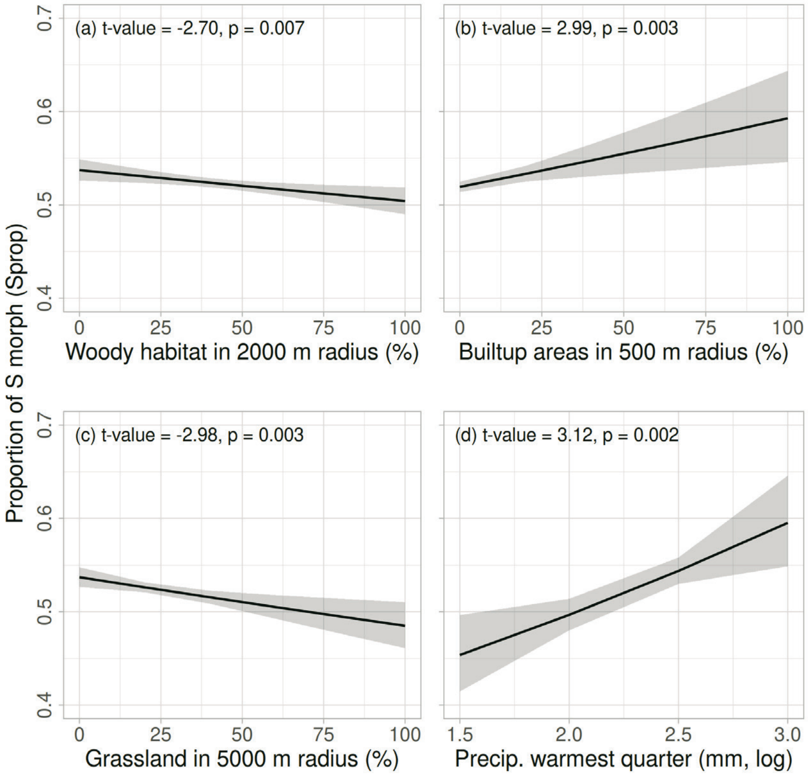

Figure 9. Relationship between the proportion of woody habitats (a), built-up areas (b), grasslands (c), precipitation of the warmest quarter of the year (d) and the proportion of S-morphs (Sprop) of *Primula veris* populations in the pan-European citizen science campaign 'Looking for Cowslips' (**III**). The graph represents the effect of variables with p-value < 0.01 in GLMM model about the effects of climate, land use and environment on the proportion of S-morphs. T- and p-values originate from the final GLMM model. Black lines depict the partial predicted marginal effects for each explanatory variable from the mixed model and grey areas indicate the 95% confidence intervals.

The absolute deviation of morph frequencies from balance increased with a higher proportion of built-up areas (p = 0.002; Figure 10a), higher precipitation in the warmest quarter (p = 0.001; Figure 10b), higher average spring temperatures (p = 0.034) and a higher proportion of cropland (p = 0.028; Table 1). The elevation negatively affected the absolute deviation, i.e., more equal morph frequencies were observed at higher elevations (p < 0.001; Figure 10c) and higher wind speed led to more balanced morph frequencies (Table 1).

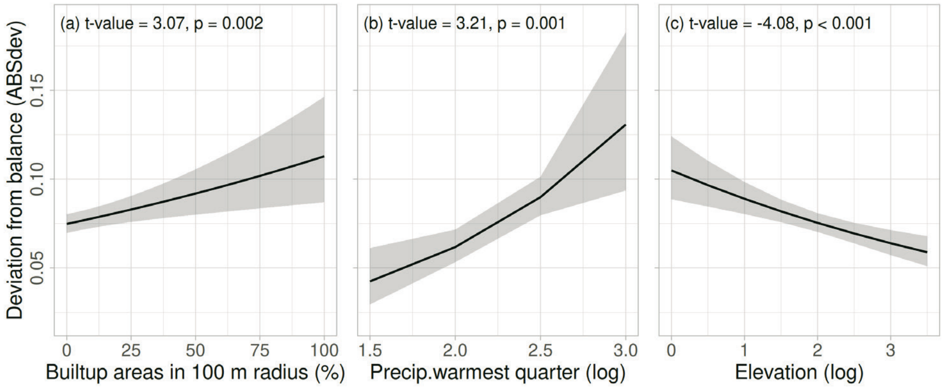

Figure 10. Relationship between the proportion of built-up areas (a), precipitation during the warmest quarter of the year (b) and elevation (c), and the deviation of morphs from equal frequencies/balance (ABSdev) in the populations of *Primula veris* populations observed in the pan-European citizen science campaign 'Looking for Cowslips' (**III**). The graphs represent the effects of variables with *p*-value <0.005 in GLMM model about the effects of climate, land cover and environment on the deviation from morph balance (ABSdev). T- and *p*-values originate from the final GLMM model. Black lines depict the partial predicted marginal effects for each explanatory variable from the mixed model linear model fit, and grey areas indicate the 95% confidence intervals.

Table 1. The directions of significant effects of different land cover and climatic factors on the proportion of S-morphs and the absolute morph ratio deviation of the *P. veris* populations observed in the citizen science campaigns (**II, III**). For paper **II**, the results for the SES_{ABS} and $SES_{S\text{-morphs}}$ indices are shown. A positive direction of the effect means that this factor increased the proportion of S-morphs or increased the morph ratio deviation. A negative direction indicates more balanced morph ratios.

	Proportion of S-morphs		Absolute morph ratio deviation	
	Direction of the effect	*p*	Direction of the effect	*p*
Log (human density) **II**			+	0.019
Grassland (r = 100 m) **II**	+	**<0.001**		
Grassland (r = 100 m): log (human density) **II**	+	**<0.001**	+	**<0.001**
Precipitation in the warmest quarter (mm) **III**	+	**0.002**	+	**0.002**
Average spring temperature **III**			+	**0.034**
Wind speed (m/s) **III**			–	**0.019**
Built-up areas (%; r = 100 m) **III**			+	**0.002**
Built-up areas (%; r = 500 m) **III**	+	**0.003**		
Grasslands (%; r = 5000 m) **III**	–	**0.003**		
Woody elements (%; r = 2000 m) **III**	–	**0.007**		
Cropland (%; r = 1000 m) **III**			+	**0.028**
Mean shape index (r = 2000 m) **III**	+	**0.017**		
Elevation (MASL) **III**			–	**<0.001**

3.4. Findings and genotyping of homostylous phenotypes

Short homostyles (i.e. stigma and anthers at the same position low inside the flower) were found and collected from one population in Sweden and Germany and three populations in Poland (constituting about 10–20% of the individuals in a population). Genotyping of the homostylous samples in parallel with L- and S-morphs from the same populations showed that all homostylous plants lacked the CYP734A50 gene and, thus, were assigned an L-morph genotype.

3.5. The effect of morph bias and morph identity on genetic diversity and differentiation

The observed heterozygosity (H_O) of the populations of *P. veris* in the grasslands of Saaremaa and Muhu islands, Estonia, was affected by the interaction between morph bias and region (**IV**). The H_O of populations in Saaremaa was negatively related to absolute morph bias ($p = 0.019$) but was not correlated with morph bias in Muhu (Figure 11a). I observed the same trend in models with directional morph ratio bias, which showed that H_O was the lowest in the populations of Saaremaa, which were more skewed towards S-morphs ($p = 0.018$; Figure 11b). The inbreeding coefficient (F_{IS}) of the study populations was explained by the interaction between morph bias and region. F_{IS} increased in Saaremaa populations in response to absolute morph bias ($p = 0.002$; Figure 11c) and decreased in response to directional morph bias ($p = 0.006$; Figure 11d), indicating that the highest F_{IS} values were observed in populations dominated by S-morphs.

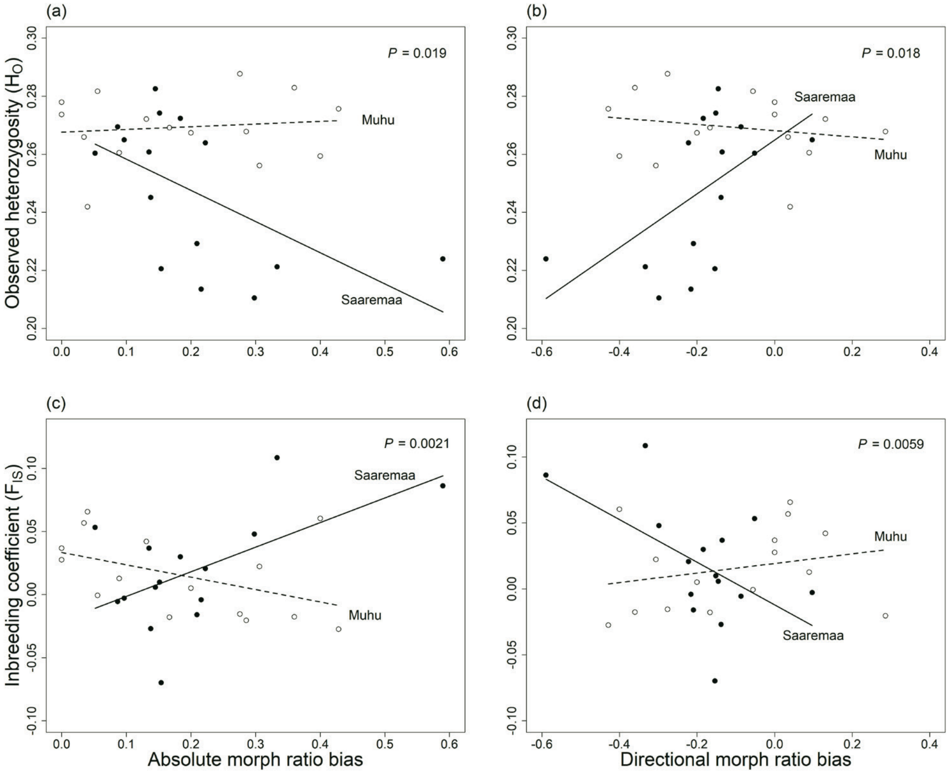

Figure 11. Effects of absolute and directional morph ratio bias in the study populations of *Primula veris* on Muhu and Saaremaa, Estonia (**IV**), on (a, b) observed heterozygosity (Ho) and on (c, d) inbreeding coefficient (F_{IS}). Negative deviation values express the dominance of S-morphs, and positive values indicate the dominance of L-morphs. Empty dots stand for populations from Muhu and filled dots from Saaremaa. Dashed and solid lines represent linear regression lines between observed heterozygosity or inbreeding coefficient and morph ratio bias for Muhu and Saaremaa, respectively. The p-value shows the significant effect of the interaction of morph ratio bias and region on the measures of genetic diversity from the respective best model.

I found no significant differences between the genetic diversity of S- and L-morphs (**IV**). However, the models revealed a significant interaction between morph type and study region (Muhu and Saaremaa). L-morphs in Muhu had higher genetic diversity than L-morphs in Saaremaa. Pairwise genetic differentiation (F_{ST}) was significantly higher in S- than in L-morphs (t-test: $t = –4.57$; $df = 495$; $p < 0.001$). F_{ST} was affected by the interaction between region and morph type ($p = 0.001$), with significantly higher F_{ST} values between S-morphs than L-morphs in the populations of Muhu island but not in Saaremaa.

4. DISCUSSION

Global change has severe consequences for different aspects of biodiversity. My thesis demonstrates the short- and long-term vulnerability of a group of plants characterised by unique adaptation to animal pollination, i.e., heterostyly. One of the most unexpected findings was the dominance of S-morphs, contrary to expectations. My studies show that plant population size is one of the central factors affecting the well-being of heterostylous plant populations (**I, II, III**) not only because of the negative relationship between fitness and population size demonstrated for numerous other plant species (Leimu et al., 2006), but also through the disruption of equal balance of morph ratios in declining populations and related consequences for mating success (**I**). In addition, results based on Estonian and pan-European citizen science campaigns indicate that heterostylous plants can be affected by different landscape and climatic factors (**II, III**). Finally, I show that populations with skewed morph ratios may experience lower genetic diversity (**IV**), which, in turn, can influence populations' viability in the long term.

4.1. The prevalence of S-morphs

One of the surprising findings in my thesis was the constant excess of S-morphs (**II, III, IV**). The large datasets collected in the citizen science campaigns throughout the years (2019–2023) and across Europe provide confidence that this is not just a coincidental observation due to random fluctuations of morph frequencies but rather represents a real trend indicating some advantage of the S-morph. According to a few previous observations, L-morphs of *P. veris* have a slightly higher self-compatibility (Wedderburn & Richards, 1990). Due to the hemizygous nature of the *S*-locus in S-morphs (Potente et al., 2022), crosses between S-morphs produce both S- and L-morphs, while crosses between L-morphs would produce only L-morphs. Therefore, we would assume to see a slight dominance of L-morphs instead, should the conditions (e.g., low legitimate mate availability) favour more intra-morph crosses. Hence, the consistent S-morph prevalence was very surprising, which directed us to look for alternative factors and mechanisms favouring S-morphs, which we discuss in detail below.

First, we assumed that S-morphs may gain an advantage because of their potentially higher genetic diversity. While higher self-compatibility in L-morphs may be favourable in the conditions of limited mating opportunities, it might turn into a disadvantage in the long term when bi-parental inbreeding becomes too prevalent, and would eventually lead to inbreeding depression and related negative fitness consequences (Van Rossum & Triest, 2007). The stronger self-incompatibility in S-morphs might then be an advantage, helping to maintain genetic diversity and higher fitness. However, when comparing the genetic diversity of S- and L-morphs of Estonian grasslands to test this hypothesis (**IV**), I did not find significant morph-specific differences. Yet, we cannot fully rule out this explanation because our study grasslands in Western Estonia are still relatively well-connected, containing occasionally quite large plant populations compared to more fragmented grasslands in landscapes with intensive land use in Estonia or elsewhere in Central Europe. Thus, possible significant differences between morphs may not yet be manifested (Reinula et al., 2021). Interestingly, I did observe a region-specific effect on genetic diversity. In particular, the genetic diversity of L-morphs was higher in Muhu (characterised by higher grassland connectivity) than in Saaremaa (more fragmented grassland systems), while the genetic diversity of S-morphs did not respond to region. This finding suggests that L-morphs might be more prone to the effects of recent landscape change and related grassland connectivity, while S-morphs are able to maintain more stable genetic diversity. In addition, analysis of morph-specific genetic differentiation (F_{ST}) of study populations shows that L-morphs are genetically more similar to each other than S-morphs, indicating more gene flow and reproduction within the L-morphs.

Second, we explored whether some landscape or climatic factors might support the prevalence of S-morphs. The results from the citizen science campaign in Estonia (**II**) revealed that S-morphs were slightly more common in those grasslands, which were located in landscapes with higher human population density. This finding may indicate a possible negative human impact on morph balance. Due to stricter self-incompatibility, S-morphs may be able to better mitigate the negative effects of urban areas and, hence, better adapt to related disruptions than L-morphs. The result was confirmed in the pan-European study (**III**), which showed a correlation between a higher percentage of built-up areas and the proportion of S-morphs, suggesting a possible human impact demonstrating a higher resistance of S-morphs. There was a negative relationship between the proportion of grasslands and the proportion of S-morphs, further indicating that in less disturbed regions with higher areas of suitable habitats, morph ratios are more balanced and do not favour the dominance of S-morphs. The excess of S-morphs was also supported by the mean shape index (patch shape complexity), which might indirectly reflect the human impact through disrupting the area and connectivity of natural and semi-natural habitats.

Third, deviation of morph frequencies from isoplethy might be mediated through disrupted plant-pollinator interactions. Some of the factors we explored may have an impact on pollinators, which then, in turn, influence insect-pollinated plants through different possible pathways. Both a higher proportion of woody habitats and grasslands were related to more equal frequencies of morphs (**III**). Forests and grasslands are important habitats for pollinators, supporting landscape-scale pollinator richness (Ganuza et al., 2022). Higher abundance and richness of pollinators increase mating opportunities between legitimate partners and thus help to maintain more equal morph frequencies. The results also showed a correlation between average summer precipitation and the proportion of S-morphs. Rainfall is one of the main factors potentially influencing plant-pollinator interactions through lessening pollination activity and influencing pollination-related traits, such as nectar dilution (Lawson & Rands, 2019), thus making plants less attractive to pollinators. However, the peak flowering time of *P. veris* is usually in spring, which is why the explanation of the negative impact of summer rainfall on pollination and morph frequencies of *P. veris* is questionable. Interestingly, a study on *P. palinuri* found that relative humidity has an effect on pollen viability (Aronne et al., 2021), with the pollen of S-morphs having a substantially higher viability than the pollen of L-morph. The same study also recorded slightly more S-morphs occurring in populations of *P. palinuri* than L-morphs. The authors argue that the pollen of L-morphs, which is located lower inside the flower and thus can experience higher humidity, contributes to the higher survival of S-morphs (Aronne et al., 2021). Thus, further studies should explore the hypothesis about the role of climate change in disruptions of heterostyly and in particular, in causing the prevalence of one morph over the other.

4.2. The effect of plant population size, land use and climate on morph ratios

Plant population size is one of the most important factors determining the balance of morph ratios. This was demonstrated in studies **II, III** and **IV** and further confirmed in the meta-analysis, including data from almost 30 studies on both distylous and tristylous species (**I**). Populations at equilibrium are expected to maintain equal morph frequencies through negative frequency-dependent selection and disassortative pollination. While morph ratios can fluctuate in small populations due to stochastic processes at the local scale without further long-term consequences for the species, our studies indicate that human-induced landscape change at a larger scale can further increase the occurrence of morph biases and not only in small populations (**II, III**).

Apart from the role of plant population size, the factors impacting the absolute morph balance are, for the most part, the same as those affecting the dominance of S-morphs. Hence, these relationships might, in fact, reflect the excess of S-morphs contributing to the absolute morph balance. These common explanatory factors shared by directional and absolute morph deviation include the precipitation of the warmest quarter and the proportion of built-up areas, which probably affect absolute morph balance through the same pathways as discussed above. I expected the availability of semi-natural grasslands, which is the main habitat type for *P. veris*, to ensure more balanced morph ratios. Interestingly, the citizen science studies show somewhat contrasting results about the impact of grasslands on morph frequencies. Study **II** indicates that the availability of grasslands supports the excess of S-morphs, while paper **III** shows that increasing availability of grasslands at the study locations supports balanced morph frequencies by having a stabilizing effect on S-morphs (Figure 9c; Table 1). The difference between these studies is, however, that in study **II**, we evaluated the presence/absence of grasslands at or in the surroundings of the study location (100 m), while in study **III**, we examined the percentage of grasslands within 5000 meters.

This result supports that the higher availability of grasslands at a larger scale, possibly also indicating better connectivity of grasslands, supports more balanced morph ratios (**III**). The presence/absence of grasslands in the proximity of study populations is a more indirect proxy for the availability of suitable habitats and its effect in the model may be mediated through other factors causing the excess of S-morphs (**II**). We observed that a higher proportion of cropland was associated with stronger morph deviations (with no specific trend in favour of any specific morph), also indicating the negative consequences of intensive human impact on populations of heterostylous plants.

Higher spring temperatures were related to more biased morph ratios, which may be mediated through temperature's effect on the pollinator activity (Kammerer et al., 2021). Interestingly, higher wind speed was associated with more balanced morph ratios. We would have expected the opposite effect as strong wind would inhibit pollinator activity (Hennessy et al., 2021). However, the effect of wind speed may instead reflect the role of some other landscape or climatic factors. For example, in Northern Europe, the large intact habitats are more often near coastal areas, which are characterised by higher wind speeds. Also, contrary to our initial assumptions, we observed more deviated morph frequencies at lower elevations. We expected to see the opposite trend due to populations at higher altitudes generally exhibiting more hostile weather conditions and lower pollinator availability, leading to decreased mating opportunities in heterostylous plant populations, as demonstrated in a study on *P. oreodoxa* (Yuan et al., 2023). Higher elevations, however, might favour more balanced morph ratios due to lower land use intensity and better habitat connectivity still maintained in these regions compared to intensively managed lowland areas (Buzhdygan et al., 2020).

4.3. The consequences of morph ratio bias

Biased morph ratios have several negative consequences for heterostylous plants. Unbalanced morph frequencies decrease the pool of suitable mates and lead to fewer opportunities for reproduction, essentially lowering the effective population size (Kéry et al., 2003). Reproductive success is reduced in populations with biased morph ratios, expressed in a significant decline in the seed set (Ishihama et al., 2006). With strongly biased morph ratios, the more common morph type produces fewer fruits and seeds (Brys et al., 2004, 2007), indicating the negative frequency-dependent selection process. In addition to the direct impacts on reproductive success, the biased morph ratios can affect genetic diversity. I observed that biased morph ratios contribute to lower genetic diversity in *P. veris* (**IV**). The same has been found for other heterostylous plants, such as *Pulmonaria officinalis* (Meeus et al., 2012) and *Primula elatior* (Van Rossum & Triest, 2006a). Although morph bias is often strongly correlated with the reduction in population size (**I**), my study, along with the research by Meeus et al. (2012), suggest that the morph bias itself is a more important variable for heterostylous species explaining the genetic diversity than the population size (Meeus et al., 2012). These two factors usually occur simultaneously, thus putting heterostylous plant populations under the negative pressures of decreasing population size and deviations from equal morph balance, which may exacerbate the risk of local extinction.

We observed lower heterozygosity and higher inbreeding in populations with more biased morph ratios in Saaremaa but not in Muhu. These two islands close to one another still have relatively well-preserved grasslands left. However, the larger island of Saaremaa has experienced slightly stronger land use intensification than the island of Muhu, where grasslands and populations of grassland plants are more connected. Thus, different results observed on these two islands may represent different degrees of the effect of recent habitat fragmentation. In addition, genetic diversity can react to landscape changes with a time lag, and current genetic measures be in fact more reflective of historical landscape structure (Epps & Keyghobadi, 2015), which was also the trend observed in the patterns of plant genetic diversity in the system of our study grasslands (Aavik et al., 2019; Reinula et al., 2021). This is especially important to take into account in studies on long-lived plants, such as our study plant, *P. veris*, which can live up to around 50 years (Ehrlén & Lehtilä, 2002). Therefore, although these grassland populations are seemingly doing fine despite the rapidly changing landscapes, we must consider lagged responses and the role of life history traits of study plants when interpreting the observed patterns.

The genetic diversity of *P. veris* was lower, and inbreeding was higher in populations dominated by S-morphs (**IV**). Previous studies have observed similar trends with the highest genetic diversity in *Pulmonaria officinalis* populations in populations skewed towards L-morphs (Meeus et al., 2012), and lower inbreeding values in L-dominated populations in another study on *P. veris* (Van Rossum & Triest, 2006b). These results may be again explained by the higher intra-morph compatibility of L-morphs, which leads to more potential suitable mates and can mitigate the negative effects of fragmentation in the short term. S-morph-dominated populations can thus be more prone to the loss of genetic diversity. However, continuing higher intra-morph inbreeding may eventually lead to inbreeding depression (Van Rossum & Triest, 2007).

While partial intra-morph compatibility may temporarily relieve the negative pressures of landscape changes, more serious evolutionary consequences are expected to follow if the conditions do not improve. Due to dual negative pressures of lowered availability of suitable mates as well as insufficient pollinator services, the shift from heterostyly to homostyly has been observed in several *Primula* species (Barrett, 2019). Although sightings of homostylous *P. veris* have been rare and their genetic origin unknown, short homostyles (anthers and stigma at the same lower position inside the flower) have been found in woody habitats in Belgium (Brys & Jacquemyn, 2015). So far, the homostylous individuals of other *Primula* representatives have been observed to be long homostyles (anthers and stigma both at the upper position) (Barmentlo et al., 2018; Boyd et al., 1990), and the origin of these homostyles has been determined to have happened due to mutations in the CYP374A50 gene, which controls the length of the style and the female self-incompatibility, thus leading to self-compatible long homostyles (Huu et al., 2022). We expected to see the same result from the genotyping of homostylous *P. veris* samples collected in the citizen science study (**III**), but that was not the case. This implies that the homostylous phenotypes found in our study were probably determined by the genes located outside the *S*-locus, and their exact origin remains unknown. Therefore, we cannot say whether these homostyles had risen due to evolutionary shifts or whether they reflect the phenotypic plasticity of this trait in response to shifts from optimal environmental conditions (Jacquemyn et al., 2012).

4.4. Indices of morph ratio bias

I used different indices of morph ratio balance in the papers of this thesis. There is no best agreed-upon method in literature, as they all essentially show the same outcome. To the best of our knowledge, the more complex index used in paper **II** is the only one that has taken into account the population size aspect so far (i.e., to consider the fact that the same ratio can be observed in small and large populations, but the likelihood of getting such a ratio is much higher in smaller populations). Although most studies include population size in the analysis as a variable for explaining morph ratio bias, the same ratios are used for small and large populations when looking at other aspects to explain morph ratio variation (e.g., climatic and landscape variables). In paper **II**, I also included indices used in previous studies to compare the results. The two indices (i.e., the traditional one and the one taking into account the number of observed plants) were strongly correlated and generally showed almost the same effects. Thus, although the index considering the number of observed individuals when calculating the morph ratio balance is technically a more accurate approach, the more widely used indices (as were used in papers **I, III** and **IV**) are still appropriate.

4.5. Citizen science as a method for data collection

Citizen science (CS) has been recognised as a valuable and increasingly used method for collecting large-scale datasets, particularly in ecological and environmental studies (Bonney et al., 2009; Fraisl et al., 2022). Obtaining observation data at a large scale is often unattainable with traditional scientific methods, which is where citizen scientists can be of help. However, the CS approach poses several challenges. First of all, the main challenge concerns the scientific trustworthiness and validity of data collected in this manner (Aceves-Bueno et al., 2017). To address this possible limitation, there are many protocols and recommendations to improve CS data quality, such as proper design and preparation of protocols, validation of CS observations, participant training, and identifying and documenting limitations in the data (Downs et al., 2021; Fraisl et al., 2020). While we cannot rule out potential errors in the CS data sent to us, we aimed to reduce the error rate as much as possible. First, to ensure high-quality data, we prepared detailed protocols and instruction videos, designed a study task that could be completed by anyone interested, and launched web materials with additional background information. Second, in the pan-European study, we translated all main materials, including the web tool and instructions, into 24 local languages to avoid misunderstanding the tasks because of language barriers. Third, we performed strict data filtering to eliminate possible mistakes and ensure high data quality. We are thus confident in our results and believe that we managed to address these main limitations of CS.

In addition to data collection, another goal of CS can be to communicate different environmental and conservation concerns (Bonney et al., 2009). Although we did not directly assess whether our CS campaign had any impact on the participants' awareness of ecological knowledge, we received a lot of feedback implying it did. Many participants were from schools and kindergartens. Our project turned out to be an excellent outdoor biology lesson through which biology teachers could introduce different topics, such as floral morphology, plant reproduction, landscape changes and nature conservation. Based on the comments from the observers, providing participants with more background information seemed to make them notice even more aspects of the surrounding environment than just required in the observation form, suggesting that the CS project indeed had a broader impact.

4.6. Conservation implications

While all animal-pollinated species are affected by habitat loss and fragmentation (Rodger et al., 2021), the heterostylous mating system introduces additional threats, such as skewed morph ratios and lower availability of suitable mates, which make them even more vulnerable to rapid landscape and environmental change. Reducing pressure from the expansion of urban areas and intensive agriculture and maintaining and protecting habitats suitable for heterostylous species, such as rare semi-natural grasslands in the case of *P. veris*, is essential to support heterostylous plant populations. This helps to ensure that sufficient population sizes are maintained for short-term survival as well as for responding to environmental changes in the long term. As heterostyly is an adaptation to animal pollination, the well-being of pollinators by protecting their habitats and improving connectivity between habitat patches to support pollinator movement is critical as well.

One strategy to support small and isolated plant populations suffering from reduced genetic diversity is through supplementing populations with new individuals, either as plants, seedlings or seeds (Frankham, 2015). A population of a heterostylous species, which consists of only individuals with the same morph, principally has an effective population size of zero, as there are no suitable mating options at the population level. Introducing individuals of the underrepresented or missing morph type may be especially important for heterostylous species to relieve the consequences of biased morph ratios (Endels et al., 2002). Recording and monitoring morph frequencies, in addition to the traditional indicators of conservation success, can provide additional valuable information about the well-being and sustainability of heterostylous plant populations, as balanced morph ratios are vital for successful reproduction and long-term survival.

5. CONCLUSIONS

This thesis shows that heterostylous plant species are affected by various local, landscape-scale and climatic factors through various short- and long-term consequences. Compared to other animal-pollinated species, heterostylous plants are especially vulnerable to these processes and related shifts in pollinator abundance because they also depend on the presence of suitable morphs for reproduction. I found that the population size is of key importance for the fitness and long-term survival of heterostylous plants: both distylous and tristylous species all over the world are negatively affected by decreasing population sizes through disruptions of equal morph balance needed to secure optimal reproductive output (**I**). Besides population size, I show that several other landscape and climatic factors, such as the availability of grasslands, closeness to urban areas and changes in precipitation, can have an impact on morph ratios through stochastic as well as directional processes (**II, III**). These results indicate that preserving natural habitats and limiting negative human impact is important to support the well-being of heterostylous plants through the optimal balance of morph frequencies. The prevalence of S-morphs indicates some advantage over the L-morph. While there were no direct differences in the genetic diversity between S- and L-morphs, I observed lower genetic diversity in S-dominated populations (**IV**). This indicates that, perhaps due to higher self-compatibility between L-morphs, they may reproduce with each other more often. Although within-morph compatibility may be advantageous in the short term, it lowers genetic diversity and the ability to adapt to changing environmental conditions in the long term.

While my thesis led to insights into the heterostyly patterns, it also paves the way for new questions. First, in an era of ongoing rapid landscape and climate change, morph-specific responses to these factors should be followed by studies exploring the mechanisms causing these patterns. Second, as natural processes should ensure an equal representation of both morph types for their long-term survival, it is important to look into how the dominance of S-morphs affects the sustainability of *P. veris'* populations in the long term. Third, the dependence of population genetic diversity on the dominance of one or the other morph in the population raises questions about the level of intra-morph compatibility in S- and L-morphs. Finally, we should consider the interacting impacts of these sets of factors on heterostylous plants. As the loss and fragmentation of natural and semi-natural habitats, as well as climate change, remain persistent and growing threats to biodiversity, it is important that we understand the various consequences of these processes to take steps to prevent further biodiversity loss.

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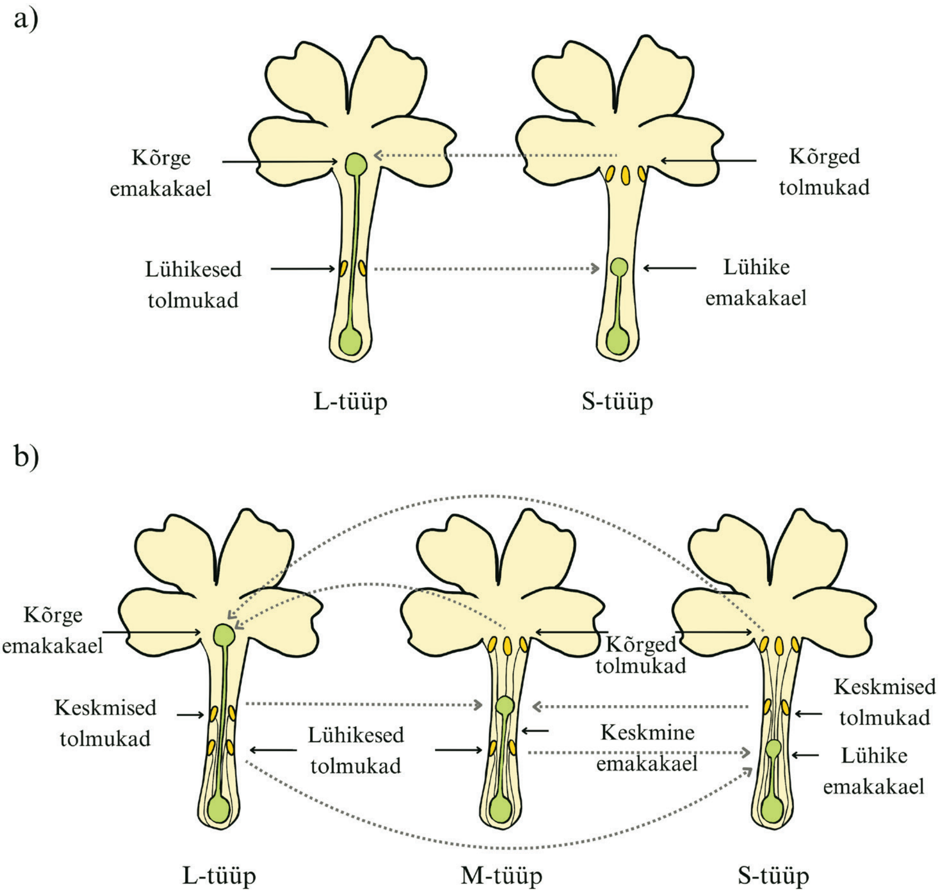
SUMMARY IN ESTONIAN

Erikaelsed taimed globaalmuutuste ajastul: kohalike, maastiku- ja kliimategurite roll

Muutused maakasutuses on põhjustanud ulatuslikku looduslike elupaikade kadu ja killustumist. Elupaikade killustumise tagajärjel on allesjäänud populatsioonid väiksemad ning üksteisest rohkem eraldatud, mis kahandab nende populatsioonide paljunemisedukust. Eriti tundlikud muutustele on loomtolmlevad taimeliigid, mis sõltuvad õietolmu levitamisel putukatest ja teistest loomadest. Selliste taimeliikide hulka kuuluvad ka erikaelsed ehk heterostüülsed taimeliigid. Heterostüülia ehk erikaelsus on taimetunnus, mille puhul koosneb taimepopulatsioon kahest või kolmest morfoloogiliselt erinevast õietüübist. Õietüübid erinevad üksteisest tolmukate ja emaka paigutuse poolest õie sees (Joonis).



Joonis. Skemaatiline joonis erikaelsete taimede morfoloogiast ja õietüüpide vahelistest sobivustest a) distüülsetel liikidel (kaks õietüüpi) ja b) tristüülsetel liikidel (kolm õietüüpi). Katkendjoon tähistab tolmeldamise suunda, mille tagajärjel saab toimuda edukas viljastumine.

Distüülsetel ehk kahe õietüübiga isenditel on ühel õietüübil emakakael lühike ja tolmukad kõrged – selliseid isendeid kutsutakse vastavalt lühikese emakakaelaga tüüpideks (*short-styled,* S-tüüp). Teine õietüüp on vastupidiste tunnustega – emakakael on pikk ja tolmukad lühikesed (*long-styled*, L-tüüp). Tristüülsetel ehk kolme õietüübiga liikidel esineb ka kolmas, keskmine õietüüp, mille puhul on emakakael keskmise pikkusega ja tolmukad emakast nii madalamal kui ka kõrgemal (*mid-styled*, M-tüüp).

Taimede erikaelsuse eesmärk on soodustada tolmlemist eri õietüüpide vahel ja takistada viljastumist sama õietüüpi taimega. Seega sõltuvad erikaelsed liigid tolmeldajatest, kes õietolmu ühelt õietüübilt teisele kannavad. Optimaalseks paljunemiseks peab ühes populatsioonis olema kõiki õietüüpe võrdselt. Elupaikade kadumise ja killustumisega kaasneb sageli taimepopulatsioonide kahanemine. Väiksemates populatsioonides võib aga õietüüpide võrdne tasakaal paigast nihkuda; ebavõrdne õietüüpide osakaal kahandab omakorda populatsiooni paljunemisedukust. See võib negatiivselt mõjutada populatsiooni geneetilist mitmekesisust ja elujõulisust.

Elupaikade kadumine ja killustumine vähendavad ka tolmeldajate liigirikkust ja arvukust. Heterostüülseid liike mõjutavad seega samaaegselt mitu erinevat tegurit: elupaikade killustumise tagajärjel kahanevad populatsioonid, paljunemiseks sobilike partnerite vähenemine, tolmeldajate arvukuse langus ning muutused maastikus ja kliimas. Eelpool nimetatust näeme, et killustunud maastikes ja tolmeldajate arvukuse vähenemise tingimustes võib erikaelsus muutuda ebasoodsaks – tõhusam on olla tolmeldajatest sõltumatum. See võib soodustada evolutsioonilisi muutusi erikaelsuse kaotamiseks ja homostüülia väljakujunemiseks. Homostüülsetel taimedel on emakas ja tolmukad õies samal kõrgusel, mis aitab kaasa isetolmlemisele ja toetab ka sobivust teiste homostüülsete isenditega. Kui erikaelsed taimepopulatsioonid ei suuda uute tingimustega kohastuda, võib neid ees oodata väljasuremine.

Käesoleva doktoritöö eesmärk oli uurida, kuidas mõjutab elupaikade kadumine ja killustumine ning sellega kaasnev populatsioonide kahanemine erikaelseid taimeliike ning millised teised maastikulised ja klimaatilised tegurid võivad õietüüpide sagedusi mõjutada. Samuti soovisin saada põhjalikumat ülevaadet, kuidas mõjutab õietüüpide tasakaalust kõrvalekaldumine erikaelsete taimede geneetilist mitmekesisust, aga ka seda, milline on erinevate õietüüpide geneetiline mitmekesisus. Lisaks soovisin tuvastada võimalikke evolutsioonilisi muutusi erikaelsusega seotud tunnustes. Eelnimetatud küsimustele vastuste saamiseks kasutasin ma erinevaid meetodeid, nagu kirjanduse ülevaate koostamine (**I**), metaanalüüsi tegemine (**I**), harrastusteaduse projektide läbiviimine (**II, III**) ning taimeproovide kogumine ja geneetiline analüüs (**IV**).

Doktoritöö esimene artikkel (**I**) sisaldab põhjalikku ülevaadet paljudest elupaikade kadumise ja killustumise tagajärgedest erikaelsetele liikidele. Koostatud kirjanduse ülevaade on aluseks doktoritöö järgnevatele osadele: ülevaates tuvastati puudujäägid senistes teadmistes ja jõuti järgmiste uurimisküsimuste ja hüpoteesideni. Doktoritöö esimene artikkel hõlmab ka metaanalüüsi populatsioonisuuruse ja õietüüpide tasakaalu seostest. 28-l uuringul põhinev analüüs näitas, et populatsiooni kahanemisel on oluline negatiivne mõju nii distüülsete kui ka tristüülsete liikide õietüüpide tasakaalule. Sama tulemus avaldus ka teistes doktoritöö artiklites (**II, III, IV**). Nimetatud järeldus tõestab, et populatsioonisuurus on üks tähtsamaid erikaelsete liikide õietüüpide sagedusi mõjutavaid tegureid.

Harrastusteaduse projektide elluviimine andis võimaluse uurida erikaelsuse mustreid laiaulatuslikult ning seeläbi tuvastada, millised maastikulised ja klimaatilised tegurid enim erikaelseid taimeliike mõjutavad (**II, III**). Mõlema projekti andmete analüüsis ilmnes maakasutuse oluline roll hariliku nurmenuku õietüüpide sageduste kujunemises – suurema inimmõjuga piirkondades olid õietüüpide sagedused rohkem tasakaalust nihkunud ja ülekaalus olid S-tüüpi isendid. Suurem rohumaade osakaal uuritavate populatsioonide ümber aga soodustas õietüüpide võrdsemat esinemist. Need tulemused viitavad selgelt intensiivse maakasutuse negatiivsele mõjule ja looduslike elupaikade säilitamise olulisusele. Samuti tingis õietüüpide tasakaalust hälbimist ja S-tüüpide suuremat osakaalu suurem sademete hulk. See seos võib peegeldada nii kõrgema niiskuse otsest mõju erinevatele õietüüpidele kui ka sademete mõju tolmeldajate tegevusele, mis omakorda kaudselt õietüüpide tasakaalu võib mõjutada. S-tüüpide ülekaal viitab asjaolule, et õietüübid ei reageeri keskkonnamuutustele ühtemoodi ning õietüüpidevahelised erinevused võivad omakorda mõjutada erikaelsete populatsioonide pikaajalisemat käekäiku.

Taimepopulatsioonides õietüüpide võrdsest tasakaalust hälbimisel võib olla mitmeid tagajärgi. Sobilike partnerite vähenemisel võib killustunud populatsioonides toimuda rohkem ristumist geneetiliselt sarnaste isenditega, mis võib kahandada geneetilist mitmekesisust ja mõjutada populatsiooni võimekust kohastuda muutuvate keskkonnatingimustega. Nimetatud seos õietüüpide tasakaalu ja geneetilise mitmekesisuse vahel ilmnes ka doktoritöö neljandas artiklis (**IV**) – nihkes tasakaaluga populatsioonides oli geneetiline mitmekesisus madalam ning esines rohkem lähiristumist. Sealjuures ilmnes madalam geneetiline mitmekesisus huvitaval kombel just sellistes populatsioonides, kus esines rohkem S-tüüpe. L-õietüüpidel on tähendatud võimekust ristuda teiste L-tüüpi isenditega, mis võib väikestes killustunud populatsioonides olla ajutiselt kasulik ja soodustada paljunemist ning toetada geneetilist mitmekesisust, kuid pikema aja jooksul mõjuda geneetilisele mitmekesisusele hoopis pärssivalt, kui lähiristumine jätkub. See võib olla ka üks põhjusi, miks senistes uuringutes oleme täheldanud just S-tüüpide suuremat osakaalu – S-tüübid võivad tänu oma väiksema võimekuse poolest paljuneda teiste S-tüüpidega olla geneetiliselt mitmekesisemad ja seetõttu erinevates tingimustes tõhusamalt hakkama saada.

Jätkuvad maastikumuutused ja tolmeldajakoosluste üheülbastumine võivad uute tingimustega kohastumiseks kutsuda erikaelsetes liikides esile evolutsioonilisi muutusi – välja võivad kujuneda homostüülsed isendid, mis ei ole enam tolmeldajatest sõltuvad. Üleeuroopalises harrastusteaduse kampaanias (**III**) leiti hariliku nurmenuku homostüülseid isendeid, mille päritolu tuvastamiseks teostasime geneetilised uuringud. Samas ei leidnud me vastupidiselt eeldustele muutusi geeniregioonis, mis teiste nurmenuku perekonna liikide puhul on varem tuvastatud kui piirkond, milles toimuvad mutatsioonid homostüüliat võivad põhjustada. Kuigi homostüülsete hariliku nurmenuku isendite leid on seniste väheste leidude tõttu teaduslikult väga huvitav, ei suudetud selle uuringuga tuvastada hariliku nurmenuku homostüülia tekke geneetilist päritolu.

Käesoleva doktoritöö kirjutamisega saadi mitmeid uusi teadmisi erikaelsetest liikidest ja muutuva keskkonna mõjust neile. Samal ajal tõstatas doktoritöö ka mitmeid uusi uurimisküsimusi – näiteks vajavad veel lähemalt uurimist ühe õietüübi valdav ülekaal ja õietüüpide erinev reageerimine maastiku muutumisele. Looduslikud protsessid peaksid tagama mõlema õietüübi võrdse esinemise ning selle läbi eduka paljunemise ja populatsioonide säilimise. Samas oleks tarvis välja selgitada, kas on veel teisi, näiteks geneetilisi tegureid, mis mõjutavad õietüüpe erinevalt ja aitaksid tasakaalustada S-tüüpide ülekaalu. Samuti aitaksid edasised geneetilised uuringud välja selgitada, kas leitud homostüülid on teistest nurmenuku perekonna homostüülidest evolutsioneerunud teistmoodi muudes geeniregioonides toimunud mutatsioonide tõttu või on tegu keskkonnatingimustest põhjustatud muutustega fenotüübis ehk plastilisusega.

Kuigi maastikumuutused ja tolmeldajate kadumine mõjutab kõiki loomtolmlevaid taimeliike, on erikaelsed liigid nimetatud tagajärgede suhtes eriti tundlikud, kuna nende paljunemisedukus sõltub lisaks tolmeldajatele ka sobilike partnerite ehk sobiva õietüübi olemasolust ja sagedusest populatsioonis. Paigast nihkunud õietüüpide tasakaal kiirendab veelgi tolmeldajakoosluste muutuste võimalike negatiivsete mõjude ilmnemist. Seetõttu võivad erikaelsed taimeliigid olla omamoodi indikaatorliigid ka teistele loomtolmlevatele taimedele, prognoosides nende käekäiku praeguste keskkonnatingimuste muutuste jätkudes. Kuna elupaikade kadumine ja killustumine ning kliimamuutused on üha kasvavad ohud elurikkusele, on oluline mõista nende tegurite erinevaid tagajärgi.

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PUBLICATIONS

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List of publications:

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Conference presentations:

Kaldra, M., Viljur, M.-L., Reinula, I., Aavik, T. (2024). The 'marriage' of heterostylous plants in an era of habitat fragmentation. The 36th annual conference on Plant Population Biology, 02.–04.05.2024. Frankfurt, Germany.

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Other publications:

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Aavik, T.; **Kaldra, M.**; Reinula, I.; Träger, S. (2020). 155 000 nurmenukku aitavad mõista niidukoosluste kadumise mõju. Novaator | ERR.

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Professional self-improvement:

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Training school “Flower Biology and Pollination Ecology: From concepts to practice – module II”, 27.02–03.03.2023, Coimbra, Portugal.

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Reviewer in Heredity, 2024–

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Konverentsiettekanded:

Kaldra, M., Viljur, M.-L., Reinula, I., Aavik, T. (2024). The 'marriage' of heterostylous plants in an era of habitat fragmentation. The 36th annual conference on Plant Population Biology, 02–04.05.2024. Frankfurt, Saksamaa.

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Muud publikatsioonid:

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Bakalaureusetöö juhendamine: Roland Lehemets (2022). Jätkusuutlikkusele suunatud trendid Euroopa põllumajanduses. Tartu Ülikool, Ökoloogia ja maateaduste instituut, Botaanika osakond

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Tartu üliõpilaste looduskaitseringi liige, 2016–

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