



Original article

Region and site conditions affect phenotypic trait variation in five forest herbs

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ABSTRACT

Phenotypic plasticity is the ability of organisms to express different phenotypes under different environmental conditions. It may buffer individuals both against short-term environmental fluctuations and long-term effects of global change. A plastic behaviour in response to changes in the environment may be especially important in species with low migration rates and colonization capacities, such as in many forest plants in present-day fragmented landscapes. We compared the phenotypic trait variation (used as a proxy for the amount of phenotypic plasticity) of five forest herbs (*Brachypodium sylvaticum*, *Circaea lutetiana*, *Impatiens noli-tangere*, *Sanicula europaea* and *Stachys sylvatica*) between two regions in Germany that differ in their overall environmental conditions (Bremen in the northwest, Freiburg in the southwest; 5 species \times 2 regions \times 8–15 populations \times 25–50 individuals). In addition, we measured light intensity and important soil parameters (soil pH, moisture, K, P and N) in all populations. We found consistent differences in trait variability between the two regions in several species. In *Brachypodium* and *Stachys* both vegetative and reproductive traits were more variable in Freiburg. Similarly, reproductive traits of *Impatiens* and *Sanicula* appeared to be more variable in Freiburg, while in both species at least one of the vegetative traits was more variable in Bremen. Mean local environmental conditions also affected trait variation; in most of the species both vegetative and reproductive traits were more variable in sites with higher nutrient contents and higher light availability. Across all traits and both regions, seed or fruit production was most variable. In summary, at least some of the studied forest herbs appear to respond strongly to large-scale environmental differences, showing a higher trait variability in the more southern region. Given the assumption that phenotypic trait variation is positively associated with phenotypic plasticity, we conclude that these populations may more easily respond to changes in the environment.

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1. Introduction

In the face of human-induced global environmental change, natural plant populations have to respond and adapt to multiple changes in the abiotic and biotic environment. For instance, changing temperature regimes and increasing climatic variability (Walther et al., 2002), as well as changes in the environment associated with habitat destruction and fragmentation (Travis, 2003), have been shown to threaten local populations and overall biodiversity (Parmesan, 2006). To cope with the predicted increase in temperature plant species may shift their range to higher elevations or latitudes (Thuiller et al., 2008; Lenoir et al., 2008; Harrison et al., 2010). However, because of low dispersal rates or colonization capacities not all species will be able to track the climate to which they are currently adapted, especially if landscapes are highly

fragmented (Jump and Peñuelas, 2005). Hence, to forecast the distribution of species in a changing environment, one has to consider not only the ability of species to colonize new sites, but also their ability to persist in current sites (Thuiller et al., 2008), especially in less mobile species groups such as plants.

Local persistence is to some extent determined by phenotypic plasticity, i.e. the ability of a given genotype to render different phenotypes depending on the environment (Schlichting, 1986). Plastic responses enable plants to respond to environmental changes in the short-term and, if the populations exhibit genetic potential for adaptive phenotypic plasticity, ultimately allow their long-term persistence (Davis and Shaw, 2001; Nicotra et al., 2010; Matesanz et al., 2010). Correspondingly, Lenoir et al. (2010) found no major changes in overall species distribution within mid-elevation forest communities during 1989–2007 in response to climate warming in the Swiss Jura mountains, indicating that species are able to persist locally despite changes in the environment. Stöcklin et al. (2009) pointed out that a plastic response to growth conditions may be crucial for the survival of alpine plants, and Rehfeldt et al. (2001)

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showed that high phenotypic plasticity in traits crucial for fitness may result in a lower probability of population extinction.

Large-scale environmental conditions, for example in terms of climate and overall soil conditions, often differ between distinct geographical regions and are likely to be altered following global environmental change. Comparisons of phenotypic variation between different regions may thus give a first insight into how plant species may respond to changes in the environment. If species differ in their phenotypic trait variation, which we here use as an indicator for the amount of phenotypic plasticity (Schlichting and Levin, 1984), they may more easily adapt to future broader-scale changes in the environment, compared to species that show no or less pronounced differences in their trait variability. Previous studies suggest that phenotypic trait variation and the amount of phenotypic plasticity are positively correlated (Richards et al., 2005, 2010), although such relationships may be complicated by differences in the underlying genetic variation (e.g. Scheepens et al., 2010).

In this study, we were interested in the ability of plant individuals to vary their phenotypes depending on broad-scale environmental conditions and we therefore compared trait variation within populations of one region with that observed in populations of another region. Environmental conditions of course also vary on more local scales (Macel et al., 2007; Jongejans et al., 2010), and we therefore also investigated effects of the local environment (in terms of light availability and soil conditions of sites within a given region) on trait variation. We compared patterns between vegetative and reproductive traits, since these have been shown to differ in their extent of phenotypic variation (Rice and Mack, 1991; Mal and Lovett-Doust, 2005; Zhang et al., 2011). We chose five forest herb species for this study, a group of organisms with generally low colonization capacities, very specific habitat requirements (Hermy et al., 1999), and adaptations to the relatively stable environmental conditions in forests (Honnay et al., 2002). Such species will likely not be able to track changes in climate, especially when landscapes are highly fragmented, and their survival will therefore depend to a large extent on their environmental tolerance (Honnay et al., 2002). We considered several species, since the extent of a response to environmental variation may differ considerably between species (Alpert and Simms, 2002; Lehmann and Rebele, 2005; Van der Veken et al., 2007; Baeten et al., 2010). Specifically, the main aim of our study was to examine how large-scale environmental differences and mean local environmental conditions affect the variation of vegetative and reproductive traits in forest herb species. Furthermore, we were interested whether vegetative and reproductive traits differ in their overall phenotypic variability and whether patterns are consistent among species.

2. Methods

2.1. Study species

For our study we chose five herbs: *Brachypodium sylvaticum* (Huds.) Beauv. (Poaceae), *Circaea lutetiana* L. (Onagraceae),

Impatiens noli-tangere L. (Balsaminaceae), *Sanicula europaea* L. (Apiaceae) and *Stachys sylvatica* L. (Lamiaceae) (Table 1); hereafter, the species will be referred to by their genus name. All species are widespread within Europe, common in Germany and more or less restricted to ancient deciduous hardwood forests (Hultén and Fries, 1986; Hermy et al., 1999). The species differ in terms of their life span (annual vs. perennial), reproduction mode (sexual vs. both sexual and asexual) and dispersal strategy (short-distance vs. long-distance) (Table 1).

2.2. Study regions and populations

We conducted our study in 2009 in two regions of Germany. One area was located in northwestern (NW) Germany (Bremen, 40 × 40 km, centre of study area: 53°15'N, 9°05'E), the other area was located approximately 600 km further south in southwestern (SW) Germany (Freiburg, 30 × 40 km, centre of study area: 48°00'N, 7°45'E). The regions are characterized by different overall environmental conditions, e.g. in terms of climate and geological substrate. Both mean annual temperature and precipitation are lower in the north (Bremen, means across 1971–2000: 9.2 °C and 672 mm, means for 2009: 10.0 °C and 645 mm) than in the south (Freiburg, 1971–2000: 11.1 °C and 900 mm, 2009: 10.9 °C and 908 mm). The northern region is mostly covered by Pleistocene deposits and has a highly fragmented forest cover. The landscape is primarily used for agriculture, with arable land prevailing, but also with large areas of grassland. The southern region is located in the Upper Rhine Lowlands including the volcanic region “Kaiserstuhl” and the adjacent foothills of the Black Forest. The study area is mostly covered by loess soils. Both lowlands and hill slopes are primarily used for agriculture and wine growing, presenting a mosaic with the fragmented forest cover. Furthermore, both mean altitude and altitudinal variation across sites differ between the two regions (Bremen: 6–53 m a.s.l.; Freiburg: 192–616 m a.s.l.).

In both regions we selected 15 populations per species (except 8 populations for *Sanicula* in Freiburg, and 11 populations for *Impatiens* in Bremen) in mature deciduous hardwood forests with at least 50–60% crown cover and little disturbance. The populations of a given species were located in different forests or, if in the same forest, at least 1 km apart from each other.

2.3. Trait measurements

Within each population of each species we selected an area that appeared to be homogeneous in terms of structure of the field layer vegetation, light environment and other environmental parameters. Within this area, at the time of seed maturity (here defined as the time when seeds came off easily from the plant; for data collection dates see Appendix A), we sampled 50 individuals of *Sanicula*, 25 individuals of *Impatiens*, 35 tussocks of *Brachypodium* and 50 ramets of both *Circaea* and *Stachys*. Hereafter, ramets and tussocks will be referred to as individuals. Individuals were

Table 1
Characteristics of the five study species (Grime et al., 1988).

	<i>Brachypodium sylvaticum</i>	<i>Circaea lutetiana</i>	<i>Impatiens noli-tangere</i>	<i>Sanicula europaea</i>	<i>Stachys sylvatica</i>
Life form	Perennial hemicyptophyte	Perennial hemicyptophyte	Annual therophyte	Perennial hemicyptophyte	Perennial hemicyptophyte
Asexual reproduction	Non-clonal, but occasional production of new shoots	Clonal, extensive vegetative spread via rhizomes and stolons	Non-clonal	Non-clonal, but occasional rhizome cleavage possible	Clonal, extensive vegetative spread via rhizomes and stolons
Sexual reproduction					
Pollination	Wind	Insect and self	Insect	Insect and self	Insect and self
Seed dispersal	Seed dispersal via epizoochory	Long-distance seed dispersal via epizoochory possible	Ballistic dispersal, seeds scattered up to 2–3 m	Long-distance seed dispersal via epizoochory possible	Gravity dispersal, i.e. seeds fall close to the parent plant
Seedbank	Absent	Absent	Absent	Absent	Present

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