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RESEARCH ARTICLE

Large Scale, Open Data, and a Big Tent: Leveraging Collaboration, Transparency, and Inclusion to Advance Macrosystems Biology

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*

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Abstract

1. The distylous plant *Primula veris* has long served as a model species for studying heterostyly, that is the occurrence of multiple floral morphs within a population to ensure outcrossing. Habitat loss, reduced plant population sizes, and climate change have raised concerns about the impact of these factors on morph ratios and the related consequences on fitness of heterostylous species.
2. We studied the deviation of floral morphs of *P. veris* from isoplethy (i.e. equal frequency) in response to plant population size, landscape context and climatic factors, based on a pan-European citizen science campaign involving observations from 28 countries. In addition, we examined the relative frequency of morphs to determine whether landscape and climatic factors disrupt morph frequencies or whether a specific morph has an advantage over the other.
3. Theory predicts equal frequencies of short-styled S-morphs and long-styled L-morphs in populations at equilibrium. However, data from >3000 populations showed a substantial morph deviation from isoplethy and a significant excess of S-morphs (9% higher compared to L-morphs). Deviation of morph frequency from equilibrium was substantially stronger in smaller populations and was not

affected by morph identity. Higher summer precipitation and land use intensity were associated with an increased prevalence of S-morphs.

4. Five populations containing individuals exhibiting short homostyle phenotypes (with the style and anthers in low positions) were found. Genotyping of the individuals at *CYP734A50* gene of the *S* locus, which determines the length of the style and the position of anthers of *P. veris*, revealed no mutations in this region.
5. Our results based on an unprecedented geographic sampling suggest that changes in land use and climate may be responsible for non-equilibrium morph frequencies. This large-scale citizen science initiative sets foundations for future studies to clarify whether the unexpected excess of S-morphs is due to partial intra-morph compatibility, disruption of heterostyly or survival advantage of S-morphs.
6. *Synthesis*. Human-induced environmental change may affect biodiversity indirectly through altering reproductive traits, which can also lead to reduced fitness and genetic diversity. Further research should consider the possible role of pollinators in mediating the ecological and evolutionary consequences of recent landscape and climatic shifts on plant reproductive traits.

KEYWORDS
citizen science, climate change, habitat loss, heterostyly, homostyly, pollination, population size, *Primula veris*

1 | INTRODUCTION

The last century has witnessed unprecedented habitat loss and fragmentation as a result of global land use change (Haddad et al., 2015). Along with climate change, this trend adversely affects several aspects of biodiversity, causing the loss of genetic diversity (Des Roches et al., 2021; Laikre et al., 2020; Schlaepfer et al., 2018), species richness (Tilman et al., 2017), and related ecosystem services (Cardinale et al., 2012). However, not all species respond in the same way to these factors, with some species being more vulnerable to the mentioned threats than the others. In plants, the response of certain species may depend on their life history, functional traits, phenotypic plasticity, and biogeographic origin (De Kort et al., 2021; Hamrick & Godt, 1996). In addition, the effects of fragmentation and climate change on plant mutualistic partners, such as pollinators (Bennett et al., 2020; Rodger et al., 2021), seed dispersers (Donoso et al., 2022) or mycorrhizal fungi (Kiesewetter et al., 2023; Outhwaite et al., 2022; Senapathi et al., 2017), may affect the relative vulnerability of plant species to the factors of global change. Outcrossing, animal-pollinated plants may be more susceptible to climate change and habitat fragmentation than clonally reproducing, selfing, or anemophilous plants due to potential negative impacts of habitat loss and climate change on pollinators (Aguilar et al., 2008; Bennett et al., 2020; Rodger et al., 2021). Furthermore, reduced pollinator abundance and diversity may ultimately cause shifts in plant–pollinator networks (Zoller et al., 2023), potentially triggering selection of phenotypes with reduced herkogamy or self-incompatibility (Bodbyl Roels & Kelly, 2011; Cheptou, 2021; Jacquemyn et al., 2012; Opedal, 2019). However, our understanding of how reproductive plant traits respond to climate change and land use shifts in contemporary landscapes is still limited (Pontarp et al., 2023).

Insufficient pollination poses a particular threat to plant species with floral traits preventing self-pollination, such as heterostyly. Heterostyly is a genetically determined floral polymorphism expressed in the reciprocal positioning of female and male reproductive organs (Barrett, 2019). It has evolved independently across at least 28 plant families (Barrett, 2019). Populations of heterostylous plants comprise two (distylous species) or three (tristylous species) morphs with reciprocal lengths of style and anthers. Differences between morphs may also be expressed in the size and morphology of stigmatic papillae and pollen grains (Costa, Castro, et al., 2017). The study of floral polymorphism has a long history with Charles Darwin being the first to suggest that such reciprocal floral polymorphism helps to ensure outcrossing among plant individuals (Barrett & Shore, 2008; Darwin, 1862; Simón-Porcar et al., 2022). Recent research has shown that heterostylous plant species are often characterised by a genetically determined incompatibility system, promoting disassortative mating (Costa, Ferrero, et al., 2017; Huu et al., 2016, 2022; Keller et al., 2014). Self-incompatibility and associated traits in heterostylous plants, including the position of anthers, the height of style, pollen size differences between morphs, and biochemical self-incompatibility are controlled by a set of tightly linked genes located in the *S* locus, which is hemizygous in one morph type (S-morph) but absent in the other morph (L-morph) in distylous plant species (Huu et al., 2016).

Different morphs usually have balanced morph frequencies in populations at equilibrium (isoplethy). However, drastic landscape changes and a decline in plant population size can cause stochastic deviations from isoplethy (Endels et al., 2002; Kéry et al., 2003), or even lead to a complete loss of one (in distylous species) or two morphs (tristylous plants; Ferrero et al., 2020; Heuch, 1980). Unbalanced morph ratios can reduce the number of suitable mating partners, reproductive output and genetic diversity in populations of heterostylous plants (Kaldra et al., 2023; Kéry et al., 2003; Meeus et al., 2012). Due to disassortative mating and a strong dependence on pollinators, heterostylous plants are thus particularly vulnerable to the negative consequences of habitat loss (Brys et al., 2004), which may eventually lead to increased self-compatibility and a breakdown of heterostyly under conditions of severe pollen scarcity (Wang et al., 2020). Furthermore, shifts in climatic conditions may have significant effects on plant–pollinator interactions. Changes in temperature and precipitation, but also an increasing frequency of extreme weather events may cause phenological decoupling of plant–pollinator networks, altered pollinator foraging patterns, increased pollen degradation and stronger nectar dilution (Lawson & Rands, 2019; Settele et al., 2016). In heterostylous species, higher humidity caused by shifts in precipitation patterns can lead to distinct viability of pollen of different morphs (Aronne et al., 2020). The combined effects of land use and climate change may thus impose an increased threat to plants with complex mating systems, such as heterostyly (Aronne et al., 2020; Stefanaki et al., 2015; Thomann et al., 2013).

Primula veris L. is a distylous commonly used model species in heterostyly research (e.g. Kéry et al., 2003; Nowak et al., 2015; Potente et al., 2022). This herbaceous plant occurs in Eurasian rural and mountainous (particularly in Southern Europe) landscapes with semi-natural grasslands and semi-open forests among their preferred habitats. However, 90% of European semi-natural grassland areas are lost (Dengler et al., 2020) with adverse effects on the occurrence and genetic diversity of many grassland species (Kiviniemi, 2008; Lienert, 2004; Lindborg et al., 2005), including *P. veris* (Brys & Jacquemyn, 2009; Kery et al., 2000; Van Rossum et al., 2004). In populations of *P. veris* at equilibrium, an equal ratio of the two morphs can be expected due to negative frequency-dependent balancing selection (Heuch, 1979). Deviations from isoplethy have been associated with declining *P. veris* population sizes (Aavik et al., 2020; Kaldra et al., 2023; Kéry et al., 2003). Such stochastic deviations of morphs from equal frequencies are not expected to affect the general proportion of morphs across populations because the relative loss of one or the other morph is completely random. A recent study exploring the morph ratio of *P. veris* in more than a thousand populations at its northern distribution limits (Estonia) has demonstrated an overall excess of short-styled S-morphs over long-styled L-morphs as well as an excess of populations where S-morphs dominated (Aavik et al., 2020). This finding suggests that other deterministic processes shape the deviation of morphs, leading to non-random prevalence of one specific morph type over the other. Previous research has found considerable variation of between- and within-morph compatibility and self-fertilisation in the populations of other *Primula* species near their distribution range margin (Shao et al., 2019; Van Daele et al., 2024; Zhang et al., 2021) or along elevation gradients (Yuan et al., 2017). Such disruptions of mating systems can occur when colonisation events lead to small and isolated populations, where self-compatibility is advantageous. Such shifts may further be facilitated by the scarcity of pollinators, favouring the adoption of selfing and homostyly as strategies to ensure successful reproduction (Yuan et al., 2017). Recent evidence shows that these shifts can occur as a result of mutations or rearrangements in genes associated with *S* locus (Mora-Carrera et al., 2023). Besides the natural causes of pollinator shortage, human-induced land use changes decrease pollinator abundance and may cause shifts towards decreased pollinator dependence (Brys & Jacquemyn, 2012; Cheptou, 2021). Despite the demonstrated effect of pollen limitation on plant reproductive strategies and its adverse fitness consequences (Rodger et al., 2021), the shifts in plant mating system have rarely been examined in landscapes strongly altered by human activities (Cheptou, 2021).

To fill the gap in knowledge about the large-scale patterns of morph ratios in heterostylous plants, we explored within-population morph frequencies of *P. veris* across most of its European distribution range. We launched a citizen science campaign in 28 European countries, enabling a broad-scale data collection of morph ratios in European *P. veris* populations. In particular, we aimed to test the following hypotheses:

1. Small population size could lead to significant deviations of morphs from balanced frequencies (Kéry et al., 2003). We hypothesise that these deviations will be stochastic, that is not in favour of one or the other morph.
2. In landscapes with limited grassland and woodland habitats, that is homogeneous landscapes with a higher proportion of arable land and built-up areas, it is expected that there is a stronger deviation from isoplethy as a result of habitat fragmentation. These effects may be both stochastic (independent of one specific morph) or deterministic, that is in favour of one particular morph (Aavik et al., 2020), mediated through the effects of landscape composition on pollinators as shown in research on other distylous species (Shao et al., 2019; Yuan et al., 2017; Zhang et al., 2021). Alternatively, partial intra-morph compatibility in L-morphs in *P. veris*, as shown by limited evidence (Brys & Jacquemyn, 2015; Wedderburn & Richards, 1990), may lead to the dominance of L-morphs over S-morphs in landscapes with low habitat availability. In such conditions, a relatively higher number of suitable mating partners for L-morphs would give an advantage for this morph type compared to S-morphs with almost complete intra-morph compatibility. Another possibility, demonstrated, however, only in

P. elatior (Van Daele et al., 2024), is that S-morphs may become overrepresented in fragmented populations due to combined effects of evolving lower herkogamy, reduced physiological self-incompatibility and more autonomous self-pollination by pollen falling onto the low stigma from the high anthers.

3. Relative morph frequencies, either stochastic or deterministic, can be affected by climatic factors, such as precipitation and temperature, through the possible impact of these factors on plant–pollinator interactions as pollinators are less active in high temperatures and rainy conditions (Ganuza et al., 2022; Jiao et al., 2023; Kammerer et al., 2021; Lawson & Rands, 2019; Teixido et al., 2022). In addition, plant–pollinator interactions can be disrupted by increasing speed of wind due to its negative effect on pollinator activities (Hennessy et al., 2021). We hypothesise that populations in regions with higher wind speed will show greater deviations from equal morph frequencies (isoplethy), as wind-mediated pollen dispersal or disrupted pollination service due to limited pollinators may differentially affect the reproductive success of the two morphs.
4. Finally, we expect that, due to increased human pressure on European rural landscapes and resulting decline in pollinator richness and abundance, we will find homostylous individuals of *P. veris* indicating disruption or breakdown of heterostyly.

2 | MATERIALS AND METHODS

2.1 | Focal species

Primula veris (cowslip) is a perennial light-demanding plant species growing in semi-natural grasslands or semi-open woodlands (Brys & Jacquemyn, 2009; Deschepper et al., 2017) and other semi-open habitats, such as road verges, woodland edges and field boundaries (Van Rossum et al., 2004). Its native range covers most of Europe and parts of Asia, while its introduced range includes the northeastern parts of the USA and Canada (Kew Plants of the World Online, 2023). Here, we focused on the native distribution of the wild-growing populations of *P. veris* (Brys & Jacquemyn, 2009). *Primula veris* is dispersal-limited and its mechanism is mainly restricted to barochory (gravity). Pollen flow contributes to gene flow at further distances (Brys & Jacquemyn, 2009). Floral polymorphism in *P. veris* is governed by an *S* locus supergene encompassing several closely spaced loci determining the traits related to heterostyly (Huu et al., 2020; Li et al., 2016). Long-styled L-morphs (or pins) have a visibly elongated style and short anthers hidden deep in the sympetalous corolla. Short-styled S-morphs (or thrum plants) are characterised by long anthers exceeding the corolla throat and a short style hidden within the latter. The heterostyly supergene (*S* locus) is hemizygous, that is present in short-styled S-morphs and absent in long-styled L-morphs (Huu et al., 2016; Nowak et al., 2015; Potente et al., 2022). In S-morphs, the *S* locus supergene occurs only in one haplotype and is missing in the other, while in L-morphs, both haplotypes lack the supergene.

2.2 | Data collection

2.2.1 | Collection of heterostyly data

To obtain a data set best representing the entire range of the species in Europe, we launched a citizen science initiative 'Looking for Cowslips' in 2021 and 2022 based on a previous successfully implemented campaign in Estonia (Aavik et al., 2020). Citizens from the following countries contributed data: Austria, Belgium, Bulgaria, Croatia, Czech Republic, Denmark, Estonia, Finland, France, Germany, Greece, Hungary, Ireland, Italy, Latvia, Lithuania, Luxembourg, Netherlands, North Macedonia, Norway, Poland, Romania, Slovakia, Slovenia, Sweden, Switzerland, Ukraine and the United Kingdom (Figure 1; Table S1). Due to the absence of active local coordinators, we could not obtain data from all European countries in which *P. veris* occurs, thus lacking data from some countries such as Moldova, Serbia, Kosovo, and Bosnia and Herzegovina.

To enable an easy submission of data via different electronic devices, we created an international website (https://cowslip.science/), encompassing a tool for uploading heterostyly data and geographic coordinates (Methods S1), explanations about the task, and several popular-scientific articles and videos (Methods S2). The tool and the materials were translated into 24 European languages (Methods S2). In addition, longer explanatory videos in Estonian, English, German and Russian provided instructions on morph identification, guidelines on conducting nature observations in an environmentally responsible manner, relevant scientific context for the study, and information about the historic background of heterostyly studies on *P. veris* (Methods S2).

Observers were asked to provide information about the approximate size of the observed population (Small: some plants, up to 100 individuals; Medium: about 100–200 individuals; Large: more than 200 to thousands) and the morph identity of 100 randomly chosen cowslip individuals (or fewer in case of small populations) occurring at least 0.5 meters apart from each other to avoid observations of the same individuals. With appropriate guidance and background materials, identifying S- and L-morphs can be carried out by observers without any prior experience (Aavik et al., 2020). In the northern part of the distribution range of *P. veris*, there are no other morphologically similar species flowering simultaneously and thus, the risk of observing a different species was low in this region. However, to enable the exclusion of misidentified occurrence records in central and southern Europe where other genus members, for example *P. elatior* (L.) Hill or *P. vulgaris* Huds., may co-occur with *P. veris*, the participants were strongly encouraged to upload up to three representative photos of their observations. The multilingual website was accessible for data uploading from the end of March 2021 until the end of June 2022 to account for occurrence records of the phenological variation of *P. veris* along the study's longitudinal, latitudinal and climate gradients.

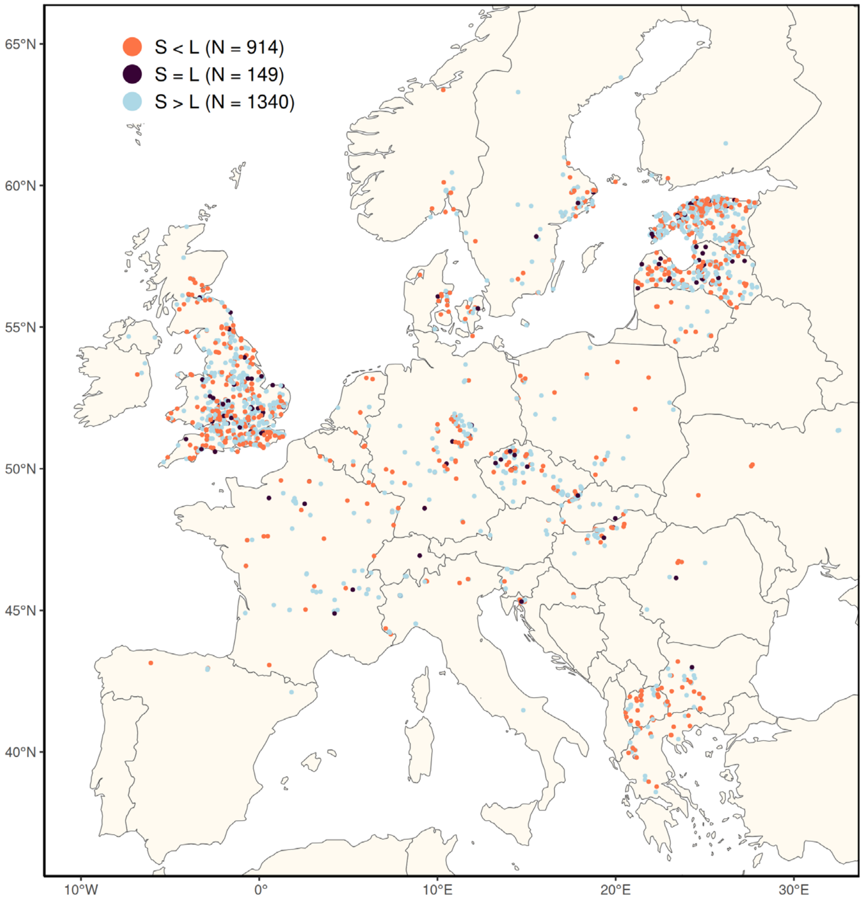

FIGURE 1 Overview of the observed populations of *Primula veris* within the frames of the citizen science campaign 'Looking for Cowslips' in 2021 and 2022. Only populations associated with geographic coordinates retained after quality filtering are depicted (Methods S3). 'S < L' denotes populations where 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. WGS84 was the coordinate system used for creating the map and respective coordinates are expressed in degrees. Figure S1 represents the observations with deviation of morphs as a continuous variable.

2.2.2 | Citizen science data validation

We carefully inspected the quality of all submitted observations before further statistical analyses. The data revision, outlined in detail in Methods S3, included the following steps: (1) exclusion of populations where wrongly identified species were detected based on submitted digital photographic material (about 80% of observations included photos of the study species), (2) revision and correction of any mistakes in geographical coordinates of the observations performed, (3) omission of empty observations or observations with too few observed plant individuals (defined as <10), (4) exclusion of observations with unrealistic number of observed plant individuals and low-quality observations, and (5) retaining only one of spatially adjacent observations (defined as located closer than 100 m to each other) in case of those populations, which were submitted together with spatial coordinates. The campaign platform received information from 5269 sites (i.e. populations; 3475 in 2021 and 1794 in 2022). In 2021, observations were submitted from a total of 32 countries, but observations from only 28 countries qualified for further analysis. In 2022, we received observations from 29 countries, from which 27 were retained for subsequent analysis. In total, 3014 populations were retained after filtering criteria for morph ratio bias assessments. Among these, 2403 had spatial coordinates, enabling a more in-depth analysis of the impact of environmental, landscape and climatic variables.

2.2.3 | Detection and genotyping of homostylous individuals

To encourage observers to report any unusual phenotypes potentially representing a transition from heterostyly to homostyly (flowers lacking the spatial separation of reproductive organs, i.e. exhibiting style and stamens with the same height) in *P. veris*, a description of homostylous individuals was uploaded on the instruction page of the website with guidelines about which steps to follow when such individuals were found. Short homostyles (i.e. with male and female organs with the same height occurring at the lower position) of *P. veris* were encountered in several locations during the campaign. Plant samples from Poland, Germany and Sweden representing the phenotypes of homostyles as well as S- and L-morphs for comparison were collected and genetically analysed at the University of Potsdam. For morph identification, the hemizygous nature of the *S* locus determining heterostyly (Huu et al., 2016; Potente et al., 2022) was used to assign *S* locus genotype to each sample (Methods S4). Specifically, one of the genes in the *S* locus, *CYP734A50*, is present only in S-morphs and absent in L-morphs, and determines the breakdown of plant hormones promoting style growth (Huu et al., 2016). Amplification of this gene of the short homostyles enabled the determination of whether these individuals had a shortened style due to a mutation in this genomic region.

2.2.4 | Climatic, land use and environmental data

To analyse the relationship between heterostyly patterns and land use, climate and environmental context, we extracted different parameters from open-source global databases (Table 1). Information on climate, soil parameters and elevation were obtained for the observation points of *P. veris* populations, for which the geographical coordinates were available. To extract variables characterising landscape structure and land use (land cover, landscape diversity and human population density), we first generated buffer zones with radii of 100, 500, 1000, 2000 and 5000 m around the observation points (1000, 2000 and 5000 m for human population density), and calculated landscape variables for the respective buffers (Table 1). Different buffer sizes were used because we lacked sufficient information on how morph frequencies are affected at different spatial scales.

To determine to what extent spatial patterns in heterostyly depend on temperature and precipitation, we extracted bioclimatic variables (Table 1) from the global WorldClim dataset version 2.1 providing long-term averages for the recent period of 1970–2000 (Fick & Hijmans, 2017). To identify land cover characteristics around every observation point, we used ESA WorldCover, a high-resolution (10 m) land cover dataset (Zanaga et al., 2021). The ESA WorldCover dataset was also used to calculate landscape metrics (Table 1) describing the composition and spatial configuration of the surveyed landscape units. Edge and patch density, mean shape index and mean patch size as measures of landscape configuration and heterogeneity were chosen because these metrics have previously shown good correlations with various aspects of biodiversity (Uuemaa et al., 2009; Walz, 2011), including the genetic variation of *P. veris* (Reinula et al., 2021). For data extraction and calculation, we used Google Earth Engine (Gorelick et al., 2017), Python and QGIS 3.22. Landscape metrics were calculated using the Python library PyLandStats (Bosch, 2019). Human population density data was extracted from the population grid of the Global Human Settlement Layer (GHS; Schiavina et al., 2022). Elevation data, which has been shown to shape pollinator-mediated impact on morph frequency patterns, genetic variation and intra-morph compatibility of distylous plants (Yuan et al., 2023), were obtained from an open-access global dataset AW3D30 (ALOS; Takaku et al., 2020), one of the most accurate free global elevation models (Uuemaa et al., 2020). Information on soil pH and soil organic carbon content (SOC) was extracted from the layer of the global SoilGrids dataset (Hengl et al., 2017). Topographic Wetness Index (TWI) was used to assess terrain-driven variation in soil moisture in the surroundings of the study populations (Kopecký et al., 2021). Note that many of these variables characterising the environment and habitat are based on interpolated data and can thus deviate from the real experienced conditions at the sites. In the final dataset, 2403 *P. veris* populations had information about all landscape, climate and environmental variables.

2.3 | Statistical data analyses

R environment was used for all statistical computing (R version 4.3.1; R Core Team, 2023). As response variables, we used (1) the proportion of S-morphs calculated as $S/(S+L)$ where S and L are absolute counts of S- and L-morphs, respectively (later referred to as 'Sprop'); and (2) 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'). These two different metrics were used to discriminate between the random deviations of morph

TABLE 1 Data sources, spatial resolution and parameters used to associate the climatic, land use and environmental variables within the designated buffers with different radii around the observed populations of *Primula veris* in the pan-European citizen science initiative 'Looking for Cowslips'.

	Dataset	Resolution	Parameter	Metrics	Buffers
Climate	WorldClim	1000 m	Min., max. and average temperature, precipitation, solar radiation, wind speed, water vapour pressure, bioclimatic variables (Table S1)	Mean	Point
Land use	GHS population grid	250 m	Human population density	Mean	Point, 1000, 2000, 5000 m
	ESA Worldcover	10 m	Land cover (crop, built-up, woody, grassland)	Proportion	100, 500, 1000, 2000, 5000 m
			Landscape configuration	Edge density, Patch density, Mean shape index, Mean patch size	100, 500, 1000, 2000, 5000 m
Environment	AW3D30	30 m	Elevation	Mean	Point
	SoilGrids	250 m	Soil organic carbon (SOC)	Mean	Point
			pH (O2)	Mean	Point
	Topographic Wetness Index (TWI)	250 m	Soil moisture	Mean	Point

frequencies from isoplethy (ABSdev) and systematic deviations in favour of one particular morph type (Sprop). Higher values of Sprop would indicate the higher proportion of S-morphs, while lower values refer to the prevalence of L-morphs. Therefore, Sprop can be used for studying the deterministic deviations of morph frequencies from isoplethy as it shows which morph is systematically prevalent. General deviation from isoplethy (ABSdev) does not take into account the fact whether the deviation occurs in favour of S- or L-morphs, and is therefore more suitable for exploring the random deviations of morph frequencies occurring due to stochastic processes (abrupt population collapses as well as colonisation events).

Due to a high number of potentially correlated variables, several steps were carried out to select the final set of variables to be included in the analyses. Because the number of intercorrelated variables was especially high among the climate variables, we first implemented correlation analysis accompanied by Principal Component Analysis (PCA) to select a set of independent climatic parameters as explanatory variables for further analyses (Table S2). The following variables for which the absolute values of intercorrelations did not exceed 0.6 were chosen: mean temperature of the warmest quarter (Bio10), precipitation seasonality (Bio15), precipitation in the warmest quarter (Bio18), average yearly wind speed, average temperature and average solar radiation of the 3 months at the peak flowering time of *P. veris* (i.e. March, April and May), and sum of precipitation of March, April and May.

The landscape structure and land cover parameters estimated in nested buffer radii were highly intercorrelated. We therefore chose one radius for further variable selection based on Akaike Information Criterion (AIC) values of general linear models (GLM) of the response variable in relation to explanatory variables in each buffer radius separately. The buffer radius with the lowest AIC value was chosen for further analysis. The best radius for a given landscape variable could differ between the two response variables, that is Sprop and ABSdev. Variables with substantially right-skewed distribution were log-transformed (human population density, precipitation of the warmest quarter, and precipitation in March, April and May). Correlation analyses between the selected explanatory variables (Tables S2 and S3) indicated that the four landscape configuration measures were intercorrelated, which is why only two of them least correlated with each other (mean shape index and patch density; $r = -0.004$ for Sprop and $r = -0.14$ for the model using ABSdev) were kept for further analysis. This procedure resulted in 18 spatially explicit numerical explanatory variables. In addition, the population size of *P. veris* estimated by the observers was used as a categorical variable with three levels: '<100' (small population size), '100–200' (medium) and '>200' (large).

For both response variables, Sprop and ABSdev, we implemented a general linear mixed model (GLMM) with observation year (2021 or 2022) as a random factor and applied spatial autocorrelation structure. We used the negative binomial family with a log-link function for Sprop because the data was over-dispersed, with the variance greater than the mean. Because the data was strongly right-skewed for ABSdev, we used the GLMM with Gamma family and a log-link function with the function glmmPQL() from R package MASS (Venables & Ripley, 2002). Following the variable selection procedure suggested in Zuur et al. (2009), we first tested different spatial autocorrelation structures using the full model including all explanatory variables. Exponential correlation structure (corExp) gave the best fit and was included in the model. For both response variables, we used 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 ($p < 0.05$) response variables were included in the final models. The results are illustrated with the help of the R package sjPlot (Lüdecke, 2024) using the partial predicted marginal effects plots where the association of each explanatory variable with response variable is demonstrated holding other variables constant. To calculate the marginal and conditional variance explained by the GLMM models, we used r.squaredGLMM() command from the 'MuMIn' package (Barton, 2023). Given that the size of *P. veris* populations is expected to be highly important for explaining morph frequencies yet potentially playing a different role depending on landscape and environmental context, we also tested for significant interactions with population size for each of the 18 spatially explicit numerical explanatory variables. The interactions were tested before the backward selection and because none of the variables showed significant interactions with population size, the interaction terms were not included in the models for backward selection. To clarify which groups of variables affected the response variables most, we extracted R^2 values separately for three sets of models: with (1) the size of the study populations, (2) climatic and environmental variables, and (3) land use variables (land cover as well as human population density) as explanatory datasets, and assessed the relative proportion explained by each of the three explanatory sets of variables through variation partitioning.

To clarify whether Sprop and ABSdev differed significantly from expected values (i.e. 0.5 for Sprop and 0 for ABSdev) in each population, we used exact binomial test and Pearson's chi-squared test, respectively. This analysis was performed separately within each *P. veris* population size class to examine whether the proportion of significant deviations from the expected values differed among small, medium and large populations.

3 | RESULTS

Observations from 3014 sites (considered as populations in analysis) retained after data filtering were used for assessing morph ratio bias, including sites without GPS coordinates, which could not be included in the next step of the analysis about the effect of climate, environment and land cover. Of the 344,757 flowers observed at 3014 sites, 179,796 were S-morphs and 164,961 were

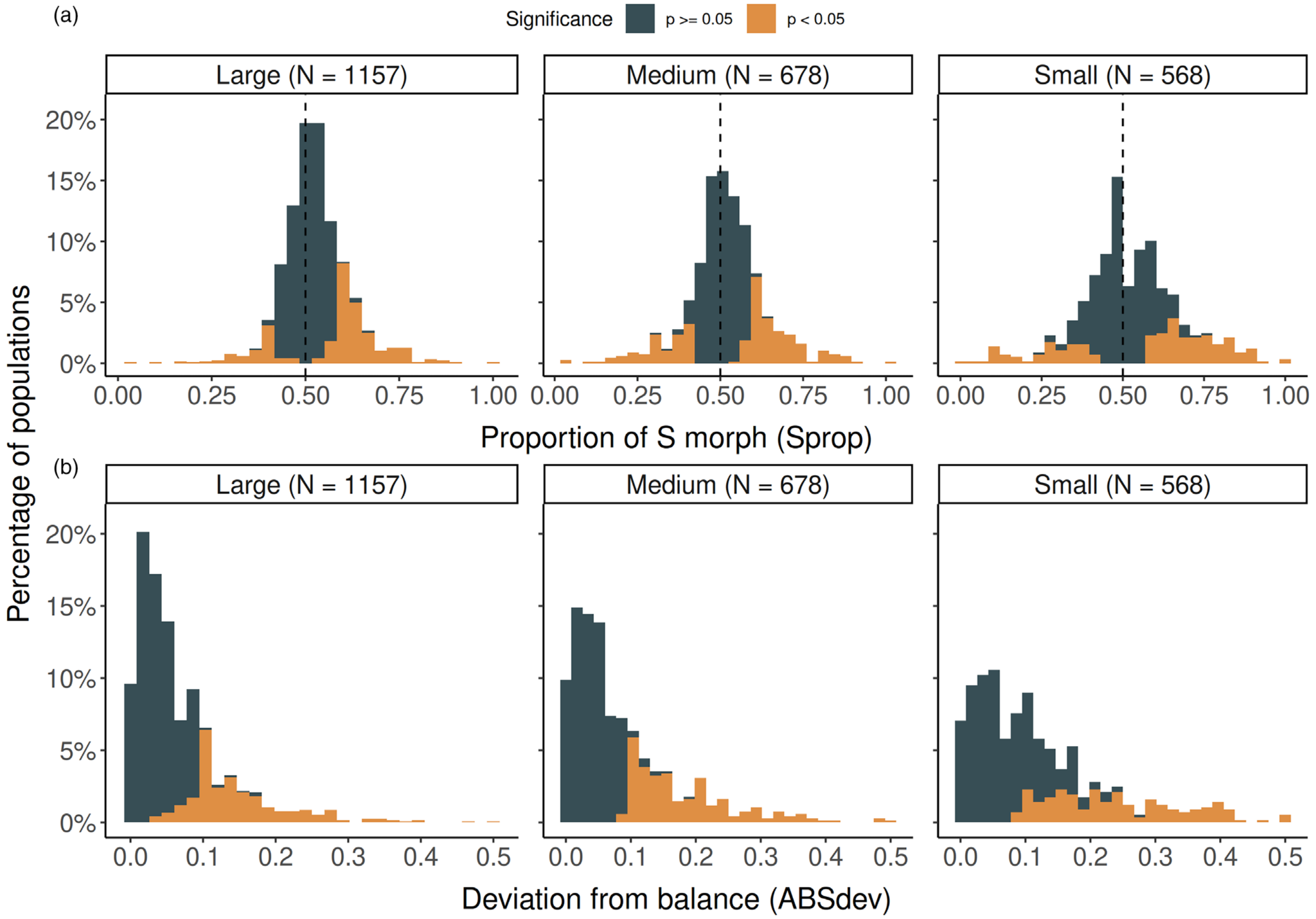

FIGURE 2 The percentage of populations of *Primula veris* in which the proportion of S- and L-morphs (a), and the deviation from equal frequencies/balance (isoplethy) (b) was significantly (orange) or non-significantly (dark blue) different from equal morph frequencies depending on the size class (small: <100 individuals; medium: 100–200 individuals; large: >200 individuals). In panel (a), *x*-axis values <0.5 indicate that there were more L-morphs than S-morphs, *x*-axis values >0.5 indicate that there were more S-morphs than L-morphs. We used exact binomial test (Sprop) and Pearson's chi-squared test (ABSdev) to test the significance of the differences from the expected values (i.e. 0.5 for Sprop and 0 for ABSdev).

L-morphs (i.e. about 100:91 ratio of S- and L-morphs, accordingly). A total of 1667 populations (55.3%) were biased in favour of S-morphs, while in 1107 (36.7%) populations L-morphs dominated. The significant deviance of morph frequencies from isoplethy in favour of S-morphs in the majority of populations was further substantiated by the results of the exact binomial test (Figure 2a). This test also showed that deviations from isoplethy (ABSdev) were observed in all population size classes (small, medium and large). However, the percentage of populations where deviations from isoplethy were not significant was higher in larger populations of *P. veris* (Figure 2a,b).

The analysis of information on climate, land cover and environment based on 2403 observations with known coordinates revealed that the proportion of S-morphs (Sprop) significantly increased with higher precipitation of the warmest quarter (Bio18) (Table 2; Figure 3d). Among the land cover variables, the higher proportion of grasslands (Figure 3a) as well as woodland habitats (Figure 3c) was associated with a reduced proportion of S-morphs, while the higher proportion of built-up areas ($r = 500$ m; Figure 3b) was related to an increase in this response variable (Table 2). In addition, the proportion of S-morphs increased with patch shape complexity (mean shape index). There was a lot of unexplained variation: both marginal (i.e. variation explained by the fixed effects) and conditional (variation explained both by fixed and random effects) pseudo-R^2 was very low (0.0002). Further variation partitioning showed that the variance was equally explained by the set of land use variables and the set of climatic and environmental variables (both of them explaining about 50% each), while the size of populations was of minor importance (6%).

Similarly to the results of the Pearson's Chi-squared test, the GLMM model about the most important predictors of the deviation of morph frequencies from equal (i.e. isoplethy; ABSdev) confirmed that *P. veris* population size significantly affects morph deviation (Table 2). In particular, the highest deviation from equal was found in small populations (<100 individuals) and the lowest in large populations (>200 individuals; Figure 4), with a significant difference between the small and large populations as well as between the medium (100–200 individuals) and large populations. ABSdev increased

TABLE 2 Results (parameter estimate ± standard error, *t*-value and *p*-value) of the final GLMM model on the effects of population size, land use and climatic variables, and elevation on the proportion of S-morphs (Sprop) and on the deviation of morph frequencies from equal, that is isoplethy (ABSdev) in *Primula veris* populations observed in the pan-European citizen science campaign 'Looking for Cowslips'.

	Proportion of S-morphs (Sprop)			**Deviation from isoplethy (ABSdev)**		
	Estimate ± SE	***t*-value**	***p***	**Estimate ± SE**	***t*-value**	***p***
(Intercept)	−0.648 ± 0.005	−135.74	<0.001	−2.572 ± 0.032	−72.32	<0.001
Pop. size (100–200)	—	—	—	0.222 ± 0.042	4.96	<0.001
Pop. size (<100)	—	—	—	0.492 ± 0.045	10.88	<0.001
Precipitation in the warmest quarter (mm)	0.016 ± 0.005	3.12	0.002	0.065 ± 0.021	3.21	0.002
Average spring temperature (°C)	—	—	—	0.049 ± 0.023	2.42	0.034
Wind speed (m/s)	—	—	—	−0.054 ± 0.023	−2.51	0.019
Built-up areas (%; $r=100$ m)	—	—	—	0.054 ± 0.018	3.07	0.002
Built-up areas (%; $r=500$ m)	0.014 ± 0.005	2.99	0.003	—	—	—
Grasslands (%; $r=5000$ m)	−0.016 ± 0.005	−2.98	0.003	—	—	—
Woody elements (%; $r=2000$ m)	−0.015 ± 0.006	−2.70	0.007	—	—	—
Cropland (%; $r=1000$ m)	—	—	—	0.041 ± 0.019	2.43	0.028
Means shape index ($r=2000$ m)	0.012 ± 0.005	2.39	0.017	—	—	—
Elevation (MASL)	—	—	—	−0.092 ± 0.025	−4.08	<0.001

Note: The estimates of the effect of population size has been brought for medium- (100–200) and small-sized (<100) populations and intercept represents the reference (i.e. large population; >200), in relation to which the other estimates are made in both models. The set of variables chosen during the backward selection into the final models were not the same, hence these variables missing in the results of one or the other model are denoted with '—'.

Abbreviations: MASL, meters above sea level; Pop. size, the categorical estimate of the population size of *P. veris* (<100; 100–200; >200); *r*, radius of the buffer for calculating land use variables; SE, standard error.

with higher precipitation in the warmest quarter (Figure 5b) and elevated temperatures during the spring months (March, April, and May; Table 2). Higher wind speed, however, was associated with lower ABSdev (Table 2). Landscape context had a significant effect on ABSdev. In particular, a higher proportion of land under agricultural crops in the surrounding landscape (buffer $r=1000$ m) was related to higher ABSdev (Table 2). Similarly, an increasing proportion of built-up areas led to a higher ABSdev (Table 2; Figure 5a). Elevation had a negative effect on ABSdev, that is more equal morph frequencies were observed at higher elevations (Table 2; Figure 5c). The values for the marginal and conditional pseudo-R^2 were 0.09 and 0.092, respectively. Contrary to the models explaining the variation of the proportion of S-morphs, the variation of the general deviation of morphs from isoplethy was largely explained by the size of the study populations (nearly 75%), while the sets of land cover variables as well as climatic and environmental variables were of much lower importance.

Short-homostylous plants were reported from one population in Sweden and Germany, and in three populations in Poland (constituting about 10%–20% of the individuals in a population). As one of the possible causes of homostyly may arise as a result mutations in the *S* locus, the samples of homostylous individuals were collected for finding evidence for this most frequent cause of homostyly. Genotyping of 10 samples of phenotypically short-homostylous plants in parallel with 6 L- and 6 S-morphs from the same populations showed that all the short-homostylous plants lacked the *CYP734A50* gene at the *S* locus and thus had an L-morph genotype instead (Figure S2).

4 | DISCUSSION

Our study engaged thousands of people in the pan-European citizen science campaign 'Looking for Cowslips'. We explored a fascinating and complex pollination-related plant trait, heterostyly, in different landscapes and across a wide climatic gradient. Citizen science initiatives offer an excellent opportunity to collect data on large-scale ecological processes and to enhance public knowledge about biodiversity outcomes in changing environments (Fraisl et al., 2022; Puchałka et al., 2022; Turrini et al., 2018). The study of morph ratios in *Primula veris* at European scale confirmed that different climatic variables influence the proportion of morphs at European scale. However, at landscape and local scale, plant population size plays the most significant role in maintaining the optimal equal frequencies of S- vs. L-morphs within populations (Aavik et al., 2020; Kéry et al., 2003). However, it also revealed an excess of S-morphs as well as a slight dominance of populations where S-morphs were more abundant (Figure 2), which has not been observed for *P. veris* in studies of comparable spatial extent. In addition, we found that the excess of S-morphs and absolute morph frequency deviations were associated with various land cover and climatic parameters.

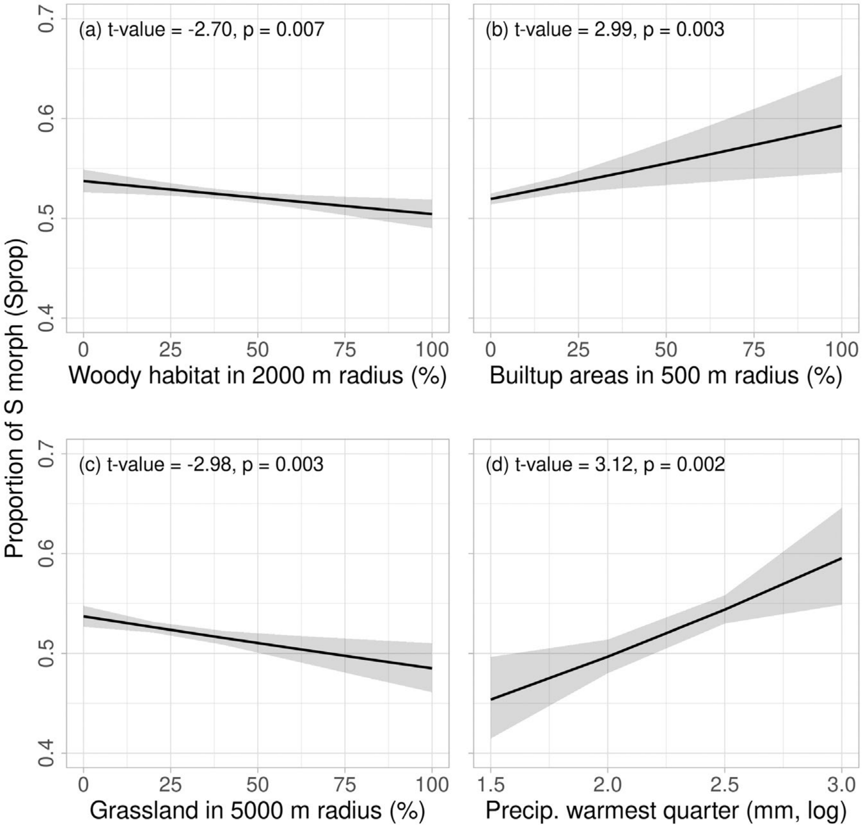

FIGURE 3 Relationship between the proportion of woody habitats (a), built-up areas (b), grasslands (c), precipitation of the warmest quarter of the year (d) and the proportion of S-morphs (Sprop) of *Primula veris* populations in the pan-European citizen science campaign 'Looking for Cowslips'. The graph 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 (Table 2). 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 (Table 2) and grey areas indicate the 95% confidence intervals. The same figures showing also the data points are presented in Figure S3.

4.1 | The excess of S-morphs

Since Darwin's seminal study of floral polymorphisms (Darwin, 1862), *P. veris* has been one of the main model systems for exploring the phenomenon of heterostyly in plants (Barrett, 2019). Subsequent research found morph frequencies in populations of *P. veris* to be equal, though with stochastic morph deviations occurring at the population level (Kéry et al., 2003). Only a study by Lees (1971) in United Kingdom reported an excess of S-morphs, however, in a small number of populations (i.e. 4 populations). In accordance with our findings, a nationwide citizen science study on >1000 *P. veris* populations in Estonia also showed an excess of S-morphs (Aavik et al., 2020). The current study demonstrates that these national snapshots are in fact part of a more general trend. The results, nevertheless, are surprising. The progenies of intra-morph crossings between S-morphs would include both S- and L-morphs because of the hemizygous nature of *S* locus in S-morphs (Potente et al., 2022), while intra-morph crosses between L-morphs would yield only L-morphs due to the lack of *S* locus in the parental L-morph genotypes. The level of intra-morph compatibility is highly variable in different species of *Primula* (Wedderburn & Richards, 1990), but in *P. veris* it has previously been reported that L-morphs have higher partial intra-morph compatibility than S-morphs. Specifically, Wedderburn and Richards (1990) showed that 14.5% of intra-morph crosses between L-morphs were successful compared to that of S-morphs (0.6%). Similarly, Brys and Jacquemyn (2015) observed seed set in about 10% of intra-morph crosses of L-morphs, while no progenies were yielded as a result of the crosses between S-morphs. Thus, L-morphs rather than S-morphs should gain advantage in the conditions of limited legitimate mate availability as a result of intra-morph crosses or even selfing. It may be speculated that the opposite results observed in our study are caused by possible biparental inbreeding arising from such a mating pattern in L-morphs. This, in turn, may give some indirect advantage to S-morphs with strong intra-morph incompatibility, thus resulting in lower inbreeding compared to that of L-morphs. Lower inbreeding in fully outbred progeny, in turn, is related to higher fitness (Angeloni et al., 2011) and can eventually lead to the excess of S-morphs. Nevertheless, a study by Kaldra et al. (2023) did not find significant differences between the genetic diversity of S- and L-morphs in *P. veris* despite a slight dominance of S-morphs in their study system. Hence, this may not be the most plausible explanation for the higher proportion of S-morphs.

Another possible explanation for the S-morph excess is suggested by the recent finding in *P. elatior* where S-morphs in fragmented populations had both reduced herkogamy and lower self-incompatibility compared to S-morphs in connected populations (Van Daele et al., 2024). These trends were less strong for L-morphs. Thus, a combination of three factors, that is (1) the greater chance of autonomous self-pollination from the high anthers to the low style in S-morphs, (2) the reduced herkogamy and (3) reduced self-incompatibility in S-morphs in more fragmented populations could contribute to the S-morph excess, especially in disturbed landscapes. However, S-morphs were slightly more prevalent in all size classes of the current study. Therefore, this explanation would need further studies to confirm its relevance in the system of *P. veris*, including the assessment of herkogamy (i.e. the distance between

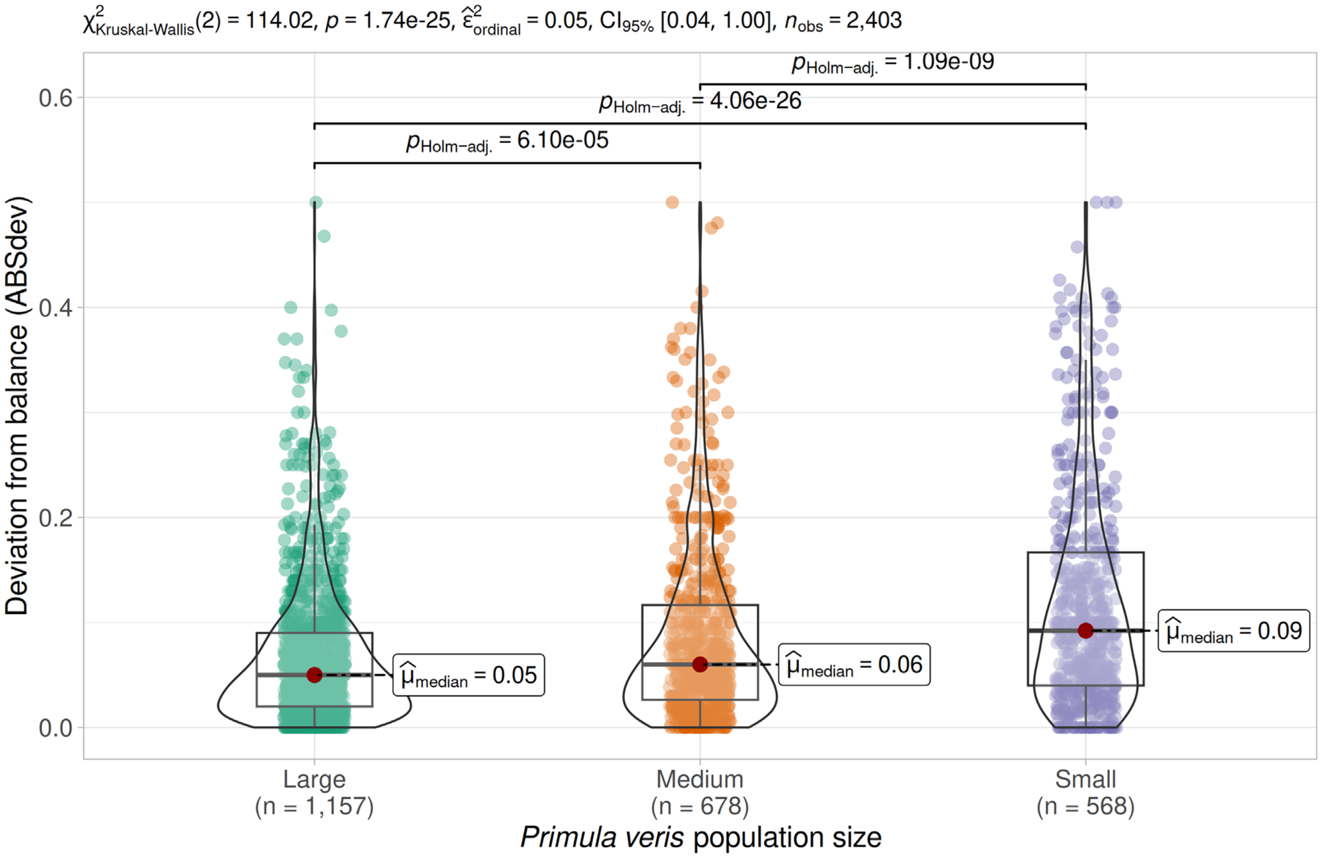

FIGURE 4 Effect of population size, that is the categorical estimate of population size (small: <100 individuals; medium: 100–200 individuals; large: >200 individuals) on absolute deviation from even morph frequency (ABSdev) in *Primula veris* populations recorded in the frame of the pan-European citizen science campaign 'Looking for Cowslips'. The graph represents the results of Kruskal–Wallis test; adjusted *p*-values for pairwise comparisons have been estimated based on Dunn's pairwise test (Dinno, 2015).

anthers and stigma) jointly with evaluating the level of possible self- and within-morph compatibility.

Research in other distylous *Primula* species has shown that considerable variation of intra-morph incompatibility may occur across the gradient from the centre to the periphery of the species' overall distribution range (Shao et al., 2019; Van Daele et al., 2024; Zhang et al., 2021). Estonia, where the dominance of S-morphs has recently been reported (Aavik et al., 2020), represents a hemi-boreal vegetation zone close to the northern edge of *P. veris* distribution (Brys & Jacquemyn, 2009). It may therefore potentially host populations with higher intra-morph compatibility, expectably leading to more skewed morph ratios across populations. If this were the case, S:L ratios would be closer to equilibrium in countries southward from Estonia. Surprisingly, S-morphs were also more prevalent in the core of Europe similarly to the northern part of the study in both years of the campaign. Thus, this finding does not confirm the possible breakdown or disruption of heterostyly when closer to the edge of the distribution range of the studied species. In some other heterostylous species, a huge variation has been shown to occur across species' distribution range. For example, *Oxalis pes-caprae*, which is a tristylous species in its native range, exhibits a full dominance of S-morphs in its introduced range. This has been explained by the occasional founder effects of this particular morph followed by a quick clonal reproduction of the colonising individuals (Ferrero et al., 2020). Founder as well as bottleneck effects are increasingly likely in spatially dynamic landscapes characterising Europe over the past century. Nevertheless, as clonal reproduction is relatively rare in *P. veris* and occurs only over very short distances (Brys & Jacquemyn, 2009), the impact of founder and bottleneck effects cannot fully explain the dominance of S-morphs throughout its whole distribution range.

The abundance and composition of pollinators is an important factor affecting the spatial separation of reproductive organs in plants (Brys & Jacquemyn, 2012). The effects of land use and climate on morph frequencies observed in this study may hence be mediated by the impact of these factors on pollinator communities. A higher proportion of woody habitats and grasslands led to a more balanced frequency of S-morphs (Figure 3). An increase in the proportion of built-up areas, in contrast, was related to a stronger excess of S-morphs (Figure 3). As the proportion of built-up areas was uncorrelated to any of the other land cover variables (Table S3), the result points to the need to explore the role of urbanisation on directing ecological and evolutionary processes, mediated to a large extent by the loss and fragmentation of natural and semi-natural habitats of populations of native species (Rivkin et al., 2019). Forest as a habitat type as well as a higher proportion of forests in the landscape

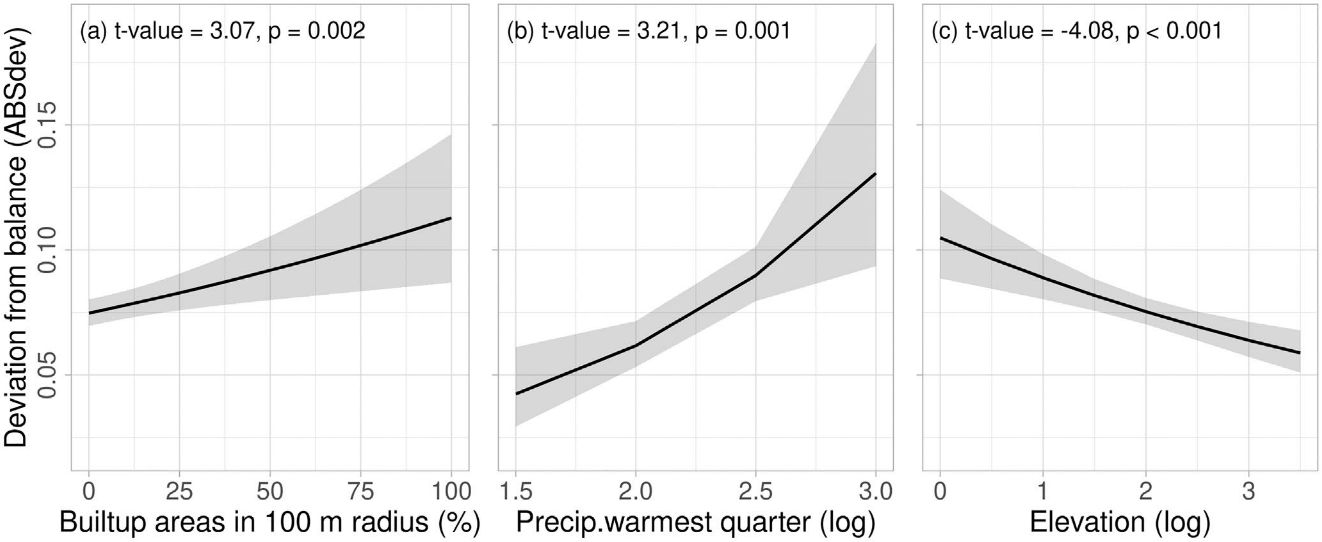

FIGURE 5 Relationship between the proportion of built-up areas (a), precipitation during the warmest quarter of the year (b) and elevation (c) on the deviation of morphs from equal frequencies/balance (ABSdev) in the populations of *Primula veris* populations observed in the pan-European citizen science campaign 'Looking for Cowslips'. 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 (Table 2). Black lines depict the partial predicted marginal effects for each explanatory variable from the mixed model (Table 2) linear model fit and grey areas indicate the 95% confidence intervals. The same figures with data points are presented in Figure S4.

has been shown to support greater richness of pollinators across different pollinator groups, while crops and settlements generally exhibit lower richness of pollinating insects (Ganuza et al., 2022). Similarly, the diversity of most pollinator groups benefits from semi-natural grasslands in contemporary European landscapes (Larkin & Stanley, 2021; Sexton & Emery, 2020). Furthermore, it is not only the diversity, but also the functional composition of pollinators that responds to landscape change. For example, the diversity and abundance of insects with long proboscis – effective pollinators for plants with long-tubed corollas, such as *P. veris* – have experienced a dramatic decrease compared to historic levels in European agricultural landscapes (Dupont et al., 2011).

We also observed a positive effect of precipitation in the warmest quarter on the proportion of S-morphs (Figure 3). Precipitation is one of the main climatic factors with a potential to influence different components of plant–pollinator interactions (Lawson & Rands, 2019). For example, wild bees that are more active in spring are negatively affected by higher precipitation (Kammerer et al., 2021), which may adversely affect pollination of plants flowering at that time. Precipitation may also influence pollination-related traits of plants, leading to diluted nectar, thus discouraging pollinators from visiting the flowers (Lawson & Rands, 2019). However, as most populations of *P. veris* flower before the warmest quarter of the year, the direct effect of precipitation at this time on cowslip pollinators cannot fully explain the relative frequency of pollinator visitation during the peak cowslip flowering. Alternatively, the same pollinator communities may suffer from the negative effects of higher summer rainfall, which may affect their overall viability to persist until the next spring.

The effects of precipitation in the warmest quarter of the year on the different morphs of *P. veris* can also occur via other pathways than mediated through pollinator communities. It is mainly the summer precipitation that determines percolation and retaining of water at a specific location, enrichment of water reservoirs and soil humidity, thus affecting plants during the rest of the vegetation period. This could explain why the precipitation of the warmest quarter is the factor most strongly influencing the geographic distribution of various spring-flowering plants (Puchałka et al., 2023). In *P. palinuri*, a strictly distylous relative of *P. veris*, a previous study (Aronne et al., 2020) found a significant negative effect of relative humidity and temperature on pollen viability. In the same study, substantially higher viability was reported in pollen from short-styled individuals (S-morphs) compared to the pollen from L-morphs. Additionally, there is a slight excess of S-morphs in *P. palinuri* populations (Aronne et al., 2013). The authors suggest that a distinct response of pollen from different morphs to humidity and temperature in the context of climate change and habitat isolation may further contribute to the disruption of distyly syndrome in heterostylous plants. Furthermore, it is not only the external humidity that matters for pollen survival, but also the humidity inside the floral tube (Dahake et al., 2022). If so, we expect that pollen (located deep in the floral tubes) in L-morphs experiences conditions of higher humidity compared to the pollen of S-morphs, and thus pollen viability in L-morphs is further challenged (Aronne et al., 2020). Other previous studies on pollen in heterostylous plant species have observed no difference between the viability and germination of S- and L-morph pollen (Silva et al., 2010; Silva & Vieira, 2013; Wu et al., 2010). Yet, in these studies, the morph frequencies were equal in contrast to the findings of the study by Aronne et al. (2020). Hence, additional research is needed to clarify whether differences in pollen viability occur in *P. veris* and how such patterns could impact the frequencies of S- and L-morphs. Furthermore, it is important to determine the intra-morph fertilisation probability in S- and L-morphs of *P. veris* in order to explore the possible interacting effects of distinct pollen viability and the strictness of inter-morph incompatibility on morph frequencies. When distinct morph-dependant pollen survival along with higher intra-morph self-compatibility in S-morphs finds confirmation in *P. veris*, it can be hypothesised that the disruptions in heterostyly will increase because of climate change.

4.2 | The role of plant population size, land use and climate on morph isoplethy

While S- and L-morphs are expected to occur at equal frequencies in distylous plant populations at equilibrium conditions, it has been demonstrated that in smaller populations, morph frequencies may be unequal in both distylous (Kéry et al., 2003) as well as tristylous species (Balogh & Barrett, 2016). Our results generalise this phenomenon as unbalanced morph ratios, regardless of morph identity, differed between all population sizes, with small populations showing the highest and large populations the lowest deviations (Figure 4). Although a 1:1 morph ratio was also observed in small populations, stronger deviations were much more likely in populations with fewer individuals (Figure 2b), suggesting that population size indeed helps buffering against stochastic deviations in morph frequencies. It also indicates that to facilitate balanced morph ratios and related fitness, populations should be much larger than one hundred individuals to consider the lower effective population size (Ne) caused by the disassortative mating pattern of *P. veris*. The findings herein support recent suggestions referring to populations with $Ne < 50$ as extremely susceptible to genetic erosion (Hoban et al., 2020), which can further be exacerbated by skewed morph ratios in heterostylous plants (Kaldra et al., 2023; Meeus et al., 2012).

Among land cover variables, higher proportion of cropland and built-up areas in the surroundings of the study populations were associated with stronger deviations of morph frequencies (Figure 5). This finding further confirms the negative consequences of intensive human impact on plants with a heterostylous mating system. In particular, the conversion of former grasslands into intensive agricultural land or/and urban sprawl may have led to population collapses, thus causing stochastic changes in the frequency of one or the other morph (Kéry et al., 2003). Nevertheless, more detailed evaluation on the distribution and connectivity of habitats suitable for *P. veris* should be carried out to explain the potential mechanisms leading to the deviations of morphs in response to specific local and national land cover changes. It has to be noted that, although the ESA WorldCover spatial dataset was shown to perform the best compared to the other global land cover maps after validation (Xu et al., 2024), this data still represents a coarse proxy of habitat suitability. First, the accuracy of ESA WorldCover data at global scale was shown to be about 84% compared to national and regional maps used as the reference for validation (Xu et al., 2024). Second, higher inaccuracies are more likely to involve such land cover types, which are spectrally more similar, including grasslands, flooded vegetation and shrubs, and thus prone to misclassification. Such inaccuracies, particularly in land cover classes encompassing the likely habitats of *P. veris*, may partly explain the relatively low proportional variance unravelled by land cover variables, and warrant using more detailed spatial data at local- and national-scale studies to assess the effects of the loss and isolation of habitats on the patterns of morph frequency deviations.

Higher precipitation in the warmest quarter of the year and increased spring temperature were related to stronger deviations of morph frequencies from isoplethy. The effect of precipitation is likely partly reflecting its role in causing S-morph excess. It thus may also be explained by higher rainfall and general humidity influencing either plant–pollinator interactions in general and/or higher pollen survival of S-morphs in particular, as described above. Nevertheless, higher spring-time temperature was observed to be associated with random deviations of morph frequencies unrelated to morph type. While increasing temperature may also lead to negative consequences for pollinators by causing overheating (Kammerer et al., 2021), the spring temperatures should not reach as critical values. Alternatively, warmer spring temperature may indicate that the conditions for pollinator overwintering have also been warmer, which in turn can have adverse effects on those wild bee species, which are more active in spring and hence important pollinators of *P. veris* (Kammerer et al., 2021). Yet, mechanisms leading to stochastic deviations of morph frequencies remain unexplained. Interestingly, we observed a higher average wind speed to be related with more balanced morph ratios, although we expected that due to the negative effects of high wind speed on pollinator activities (Hennessy et al., 2021), this parameter would tend to cause skewed morph ratios. It is, however, possible that the wind speed gradient resembles variation in some other unmeasured variable. For example, in Northern Europe (e.g. Sweden, Estonia and Denmark), more intact habitats suitable for cowslips and their pollinators are likely to occur near coastal areas, which are characterised by higher wind speed.

Surprisingly, we observed a stronger deviation of morph frequencies from isoplethy at lower elevations (Table 2). Populations at higher altitudes may exhibit increased stochasticity in pollinator availability and visitation rate due to hostile weather conditions with consequent effects on morph ratio patterns. For example, populations of the Chinese endemic, *P. oreodoxa*, a congener of *P. veris*, have more variable morph ratios at higher altitudes, which is directly related to the lower effectiveness of pollination in these regions (Yuan et al., 2023). However, contrary to the findings of Yuan et al. (2023), we observed a general stabilising effect of elevation on morph deviation in our study (Table 2). This is most probably related to lower land use intensity and better habitat connectivity at higher altitudes compared to lowland regions (Buzhdygan et al., 2020). It is also possible that other altitude-related variables not considered in the present study, but with possible impact on pollinator communities, for example aspect (Minachilis et al., 2021), would help to shed more light on morph frequency patterns along elevation gradients.

4.3 | Occurrence of homostylous individuals of *P. veris*

Several populations of *P. veris* observed in the campaign contained homostylous individuals. All of these individuals were short homostyles, that is with both style and anthers situated at the lower position. Genotyping of these individuals at the gene *CYP734A50* of *S* locus revealed that all of them had a L-morph genotype (Figure S2), suggesting that their low styles were most probably due to mutations outside of the *S* locus. Heterostyly has shifted to homostyly in several *Primula* species (Barrett, 2019; de Vos et al., 2014; Gilmartin, 2015; Mast et al., 2006), generally as a result of insufficient pollinator service or low availability of compatible mates in small populations. Essentially all these transitions occurred by mutations to the *CYP734A50* gene, which jointly controls style length and female self-incompatibility type, thus leading to self-compatible long homostyles (i.e. homostyles with both male and female organs at the upper position) that reproduce predominantly by selfing (Huu et al., 2022). For example, in the closely related *P. vulgaris*, this transition due to mutations in *S* locus has occurred multiple times by independent mutations (Mora-Carrera et al., 2023)—a finding that, unexpectedly, found no confirmation in our study involving more than 500,000 individuals of *P. veris*. Similar *P. veris* homostyles with a low positioning of anthers and stigma have previously been found in woody habitats (about 10% of observed individuals) in Belgium, while reciprocity of reproductive organs in adjacent grassland populations was strict and stable (Brys & Jacquemyn, 2015). The self-incompatible short homostyles in this latter study represented an L-morph genotype similar to those discovered in the present study (Figure S2). By analogy, it therefore appears likely that the short homostyles found in the Polish populations (making up 10%–20% of the number of individuals in these populations), in Germany and in Sweden, also remain self-incompatible, even though this was not examined. It is hence likely that homostylous phenotypes in the present study were determined by genes located outside *S* locus, which has been offered as a possible explanation for the occurrence of self-incompatible homostyles (Barrett, 2019; Matsui et al., 2004).

Other studies have shown that heterostylous species may respond to strong shifts in pollinator communities after only a few generations by evolving towards self-compatible long homostyly (Liu et al., 2022). Against this background, the absence of self-compatible long homostyles of *P. veris* remains an intriguing issue. Consistent with the latter, we are only aware of a single old literature report of such a long homostyle of *P. veris* (Scott, 1864). Thus, it still seems unclear whether the shift from heterostyly to self-compatible homostyly could represent a viable evolutionary path for *P. veris* to 'escape' from low-pollinator or low mate-availability environments, becoming increasingly frequent due to environmental change.

5 | CONCLUSIONS

At an evolutionary time scale, heterostyly has an advantage over homostylous mating system and selfing (de Vos et al., 2014; Yuan et al., 2017). However, land use and climate change may threaten the balance of equal morph frequencies needed to ensure these benefits. The current study explored morph ratios in *P. veris* populations with the help of thousands of citizen scientists throughout Europe and detected a significant excess of S-morphs across the species distribution range. The proportion of S-morphs was close to equal with L-morphs in landscapes covered by a higher proportion of grassland and woodland habitats, while an increase of built-up areas led to the prevalence of S-morphs. The relationship between precipitation of the warmest quarter and the proportion of S-morphs may be due to a shift in plant–pollinator interactions responding to precipitation, or the differential reaction of pollen from distinct floral morphs to overall humidity. The significant role of land use and climatic variables in determining the systematic higher frequency of one morph over the other implies that these factors require further attention to explain the mechanisms causing these unexpected patterns. The stronger impact of plant population size on general morph frequency in populations of *P. veris* compared to the role of other sets of factors (such as climate and land cover) confirm the vulnerability of small populations to stochastic shifts of morph ratios. This study carried out at an unprecedented geographic scale is setting solid foundations for future studies assessing the susceptibility of the plants with heterostylous breeding system to climate change and landscape alteration not only in *P. veris*, but also in other plants characterised by such a complex mating system.

AUTHOR CONTRIBUTIONS

Tsipe Aavik was responsible for leading the campaign. Tsipe Aavik, Marianne Kivastik, Iris Reinula and Martin Zobel conceived the project idea. Marianne Kivastik, Iris Reinula, and Kertu Hool helped to set up the citizen science campaign and to promote the campaign among different target groups. Sara A. O. Cousins, Jan Plue, Sabrina Träger, Marta Barberis, Arjen Biere, Anikó Csecserits, Eleftherios Dariotis, Grzegorz Grzejszczak, Živa Fišer, Margaux Julien, Marcin Klisz, Nikos Krigas, Attila Lengyel, Zuzana Münzbergová, Baudewijn Odé, Hana Pánková, Radosław Puchałka, Theodora Petanidou, Ricarda Pätsch, Froukje Rienks, Ioulietta Samartza, Julie K. Sheard, Bojana Stojanova, Joachim P. Töpper, Georgios Tsoktouridis and Spas Uzunov were responsible for the country-level communication and management of the campaign. Michael Lenhard and Cuong Nguyen Huu were responsible for genotyping the homostylous phenotypes of *Primula veris*. Triin Reitalu carried out the statistical analyses. Marianne Kivastik, Iris Reinula, Evelyn Uuemaa, Desalew M. Moges, Alexander Kmoch and Tsipe Aavik contributed to the collection of additional spatial data and filtering of citizen science data. Tsipe Aavik wrote the first draft and all authors, including Sílvia Castro, Hans Jacquemyn, Ülo Niinemets and Meelis Pärtel, provided input and approved the final version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interests. Hans Jacquemyn is an Associate Editor for *Journal of Ecology*, but took no part in the peer review or decision-making process for this manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Heterostyly data is available at the Dryad Digital Repository: https://doi.org/10.5061/dryad.k3j9kd5jj (Aavik et al., 2024). Climatic, land use and environmental data is available upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. The distribution of sampled study populations of *Primula veris* along with the deviation of morph frequencies from isoplethy.

Figure S2. The results of the genotyping of *CYP734A50* of the samples of *Primula veris*.

Figure S3. Relationships between the proportion of S-morphs and land use and climatic variables with model prediction and raw data points.

Figure S4. Relationships between morph deviation from equal frequency and land use and climatic variables with model prediction and raw data points.

Methods S1. The list of questions asked from the citizen scientists on the data uploading platform of the citizen science campaign “Looking for Cowslips”.

Methods S2. The list of the main communication channels and tools with corresponding web links used in spreading the information.

Methods S3. Data filtering criteria and the corresponding number of excluded observations of the *Primula veris* heterostyly observations.

Methods S4. Laboratory protocol for the determination of mutations at S locus of *Primula veris*.

Table S1. The list of institutions who contributed to the citizen campaign ‘Looking for Cowslips’.

Table S2. Correlation coefficients and principal coordinate analysis (PCA) of the preliminary set of climatic variables in the citizen science campaign ‘Looking for Cowslips’.

Table S3. Correlation coefficients of variables included in the analysis about the effect of climatic, environmental and land-use variables on the proportion of S-morphs.

Table S4. Correlation coefficients of variables included in the analysis about the effect of climatic, environmental and land-use variables on the deviation of morphs from isoplethy.

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