Heathlands confronting global change: drivers of biodiversity loss from past to future scenarios

Jaime Fagúndez*
Departamento de Biologías Animal, Biología Vexetal e Ecoloxía, Facultade de Ciencias, Universidade da Coruña, 15071 – A Coruña, Spain
* E-mail jaime.fagundez@gmail.com

Received: 3 July 2012 Returned for revision: 23 August 2012 Accepted: 18 October 2012 Published electronically: 6 December 2012

• Background Heathlands are dynamic plant communities characterized by a high cover of sclerophyllous, ericoid shrubs that develop over nutrient-poor soils. Interest in the preservation of these habitats in Europe has increased over the last decades, but over this time there has been a general decline in habitat quality, affecting community structure, ecosystem functions and biodiversity. Negative drivers that trigger these changes include land-use changes (i.e. habitat destruction and fragmentation), pollution, climate change, natural succession and human management, as well as the presence of invasive exotic species.

• Scope Based on recent scientific literature, the effect of each of these potential drivers on a wide set of factors, including physiological traits, species richness and diversity, community structure, ecosystem functions and soil conditions, is reviewed. The effects of these drivers are generally understood, but the direction and magnitude of factor interactions, whenever studied, have shown high variability.

• Conclusions Habitat loss and fragmentation affect sensitive species and ecosystem functions. The nature of the surrounding area will condition the quality of the heathland remnants by, for example, propague pressure from invasive species. The dominant ericoid shrubs can be out-competed by vigorous perennial grasses with increased atmospheric nitrogen deposition, although interactions with climate and management practices may either counteract or enhance this process. Grazing or periodic burning promotes heath loss but site-specific combined treatments maintain species diversity and community structure. Climate change alone moderately affects plant diversity, community structure and ecosystem functions. Combined with other factors, climatic changes will condition heath development, mainly with regard to key aspects such as seed set and seedling establishment, rare species occurrence and nutrient cycling in the soil. It is essential to address the effects of not only individual factors, but their interactions, together with land-use history, on heathland development and conservation in order to predict habitat response to future scenarios.

Key words: Heathlands, Europe, pollution, climate change, land-use change, natural succession, biological invasions, grazing, burning, biodiversity, fynbos, environmental interactions.

INTRODUCTION

Heathlands are human-shaped habitats that play a crucial role in the traditional European landscape, with a widely recognized strong cultural and natural value. Heathlands add substantially to many ecosystem services, such as food and water supply, carbon sequestration, recreation, hunting, landscape and biodiversity conservation (Webb, 1998; Alonso et al., 2001; Wessel et al., 2004). The importance of heathland conservation has been highlighted in the last decades as a general process of habitat loss and degradation is taking place. These habitats, with their narrow specialist organisms and complex interactions, are now threatened (De Graaf et al., 2009). Protection and restoration plans for European heathlands have been promoted by the European Union and individual countries to counteract the negative effects of different drivers of biodiversity loss over habitat quality (Pywell et al., 2011). This interest has also been reflected in scientific literature with many papers, especially in the 1990s and 2000s, dealing with heathland biodiversity, conservation and restoration (Fig. 1).

The term heathland has been applied to a wide range of habitats with some characteristics in common. From an ecological and physiognomic view, these are here taken as communities in which perennial sclerophyllous shrubs are dominant and which develop over nutrient-poor soils (Specht, 1979). These communities are usually dominated by species included in the Ericaceae tribe of the Ericaceae family (Calluna, Daboecia and Erica genera; Oliver, 2000; Stevens et al., 2004). Here, the focus is on the European temperate heathlands, although some studies are discussed from other similar habitats (i.e. other heathland types) such as the fynbos biome from South Africa. The different heathland communities within temperate Europe are associated with different climatic conditions (Mediterranean, oceanic or continental heaths), edaphic conditions (acid or basic soils), waterlogging (wet or dry heaths), altitudinal range (lowland, upland or alpine heaths) and other ecological variables that condition the community structure and composition. Heathlands are mainly successional communities that replace woodlands, except in the latitudinal and altitudinal tree limits, or hyper-oceanic temperate areas in Scotland and in the west of
Ireland, when heathlands may become the climax vegetation (Specht, 1979; Cross, 2006; Fenton, 2008). The oceanic climate of Atlantic regions depresses the potential tree-line but, rather than temperature extremes, wind is a key factor controlling the vegetation type (Grace, 1997; Crawford, 2000). Sclerophyllous ericoids predominate except in the most exposed mountain areas (Hodd and Sheehy Skeffington, 2011). In extreme montane oceanic environments, such as in western Ireland and Scotland and the Faroes, the ericoid vegetation gives way to bryophyte heath (Averis et al., 2004; Hodd and Sheehy Skeffington, 2011) A description of the different European heathland communities is beyond this review and may be obtained from other sources (Gimmingham et al., 1979; Thompson et al., 1995; Díaz, 1998; Loidi et al., 2007, 2010). The location of the study sites from a selection of the papers reviewed here, covering most of the geographic area studied, is shown in Fig. 2.

A large number of studies deal with different aspects of heathland conservation, considering different threats, most of which are included in the main drivers of biodiversity loss as described by the Convention of Biological Diversity (Secretariat of the Convention on Biological Diversity, 2006): (a) land-use changes (habitat loss and fragmentation); (b) biological invasions; (c) climate change; (d) pollution and eutrophication; (e) overexploitation of natural resources. Habitat loss has been extensively described throughout Europe (e.g. Rose et al., 2000; Piessens et al., 2004) leading to a strong fragmentation and isolation of the remaining heath patches. The consequences of this process on the community have been studied and different responses for ecological groups recorded (e.g. Piessens et al., 2005). Pollution, mainly from nitrogen (N) deposition, is a major driver of heathland conversion to grasslands and has received much attention for this reason (Heil and Diemont, 1983; Moore, 1995;...
Britton and Fisher, 2007), while increasing CO₂ concentrations and climate change have shown a high variability whenever measured across Europe, with several experimental studies performed during the last decade (e.g. Peñuelas et al., 2004; Albert et al., 2011a, b). As heathlands are not particularly prone to species invasions, they are rarely referred to in that context (e.g. Carvalheiro et al., 2010), but species such as Rhododendron ponticum are recognized as important disruptors of heathland diversity and structure. Management (i.e. resources exploitation) is in turn a very important issue for heathland maintenance, and is related to all other drivers and key processes such as fire occurrence (e.g. Mitchell et al., 2009).

The effects of these drivers have been measured using a wide range of traits, the most common of which being cover of the key shrub species in relation to trees or grasses (e.g. Alonso et al., 2001; Britton et al., 2003). Other studies measure plant diversity on heathlands (e.g. Britton and Fisher, 2007; Calvo et al., 2007) and/or focus on target species considered as to be restricted to heathland habitats (e.g. Kleijn et al., 2008; Tsaliki and Diekmann, 2011). Different physiological variables have also been measured as direct indicators of plant response to drivers, such as photosynthesis and respiration rates (e.g. Albert et al., 2011a, b), or development such as key steps of the plant’s life cycle, such as the soil seed bank and seedling survival (e.g. del Cacho et al., 2012). Changes in plant contents of different nutrients have been related to soil composition, which is an indirect measure of habitat quality (e.g. De Graaf et al., 2009), considering parameters such as acidity and nutrient availability (Kleijn et al., 2008). Moreover, soil biota is also an important indicator of habitat quality (Payne et al., 2011), including the crucial presence and diversity of ericoid mycorrhiza (Read et al., 2004). Changes in ecosystem services can also be used as a measure of heathland condition (e.g. Wessel et al., 2004) as well as biotic interactions such as pollination activities (Forup et al., 2008) or food webs (Carvalheiro et al., 2010).

The key threats to heathland ecosystems are now relatively well known, but less information is available on how these effects will interplay and whether synergistic, antagonistic or additive interactions will result from its confluence in future scenarios. Information on the evolution of these drivers from past times is also scarce but necessary for understanding on-going processes and their possible future effects. Here, the main factors influencing heathland conservation and biodiversity are reviewed, and a first approach to a holistic view, considering past processes, recent drivers and projections for the future of heathland ecosystems is outlined.

ORIGIN AND DEVELOPMENT OF PRESENT-DAY HEATHLANDS IN EUROPE

Heathland flora evolved during the Mesozoic, a particular evergreen sclerophyllous vegetation adapted to dry environments and poor soils, especially with limited phosphorous (P) availability (Specht, 1979). Sclerophyllous characteristic elements from fossil records in Europe have been dated from up to 40 Mya BP (million years before present), a period of subtropical climatic conditions in the northern hemisphere (Dallman, 1998). During the cold and warm alternating phases of the Pleistocene, heathland vegetation dominated the intermediate periods between woodland expansions at the warmest moments and the xerothermic grasslands of the colder phases (Daniau et al., 2010). Traits such as the ericoid leaves developed as an efficient adaptation to the physiological water stress derived from low temperatures. Evergreen sclerophyllous shrubland communities also became adapted to the Mediterranean climate, which appeared on earth only approx. 3 Mya BP, characterized by the arid conditions of the warm season (Mariotti and Dell’Agata, 2012). Typical heath components such as the Ericaceae (Calluna, Daboecia and Erica) have undergone different colonizing and retreat episodes across the northern European region concurrently with the climatic shifts that took place during the late Tertiary. As an example, Erica scoparia shows narrow genetic variation among the continental Mediterranean populations compared with Macaronesian populations (Désamoré et al., 2012). This suggests that the present-day distribution is the result of different episodes of expansion and retreat, and a recent recolonization which probably ended at the last glacial period. This process of rapid recolonization also occurred with the tree heath (Calluna arborea), which originated in the East African mountain region approx. 5–2 Mya BP and colonized the Mediterranean and adjacent areas in Europe several times, with the Iberian Peninsula serving as late-Tertiary refuges (Désamoré et al., 2011). However, a rapid recolonization during the Holocene did not come from these refuges but from eastern African/Arabian populations. Southern populations of Calluna vulgaris (hereafter Calluna) also show a higher allozyme variation than northern ones, suggesting the existence of refuges and rapid south–north recolonization after the ice retreat (Mahy et al., 1999).

The last glacial period ended approx. 10 000 years BP and a general expansion of broadleaf deciduous forests took place, replacing open habitats such as heathlands. Heathlands have been present in Europe during the entire Holocene period, although changes in their extension and dominance occurred in association with climatic shifts and human occupancy. Holocene pollen records show a general presence of Calluna along its entire modern distribution, only limited by ice-cover at the northern-most region of Europe (Fig. 3). From approx. 5000 years BP there is a general increase in the Calluna–Erica pollen records throughout Europe (Prösch-Danielsen and Simonsen, 2000; Karg, 2008; Carrión et al., 2010), which coincides with human settlements and the beginning of a generalized deforestation process. The heathland extent reached its peak during the Bronze age and the early Iron age, approx. 4000–2000 years BP in western Europe (Webb, 1998; Odgaard and Rasmussen, 2000; Karg, 2008; Nielsen and Vad Odgaard, 2010), although its expansion was highly asynchronous: some areas were not transformed into heaths until the Middle Ages, approx. 1000 years BP, mainly uplands (Muñoz-Sobrino et al., 1997; Kooistra, 2008; Olsson and Lemdahl, 2009; Sköld et al., 2010), a period at which lowlands were losing heath extent by transformation into agrosystems (Fyle et al., 2003). The strong leaching process after the removal of large wooded areas resulted in the acidification and impoverishment of the soils, favouring heathlands. The heathland landscape became dominant in many parts of Europe, especially in the east, and the heathland landscape became characteristic of much of the northern parts of Europe.
western and southern Europe until a generalized decline started around 400 years BP, but most evidently since the 18th century as a result of land-use changes related to the industrial revolution, urban development and intensification of forestry and agriculture practices (Stevenson and Thompson, 1993; Prøsch-Danielsen and Simønsen, 2000; Berglund et al., 2008; Nielsen and Vad Odgaard, 2010).

There is evidence of human use of heathlands since the Bronze Age in western Europe (Karg, 2008). In the northern oceanic stands such as the Faroe Islands, pre-human settlement heathland expansion has been related to climatic shifts (Hannon et al., 2005), but is mostly explained by human-induced clearances of woodlands (Kooistra, 2008). The traditional management of heathlands was similar for
approx. 2000 years, and included different grazing systems, peat and turf cutting and removing, mowing to provide cattle with winter feeding, periodical burning to promote young regrowth and wood extraction for different uses such as the manufacture of smoking pipes or as a source of charcoal (Webb, 1998; Izco et al., 2006; La Mantia et al., 2007). In the Mediterranean, fluctuating pollen records show complex vegetation pattern changes during the Holocene (Carrión et al., 2010; Kouli, 2011). A higher presence of the sclerophyllous shrub vegetation extension may be explained by an increasingly arid period during the mid-Holocene at approx. 5000 years BP (Sadori and Narcisi, 2001; Fletcher, 2007; Carrión et al., 2010; Kouli, 2011). However, the human-induced increase in fire frequency was probably a major cause of evergreen Quercus woodland depletion and the promotion of shrublands in Mediterranean areas (Fletcher, 2007; Colombaroli et al., 2008) and, therefore, a major force of landscape shaping. Fire is also strongly related to the human management of northern and western heathlands, such as those at the Baltic coasts (Savukyniute et al., 2003; Olsson and Lemdahl, 2009), but differences with the Mediterranean region rely on the frequency of fires and the extent of the burned areas.

An understanding of the role of past human uses and climate on present-day heathlands may provide a basis for predicting future changes in relation to land-use changes, global climate change and other drivers. The implementation of this information on modelling the future of dynamic vegetation such as that of heathlands can be a powerful tool that is yet to be fully explored (Marinova et al., 2012).

**DRIVER 1: HABITAT DESTRUCTION AND FRAGMENTATION**

Heathlands were once a widely extensive habitat in a human-made cultural landscape, but a general substitution of traditional by other land-use management types has taken place in recent times. A general decrease in heathlands throughout temperate Europe during the last two centuries has been extensively reported. In Belgium, only 1 % of the heathland area from 1775 remains (Piessens et al., 2004) and in England only 16 % of the lowland heathland extensions from the early 19th century are left (Alonso, 2004), as most of the area has been transformed by afforestation, urban development or agricultural intensification. The heathland area has declined by 60–70 % in Sweden and Denmark from 1900 to 1960, and by 95 % in The Netherlands during the same period (Newton et al., 2009). Upland heathlands (moorlands) have also declined significantly, by as much as 90 % in Ireland and England during the last 200 years (Thompson et al., 1995). On the other hand, in certain areas like montane Mediterranean regions, heathlands have increased their extension due to land abandonment (Mouillot et al., 2005; Azevedo et al., 2011). Besides the obvious negative effect of a general reduction of heathland’s extension, habitat fragmentation and isolation are a key aspect of heathland conservation (Cristofoli et al., 2010a). The remaining areas of heathlands throughout Europe are strongly fragmented, with remnants alternating with other natural or mainly managed habitats (Veitch et al., 1995; Piessens et al., 2006). In Dorset, South-West England, a general decline of lowland heathlands has been documented since the 19th century (Webb, 1990; Veitch et al., 1995; Rose et al., 2000; Hoofman and Bullock, 2012). An accurate analysis of land-use change performed by Hoofman and Bullock (2012; Fig. 4) showed an overall habitat loss of 56 % for heathlands, but also a decrease in the mean patch size of 88 %, an increase in the distance between patches, and a lower heathland occupancy on the surrounding area of each heathland patch. Heaths have mainly been transformed to woodlands (broadleaf and coniferous) and to more anthropogenic land uses (arable land, improved grasslands or built-up areas). Overall, semi-natural habitats decreased by 74 % and were substituted by anthropogenically made habitats in the region. Therefore, heathlands have decreased in extension, fragment size, connectivity and species’ suitability with regard to the surrounding habitats.

**Habitat fragmentation affects diversity and community structure**

One of the negative effects of fragmentation generally described in the literature is regarding species richness. Piessens et al. (2004) stated that plant species richness of heathland areas is affected by fragmentation, but that this negative effect relies mainly on isolation and not on patch size. However, species richness is not a clear indicator of habitat quality as a response to habitat fragmentation (Kemper et al., 1999; Piessens et al., 2005) because it may be strongly influenced by an increasing edge effect, since species richness may be augmented by generalist or invasive species from external habitats, which strongly depends on the perimeter/area ratio, i.e. fragment size and shape. In contrast, community composition, measured as a shift in biological traits such as dispersal mode or pollination syndrome, may better explain habitat changes. According to Piessens et al. (2005), a given biological trait may determine the survival of a certain species for an isolated heath area. Plants with a persistent soil seed bank showed the highest survival rates for isolated patches. Other traits, such as long-distance dispersal abilities, seem to play a weak role in patch colonization. The soil seed bank is a key factor in the maintenance or recovery of European heathlands (Willems, 1988; Aerts et al., 1995; Valbuena and Trabaud, 2001; Måren and Vandvik, 2009). A persistent soil seed bank is characteristic for most of the dominant species in heathlands such as Calluna or Erica (Thompson and Band, 1997). Whenever the seed bank has been removed or depleted, heathland recovery will be severely retarded (Aerts et al., 1995; Pakeman and Marshall, 1997; Mitchell et al., 1998; Degn, 2001; del Cacho et al., 2012). If fragmentation takes place, the seed bank will play a key role in the long-term survival of the species (Bossuyt and Hermy, 2003; Cristofoli et al., 2010b). The rarest species are, however, under-represented in the seed bank compared with their occurrence in the community (Bakker and Berendse, 1999) and may therefore undergo local extinction even if recovery from the seed bank is achieved. Again, rare species are more sensitive to processes that may only marginally affect the community structure.
Population genetics and fragmentation

In a strongly fragmented landscape, the potential genetic-diversity loss associated with species population isolation will also negatively affect biodiversity. Genetic drift, inbreeding depression and allelic impoverishment will eventually cause the extinction of a given species, and an overall genetic-diversity loss. Rare species, such as *Gentiana pneumonanthe*, did not show a direct relationship between genetic variation and population size in Belgium, probably because isolation has taken place in recent times, and the species is a long-living perennial (Raijmann et al., 1994). However, it is clear that there is a low gene flow between populations, meaning that inbreeding depression from isolation will eventually take place.

Three recent papers deal with population genetics related to habitat fragmentation of three different heathland specialist species: the ground beetle (Drees et al., 2011), a heath bee (Exeler et al., 2010) and the smooth snake (Pernetta et al., 2011). In a study of the genetic-diversity pattern among smooth snake (*Coronella austriaca*) populations in a southern England landscape dominated by pine plantations with heathland remnants, Pernetta et al. (2011) found a significant correlation between allozymic differentiation and geographical distance, the so-called isolation-by-distance model, which corresponds to a continuous genetic population structure. This suggests that the smooth snake is capable of using corridors such as roadside verges to range between heathland patches and therefore minimizing the genetic diversity loss for the species. They also found a sex-biased population structure explained by the sedentary behaviour of females in contrast to a higher capacity of dispersal by males, promoting gene flow between populations.
A strong gene flow between populations was also found for a heathland specialist bee (*Andrena fuscipes*) in north-western Germany (Exeler et al., 2010). Again, the isolation-by-distance model better explains the genetic differentiation among patches in a common structure for a long-distance flying species with no effective barriers to gene flow. The relation to geographic distance was, however, weak and it is understood that other non-measured ecological variables may play a role in the population structure of the species. A study of the ground beetle (*Poecklius lepidus*) populations established that the main factor to explain genetic variability was the heathland patch size where the species was present (Drees et al., 2011). Patch size was positively correlated to allelic richness and heterozygosity. In contrast, Exeter et al. (2010) found no correlation with fragment size, although a recent bottleneck event was deduced at the smallest recorded heathland patch of only 300 m². A minimum patch size is thus critical for habitat quality, although this effect greatly varies among ecological groups such as the flying bees or the sedimentary beetles. Drees et al. (2011) concluded that heath fragments of <50 ha are ineffective for the long-term conservation of genetic variability of the ground beetle. Heathlands are dynamic ecosystems with recurrent episodes of disturbance such as fire or management changes. Thus, a minimum effective population size must be calculated over predictions of fluctuations with strong population declines to avoid the genetic erosion of specialist species. On the other hand, the population size of specialist species is not always in accordance with patch size, as this correlation was not observed in two heathland *Genista* species studied in Germany by Tsaliki and Diekmann (2010, 2011).

Matrix and corridors are determinant in the fragmentation effect

In addition to fragment size and isolation, the existence of corridors and the nature of the matrix strongly affect the habitat quality and species’ populations of heathland remnants. Piessens et al. (2006) studied a set of heathland patches with different land uses in the adjacent areas. A strong edge effect was recorded in heath patches adjacent to the different land uses, reflected in plant community composition changes and soil properties. The abundance of heather (*Calluna*) decreased towards the edge in all cases, and it was mostly replaced by grasses. Available P, nitrates and soil pH, as eutrophication indicators, increase towards the edge. The authors determined the same average distance from the margin as the edge effect limit for all bordering land uses. However, the negative effect within this belt was higher for heath patches adjacent to cropland, with higher eutrophication in the soil. The nature of the matrix (i.e. surrounding landscape) in a heathland mosaic was also important for a wide range of flower-visiting insects (Dupont and Nielsen, 2006). Patch size was not correlated with species richness but community composition and, therefore, plant-insect assemblages are affected by fragmentation. Small remnants have a higher diversity, although this is explained by the occurrence of generalist species against heath-specialists. External habitats are therefore enriching patches with a higher edge percentage, which highlights the importance of the surrounding habitats.

Conversely, the need for patch connection through corridors to maintain species in heath patches has been stated for different ecological and taxonomic groups (Noordijk et al., 2011; Pernetta et al., 2011). The permeability of the surrounding areas and the existence of suitable corridors, will determine the effective connectivity between patches.

The classical approach to island biogeography, which involves considering isolation-by-distance alone, is not suitable for a complex landscape such as heathlands. The matrix composition is therefore critical (Ricketts, 2001). An approach to the fragmentation effect over heathland landscapes should consider the surrounding habitat types in terms of effective corridors for key species such as pollinators (Webb and Vermaat, 1990). For example, a complex interaction exists between populations of the Dartford warbler (*Sylvia undata*) in Dorset and the different surrounding habitats (van der Berg et al., 2001).

The heathland plant community is highly resilient to fragmentation and isolation, with a resultant low diversity loss (Piessens et al., 2005). It also means that a big effort is needed to restore the heath plant community after habitat destruction (Cristofoli et al., 2010b). It may be the case that local extinctions are taking place over a long time period and, therefore, there is an actual extinction debt in heathland ecosystems (Piessens and Hermy, 2006; Cristofoli et al., 2010a), but this theoretical effect needs testing.

Fragmentation affects other taxonomic groups that may act as dispersers or pollinators (Webb and Vermaat, 1990; van der Berg, 2001; Noordijk et al., 2011), but plant reproduction success is weakly influenced by population size (Tsaliki and Diekmann, 2011). However, other studies point to an interaction effect of eutrophication and fragmentation that may affect the reproductive success of rare heath species (Vergeer et al., 2003).

Soil conditions are related to habitat quality independent of fragment or population size (Piessens et al., 2004; De Graaf et al., 2009; Tsaliki and Diekmann, 2010). Thus, species diversity and habitat quality of heathland patches are, as a general rule, little or not dependent on patch size as long as the key environmental factors (mainly soil properties) are maintained. Land-use changes may strongly affect the habitat quality of the surrounding landscape (i.e. matrix and corridors) resulting in a higher environmental pressure to heathland remnants.

**DRIVER 2: POLLUTION AND EUTROPHICATION**

One of the main characteristics of heathlands is that they develop over poor soils, with low values for most nutrients and pH (Mitchell et al., 1999; De Graaf et al., 2009). Although some heathlands occupy basic soils, especially around the Mediterranean basin (Canals and Sebastià, 2002; Sardans et al., 2008a–c) most temperate heaths live on acid soils (De Graaf et al., 2009). The main limitations to plant growth in these conditions are exchangeable P, potassium (K) and N (Bobbink et al., 2010). Other edaphic chemical variables that limit plant growth in heathlands are aluminium toxicity, low contents of minor nutrient concentrations such as calcium (Ca²⁺) or magnesium (Mg³⁺), or the ratios between these nutrients (Kleijn et al., 2008). Moreover, different hydrological conditions such as slow-draining soils of wet
heathlands diminish the acidification process and, whenever drained, result in a high acidification, higher soil respiration rates, and lower N availability (Jansen et al., 2004). Soil conditions are particularly important in maintaining heathland habitat quality, as stated for habitat fragmentation.

Several pollutant sources globally affect the temperate biomes, mainly through the atmospheric deposition of sulphur (S) or N. Atmospheric N deposition is today considered one of the main drivers of biodiversity loss in northern temperate biomes (De Schrijver et al., 2011; McClean et al., 2011). Reduced and oxidized forms of organic nitrogen have increased the deposition rates of N and will most likely continue for the following decades (Tilman et al., 2002). High atmospheric N depositions result in a higher N concentration in the leaves of ericaceous species and a subsequent increase in N : P and N : K ratios in leaf tissues (Britton et al., 2008) which may result in a higher herbivorous pressure over the species. Litter deposition then adds to organic soil N inputs where higher decomposition rates are recorded, which in turn decreases the C : N ratio (Power et al., 2001). Nitrogen leaching increases, eventually affecting water quality, especially in upland landscapes (Britton et al., 2008), although this has not always been observed (Power et al., 2004). The complete cycle is thus affected on the system, with a strong negative effect over the habitat quality.

Atmospheric N deposition alters heathland community structure

The increase in atmospheric N depositions affects community structure and composition in heathlands by enhancing grass species over shrubs (Heil and Diemont, 1983; Roelofs, 1986; Heil and Bobbink, 1993; Moore, 1995; Bakker and Berendse, 1999; Britton et al., 2001; Terry et al., 2004). Nitrogen addition increases shoot growth, biomass and flowering of ericaceous species such as Calluna (Power et al., 1995; Gidman et al., 2005; Britton and Fisher, 2008; von Oheimb et al., 2010), but there is a resultant overall negative effect due to competition with grass species such as the purple moor grass (Molinia caerulea) against heather (Calluna), especially at the seedling stage when Molinia more efficiently uses N inputs (Friedrich et al., 2011). This is of particular importance since germination and seedling establishment is crucial for heath development (Power et al., 2001; Roem et al., 2002; Britton et al., 2003; Friedrich et al., 2011). Seedling establishment of Deschampsia flexuosa also increased significantly with higher N deposition values, especially when combined with uncontrolled fire (Power et al., 2001). The switch from heather dominance to heath grasses is therefore conditioned to a certain level of disturbance in the community (Power et al., 1998; Britton and Fisher, 2007) from intensified management (grazing or cutting), accidental fire, or by heather beetle (Lochmnaea saturalis) attacks. Any of these factors can break up the canopy cover of the shrub, promoting the germination of grass seeds (Terry et al., 2004). In addition, the plant-community changes observed with higher N availability may serve as indicators for negative effects on soil biota (Payne et al., 2011).

Species richness decreases with increasing N deposition for all vegetation types, but in heathlands this negative effect is among the highest (Maskell et al., 2010). Species richness, as an indicator of habitat quality, decreases when eutrophication occurs (De Graaf et al., 2009), especially with a loss of heath specialists (De Graaf et al., 2009) and rare and endangered species (Kleijn et al., 2008). Overall, acidity and A1 : Ca ratio determine community composition and species richness, but NH4 concentration and the NH4 : NO3 ratio are the key factors affecting rare species that show a much narrower tolerance for changes in these parameters (Kleijn et al., 2008). Species composition may also be altered by high N availability, by shifting from an N-limited to a P-limited or an NP-co-limited environment (Power et al., 2001; Härdtle et al., 2009; von Oheimb et al., 2010), although this effect needs further experimental work (von Oheimb et al., 2010). Eutrophication also promotes invasion by generalist species with a negative effect on heath specialists (Mitchell et al., 2000). However, markedly different results may be observed in different heath communities, since N addition resulted in higher species richness in an alpine Cantabrian heathland (Calvo et al., 2007). Perennial herbs were enhanced, but no negative effect over ericoid shrubs was recorded, suggesting that the species loss associated with N addition needs to be ascertained locally.

DRIVER 3: INCREASING CO2 AND CLIMATE CHANGE

Increasing atmospheric CO2 as a result of human intervention is affecting the climate by global warming, changes in precipitation amounts and annual distribution, as well as extreme climatic events. Over the last century, an increase in the mean annual temperature of 0.9 °C has been recorded in continental Europe, and future scenarios predict an increase of the mean annual temperature of 0-1 to 0.4°C per decade for the 21st century (Harrison et al., 2006; Alcamo et al., 2007). The mean annual precipitation is predicted to increase in northern Europe and decrease in southern Europe, but the summer drought will be drier and last longer throughout the region (Alcamo et al., 2007). Global change is affecting biological systems throughout the world according to a wide set of indicators, including plant communities (Rosenzweig et al., 2007). Direct consequences are changes in phenology, plant productivity or metabolic rates, and these effects determine the species distribution, competition and community structure (Peñuelas and Filella, 2001; Walther, 2003; Feehan et al., 2009). These changes will probably disrupt ecological functions, species interactions and ecosystem services (Fitter and Fitter, 2002; Memmott et al., 2007; Feehan et al., 2009). The projected biodiversity losses in alpine and boreal biomes are among the most directly affected by global warming, whereas others such as tropical forests will be mainly affected by land-use changes (Sala et al., 2005). In contrast, biodiversity loss in temperate heathlands seems to be balanced between these two main drivers, and is highly dependent on their interaction.
effects (Sala et al., 2005; de Chazal and Rounsevell, 2009). The diversity and structure of heathlands will be affected by climatic changes, e.g. arctic-montane vascular plant species in oceanic heaths are likely to decrease in extent due to predicted temperature rises, which will also favour the expansion of more generalist competitive species (Walther et al., 2005). These will affect bryophyte-rich heaths, which will also reduce in extent due to a greater seasonality of rainfall (Hodd and Sheehy Skeffington, 2011).

Climate change effects have been measured in heathlands from historical records (Berry et al., 2002; Peñuelas and Boada, 2003), manipulating experiments (Beier et al., 2004; Jentsch et al., 2007; Mikkelsen et al., 2008; Albert et al., 2011a) and the implementation of predictive models [Coquillard et al., 2000; Berry et al., 2002; also Midgley et al. (2002) in fynbos]. This large set of published data provides the basis for understanding recent changes in heathlands associated with climate change, and to predict, to a certain extent, the future of heathlands under global change scenarios.

Climate-change effects over phenology of heath species are heterogeneous

The distribution of plant-cycle events throughout the year (i.e. phenology) is markedly dependent on temperature and precipitation (Peñuelas and Filella, 2001; Walther, 2003; Feehan et al., 2009). Phenology is a key ecological process that involves plant growth and ecosystem functions such as plant–pollinator interactions (Memmott et al., 2007). Moreover, shifts in plant phenophases are one of the most accurate biological indicators of climate change (Walther, 2003; Jentsch et al., 2009). In heathlands, drought alters the flowering time span and the vegetative growth period of common shrub species (Peñuelas et al., 2004), but these are less affected by warming. The growth period may last longer as early spring temperatures rise, but this does not necessarily result in higher productivity because overall growth is limited by lower water availability in drier regions (Bernal et al., 2011). In a Mediterranean heathland experiment, warming and drought benefitted Erica multiflora over Globularia alypum (Llorens et al., 2004b). Both are sclerophyllous shrub species common in basic poor soils of the western Mediterranean basin, but E. multiflora is a resprouter species with a thick lignotuber to store reserves (Sardans et al., 2006) and therefore less dependent on short-term resources, such as soil-water availability. This apparent disruption of species competition due to climatic changes must be considered in the specific conditions of the Mediterranean climate, which is characterized by a strong inter-annual variation and unpredictability (Mariotti and Dell’Aguila, 2012). Globularia alypum, a species with both seeder and resprouter strategies (Saura-Mas and Lloret, 2007) may compensate for changes with a higher ecological plasticity.

Flowering time is affected in a species-specific manner, either delayed or advanced by warming or drought whenever extreme climate events take place (Jentsch et al., 2009). However, there is a strong interaction between the plant community and phenological shifts. A drought event significantly delayed mean Calluna flowering peak and extended flowering time, but only in complex stands with high functional diversity (Jentsch et al., 2009). Delays and increasing lengths of flowering time occur in heath species under drought treatments (Peñuelas et al., 2004), while general patterns show an overall earlier bloom in a warmer climate (Fitter and Fitter, 2002; Peñuelas et al., 2002). The delay on flowering of the ericaceous species is stronger under a Mediterranean climate (Peñuelas et al., 2004; Prieto et al., 2008) but it is either unaffected or slightly brought forward in temperate heaths. Water availability during the flowering season is the main limitation for flowering in the Mediterranean stands, whereas northern heaths are less affected by drought and are favoured by mild spring temperatures.

Climate changes nutrients cycles and limitants in heathland soils

Global warming and rising CO₂ concentration increases soil biological processes, enhancing litter decomposition and nutrient availability. On the other hand, water stress lowers biotic activity in the soil (Peñuelas et al., 2004; Sowerby et al., 2008). Complex site-specific interactions are found for warming and drought in soil respiration rates (Sowerby et al., 2008). In oligotrophic plant formations such as heathlands, higher rates of mineralization may increase the N : P ratio in the soil and eventually drive a change from N-limited to N-P limitation (von Oheimb et al., 2010). This process is accelerated by increasing air temperature whenever water stress is kept under critical values, mainly in non-Mediterranean climates (Schmidt et al., 2004). The negative effects of high N deposition on habitat quality is thus conditioned by climate (Britton et al., 2001; Schmidt et al., 2004; Sardans et al., 2008a–c).

Plant physiological response to CO₂, warming and drought differ in magnitude and direction

Increasing CO₂ atmospheric concentrations result in higher plant productivity and increasing rates of photosynthesis and respiration (Albert et al., 2011a, b), which is enhanced by warming but reduced by drought in experimental treatments on a Calluna Atlantic temperate heath. A non-additive response to interactions between these treatments was recorded for photosynthetic performance (Albert et al., 2011b), suggesting complex interactions between warming, drought and rising CO₂ levels.

Warming treatment resulted in a higher plant productivity in another controlled experiment on different European heathlands (Peñuelas et al., 2004; Wessel et al., 2004), while drought reduced plant productivity, respiration rates and photosynthesis, mainly in Mediterranean heathlands. However, the interaction between warming and drought factors was not studied in this experiment.

Sclerophyllous shrubs are less affected than grasses with regard to photosynthesis performance (Ninemets et al., 2011), but the production of secondary compounds such as terpenoids lowers under drought treatments, which is an effect that is also observed under increasing N addition (Hofland-Zijlstra and Berendse, 2009). Warming and drought increased herbivore attack by the heather-beetle in temperate Calluna stands (Peñuelas et al., 2004), probably due to the depletion...
of phenolic compounds which constitute a defence against herbivores. Moreover, a decline in the allelopathic compounds of heather litter increases the mineralization rate and promotes germination of other species. However, positive competition of heather against heath graminoid species relies more on its higher efficiency under nutrient-poor soil conditions than on the allelopathic properties of its litter (Berendse et al., 1994; Hofland-Zijlstra and Berendse, 2010).

Plant diversity is altered mainly due to effects at the seedling stage

Plant responses to climate change are asymmetric, with differences across regions and ecosystems (Walther, 2003). Moreover, different species co-occurring in a single habitat may be affected differently by climatic shifts (Llorens et al., 2004a, b). Species richness, as the general sum of species occurring at a site, is therefore a complex measure to indicate habitat changes and must be contrasted with species composition. Plant diversity changes were measured under experimental manipulation for warming and drought over different European heathlands (Peñuelas et al., 2007). No significant differences due to warming or drought were recorded in the 7-year experiment across sites. However, recovery after fire in a Mediterranean site of the north-east Iberian Peninsula decreased under both treatments, but mainly under the drought conditions. Contrary to biomass, plant cover or net primary productivity, which responded significantly to treatments and time, plant richness was unaffected by climatic changes. Disturbances such as wildfires will delay regeneration processes and decrease plant richness at least during the early stages in Mediterranean stands subjected to increasing aridity (i.e. summer drought). Heathland regeneration relies both on resprouting and seed germination (Ojeda et al., 2001; Lloret et al., 2004). Seedling diversity lowers under drought and warming treatments (Lloret et al., 2004; Prieto et al., 2009; del Cacho et al., 2012). Long-term changes on plant richness and diversity will occur due to climatic shifts, not over mature stages but during early phases of vegetation recovery from disturbance such as wildfires.

**DRIVER 4: VEGETATION DYNAMICS AND MANAGEMENT**

Most heathlands are commonly described as successional vegetation types, intermediate steps within dynamic succession series that end in the climax vegetation (Mallik, 1995; Pakeman and Nolan, 2009). Potential drivers of change over heathland vegetation are therefore the natural forces that affect community structure towards a highly mature vegetation type such as broadleaf or coniferous woodlands. Changes may also point towards a regression in natural succession, by means of a general loss in shrub cover and substitution by pastures or bare soils. In other cases, succession takes place favouring heathlands. Mountain meadows, where summer grazing was the traditional management, are now switching towards a dwarf shrub heath community due to the abandonment of these practices (Pasche et al., 2004), although this represents a transition phase that will eventually continue succeeding to woodlands.

However, natural succession is a complex transition between community types conditioned by climate, soil properties, species seed bank or dispersal, and local management, and has therefore been described as site-specific (Britton et al., 2000; Manning et al., 2005; Britton and Fisher, 2007). This is in accordance with other views that discuss the generally accepted phytosociological approach of a straight succession towards a single potential vegetation type (Carrión and Fernández, 2009). Mitchell et al. (1997, 1999, 2000) described more than one successional trajectory (i.e. transitions between communities) in lowland heaths (Fig. 5). Soil properties explained most of the community variation on a canonical multivariate analysis. Higher pH values and available Ca and Mg is associated with birch woodlands, while higher N concentrations (NH₄ and NO₃) are found in sites invaded by bracken. Low pH and high N values were found on plots invaded by Pinus sylvestris and Rhododendron ponticum. In a different study, a transition towards a Betula-dominated scrub was limited by both seed availability of the invasive species and the heath age and structure (Manning et al., 2005).

Time span is not the main factor for transition between communities, as several biotic and abiotic factors may act as limitants or promoters of succession. Management plays a critical role in heathland existence, preservation and/or restoration as it has been considered in the scientific literature (Webb, 1998). European heathlands have been periodically controlled by grazing, burning or cutting, all of which are actions that remove plant biomass and prevent natural succession.

**Grazing maintains community structure when other factors are controlled**

The use of grazing, generally associated with other management practices such as periodic burning, is one of the main factors that have shaped the European heathland landscape for millennia (Thompson et al., 1995; Webb, 1998; Evans et al., 2006). During the last two centuries, a general transformation process towards a higher intensification has taken place, leading to higher stocking rates and the change of mixed grazing by wild and domestic herbivores to a single-species grazing use (Gordon et al., 2004). On the other hand, abandonment of traditional pastoral practices in heathlands implies a transition towards scrub and woods (Marrs et al., 1986; Webb, 1998; Bokdam and Gleichman, 2000).

Evidence shows that intense grazing results in a loss of cover of shrub species and an increase in graminoids (Bullock and Pakeman, 1997; Bokdam and Gleichman, 2000; Newton et al., 2009). These changes are conditioned by grazing species, stocking rates, management (herding, seasonal free ranging) or in combination with other practices such as cutting or burning (Bullock and Pakeman, 1997; Newton et al., 2009; Celaya et al., 2010). The use of different grazing animals affects heathlands in different ways, promoting transitions towards other vegetation types at different time rates (Putman et al., 1987; Jáuregui et al., 2009; Celaya et al., 2010; DeGabriel et al., 2011; Wehn et al., 2011). There is also a strong interaction between grazing species and season (Putman et al., 1987; Hester and Baillie, 1998). For example, cattle use heathers evenly throughout the year, while other herbivores such as ponies have foraging peaks in
the spring, when the growth of grasses gets higher (Pratt et al., 1986; Putman et al., 1987).

DeGabriel et al. (2011) compared the plant community structure and species diversity in Scottish upland heathlands with the presence or absence of sheep grazing on different scales. Sheep removal was correlated with a higher grazing pressure from deer, but an overall lower heather utilization. Alpha diversity was correlated to the sheep livestock, mostly due to a switch towards grasslands when the number of sheep increased. Deer and moderate sheep grazing is the optimal scenario to maintain community structure and alpha and beta diversity. Higher diversity values were recorded in intermediate stages during the transition towards grasslands, a richer community, whereas absence of sheep may cause a turn towards the degenerate phase of the Calluna cycle.

Newton et al. (2009) described great variation in the response of communities subjected to different experimental grazing studies and concluded that it would be difficult to give an exact general prescription for maintaining heath by grazing. Grazing is an effective management practice for heathlands but, in general, it requires to be combined with other practices such as burning (Barker et al., 2004; Hårdtle et al., 2009). Again, this depends on local conditions and the particular heathland type. Traditional grazing practices may be sufficient for heathland maintenance in the Erica scoparia community in central France (Gachet et al., 2009) but not, for example, in Calluna stands in north-east Iberian mountain heathlands (Bartolomé et al., 2000).

Fire may promote both regressive and progressive successional stages

Fire is a key factor in the existence of most heathland vegetation types (Schwilk et al., 1997; Harris et al., 2011). The sclerophyllous vegetation under Mediterranean climates, such as fynbos in South Africa, chaparral in California or Mediterranean heathlands, are generally fire-prone habitats with high fire frequencies (Delitti et al., 2005; Mouillot et al., 2005; Azevedo et al., 2011). Fire regimes range from large, intense wild-fires to prescribed winter burning performed to maintain heath structure. Successional dynamics on heathlands are directly correlated to fire regimes (Sedláková and Chytrý, 1999; Mohamed et al., 2007; Mären and Vandvik, 2009; Mitchell et al., 2009) and the use of controlled fire is an effective management tool for heathland preservation (Sedláková and Chytrý, 1999; Mohamed et al., 2007; Davies et al., 2008). On the other hand, a general increase in fire frequency associated with global warming may benefit
certain heath communities against other habitats such as woodlands, particularly under a Mediterranean climate (Mouillot et al., 2002).

The increasing frequency of fire regimes generally causes a regression on succession, promoting grasses against shrubs (Power et al., 2001; Brys et al., 2005; Jacquemyn et al., 2005). However, recent evidence supports the positive effect of fire on tree encroachment on heathlands, promoting progressive succession (Borghesio, 2009; Ascoli and Bovio, 2010). Ascoli and Bovio (2010) studied birch (Betula pendula) and aspen (Populus tremula) encroachment on Calluna-dominated heathlands on the Alps piedmont. Fire reduced the continuous vegetation canopy, removed allelopathic compounds and promoted tree encroachment via the facilitation of seed germination and seedling establishment. Later, strong suckering regeneration of aspen resulted in a general loss of Calluna cover and the presence of characteristic heath species such as Genista tinctoria or Gentiana pneumonanthe. It is notable that the effect over Molinia shows the opposite sign, with higher cover values underneath the tree stands. Fire therefore causes a regressive succession from heathlands to pastures, but also promotes positive succession favouring different tree species. Below critical values, there is a risk that fire may transform the heathland landscape into a mosaic of woodlands and pastures. However, this particular response may be associated with this particular heathland type, and thus new contrast studies are needed in other regions.

A need for combined treatments on heathland management

Several studies have revealed that incorrect policies have been developed regarding heathland conservation. In Montseny Natural Park, an isolated heathland region in a Mediterranean area in eastern Spain, prohibition of fire has resulted in a general transition of the Calluna heath towards a Mediterranean forest or bracken invasion (Bartolomé et al., 2005). Grazing alone has not resulted in the maintenance of heath but a generalized transition towards scrub and forest. Bokdam and Gleichman (2000) stated that grazing by free-ranging cattle is not enough to prevent heath transition, both towards grassland or woodland, in Dutch lowland heathlands. They predict a future landscape formed by a wood–pasture mosaic unless additional management is implemented, such as limiting grazing to seasonal and day-time herding. Sedláková and Chytry (1999) state that the use of cutting as an alternative to fire for biomass out-take retards Calluna recovery and enhances grass encroachment. A combined management of prescribed burning and grazing is proposed to maintain heath structure and diversity. However, cutting may be an efficient substitute to grazing for biodiversity conservation according to Calvo et al. (2007) who performed a manipulated experiment in an alpine Calluna stand in northern Spain. A combined fertilization and cutting treatment showed the highest biodiversity. Graminoid species and forbs were enhanced, but no competition effect was observed with Calluna, although the field experiment lasted for 5 years and projections on long-term process should show cautiousness.

Heathland management is, without doubt, the key instrument for habitat maintenance, but the appropriate practices to be used are strongly correlated to climate and regional environmental characteristics. Lessons from traditional practices are especially useful regarding fire frequency, grazing levels or cutting intervals, and may provide practical information on the conservation plans to be implemented.

DRIVER 5: INVASIVE EXOTIC SPECIES

The presence and spread of non-native species disrupting ecological processes throughout biomes worldwide is considered one of the main causes of biodiversity loss (Hulme et al., 2001; Butchart et al., 2010), even though these invasions are, to some extent, not always a driver but a consequence of a habitat quality loss triggered by other factors (Didham et al., 2005). Heathlands are among the habitats with a lower frequency of exotic invaders and are less affected with regard to its ecosystem functions (Lambdon et al., 2008; Chytry et al., 2009). Mediterranean heathlands have a low number of invasive species when compared with other Mediterranean areas, and some heath types have no invasive species ever recorded (Vilà et al. 2007). In contrast, the high impact invasive exotic vascular plants are having on the South African fynbos habitat threatens endemic native species (Roura-Pascual et al., 2009).

In spite of its low invasiveness, European temperate heathlands occur on highly managed landscapes, and some important biological invasions have been recorded with a high environmental and economic cost (Tyler et al., 2006). However, this driver has not been given as much attention by heathland ecologists as other issues, and the term ‘invasion’ is frequently used without distinction for the appearance of native species as a result of natural succession and the spread of exotic species that alter the community (e.g. Mitchell et al., 2000).

Trees such as Prunus serotina or Robinia pseudoacacia, shrubs like Gaultheria shallon, Rosa rugosa or Rhododendron ponticum and grasses such as Panicum acuminatum are among the alien species naturalized in temperate European heathlands. Some invasions are from coniferous species such as Pinus strobus, Picea stichtensis or Douglas fir (Pseudotsuga menziesii) (Broncano et al., 2005; Carrillo-Gavilán et al., 2011), which compete with other native gymnosperms involved in the natural succession process. A favourable competition between Douglas fir and the native silver fir (Abies alba) was described by Carrillo-Gavilán et al. (2011) for a montane heathland landscape in north-east Spain. Higher germination rates were found for Douglas fir, while the two species showed high mortality at early seedling stages. Success of the Douglas fir is probably limited to the amount of available seeds. Propagule pressure from nearby areas is thus the key process for invasiveness of the species, in accordance with the general view that considers propagule pressure as a major factor on plant invasions (Simberloff, 2009).

Invasions in heathlands are driven mostly by habitat suitability directly influenced by soil conditions, as observed for Rhododendron ponticum (Mitchell et al., 2000; Erfmeier and Bruehleide, 2010). A negative feedback is promoted because Rhododendron-invaded areas showed the lowest values of plant diversity, either for total species or for heath specialist numbers (Mitchell et al., 2000). In a different study, cover
of dominant species, either shrub or perennial grasses, was directly inverse to the presence of the alien *Panicum acuminatum* in *Calluna* heathlands of northern Italy (Lonati et al., 2009). Management should therefore limit tree encroachment (Ascoli and Bovio, 2010) but also extend the loss of dominant species’ cover to prevent spreading of the invasive species. Whenever large amounts of biomass are removed by combined factors such as fire and grazing in short intervals, *P. acuminatum* will succeed in that particular region.

The negative effects of invasive species, however, go beyond competition with native species, as complex interactions at trophic levels (i.e. food webs) are altered in invaded heathlands. A significant negative effect of the invasive species *Gaultheria shallon* over certain specialist parasitoid and herbivorous species was recorded in a lowland heath in Southern England (Carvalheiro et al., 2010). In contrast, and to a certain level of invasiveness, generalist groups were positively affected by *G. shallon*. A lack of resources for specialist herbivores, which do not feed on the exotic species, and disruption of the food chain by parasitoids—herbivores—plants, causes a major threat to the habitat quality, and probably affects other organisms and ecosystem functions. Disruption of species assemblages in the community, including parasite and host interactions, is thus a major cause of habitat quality loss (Henson et al., 2009). An indirect effect of the presence of an invasive species is the spread of *Phytophthora* spp., which infects *Rhododendron ponticum* and also other heathland species in the British Isles (Beales et al. 2009). The direct impact of the invasive parasite may be enhanced by the presence of the invasive plant species.

**INTERACTION BETWEEN DRIVERS**

The understanding of ecological processes involving different drivers over ecosystems is a major task for ecologists in the future (Darling and Côté, 2008). When dealing with biodiversity loss, very different responses have been recorded when more than one factor is analysed, either additive effects, synergies or antagonisms. Non-additive interactions can be considered as ecological surprises, but recent knowledge points to a high prevalence of these surprises in ecological research (Lindenmayer et al., 2010). In the topics covered, many studies analyse one or few drivers with the limitation of excluding other shift sources from the study. As an example, several models have been proposed on the heathland future development under increasing N-deposition scenarios, but no effect derived from global warming, or even climate, was considered (Power et al., 2004; Terry et al., 2004; Evans et al., 2006; but see Britton et al., 2001). However, shifts occurring under high N deposition values are similar to the rising temperature effects predicted for the future, such as changes in plant growth or flowering (Peñuelas et al., 2004). Strong interactions between the described drivers are found whenever they are analysed as factors in a single model, but the magnitude and direction of interactions is generally unpredictable, as in other ecosystems (Brook et al., 2008; Darling and Côté, 2008; de Chazal and Rounsevell, 2009). Moreover, effects of different factors are frequently species specific and presumably different communities and ecosystems will respond differently to interactions (Werkman and Callaghan, 2002; Britton et al., 2003; Kreiling et al., 2008).

Among the most studied interactions, eutrophication is probably the best-known since it is directly related to management and heath dynamics and is critical for ecological restoration and conservation (Piessens et al., 2005; De Graaf et al., 2009). The increasing N concentrations in heath systems come from atmospheric depositions or other factors such as intense grazing (van der Wal et al., 2003) or burning (Mohamed et al., 2007). In particular, higher values of NH₄ are found after fire and there is a generalized loss of elements through leaching, including N. The C : N ratio in plants is not affected by fire, but C : P and N : P ratios increased in the grass *Deschampsia flexuosa*. This suggests a negative effect on *D. flexuosa* in competition with *Calluna* due to the latter’s advantage in uptake of the limitant P. The N content in *Calluna* shoots increases with N addition (Pitcairn et al., 1995; Hicks et al., 2000; Britton et al., 2008) and burning (Britton et al., 2008), but there is no interaction effect according to Britton et al. (2008). In contrast, the opposite effect of atmospheric N deposition has widely been accepted with perennial grasses favoured against heather (Heil and Bobbink, 1993; Terry et al., 2004; Bobbink et al., 2010). Plant diversity lowers with higher N availability and the soil N : P ratio (Roem et al., 2002; De Graaf et al., 2009). A higher NH₄ concentration mostly affects rare and endangered species (Kleijn et al., 2008; De Graaf et al., 2009), and may constitute a trigger factor for the spread of exotic invasive species (Mitchell et al., 2000; Perry et al., 2010). Biomass removal through other management practices, such as cutting or grazing, buffers the ecosystem from the long-term effects of N atmospheric deposition (Power et al., 2001) but, conversely, removing the shrub canopy enhances grass competition by the facilitation of seed germination, a particular stage in which grasses are favoured by higher N deposition rates (Britton et al., 2001; Friedrich et al., 2011).

Climate changes may also condition the effects of N atmospheric deposition (Whitehead et al., 1997; Gordon et al., 1999; Britton et al., 2001; Werkman and Callaghan, 2002). Drought is a key factor in the *Calluna*—grass and *Calluna*—bracken competition (Gordon et al., 1999; Britton et al., 2001). The dramatic substitution of heathlands by grasslands described in The Netherlands (Heil and Diemont, 1983) does not occur in the UK, at least to the same extent, and this may be explained by a higher annual precipitation, a factor that lowers the negative effect of N deposition (Gidman et al., 2005; Helliwell et al., 2010), together with frequent cutting (Britton et al., 2001; Fig. 6). Soil moisture is thus the key factor affecting N mineralization in the soil, although higher rates of respiration and decomposition are also recorded at higher air temperatures (Emmett et al., 2004). Carbon sequestration will increase with higher N inputs (de Vries et al., 2009), as has been seen in forest systems; however, the C : N ratio response remains unclear, both in soil and biomass, to recent changes, since increasing N deposition and a higher CO₂ concentration may act synergistically over plant productivity (Larsen et al., 2011).

Whitehead et al. (1997) measured the growth of *Calluna* under high CO₂ concentrations and N addition. Photosynthesis and growth was enhanced both by increasing CO₂ and as a
result of N and P addition (no response from N alone), but the interaction was antagonistic. In contrast, bracken was enhanced by both factors and synergistically by its interaction. This study was performed under laboratory conditions, but a field study by Werkman and Callaghan (2002), which also covered bracken and heather response, suggests that competition between the species alters the specific response to each factor. Heather growth was neither affected by increasing temperature or N addition, nor by its interaction, in pure stands. In mixed plots with bracken, growth was negatively affected by both factors due to the competition effect, since bracken reacted positively to rising temperature and comparatively to N addition. Flowering showed a different response, as it increased with higher temperature in pure stands, but showed no significant response on mixed plots. Bracken’s frond height increased and shaded heather, which was the major cause for the negative effect over Calluna.

More long-term field experiments are needed to provide a scientific-based approach to interactions between drivers of biodiversity changes in heathlands. The system response to higher nutrient availability together with different management types or climatic conditions are best known, but restricted to competition, plant and soil chemical composition, and effects over single species (Alonso et al., 2001; Werkman and Callaghan, 2002; Barker et al., 2004; Härdtle et al., 2009). Other factor interactions, such as the presence of invasive species combined with climate change, are desirable for future predictions on heathland responses to these drivers.

**Fig. 6.** Interactive effect of cutting-time intervals, N deposition and precipitation in the maintenance of Calluna cover in a modelled lowland heathland. Three scenarios with mean annual rainfall values of 550 mm, 700 mm and 900 mm where modelled. The frequency of cutting needed to maintain Calluna cover decreases with higher precipitation values and higher N deposition. The 700-mm scenario showed a high sensitivity to N deposition, with a management change needed at low levels of N deposition (20 kg N ha\(^{-1}\) year\(^{-1}\)). Modified from Britton et al. (2001).

Heathlands are highly dynamic habitats, with strong biotic and abiotic interactions affected by external drivers, despite its appearance as a homogeneous, stable ecosystem. All of the factors studied influence diversity patterns, community structure and the general quality of the habitat. However, most of these factors are species specific, site specific or strongly dependent on other factors such as local climate. Moreover, shrubland types of markedly different climatic and geographic areas with different species composition, as covered here, may be affected differently by these drivers. As an example, a different response to experimental warming and drought in a north–south gradient of European heathlands was recorded for factors such as primary productivity, plant richness or soil microbial activity (Peñuelas et al., 2004, 2007; Sowerby et al., 2005). Even in stands from similar latitudes, differences are observed due to abiotic local conditions or stochastic forces such as heather-beetle attacks (Peñuelas et al., 2004). Moreover, studies on interactions among factors are still insufficient but point to unpredictable and locally specific responses. A summary of the general tendencies and future projections that can be cautiously extracted from the available information follows.

**No clear effects on species richness and diversity but rare and endangered species will decline**

Overall species richness and diversity is a key indicator of habitat quality, and the benefits of diversification in plant communities are many (Isbell et al., 2011). However, the temperate European heathlands are relatively species poor, moderately homogeneous and with a low species turnover (Webb and Vermaat, 1990; De Graaf et al., 2009; Loidi et al., 2007, 2010). The overall number of species will probably increase under intensely managed areas where a mosaic of grass and shrubs is created (Calvo et al., 2005, 2007; Celaya et al., 2010; Muñoz et al., 2012), but this does not necessarily...
mean a higher habitat quality. For example, a higher number of species was recorded in Betula-dominated and Pteridium-invaded plots, although the heath-specialist species decreased at both stages compared with the pure heathland stands (Mitchell et al., 1999). A general species loss will take place under higher N-deposition scenarios (Maskell et al., 2010). Soil conditions, particularly higher NH$_4$ concentrations, are the key factors that affect plant richness. Rare and specialized species will decline and most probably undergo local extinction processes under future conditions of soil eutrophication (Roem and Berendse, 2000; van der Berg et al., 2005; Kleijn et al., 2008; De Graaf et al., 2009). However, this effect shows a high variability between regions and may depend strongly on local climate and historical land-use (Britton et al., 2001; Calvo et al., 2007).

Habitat fragmentation will affect heath species richness but these changes have been retarded and thus heathland flora in western European remnants show a case of extinction debt (Piessens and Hermy, 2006; Cristofoli et al., 2010a). A longer time span is needed for an accurate quantification of biodiversity loss derived from an absence of connectivity (Lindborg and Eriksson, 2004). On the other hand, restored heathland patches will need time to recover diversity values similar to undisturbed areas (Cristofoli et al., 2010b). However, although fragmented and continuous patches are similar in species richness even for heath specialists (Dupont and Nielsen, 2006), other trophic or plant-associated groups such as pollinators will decline, affecting all trophic levels and plant–animal interactions (Piessens et al., 2005). The surrounding habitats at different scales, which buffers remnants but may also provide propagule pressure of invasive species and facilitate succession, will be critical for habitat conservation (Mitchell et al., 2000; Dupont and Nielsen, 2006; Carrillo-Gavilán et al., 2011). Dynamics on heathland vegetation implies the alternation of different species and ecological groups and, therefore, mosaics of heaths at different mature stages together with remnants of natural and semi-natural vegetation in extensive agriculture landscapes, i.e. higher landscape heterogeneity, enhanced plant diversity (Firbank et al., 2008; Muñoz et al., 2012). Global biodiversity threats include a general switch towards intensified farming methods (Tschamtké et al., 2005), indirectly affecting plant richness and diversity in heathlands (DeGabriel et al., 2011).

Future climatic changes will not necessarily result in a decrease of species richness, but recovery after disturbances such as wildfires will be retarded (Peñuelas et al., 2007), since seedling diversity and survival will significantly decrease under warmer, but mostly drier environments (Llorens et al., 2004; Prieto et al., 2009; del Cacho et al., 2012). These effects will be particularly significant in the Mediterranean region, where wildfire frequency is predicted to rise (Delitti et al., 2005). Moreover, extreme climatic events such as the 2003 summer heat-wave will probably increase in frequency (Schär and Jendritzky, 2004) and provide the conditions for wildfires to occur (Garcia-Herrera et al., 2010). Extreme climatic events are a key factor for the future modelling of European heathlands (Peñuelas et al., 2007; Kreyling et al., 2008) but predictions on event frequency and ecosystem response will be extremely difficult.

**Community structure is affected by all drivers**

Nitrogen deposition, global warming, intensive grazing, recurrent fires or rising CO$_2$ concentrations promote a transition in which perennial graminoids benefit in their competition with shrub species (Berendse et al., 1994; Britton et al., 2001; Power et al., 2004; Brys et al., 2005; Jaquemyn et al., 2005; Hofland-Zijlstra and Berendse, 2009, 2010; Newton et al., 2009; DeGabriel et al., 2011), while nutrient-limited soils, prescribed burning or mixed grazing will benefit heather (Mohamed et al., 2007; Harris et al., 2011). In addition, lack of management, wildfires in certain areas, high N deposition and the transformation of surrounding areas promotes a transition towards scrub and woodland (Mitchell et al., 2000; Manning et al., 2005; Mobaïed et al., 2011). Some authors have suggested that both transition forces may occur simultaneously, resulting in the substitution of continuous heathland vegetation areas by a mosaic of grasslands and woodlands (Bokdam and Gleichman, 2000; Ascoli and Bovio, 2010). These changes also imply abiotic alterations such as nutrient cycles that promote a certain species or group above others, i.e. grasses versus shrubs.

Soil nutrient cycles will perform differently under a changing climate (Sardans et al., 2008a–c). For example, drought conditions will reduce P and K capture by Mediterranean heaths, reduce the concentration in leaves and stems, and add to a diminution in the rate of photosynthesis, while warming increases its concentration and promotes translocation from stems to leaves (Sardans et al., 2008b). Moreover, rates of N atmospheric deposition are predicted to increase, as is CO$_2$ concentration, and both of these parameters increase metabolic rates and biomass (Gorissen et al., 2004; Albert et al., 2011a, b). Different responses have been recorded between regions (Peñuelas et al., 2004) and species (Llorens et al., 2004a, b), which means that heathland species’ competition may depend on several environmental factors. Competition and community structure is a major factor that conditions the effects of different drivers. For example, Calluna is negatively affected by warming and N addition only when in competition with bracken (Werkman and Callaghan, 2002), and flowering time is retarded by drought only in complex-vegetation stands (Jentsch et al., 2009).

**General extent of heathlands will continue to decline**

The abandonment of traditional practices of cultivated or grazed areas is occurring in different areas, mainly in upland heaths. Heathlands may be favoured by it, and re-colonization of grasslands by different shrub communities including heathlands, will take place as a result of natural dynamics (Mouillot et al., 2002, 2005; Azevedo et al., 2011). Mouillot et al. (2002) predicted a higher heathland extent derived from a higher frequency in fire regimes in the Central Massif of France. Certain heathland communities in areas with a Mediterranean climate have also extended due to traditional land-use abandonment and increasing fire frequency (Moreira et al., 2001; Mouillot et al., 2005; Azevedo et al., 2011). In the Atlantic region, efforts have also been made to restore
heathland habitats, e.g. the programme to re-establish a substantial extension of lowland heathland in the UK (Pywell et al., 2011). However, the general decline in lowland heathland landscapes observed for the last 200 years continues (Veitch et al., 1995; Rose et al., 2000; Arianoutsou, 2001; Mobaied et al., 2011; Hooftman and Bullock, 2012), and projections for the future predict a loss of heathland occupancy. Mobaied et al. (2011) estimate a general loss of heathland

![Vegetation changes in a heathland landscape](https://academic.oup.com/aob/article-abstract/111/2/151/254946 by guest on 08 March 2019)
habitats by substitution with either grasslands or woodlands, and predict a continuous health loss measured from habitat transitions (Fig. 7). In Mediterranean areas this tendency is also observed due to profound changes in human land-use and fire regimes (Arianoutsou, 2001). As an example, machis vegetation declined by 30% in favour of Pinus brutia and Cupressus sempervirens forests in western Crete over 50 years (Arianoutsou, 2001). In fynbos, future predictions of occupancy area and species loss by Midgley et al. (2002) are even more catastrophic, with a total loss of >50% and the extinction of a large proportion of endemic species over the next 50 years considering the predicted climate change. In western Europe, where the study sites of most of the publications discussed here are located, heathland occupancy will depend on management practices, land-use and conservation policies, and social interests. A general concern regarding the importance of the heathland landscape as a natural and cultural heritage is now widely accepted, and several heathland types are among the priority habitats of the EU Habitats Directive (Ostermann, 1998). However, there is also a need to maintain habitat quality, in terms of abiotic factors and biotic interactions, in order to avoid the degeneration of existing heathlands despite efforts to preserve them. Management policies must consider past, present and future scenarios taking all possible shift drivers into account, and specific conservation plans must be designed for each area.

CONCLUDING REMARKS

The structure and biodiversity of heathlands are affected by several drivers, but the effects are remarkably different among sites, communities and species. Underlying biotic and abiotic factors and driver interactions, together with landscape history, explain the different responses recorded in the literature. As an example, eutrophication from N deposition has been widely recognized as a major cause of heathland loss by shift to grassland in The Netherlands (Heil and Bobbink, 1983, and references in the pollution paragraph), but it has not been clearly demonstrated in other areas (Stevenson and Thompson, 1993). Higher precipitation counters this negative effect to a certain extent and it has been proposed as a possible explanation for the diminishment of this process in the British Isles (Britton et al., 2001; Fig. 6). In the Cantabrian Mountains, a positive effect of N addition over diversity of heath-specialist species with no competition against heather (Calvo et al., 2007) suggests that local climate conditions or historical management are conditioning the habitat response to this driver. Whereas lowlands of western Europe had a major transformation enhancing heathlands at approx. 3000 years BP, mountain areas in the north of the Iberian Peninsula did not undergo an intense afforestation process of rare species and early stages of development (seed bank and seedlings) are key factors that are negatively affected by the main drivers and their interactions. Competition between heathers and grasses or progressive succession towards woodlands relies on a weak equilibrium affected by all drivers that must be addressed locally to provide the appropriate management practices for the future conservation of European heathlands.

ACKNOWLEDGEMENTS

M. Sheehy Skeffington (National University of Ireland, Galway), and an anonymous reviewer provided useful comments that improved this review. J. Izzo (University of Santiago de Compostela) made comments on an early draft. I thank the authors and publishers who gave me permission to use their figures.

LITERATURE CITED


Hofland-Zijlstra JD, Berendse F. 2010. Effects of litter with different concentrations of phenolics on the competition between Calluna vulgaris and Deschampsia flexuosa. Plant and Soil 327: 131–141.


Nielsen AB, Vad Odgaard P. 2010. Quantitative landscape dynamics in Denmark through the last three millennia based on the Landscape Reconstruction Algorithm approach. Vegetation History and Archaeobotany 19: 375–387.


