Forest herbs in the face of global change: a single-species-multiple-threats approach for *Anemone nemorosa*

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Background – Global environmental changes have become important drivers of plant community shifts and are considered to be threats to biodiversity. Because multiple environmental changes are acting simultaneously, they might antagonistically, analogously or synergistically affect plant populations and communities.

Approach – In this review paper, we attempt to take a single-species-multiple-threats approach to gain insights into the complex impacts of global changes. We selected a well-studied forest herb (*Anemone nemorosa*) as a case and discuss its response to several prevailing environmental threats.

Results – Changes in forest management, land use change, acidifying and eutrophying deposition and climate change are the main topics that have been studied for *Anemone*. Their impacts have basically been studied at three levels of biological organisation: populations, individual ramets and traits. An important finding that emerged in this review is that the human alterations of the environment have ambiguous effects on the performance of *Anemone*. While some environmental changes were detrimental, others were rather neutral or even beneficial. The cover of *Anemone*, for instance, increased following the conversion of coppice towards high forest management, but decreased because of soil acidification and reduced soil moisture.

Conclusion – Because the multiple threats may have ambiguous effects on plant performance, the ultimate response of an *Anemone* population turns out to be very complex. To conclude, we emphasise the need for more integrative studies that assess the impacts of multiple global changes on the different levels of biological organisation of a species.

Key words – forest biodiversity, ancient woodland, *Anemone nemorosa* L., acidification, eutrophication, forest conversion, land use change, climate change, wood anemone.

INTRODUCTION

As most of the plant biodiversity in temperate forest ecosystems is found in the herbaceous layer (e.g. Gilliam & Roberts 2003, Gilliam 2007), this stratum is pivotal for biodiversity and ecosystem functioning in general. The ecology of woodland herbs, including their response to forest canopy dynamics, has been extensively studied (for reviews see: Bierzychudek 1982, Hermy et al. 1999, Gilliam & Roberts 2003, Roberts 2004, Whigham 2004, Gilliam 2007). Yet, a suite of global environmental changes that emerge from the increasing rates of socio-economic development are progressively influencing the normal dynamics and patterns of forest plant diversity (e.g. Gilliam 2006, Hermy et al. 2008, Rackham 2008). These environmental threats to forest plant diversity include airborne pollution, forest conversion, invasive species, land use change and climate change (Rackham 2008) and lead to widespread biotic impoverishment and homogenization across forested landscapes (e.g. Wiegmann & Waller 2006, Vellend et al. 2007, Van Calster et al. 2007, 2008b, Rogers et al. 2008).

A straightforward approach to study the impact of environmental changes on the herbaceous forest vegetation is to

Figure 1 – *Anemone nemorosa* L. is one of the most abundant spring-flowering herbs in deciduous forests in northwestern Europe. Although it is not a red list species, multiple threats (management change, land-use change, acidifying and eutrophying deposition and climate change) may act antagonistically, analogously or synergistically on this species and potentially affect the future persistence and spread of its populations.

select a single factor, say, forest conversion, and to evaluate its effect on several species, functional groups and vegetation types (e.g. Decocq et al. 2004, Van Calster et al. 2008a). Addressing the impact of environmental changes the other way around, i.e. looking at the effects of several changes on a single species, is rather uncommon because this approach implies highly complicated study designs. First of all, the different environmental drivers act upon the vegetation at different spatio-temporal scales. An ideal study design would thus require an integration of different spatial and temporal scales. Second, the response rates of forest herbs depend on the nature of the environmental change, so the study of several changes implies different monitoring schemes. Nevertheless, an integrated "single-species-multiple-threats" approach may provide important insights into potentially antagonistic, analogous or synergistic effects of co-occurring environmental changes. Is the low capacity of a species to colonize recent forest patches counteracted or rather aggravated by climate change? Is the impact of chronic atmospheric nitrogen deposition obscured by excessive shade?

In this review paper, we attempt to take a single-species-multiple-threats point of view using the spring-flowering geophyte *Anemone nemorosa* L. (fig. 1). The species is widespread in Europe and is regarded as a flagship species of

deciduous forest by many people since it is an eye-catching feature of the spring vegetation. It is not our intention to provide a review of the species' autecology, which can be found elsewhere (e.g. Shirreffs 1985, Mondoni et al. 2008), but we explore its response to global changes at the trait, ramet and population level. Although *A. nemorosa* may also occur in open habitats at northerly latitudes and higher altitudes, the ecological context of this review is restricted to *A. nemorosa* populations in forested environments. We provide an overview of European literature on the species with special attention to results from a densely populated region (Belgium) in which multiple changes are to be expected. The global changes that have been studied for *A. nemorosa* are: changed forest management (including grazing), land use change, acidifying and eutrophying deposition and climate change.

STUDY SPECIES

Anemone nemorosa L. (Ranunculaceae; wood anemone; further referred to as *Anemone*) is a widespread European forest herb growing in the forest understorey. The species' distribution is mainly associated with deciduous forests, but it may also occur in moist pastures, woodland pasture, hedgerows or even coniferous forest (Shirreffs 1985, Grime et al. 2007,

Wehling & Diekmann 2009). Within Europe the perennial vernal forest geophyte occurs from the Pyrenees to northern Sweden and from Ireland to western Russia (Hultén & Fries 1986). Shoots emerge in early spring and flowering starts a few weeks later. Flowers (one per ramet) are typically white, hermaphrodite, mostly self-incompatible and insect pollinated although selfing occurs (Shirreffs 1985, Müller et al., 2000). Each ramet usually produces c. twenty achenes (further referred to as 'seeds') with a mean seed mass of 2 mg (De Frenne et al. 2010b). The species forms a branching horizontal rhizome system in the upper soil and litter layer that is used for its vegetative spread and storage, but also causes sensitivity to drought and soil compaction (Shirreffs 1985; Philip & Petersen 2007; Rusterholz et al. 2009). The vegetative growth of the species is very slow (e.g. average rhizome segment growth 30 mm.yr^{-1} in Denmark; Philip & Petersen 2007) and seed dispersal is likely to be the most important way of spread (Brunet & von Oheimb 1998a; Stehlik & Holderegger 2000). Because of its low dispersal capacity, *Anemone* is considered a very slow-colonizing 'ancient' forest herb (*sensu* Hermy et al. 1999). An extensive overview of the most important characteristics of the species' ecology can be found elsewhere (e.g. Shirreffs 1985, Mondoni et al. 2008). *Anemone* may be considered one of the most intensively studied forest herbs in Europe: a Web of Science search using the keyword 'Anemone nemorosa' resulted in 53 peer reviewed studies published in the period 1990–2009 that included the species in the title or abstract (www.isi-knowledge.com).

FOREST MANAGEMENT CHANGE

Forest management is often a dominant component of the disturbance regime in present day forests, especially in Western Europe. Management has both direct and indirect effects on the herb layer (Gilliam & Roberts 2003). An important direct impact is the (partial) destruction of populations when a stand is cut, ploughed for regeneration or when herbicides are applied. Godefroid et al. (2005) showed that the frequency and cover of several herb layer species, including *Anemone*, was reduced for at least thirteen years following a clear cut. They suggested that the low dispersal capacity of most forest species (see Land use change) coupled with the frequency and spatial scale of certain silvicultural systems (e.g. clear cut) precludes the full recovery of the populations. Intentions to replace clear cut systems by selection harvesting systems (e.g. single tree or group selection harvest) are therefore encouraging. Management has also important indirect impacts on the herb layer through the alteration of the tree species composition and structure, which modifies the light, soil and humus conditions. Tree species with base-rich litter, for instance, produced milder humus forms and supported a higher richness of understorey forest species in three forests in the Netherlands and Denmark (van Oijen et al. 2005). The dominant effect of tree species was further illustrated by the high abundance of *Anemone* underneath *Fraxinus excelsior* L. trees whereas it was virtually absent 2 m away, beneath *Quercus* spp. It is therefore clear that changing the tree species composition may have significant impacts on the persistence of forest plant populations in the understorey.

The large scale conversion of broadleaved forest into conifer plantation is likely to represent one of the most drastic management changes during the past two centuries. The conversion into coniferous high forest not only affects the light, topsoil and humus conditions, it is also associated with intensive management practices such as clear cutting and ploughing before replanting. Peterken (1993) states that planting conifers largely eliminates the spring-growing shade flora and that in productive stands the changes in the herb layer are almost as great as if the wood had been temporarily cleared away. Wulf & Heinken (2008), for instance, studied transects from ancient broadleaved stands into adjacent, thirty year old conifer stands and showed that many forest herbs, including *Anemone*, were significantly associated with the ancient broadleaved sites. Apparently, the species were unable to recolonize the conifer stands after their populations were eliminated by clear cutting the preceding stand and ploughing before planting the conifers. The limited colonization potential of forest herbs, and particularly *Anemone*, will be discussed further (Land use change).

Another form of change in forest management is the large scale conversion of coppice or coppice-with-standards management towards high forest management in much of Western-Europe during the 20th century. We will elaborate on this type of conversion as a case because we have old vegetation records as baseline data to rely on. In a coppiced system, the underwood is cut down in relatively short rotations and new shoots resprout from the cut stumps. Because the coppice system was the traditional form of forest management for centuries (e.g. Kirby & Watkins 1998, Rackham 2003), the composition of the forest flora in many forests is expected to be partly the result of the environmental conditions created by coppicing such as cyclic variations in light availability, temperature and nutrients (e.g. Buckley 1992, Decocq et al. 2004). Spring-flowering species are one of the species groups that thrived under the regular cutting regime. For instance, the proportion of flowering individuals or ramets of *Primula elatior* Hill, *Narcissus pseudo-narcissus* L., and also *Anemone* increased sharply the second or third growing season following coppicing (Barkham 1980, Shirreffs 1985, Mason & MacDonald 2002, Rackham 2003). The frequency of occurrence of *Anemone* showed, however, little response to the coppice cycle (Mason & MacDonald 2002). The gradual (neglect) or abrupt (clear cut and replanting) conversion of coppiced stands towards high forest is associated with a change in disturbance frequency and overstorey species composition. Van Calster et al. (2007, 2008a) showed that such conversions of the overstorey may lead to strong vegetation shifts in the understorey because of a decreased litter quality and an increase in shade cast by the canopy. Especially the conversion to homogeneous beech stands had a negative impact on herb layer alpha and beta diversity. Despite these negative trends, *Anemone* (together with *Hyacinthoides non-scripta* (L.) Chouard ex Rothm.) could actually benefit from the changes in forest management: the mean cover of the species increased by 20% (Van Calster et al. 2008a). Similarly, the species increased significantly in British woodlands following the abandonment of coppice management during the past hundred years (Barkham 1992a, b). The life history characteristics of the species may partly account for this

response. Because *Anemone* has a shade-avoiding strategy and is able to emerge and grow in thick litter layers (Sydes & Grime 1981, Baeten et al. 2009c) it is able to outlive the management changes. Furthermore, the decline of many competing species in the herb layer may additionally account for the spread of *Anemone* because its abundance may be determined chiefly by the limitations of its competitors (Hermy 1985, Rackham 2003). *Anemone* did, however, not always prove to profit from the conversion of coppice towards high forest management. In central Belgium, Baeten et al. (2009a) showed that the mean cover of *Anemone* decreased by 20% during five decades of gradual conversion of a coppice-with-standards management towards uneven aged high forest. A significant acidification of the topsoil layer from pH 5 to 4.3 was, at least partly, responsible for the observed decline (see Acidifying and eutrophying deposition).

The increasing numbers of deer and other ungulates are also considered to be a significant global change which may have dramatic effects on the structure and composition of forest vegetations (e.g. Watkinson et al. 2001, Rackham 2008). Changes in grazing pressure are not strictly related to forest management, but because the regulation of animal densities is a particular management option, the effects on *Anemone* are discussed here. Mårell et al. (2008) used exclosures to show that on average 30% of the flowering shoots at the population level were lost by browsing of roe deer. Van Uytvanck & Hoffmann (2009) studied the effect of cattle grazing management on the herbaceous flora and also found negative responses of *Anemone* in terms of flowering frequency and cover. Yet, *Anemone* is expected to be favoured by intermediate grazing levels that are high enough to reduce the dominance of its competitors (e.g. *Rubus* sp.), but do not create intensive disturbances such as trampling (Watkinson 2001, Van Uytvanck & Hoffmann 2009).

LAND USE CHANGE

Historical-ecological, archaeological and palynological data show that temperate forests in Europe have been disturbed by humans for millennia (e.g. Tack et al. 1993, Kirby & Watkins 1998, Rackham 2003). The massive clearance of forests for agriculture and the subsequent re-establishment of forest after the abandonment of agriculture represent the most intensive disturbance and, in fact, large parts of the present-day forest area have experienced an agricultural use at some point in their history. An overwhelming number of studies showed that forest herb diversity in post-agricultural forests is reduced for centuries to even millennia because many species fail to colonize the sites (reviews: Flinn & Vellend 2005, Hermy & Verheyen 2007). In a review of European literature, Hermy et al. (1999) showed that about 30% of the forest plant species, including *Anemone*, are more or less confined to historically continuous forests ('ancient forest species'). Basically two mechanisms may account for the slow colonization rates of ancient forest species into post-agricultural forests: (1) dispersal limitation and (2) recruitment limitation. The relative importance of both mechanisms has been tested in several observational and experimental studies and *Anemone* often served as a representative study species.

Observational studies that assessed the impact of land use history on the distribution of forest herbs showed that the probability for *Anemone* to occur in post-agricultural sites increased with decreasing distance to colonization sources (e.g. ancient forest stands, fringe relics) and with increasing forest age (Brunet & von Oheimb 1998a, b, Bossuyt et al. 1999, Honnay et al. 1999, Verheyen & Hermy 2001a, b). In ideal configurations, i.e. post-agricultural forest immediately bordering ancient forest on the same soil and similar light conditions, the colonization rate of *Anemone* was estimated at only 21–85 m per century (Brunet & von Oheimb 1998a, b, Bossuyt et al. 1999, Dzwonko 2001). The observation that the probability of occurrence increases with forest age and decreases with isolation at least suggests that dispersal may be the main limitation for colonization. In a meta-analysis of colonization rates of European and eastern North American forest herbs, Verheyen et al. (2003) showed that *Anemone* belongs to an emergent group of slow colonizing small perennials that share a number of traits related to low dispersability: few heavy seeds, no morphological adaptation for long distance dispersal and a delayed age of first reproduction. On a scale between -100 (strongly associated with post-agricultural forest) and +100 (confined to ancient forest), *Anemone* (+77) ranked among the most slowly colonizing species together with species such as *Hyacinthoides non-scripta* (+100), *Lamium galeobdolon* (L.) L. (+79) and *Paris quadrifolia* L. (+75) (Verheyen et al. 2003). The low dispersal capacity may have particular consequences for its response to climate change (see Climate change).

Once diaspores of a species have reached an unoccupied post-agricultural site, they still need to germinate and recruit into the adult life stage. These post-dispersal colonization stages might also hamper colonization success (recruitment limitation). The former agricultural land-use has persistently altered the biotic and abiotic soil conditions, which may affect plant recruitment and performance. The strong competition with competitors such as *Urtica dioica* L., which benefit from the increased nutrient availability from former agriculture, is often cited to be an important constraint for the establishment and growth of forest herbs. Hipps et al. (2005) experimentally tested whether competition with *U. dioica* reduced the growth of three forest herbs along a phosphorus gradient. Whereas the growth of two of the forest herbs (*L. galeobdolon, Veronica montana* L.) was reduced by competition, *Anemone* was unaffected. The difference in phenology enabled *Anemone* to complete its vegetative and reproductive growth phases prior to the substantial growth of its competitor. However, this strategy is not useful for colonizing sites dominated by evergreen grasses or herbs, which largely pre-empt the available growing space in spring. Brunet & von Oheimb (1998a), for instance, showed in an observational study that the migration of *Anemone* from ancient into adjacent post-agricultural sites was significantly slower if the herb layer was dominated by evergreen grass species. To test the relative importance of the recruitment stage and the role of competition experimentally, Verheyen & Hermy (2004) sowed seeds and planted adults of *Anemone* into ancient and post-agricultural forest sites and removed the competitive vegetation in half of the plots. After two growing seasons they demonstrated that neither the germination of seeds
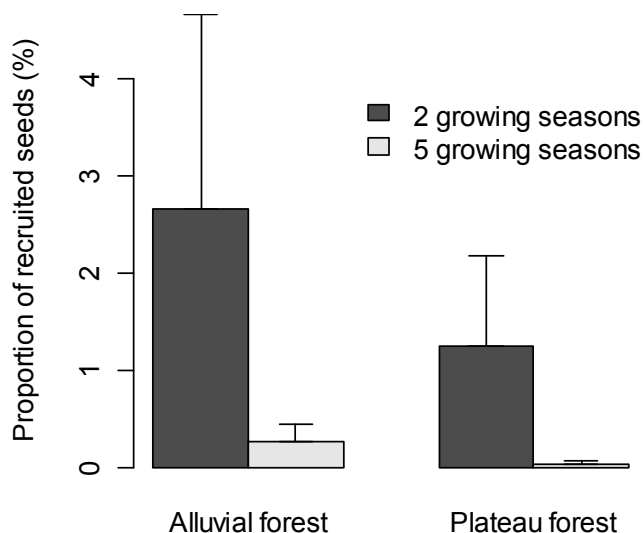
Figure 2 – The proportion of *Anemone nemorosa* seeds (%) that recruited in two contrasting forest types in central Belgium. Seeds were sown in alluvial and plateau forest in undisturbed vegetation plots. The proportion of seeds that recruited into the seedling and the adult life stage were counted after two and five growing seasons (data from Baeten et al. 2009c).

nor the performance of adults were affected by former land use and competition. A re-evaluation of the experiment after eight growing seasons, however, showed that the experimental populations of *Anemone* still persisted in the ancient sites, but had strongly declined in the post-agricultural sites (Baeten et al. 2009b). In a very similar introduction experiment, Baeten et al. (2009c) showed that only a very low fraction of seeds could develop into an adult life stage (< 0.5%; fig. 2) and they found no effect of competition on the number of recruits after five growing seasons. To summarize, it is clear that land use change has a dominant impact on the distribution of forest herbs. The recovery from former agricultural land use of species such as *Anemone* is severely hampered by a low dispersability and low recruitment success. While *Anemone* seems to be rather independent of strong competition (but see Baeten et al. 2009b), the recruitment and growth of other species may be strongly reduced by competitive species that profit from the former fertilization.

ACIDIFYING AND EUTROPHYING DEPOSITION

Because species differ greatly in their occurrence along spatial gradients of soil acidity (e.g. Ellenberg et al. 1992), the degree of soil acidification is one of the most important environmental gradients that structures plant communities. The increase in soil acidification rates in temperate forests, which are at least partly caused by the high loads of atmospheric potentially acidifying deposition during the past decades, are therefore considered an important driver of community changes in the herbaceous forest layer (e.g. Falkengren-Grerup 1986, Kuhn et al. 1987, Thimonier et al. 1994, Van Calster et al. 2007). Particularly those soils with limited buffer capacity (e.g. sandy textures) are more sensitive to soil acidification and vegetation changes. The acidification process

is driven by the cumulative input of protons (H^+), which forces the soil along a sequence of buffering systems (Bowman et al. 2008). This process is associated with a decreasing pH, depletion of nutrients (e.g. potassium, magnesium and calcium) and increasing availability of metals (e.g. aluminium) that potentially inhibit the growth of forest plants. A critical threshold for the forest vegetation is the transition from the cation exchange buffer range to the aluminium buffer range at a pH-H_2O of about 4.2 (*sensu* Ulrich 1991). When this threshold is crossed, a suite of soil properties related to soil acidification may constrain the establishment and growth of many forest herbs. Experiments, for instance, indicate that increasing concentrations of H^+ and aluminium (Al^{3+}) and mineral nutrient deficiencies might inhibit the growth of several forest plant species, which may explain the response of forest vegetations to soil acidification (Falkengren-Grerup & Tyler 1993, Falkengren-Grerup et al. 1995, Tyler 1996).

Again, *Anemone* served as an interesting case to demonstrate the significance of soil acidification for vegetation change. Although *Anemone* has a wide pH amplitude (Shirreffs 1985: pH 3.5–8.0, Ellenberg et al. 1992, Rackham 2003), some lines of evidence suggest that it is threatened by excessive acidification. For instance, the critical threshold for the occurrence of *Anemone* on acidification-sensitive soils was pH 3.4 (Merck Spezialindikator field method) and its abundance was positively correlated with soil pH in the south of the Netherlands (van Oijen et al. 2005). In the German Ruhr region, Wittig (2008) introduced rhizomes of *Anemone* into three different soil types in a beech forest and showed that soil acidification resulting from industrial air pollution inhibited the successful establishment of a population over the course of nine growing seasons. Further evidence comes from a resurvey of old vegetation records in forests with different degrees of soil acidification after five decades (Van Calster et al. 2008a versus Baeten et al. 2009a, see also Management change). The mean cover of *Anemone* had significantly increased during five decades on the well-buffered soils in Van Calster et al. (2007, 2008a), but its mean cover sharply decreased during the same time period on weakly buffered luvisols of which 85% approached or entered the aluminium buffer range (Baeten et al. 2009a). A historical-ecological study in central Belgium compared soil and vegetation differences between plots located along an historical U-shaped sunken road (probably originated during Roman times ~ 2000 year ago) and plots at 15–70 m distance from the road (Plue et al. 2009). Because the road cuts into deeper niveo-eolic calcareous loess, the soil pH was significantly higher in the plots near the road and those plots supported a higher species richness. *Anemone* and some other mesotrophic ancient forest species (e.g. *Lamium galeobdolon, Melica uniflora* Retz.) were more frequent and abundant in the plots near the road.

Because soil acidification is to a large extent caused by increased nitrogen deposition (NOX, NHX) it is often associated with eutrophication. Gilliam (2006) reviews the effects of the increased nitrogen availability on the forest herb layer. Besides the direct impact on growth, increased nitrogen supply has also indirect effects on the herb layer including decreased mycorrhizal diversity and changes in interspecific competition. In a nitrogen addition experiment in southern

Sweden, Falkengren-Grerup (1993) tested the effects of increased nitrogen availability on the performance of forest herbs. After six growing seasons, the application of 180 kg N ha^{-1}.year^{-1} significantly reduced the cover and biomass of *Anemone* and several other common species (e.g. *Maianthemum bifolium* (L.) F.W. Schmidt, *Viola reichenbachiana* Jord. ex Boreau) relative to the control. The shoot length and flower frequency of *Anemone* were also negatively affected by nitrogen addition. Although the applied level of nitrogen was much higher than the prevailing levels of atmospheric nitrogen deposition, the results indicate that chronic nitrogen deposition may have a negative impact on the performance of *Anemone*.

CLIMATE CHANGE

The Intergovernmental Panel on Climate Change (IPCC 2007) recently stated that "warming of the climate system is unequivocal as is now evident from observations of increases in global average air and ocean temperatures, widespread melting of snow and ice, and rising global average sea level". Hence, it is undisputable that climate change will have a huge impact on the performance and the distribution of both plants and animals (Root et al. 2003, Parmesan & Yohe 2003, Thomas et al. 2004). Climate change directly affects the phenology and performance of plants through increasing mean, maximum or minimum annual temperature, but also affects vegetation through altered frequency and magnitude of extreme events (e.g. summer drought) and changing precipitation and relative air humidity patterns (Hughes 2000, IPCC 2007, Lovejoy & Hannah 2005). Below, we will outline the potential effects of increased temperature (warming) and changed precipitation, soil moisture and relative air humidity on the performance of *Anemone* on a European scale in the coming decades.

Warming

The predicted rise in mean annual temperature ranges from 2.3–5.3°C in the temperate zones of northwestern Europe by 2080–2099 compared to 1980–1999 (IPCC 2007). This would result in a 300–400 km northward latitudinal and 500 m upward altitudinal shift of the isotherms (Hughes 2000). Several approaches have been applied to study the effects of climate change on the phenology and performance of *Anemone* including (1) observational studies along temporal (time series) and spatial (latitudinal and altitudinal) gradients, (2) experimental studies that manipulate temperature and (3) bio-climatic envelope and process-based computer simulations.

Due to the pan-European distribution of *Anemone*, this species may serve as an interesting case to monitor relationships between climate and phenology (using time series; Sparks & Menzel 2002) or performance (using a latitudinal space-for-time substitution procedure; Fukami & Wardle 2005). With respect to phenological changes, Ahas (1999) and Sparks & Menzel (2002) both showed a clearly negative correlation between flowering date of *Anemone* and the mean spring temperature using a 78-year and 154-year time series in Estonia and Great Britain, respectively. On the other hand,
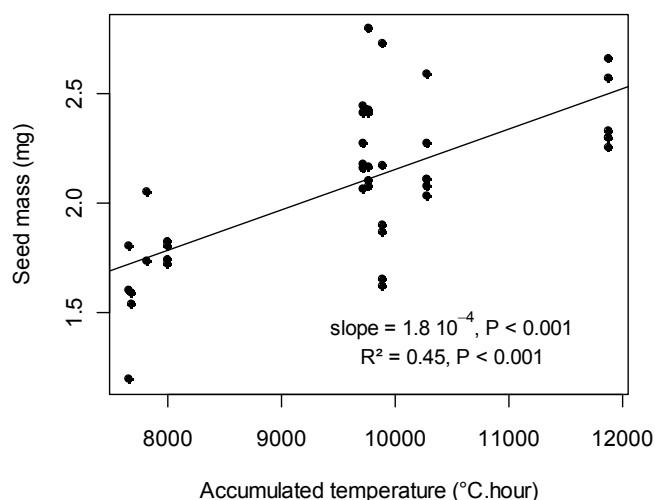
Figure 3 – The relationship between the accumulated temperature (growing degree hours above 5°C) and the dry seed mass of *Anemone nemorosa* along a latitudinal gradient from northern France (49.8°N) to northern Sweden (63.8°N) in 2008 (data from De Frenne et al. 2010b).

in a twelve-year time series in Sweden, Tyler (2001) found no effect of temperature on the timing of flowering onset of *Anemone*. Furthermore, De Frenne et al. (2009, 2010b) and Graae et al. (2009) sampled populations of *Anemone* along a large latitudinal gradient from northern France to northern Sweden and were able to unravel the effects of accumulated temperature (growing degree hours above 5°C) on a set of reproductive traits of *Anemone* (number of seeds, seed mass, germination, requirements for dormancy break, seedling mass). The results provided evidence that temperature was the main factor affecting the reproduction of *Anemone* along the latitudinal transect. An increase of 1000 growing degree hours (i.e. an increase by 1°C during 42 spring days), for instance, resulted in a 10% higher mass of *Anemone* seeds and seedlings (fig. 3). In addition, the germination percentage was higher in seeds from adults that grew in a warmer environment (De Frenne et al. 2010b). Finally, in a comparison of lowland and mountain populations of *Anemone* (altitudinal gradient) in northern Italy, Mondoni et al. (2008) showed that the intraspecific variation in the timing of germination was related to adaptation to the local climate. They found that 50% of the shoot emergence of *Anemone* seedlings in the mountain population (1350 m a.s.l.) only occurred when temperatures dropped below 5°C (cold stratification). Hence, if average winter temperatures would rise above 5°C, this may disrupt the dormancy break of *Anemone* seeds in winter.

De Frenne et al. (2010a) used open-top chambers to experimentally test the effect of increased temperature on the performance of *Anemone* in a deciduous forest in Belgium. Open-top chambers are miniature polycarbonate greenhouses that passively heat a small vegetation plot (~ 0.35 m²) with c. 1–1.5 °C before the leafing out of the tree canopy. After one growing season, the mean plant height of *Anemone* was almost 10 cm higher in the warming treatment versus the control. The flowering phenology and the other vegetative traits (aboveground biomass, SLA, leaf carbon and nitrogen concentration) were not significantly affected. Repro-

Table 1 – Non-exhaustive overview of studies that measured the response of *Anemone nemorosa* to one of the global environmental changes reviewed in this paper.

The table only shows studies for which *Anemone* was used as a study species or studies where *Anemone* was substantially discussed because of its particular response. Not all space-for-time studies related to land-use change were included here. The direction of the effects that were found in the cited studies are summarized in fig. 4.

Environmental change	Approach	Scale	Publication
Management change	Experimental – exclosures	Stand	Mårell et al. (2009)
	Experimental – exclosures	Forest	Van Uytvanck & Hoffmann (2009)
	Observational – space-for-time	Stand	Wulf & Heinken (2008)
	Observational – (semi)permanent plots	Forest	Barkham (1992b)
	Observational – (semi)permanent plots	Forest	Van Calster et al. (2007, 2008a)
	Observational – (semi)permanent plots	Forest	Baeten et al. (2009a)
Land-use change	Experimental – pot experiment	Individual	Hipps et al. (2005)
	Experimental – introduction	Stand	Verheyen & Hermy (2004)
	Experimental – introduction	Stand	Baeten et al. (2009b)
	Experimental – introduction	Stand	Baeten et al. (2009c)
	Observational – space-for-time	Stand	Brunet & von Oheimb (1998a)
	Observational – space-for-time	Stand	Bossuyt et al. (1999)
	Observational – space-for-time	Forest	Honnay et al. (1999)
	Observational – space-for-time	Forest	Verheyen & Hermy (2001a)
	Observational – space-for-time	Forest	Verheyen & Hermy (2001b)
	Observational – space-for-time	Landscape	Hermy (1985)
	Meta-analysis	European	Verheyen et al. (2003)
Acidifying/eutrophying deposition	Experimental – nitrogen addition	Stand	Falkengren-Grerup (1993)
	Experimental – introduction	Stand	Wittig (2008)
	Observational – vegetation survey	Stand	Plue et al. (2009)
	Observational – (semi)permanent plots	Forest	Van Calster et al. (2007)
	Observational – (semi)permanent plots	Forest	Baeten et al. (2009a)
Climate change	Observational – time series	Population	Ahas (1999)
	Observational – time series	Population	Tyler (2001)
	Observational – time series	Population	Sparks & Menzel (2002)
	Observational – latitudinal gradient	Population	De Frenne et al. (2009)
	Observational – latitudinal gradient	Population	De Frenne et al. (2010b)
	Observational – latitudinal gradient	Population	Graae et al. (2009)
	Observational – altitudinal gradient	Population	Mondoni et al. (2008)
	Observational – seed storage test	Population	Ali et al. (2007)
	Experimental – open-top chambers	Stand	De Frenne et al. (2010a)
	Observational – vegetation survey	Forest	Lameire et al. (2000)
	Observational – vegetation survey	Forest	Leuschner & Lendzion (2009)
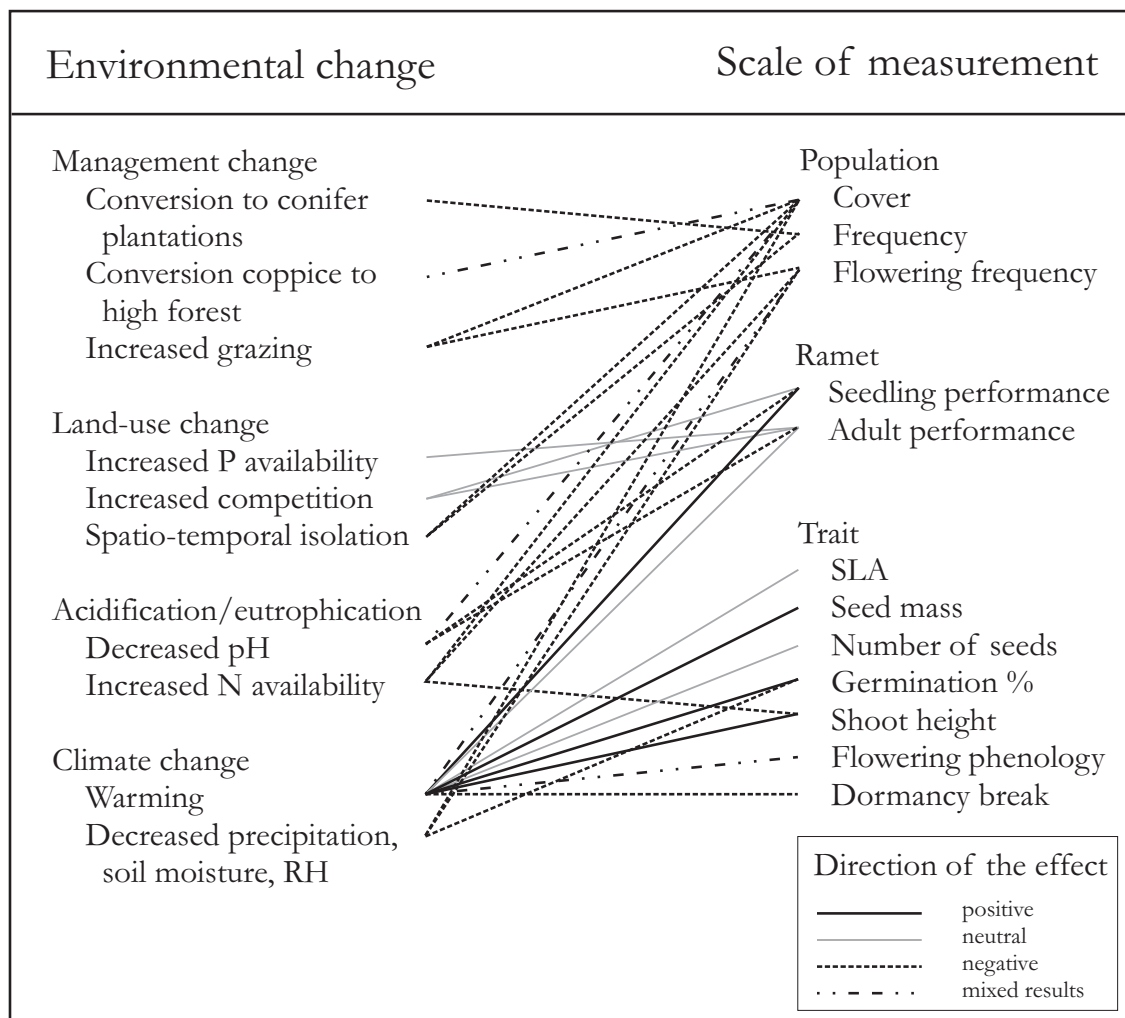
Figure 4 – Synthetic scheme of the responses of *Anemone nemorosa* to the multiple environmental changes at three levels of biological organisation (population, ramet, trait). The relations in the scheme are restricted to the studies in table 1.

ductive performance generally decreased, but this response was probably due to selfing effects or pollen limitation in the chambers rather than direct warming effects.

Plant species mainly have two options to cope with the effects of climate change: adaptation to the new climatic conditions or migration to higher altitudes or latitudes. A bio-climatic envelope model showed that the bio-climatic suitability of *Anemone* will most likely shift c. 1000 km northward from about 63 °N to 71 °N by the end of this century (Svenning & Skov 2006). However, due to the habitat fragmentation in western Europe and the low dispersal capacity of *Anemone*, it is unlikely that the distribution of *Anemone* will ever match the predicted bio-climatic envelope by the end of this century (Honnay et al. 2002). To track a warming climate (say 3°C by the end of this century), the species needs to migrate at rates of 1000–4000 m per year (Hughes 2000, Malcolm et al. 2002). These rates are much higher (up to a factor 10000) than the estimated colonization rates of *Anemone* that range between 0.21 m and 0.85 m per year (Brunet & von Oheimb 1998a,b, Bossuyt et al. 1999, Dzwonko 2001, see

Land use change). The odds are that migration is nearly impossible at such a high speed for *Anemone* and many other slow-colonizing forest species (Honnay et al. 2002), leaving no other option to the present populations than to adapt to a warmer climate in the coming decades or to get saved by assisted migration (Van der Veken et al. 2008).

Changes in precipitation, soil moisture and relative air humidity

The predicted increase in mean annual precipitation in northwestern Europe ranges between 0 and 16% by 2080–2099 compared to 1980–1999. However, summer precipitation is likely to decrease or stay equal (-21% to +16%) whereas winter precipitation is forecasted to increase in northwestern Europe (+9% to +25%; IPCC 2007). The relative air humidity and soil moisture in the forest understorey may also alter owing to, for instance, increased summer drought. A prolonged effect of a decrease in relative air humidity on the performance of forest plant species was experimentally tested by Leuschner (2002) and Lendzion & Leuschner (2008).

These studies found negative effects on forest plant performance as the studied species were well adapted to high relative air humidity values. The impact of changes in the relative air humidity and soil moisture on the performance of *Anemone* is complex. In German beech forests, Leuschner & Lendzion (2009) showed that the abundance of *Anemone* was highest in stands with high soil moisture, but low air humidity. The sensitivity of *Anemone* to decreased soil moisture was also observed by Lameire et al. (2000). In a resurvey of semi-permanent plots, they found a significantly decreased mean cover after 20 years related to the lowering of the groundwater table. Furthermore, Tyler (2001) showed in a twelve-year time series in Sweden that the flowering of *Anemone* was negatively correlated with autumn/winter precipitation in the preceding year. The predicted increase in winter precipitation by 2080–2099 may thus reduce flowering success. The predicted decrease in summer precipitation may additionally reduce the regenerative success by seeds as the life span of *Anemone* seeds is reduced by post-dispersal desiccation (Ali et al. 2007). Thus, both increased winter precipitation and summer drought may constitute a future threat to the performance of *Anemone* in Europe.

SYNTHESIS:
INTERACTIVE EFFECTS OF GLOBAL CHANGES

The nature of natural forest dynamics, e.g. the rates of canopy gap formation and closure, has a strong control on the demography of forest understorey herbs (e.g. Valverde & Silvertown 1998). In a world dominated by human activity, however, natural disturbance regimes are becoming an exception as several global changes alter forest ecosystems at different spatial and temporal scales. It is therefore particularly challenging to expand our understanding on how forest plant populations and vegetations respond to the human alteration of the forest environment. If there is one generality that emerges from the large number of studies devoted to the issue, it is that the human alteration of the forest environment is a threat to forest plant diversity (e.g. Gilliam 2006, Rackham 2008). In the present review, we emphasized two important, additional topics. First, although the different global changes are often studied separately, it should always be acknowledged that they are acting simultaneously upon the populations of a species. While some human alterations of the environment may be detrimental to forest herb performance, others may be beneficial. The ultimate response is therefore very complex. Second, the impacts of global changes are evaluated at different levels of the biological organisation of the species. Responses are measured at the population level (cover, flowering frequency), the individual level (total biomass) or the trait level (seed mass, phenology). These two topics are represented in a synthetic scheme that represents the different relationships between a specific environmental change and the level of organisation (fig. 4). The scheme relies upon the responses of *Anemone* that are outlined in this review and is restricted to the studies from table 1. There are several important conclusions that emerge from this synthesis. First of all, it is clear that multiple environmental changes simultaneously affect the performance of *Anemone*, and the direction of the effect is not always

negative. At a particular level of biological organisation, one environmental change may be detrimental while another is rather beneficial. For instance, the size of an *Anemone* population is reduced by soil acidification, but, at the same time, the species may benefit from the conversion of coppice to high forest management. Furthermore, the low proportion of seeds that can recruit and survive the seedling stage partly constrains the colonization of post-agricultural forests. Climate warming might mitigate this limitation because higher temperatures result in heavier seeds and seedlings that may be more successful. Second, studies on the effects of a particular global change are generally restricted to a single level of biological organisation. The effects of changes in forest management or soil acidification are mainly evaluated at the population level, but detailed studies at the level of individual traits are largely lacking. Similarly, the experimental study of climate warming strongly focuses on the trait level, being limited at the temporal and spatial scale due to logistical constraints. The scheme thereby indicates some important needs for future research.

To synthesise, we advocate the necessity to study the complex effects of environmental changes on plant diversity in a more integrated way. First, studies that explicitly include two or more environmental changes are the most straightforward way to gain insights into the potential, interactive effects of the changes on plant populations or communities. In this respect, Reich (2009) recently provided a good example. In a ten-year grassland experiment, he showed that elevated nitrogen supply reduced species richness more at ambient CO_2 levels compared to elevated CO_2 levels. Second, the effects of environmental changes should be measured and integrated at the different levels of biological organisation (scale of measurement fig. 4). A mechanistic understanding of global change effects on plants mainly requires observations at the trait and individual level. The consequences of trait-level responses should, however, be evaluated at the population level. The population level not only incorporates the effects of all the different global changes, it is also the scale of interest for biological conservation.

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