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Review

Climate change and nature conservation in Central European forests: A review of consequences, concepts and challenges

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ABSTRACT

With a predicted rise in average global surface temperature at an unprecedented rate, as well as changes in precipitation and disturbance regimes, climate change will bring forth new challenges for nature conservation in forest ecosystems. Species and habitats to be protected will be affected as well as related concepts and area specific objectives. Climate change impacts are likely to be aggravated by other anthropogenic stresses such as fragmentation, deposition or habitat destruction. To be reliable and effective, current objectives and guidelines of forest conservation need to be reassessed and improved. Our study analyses possible impacts of climate change on forests and identifies key future challenges for nature conservation in forests and ecosystem research. We reviewed 130 papers on climate change impacts on forest ecosystems and species published between 1995 and 2010. The geographical focus of the study is Central Europe. Papers were analysed accounting for direct and indirect impacts of gradual changes as well as stochastic disturbance events in forest ecosystems and their possible consequences for nature conservation.

Even though broader aspects of nature conservation (protected areas, biodiversity) are frequently mentioned, little attention is given to forest-specific nature conservation. Particular aspects are insufficiently represented, such as the influence of climate change on different forest succession stages, the development of dead wood volume and quality, responses of secondary broadleaved species, azonal or extrazonal forests as well as ancient woodlands or remnants of historical silvicultural systems. Challenges arise in the context of great uncertainties about future developments. Nature conservation concepts and objectives in forests need to be adapted either within a permanent evaluation process or through the inclusion of further changes *a priori*, even if they are to some extent unpredictable. In some cases adaptation measures within nature conservation (e.g. adjusting protected areas) may conflict with interests of other stakeholders. Further research, particularly on interrelations between different impacts and the adaptive capacity of current forest ecosystems, associated species and existing genotypes is urgently needed. The scale and complexity of the task at hand calls for the establishment and further strengthening of international research networks.

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1. Introduction

Current projections of climate change constitute a further increase in average global surface temperature (1.8–4 °C change by 2090–2099 relative to 1980–1999, best estimates) and atmospheric carbon dioxide concentrations, changes in precipitation as well as altered disturbance regimes (IPCC, 2007). Extreme weather events such as heat waves, hot days or nights and heavy precipitation events are predicted to likely or very likely increase, with spatial differences (IPCC, 2007). Forest ecosystems seem to be especially prone to climate change (Alley et al., 2003). This is due to the high anthropogenic imprint on forest composition, as well as the comparatively long generation times and low migration rates of many species living in forest ecosystems. These factors may cause adaptation to lag behind the predicted high rates of climate change (Jump and Penuelas, 2005; Wesche et al., 2006). Interdependencies between ecosystems, climate change and other anthropogenic impacts complicate clear projections about the responses of species and ecosystems to altered climate and disturbance regimes. For instance, increasing carbon dioxide concentrations will alter responses of forests to a changing climate and fragmentation is likely to hamper species migration responses to climate change (e.g. Kappelle et al., 1999; Noss, 2001; Boisvenue and Running, 2006).

Nature conservation in forests will face particularly difficult challenges. Besides species or habitats to be protected, related concepts and specific indicators for conservation objectives will be affected by climate change. To be efficient and reliable, nature conservation needs to take climate change and its direct and indirect implications into consideration (De Meester et al., 2010). In addition, forest ecosystems are the subject of numerous and often competing interests regarding their economical, ecological and social functions which may be even further complicated in the face of climate change. Against this background, analysing climate change impacts on forest ecosystems and their consequences for nature conservation builds a substantial basis for future conservation practice and strategies. If conservation objectives and concepts based on stable site conditions are not reassessed and refined, some may become unenforceable from a societal perspective or doomed to failure from an ecological one. Furthermore, focal points in conservation efforts may shift, e.g. from the consideration of particular species within restricted habitats to higher spatial scales (national, international) or to the overarching objective of maintaining ecosystem functionality (Huntley, 1995; Jessel, 2009).

More and more scientific papers about climate change and its impacts on species, populations or ecosystems have been published during the last decade. Several research and review papers concern the impacts of climate change on forest trees and ecosystems in Europe (e.g. Saxe et al., 2001; Hamrick, 2004; Broadmeadow et al., 2005; Millar et al., 2007; Lindner et al., 2010). Papers regarding species range shifts (e.g. Davis and Shaw, 2001; Bakkenes et al., 2002; Honnay et al., 2002; Araujo et al., 2004; Skov and Svenning, 2004; Pompe et al., 2008; Mustin et al., 2009), environmental shifts (Metzger et al., 2008a) or climate change impacts on forest productivity and management are numerous (e.g. Noss, 2001; Boisvenue and Running, 2006; Kirilenko and Sedjo, 2007; Eggers et al., 2008). Many papers have also been published on the implications of altered climatic conditions and disturbances on biodiversity (e.g. Kappelle et al., 1999; Sala et al., 2000; Hampe and Petit, 2005; Nitschke and Innes, 2006) and protected areas (e.g. Gillson and Willis, 2004; Hannah et al., 2007; Normand et al., 2007; Hannah, 2008; Mehring and Stoll-Kleemann, 2008). However, as far as we know there is no survey of climate change impacts on different aspects of nature conservation in forests focussing on Central Europe in the analysed literature.

The purpose of our review was to analyse how climate change may influence nature conservation in forests of Central Europe. The following questions were addressed:

- What are the main impacts of climate change on Central European forest ecosystems?
- What are the key challenges to be tackled by nature conservation practice and research in forest ecosystems in the face of climate change?

2. Materials and methods

A literature search was conducted within the scientific databases “Forest Science Database”, “Science Citation Index Expanded”, “BIOSIS Previews” and “GEOBASE”.

We used the search terms “climate change”, “global warming”, “forest”, “forest conservation”, “forest ecosystem”, “nature conservation” and “conservation” in different combinations to find scientific papers dealing with impacts of climate change on forest

Table 1
Geographical foci of the reviewed articles.

Geographical focus	Number of articles
Global or not specific	40
Europe (total)	68
In general or multiple parts	26
Germany	15
Switzerland, Swiss Alps	13
Great Britain, Ireland	5
Netherlands	2
Austria	2
France	2
Belgium	1
Sweden	1
Finland	1
"Northern Hemisphere"/"Boreal and temperate environments"	3
"Northern and tropical forests"	1
USA, Canada	18

ecosystems or ecosystems and biodiversity in general, but with relevance to nature conservation in forests. Papers from the year 1995 onwards were included in the review process, with emphasis on topical papers from the last 10 years (2000–2010). The geographical focus of the study was Central Europe. Throughout our review, we used Switzerland (Central European Alps) as well as eastern and central Germany as example regions. Papers focussing on non-European countries or without spatial restrictions were considered if they presented results with validity for European conditions (Table 1). Relevant papers included in the references from the selected papers were added in a pyramid scheme. More than 500 publications were preselected in a literature database and tagged with keywords. Out of all papers those with highest relevance in regard to the overarching research question and spatial reference were selected (according to Pullin and Stewart, 2006). Given that the focus of this work was the *impacts* of climate change, papers primarily concerning adaptation strategies or mitigation options were not considered.

In the end, 130 scientific papers from national and international journals were analysed in detail. They were systematically categorised. First regarding their background (base data, included information, climate scenarios if applied, spatial basis and reference level, such as species, population or ecosystem) and secondly, with regard to the content of the statements made in the papers. The categories with regard to contents comprised direct and indirect impacts of gradual shifts in site characteristics (e.g. changes in temperature and precipitation) as well as direct and indirect impacts of abrupt, stochastic changes due to altered disturbance regimes (Table 2). Impacts on nature conservation were then considered. The categories relating to nature conservation follow the indicators by Schaich and Konold (2005) compiled to evaluate the achievement of nature conservation objectives in forests. We adopted the following indicators as categories for our analysis: native tree species composition, availability of dead wood and old growth, natural regeneration and succession processes, coherence of forest areas, ecotones of conservation value, adjusted game populations, protected forest areas as well as historical silvicultural systems or ancient woodlands. They were complemented by an additional category on diversity in forests (the achievement of which is partially associated with the other indicators). The ecotones category was further extended by azonal and extrazonal forest stands in order to identify the importance of "special" forest sites in a changing climate. For the most part, papers addressed multiple subjects meaning that categories are often overlapping within papers as well as within particular statements. The order of our results follows the comparative frequency of statements in the papers relating to each category.

3. Forest ecosystems and nature conservation in a changing climate

3.1. Categorisation of the papers – an overview

Of the 130 papers reviewed, the majority (98 papers) is based on literature and modelling (Fig. 1). Consequently, predictions made about future developments will, to a greater or lesser extent, comprise uncertainties. A rather small proportion (15 of 130 papers) is based on empirical studies. A further 12 papers refer to empirical studies besides model results or literature analysis. Examples of empirical studies are the monitoring of phenological phases, tree line shifts as well as tree growth surveys (e.g. Chmielewski and Rötzer, 2001; Menzel et al., 2006; Bolli et al., 2007; Rose et al., 2009; Vitasse et al., 2009). Some empirical studies involve restricted research time-frames, making it difficult to identify climate change influences or to clearly distinguish them from other influences (e.g. Gehrig-Fasel et al., 2007). Thus, many authors stress the necessity of long-term studies (Aber et al., 2001; McCarty, 2001; Bertin, 2008; Bässler et al., 2010). Nearly all future projections refer to time peri-

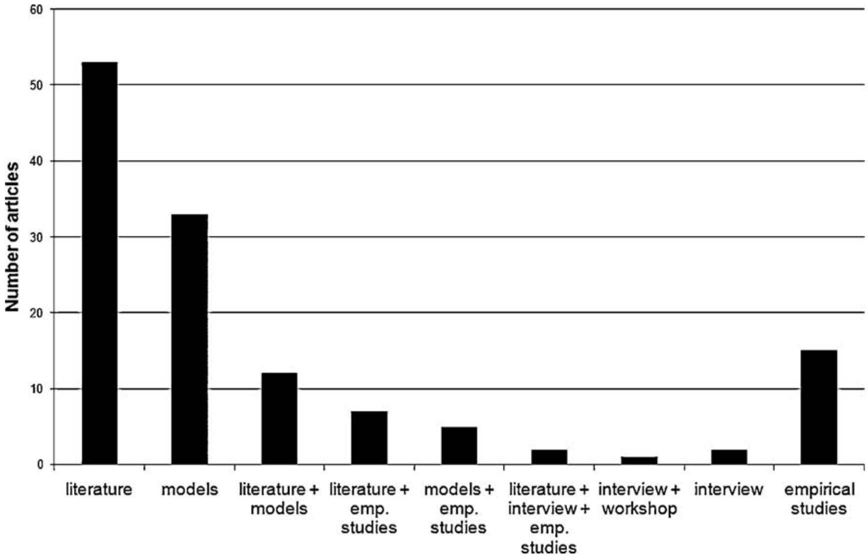

Fig. 1. Numbers of papers from the reviewed literature in which different categories of base data are applied.

Table 2
System of categories with regard to contents used in the analysis.

Character of changes	Impact character	Affected domain = category	Sub-category
Gradual	Direct	Species ranges	
		Genetic aspects	
		Phenology	
Abrupt/stochastic (alteration of disturbance regimes)	Direct	Drought/heat periods	
		Storm events	
		Forest occurrence	
		Lightning strike	
		Flooding	
	Indirect	Insects/pests/pathogens	
		Forest fires	
		Erosion/land slides	
Gradual and abrupt changes	Direct and indirect	Invasive/introduced species	
		Nature conservation	Tree species composition
			Diversity
			Azonal, extrazonal forest stands and ecotones
			Coherence of forest areas
			Natural regeneration
			Succession stages
			Ancient woodlands and historical silvicultural systems
			Dead wood
			Protected forest areas

ods or slices which conclude, at the latest, in the year 2100. Only two models employ longer time periods. Studies concerning the past mainly refer to periods during the last 150 years. Ten papers consider earlier time periods or palaeoecological data as well. Some studies are related to single events, e.g. the impacts of droughts (Saccone et al., 2009). While the majority of papers (106) refer to large areas (national to global scales) or do not have a definite reference area, 10 papers refer to “mid-scale” areas (federal state, region, landscape) and 14 papers to small-scale areas (e.g. forest stands, specific study sites). With regard to contents, the reviewed papers address different categories relating to forest ecosystems. Shifts in species ranges are mentioned most frequently, followed by disturbance regimes (Fig. 2).

3.2. *Climate change impacts on forest ecosystems and species*

3.2.1. *Species ranges*

Species distribution is determined, amongst other factors, by climatic conditions. Consequently, expansions or shifts in species ranges to higher latitudes and altitudes caused by climate change are predicted and have already been partially observed (Kappelle et al., 1999; Parmesan and Yohe, 2003; Walther et al., 2005; Parmesan, 2006; Kirilenko and Sedjo, 2007; Bertin, 2008). For example, Jurasinski and Kreyling (2007) report an upward shift of plant species in the Swiss Alps. As tree and other forest species will react individualistically, species composition and inter-specific dependencies may change (Hansen et al., 2001; Bakkenes et al., 2002; Hemery, 2008). Locally, new species compositions without a past equivalent are expected to develop (Archaux and Wolters, 2006; Keith et al., 2009). However, colonisation of suitable habitat, in particular by woodland plant and tree species with relatively slow migration rates, can lag considerably behind predicted high rates of climate change (Hansen et al., 2001; Wesche et al., 2006; Gehrig-Fasel et al., 2007). Adaptive changes at the leading edge of a species distribution will probably be faster than changes at the rear edge, and slow adaptation processes at the rear edge may lead to extinction of local populations and therefore to reductions in total geographical ranges (Davis and Shaw, 2001; Aitken et al., 2008; Bertin, 2008; Lindner et al., 2010). Currently highly fragmented and intensively used landscapes as well as the absence of so-called “chance-events” (e.g. by migrating herbivores) may additionally hamper migration of species and gene flow between populations (Kappelle et al., 1999; Davis and Shaw, 2001; Honnay et al., 2002). If species are not able to reach new suitable habi-

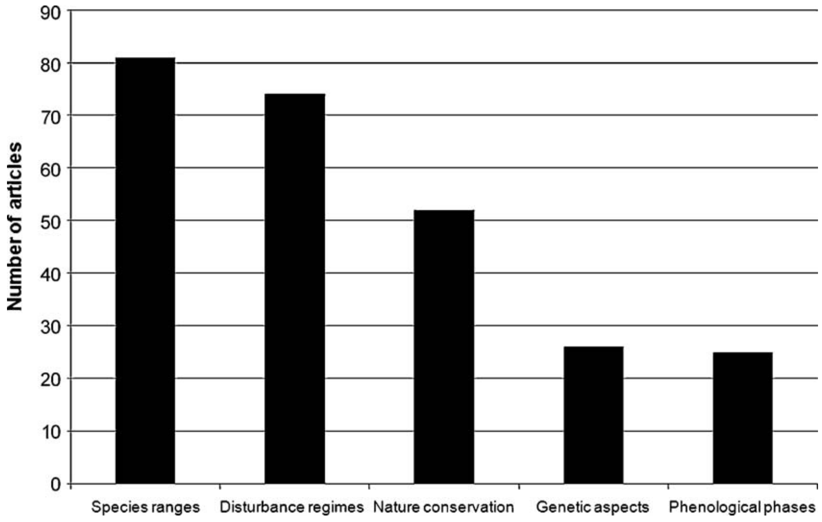

Fig. 2. Number of papers addressing the different content categories (more than one category may appear within an article).

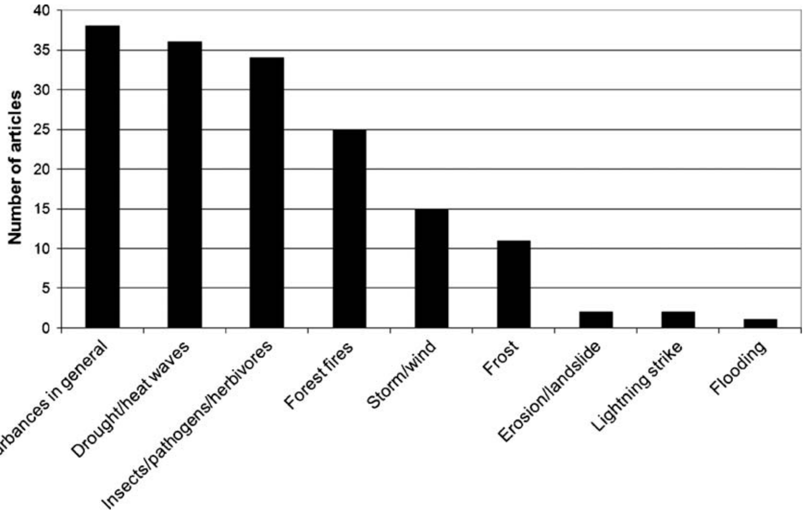

Fig. 3. Numbers of articles which address disturbances in general or particular disturbance types.

tat and fail in adapting to changing conditions, range losses and species extinctions are likely (Kappelle et al., 1999; Davis and Shaw, 2001; Hannah, 2008; Engler et al., 2009). Species which are geomorphically restricted from shifting their ranges to higher altitudes, such as montane species, are expected to be replaced by more competitive species (Bugmann, 1999; Parmesan, 2006; Verboom et al., 2007). However, other impacts on plant species distribution, such as land use, can be difficult to separate from those of climate change (Bertin, 2008). Archaux and Wolters (2006) note that besides an increase in mean temperatures, extreme weather events may provide an alternative explanation for current changes in species ranges.

3.2.2. *Alteration of disturbance regimes*

Seventy-four of the reviewed papers refer to disturbances or extreme events. Some of these do not name different types of disturbances whereas others analyse specific disturbances (Fig. 3). More than half of these papers presume that climate change, in combination with other anthropogenic influences, will likely lead to an overall increase in the frequency, intensity and duration of extreme events in Europe. Direct impacts, such as heat waves can be distinguished from indirect impacts such as insect outbreaks. It is expected that extreme events might have a greater influence on forest ecosystems than gradual shifts, particularly if multiple disturbances act together and thereby amplify each other, or follow each other in close succession (Kirilenko and Sedjo, 2007; Jentsch and Beierkuhnlein, 2008; Lindner et al., 2010). Extreme events may further facilitate natural selection for disturbance tolerant genotypes (Archaux and Wolters, 2006).

Drought periods in combination with increasing mean temperatures are likely to be particularly harmful to forests (Allen et al., 2010). It is expected that the frequency and intensity of summer droughts and heat waves in Europe, especially in Central and Southern Europe, will increase (Metzger et al., 2008b; Lindner et al., 2010). Semiarid forests seem to be particularly susceptible to climate change, as shown by studies from New Mexico, where severe drought in combination with anthropogenic fire suppression and bark-beetle attacks caused a rapid landscape-scale shift of a forest-woodland ecotone (Allen and Breshears, 1998).

As direct consequences of drought, species ranges might shift, forest species productivity and reproduction could be reduced and mortality might increase (Dale et al., 2001; Easterling and Apps, 2005; Archaux and Wolters, 2006; Jentsch and Beierkuhnlein, 2008). Intensified drought periods will further enhance the risk of forest fires (Schröter et al., 2005; Bytnerowicz et al., 2007; Kirilenko and Sedjo, 2007; Meyn et al., 2010). While elevated temperatures are expected to enhance soil fauna activity and decomposition rates, drought may counteract these effects or even lead to local extinction of some soil species (Dale et al., 2001; Hulme, 2005; Jentsch and Beierkuhnlein, 2008). Higher temperatures and water deficiency may decrease vitality and resistance of trees to secondary damages caused by pathogens and insects (Engesser et al., 2008). Reciprocal, foliar or root pathogens can predispose trees to water stress (Desprez-Loustau et al., 2006). However, Allen et al. (2010) stress the great uncertainties, which currently impede the prediction of tree mortality due to drought and its interaction with biotic stressors.

Survival, reproduction, distribution and expansion of pathogens and insect species can be influenced by changes in temperature and precipitation (Ayres and Lombardero, 2000). Species are favoured or disadvantaged depending on their life cycles and characteristics (Bale et al., 2002; Archaux and Wolters, 2006). If temperature elevates within the favoured temperature range of a species, development and winter survival will be increased. Thermophilic species ranges are likely to be extended to higher altitudes and latitudes, meaning that new species, so far considered as non-native, may occur in some locations (Bale et al., 2002; Carroll et al., 2003; Roloff and Grundmann, 2008). Multivoltine species (e.g. *Scolytinae*-species) may produce more generations within a year due to increased development rates (Bale et al., 2002; Engesser et al., 2008). Accordingly, study results from North America and Canada attribute an unprecedented outbreak of spruce beetles to a notable increase in summer temperatures during the late 20th century (Berg et al., 2006). Engesser et al. (2008) attach greater importance to extreme events in triggering bark beetle outbreaks than elevated mean temperatures in Switzerland. In contrast, Kölling et al. (2009) suggest that long-lasting temperature increases may be of greater importance for bark beetle infestations in German stands of *Picea abies* than single heat waves. The latter assumption is supported by model results from Sweden, suggesting considerable changes in activity, voltinism and geographical range of spruce bark beetle in a gradually changing climate (Jönsson et al., 2009). A local increase in wet periods may facilitate the expansion and impacts of pathogens and pests (Hulme, 2005; Hemery, 2008). Desprez-Loustau et al. (2007) suggest that most pathogen species benefit from higher temperatures, whereas reactions to changes in precipitation are different depending on species' biology. Consequently, latent fungi or species from more southern origins may be favoured and could lead to severe damage, while fungi depending on water or high moisture for development, dispersion and infection are likely to be negatively affected by increasing drought (Desprez-Loustau et al., 2006, 2007). Studies on *Dothistroma* needle blight reveal the strong influence of hydrology in the responses of pathogens to climate change. An unprecedented epidemic of *Dothistroma septosporum* in Canada is correlated with an increase in mean summer precipitation due to climate change (Woods et al., 2005). Accordingly, a modelled decrease in summer rainfall in France limits the range of *Mycosphaerella pini* (anamorph = *D. septosporum*) and offsets positive effects of warmer temperatures (Desprez-Loustau et al., 2007). Insect species overwintering in the forest litter could be disadvantaged by increasing temperatures if insulating snow depth decreases (Ayres and Lombardero, 2000). As insect populations normally show fluctuations, it might be difficult to separate the influences of particular weather events from the long-term impacts of climate change (Rouault et al., 2006; Engesser et al., 2008).

Regarding forest fires, a general increase in activity is expected, being aware that there are also regions without changes or even decreasing fire occurrence (Flannigan et al., 2009). An increase in regions where fire was not previously an important driving force, and hence where species are poorly adapted, may lead to significant ecosystem changes (Hemery, 2008; Moser et al., 2010). For example, areas with higher elevation could become dryer and therefore more susceptible to fire, as described for the Swiss Alps (Schumacher and Bugmann, 2006; Wohlgemuth et al., 2008) and the Pyrenees (Lindner et al., 2010). Consequently, species composition might in the long-term shift towards more fire-adapted, fast colonizing species (Noss, 2001; Hemery, 2008). Moser et al. (2010) illustrate the interaction of forest fires and increased drought periods in the Central Alps, concluding that drought is crucial in limiting tree recruitment after fires. Increased forest fires could further reduce carbon sequestration and forest areas could become a net carbon source (Stocks et al., 1998; Seidl et al., 2008). An increase in frequency and intensity of lightning events due to climate change is predicted for the Northern Hemisphere, which additionally increases the risk of forest fires (Nitschke and Innes, 2006; Wohlgemuth et al., 2008). However, Wohlgemuth et al. (2008) point to the fact that most forest fires in densely populated Europe are likely to be caused by humans. Management will also influence the risk of forest fires, for instance via tree species choice, modification of forest structure and density or the volume of combustible material (Schelhaas et al., 2003; Thuiller et al., 2006; Wohlgemuth et al., 2008).

Albrecht et al. (2009) found that, besides regionally severe wind damages, there is no clear meteorological evidence for a significant increase in storms in Europe during the last centuries until the present. Furthermore, they did not find significant correlation between increased storm frequency/intensity and anthropogenic climate change to date. However, they conclude that there is a slight tendency towards an increase in the importance of winter storms attended by a decrease in summer storms. Swiss studies show an increase in wind speed and intensity since the 19th century. In the meantime, winter temperature and precipitation have also increased, thus driving forest stands to be more sensitive to wind storms through wetter and more often unfrozen soils (Usbeck et al., 2009). The extent of damage also increases, which is partially attributed to an increase in forest area and growing stock. Some authors attribute increased storm damages mainly to altered forest structures, such as large-scale coniferous forest areas (Schelhaas et al., 2003; Bytnerowicz et al., 2007; Rigling et al., 2008).

An increase in heavy precipitation events could alter soil saturation and thereby increase erosion or landslides (Dale et al., 2001; Bolte et al., 2009). Regarding water supply, altered transpiration due to climate changes is expected to have effects on the entire hydrological regime of the particular ecosystem (Aber et al., 2001; Hulme, 2005).

3.2.3. Phenological phases

Several studies analysing phenological data show a lengthening in the average annual growing season for trees in Europe during the last 50 years which is attributable to changes in air temperature (Menzel and Fabian, 1999; Chmielewski and Rötzer, 2001). Phenological phases are altered with more pronounced changes in recent decades and a clear trend towards advanced spring events such as leaf unfolding or flowering in most parts of Europe (Root et al., 2003). However, some data from south-east Europe (Balkans) show a trend towards delayed spring which is attributed to the regional specifics of climate change (Menzel and Fabian, 1999; Chmielewski and Rötzer, 2001). Though less consistent, changes in autumn phases such as leaf colouring show a trend towards delayed onset (e.g. Menzel and Fabian, 1999; Chmielewski et al., 2005; Menzel et al., 2006; Bertin, 2008). The response of an organism to periodic changes in temperature is known as thermoperiodism (Lincoln et al., 1998). The primary role of temperature in early-season phenology is also shown by Green (2007) for three northern conifers. He suggests that although species show specific, unique interactions between temperature and photoperiod, they can achieve an adaptive similarity under particular climatic conditions. Advanced or delayed timing of individual phenological phases could lead to discrepancies between interacting phases of species (e.g. pollination) (McCarty, 2001; Penuelas and Filella, 2001; Theurillat & Guisan, 2001; Menzel et al., 2006). Trees may be negatively affected by disproportionally high losses of stored carbohydrates due to elevated winter temperatures and hence increased respiration. Moreover, activation of metabolism processes during dormancy could lead to physiologically stressful conditions (Kätzel, 2008). If milder winter temperatures lead to reduced frost hardening, late frost periods may cause severe damage to trees (Saxe et al., 2001; Hemery, 2008; Kätzel, 2008; Kreyling, 2010).

3.2.4. Genetic aspects

Genetic traits may be altered by directional changes in climatic conditions (Hamrick, 2004; Bertin, 2008). According to Hamrick (2004), much of the genetic variation of tree species is within rather than amongst their populations, which considerably reduces overall loss of genetic diversity in the case that partial populations go extinct. On the one hand, tree populations might be relatively adaptive or insusceptible to extinction risk due to their high genetic diversity, phenotypic plasticity, high levels of pollen flow and long lifetime of individual trees. These factors may enable them to survive periods of adverse conditions (Hamrick, 2004). On the other hand, longevity could be a disadvantage in the face of rapid and lasting directional changes in climatic conditions. Genes of long-lived, mature trees mostly reflect selection at the seedling stage (Smulders et al., 2009). Hence, Jump and Penuelas (2005) argue that longevity and long generation times of species will impede adaptation as chances for establishment of new genotypes within populations are reduced. Studies from Finland revealed a significant influence of increased mortality on evolutionary adaptation of forests to climate change (Kuparinen et al., 2010).

Analyses of palaeoecological plant species data lead to the conclusion that adaptation is mainly limited and extinction levels are highest during periods of rapid climate change (Davis and Shaw, 2001). In particular, risk of extinction is increased by impeded genetic adaptation of populations with limited ranges and reduced genetic variation for climate-related traits. Genetic variation and intensity of selection on specific traits are crucial for evolutionary adaptation (Davis and Shaw, 2001). However, selection in one trait may constrain other traits. For instance, directional and rapid changes in temperature could cause losses of genotypes of cool con-

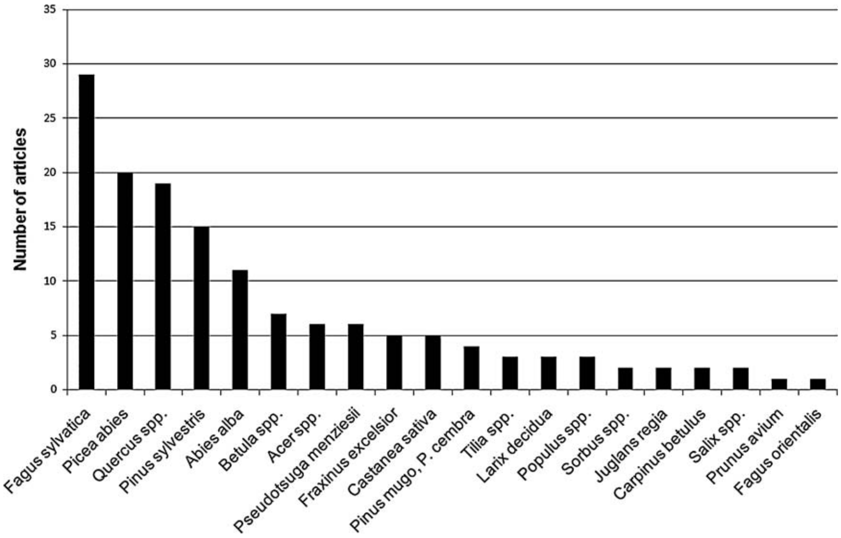

Fig. 4. Numbers of articles citing particular tree species referring to Europe.

ditions, which may reduce the overall genetic variation of tree and plant populations (Noss, 2001; Jump and Penuelas, 2005; Aitken et al., 2008). Selection for higher productivity due to increased vegetation periods may decrease frost hardiness, which could lead to severe frost damages or even dieback, given the occurrence of rare frost events (Aitken et al., 2008; Kreyling, 2010).

Additionally, tree species may display clines in adaptive traits as a result of environmental gradients and competitive selection, which influences responses to climate change (Rehfeldt et al., 1999, 2001; Theurillat and Guisan, 2001; Savolainen et al., 2007). The occupied intraspecific niche shows the discrepancy between inhabited and optimal climate and any climatic changes may alter this relation (Rehfeldt et al., 1999, 2001). Time required for long-term adjustment can therefore vary geographically; between few and scores of generations, or, as described for *Pinus contorta* in Canada, between 200 and more than 1000 years (Rehfeldt et al., 2001).

3.3. *Nature conservation in forests in the face of climate change*

3.3.1. *Tree species composition*

The 43 papers which name specific tree species referring to Europe, mainly consider species which are widespread or with current economic importance (Fig. 4) such as *Fagus sylvatica*, *Picea abies*, *Quercus* species, *Pinus sylvestris* or *Abies alba*. Future suitability of tree species to particular sites will be subject to changes, which could result in either a regional increase or decrease in the current spectrum of species (Lasch et al., 2002; Bertin, 2008). As knowledge about responses of native populations is still insufficient, assessments of the adaptive potential of particular tree species in a changing climate differ (Jump and Penuelas, 2005). *F. sylvatica* is a highly competitive species in Central Europe and relatively tolerant to moderate drought periods (Roloff and Grundmann, 2008). However, prolonged periods of severe drought may negatively affect this species. Various authors suggest that *F. sylvatica* will suffer at drier sites with low water storage capacity (Franke and Köstner, 2007; Gessler et al., 2007; Friedrichs et al., 2009). A loss in the competitive ability of *F. sylvatica* for the benefit of more drought tolerant tree species has been identified in states of eastern and central Germany (Lasch et al., 2002; Roloff and Grundmann, 2008; Friedrichs et al., 2009), southern England (Wesche et al., 2006) and sites in the Pyrenees with higher elevation (Lindner et al., 2010). Comparative analyses of different provenances of *F. sylvatica* indicate that central provenances (Germany, sub-oceanic climate) might be less adapted to drought than marginal ones (Poland, sub-continental to continental climate) (Rose et al., 2009). A seasonal increase in flooding events due to altered precipitation regimes will reduce the vitality and competitive abilities of *F. sylvatica* on water-logged sites by damaging roots and facilitating fungal pathogens (Gessler et al., 2007; Sperber and Hatzfeldt, 2007).

Out of 20 papers concerning *P. abies*, 65% report increasing unsuitability of this species for sites in Germany, and, more generally, Central Europe (Roloff and Grundmann, 2008; Bolte et al., 2009; Kölling et al., 2009). Stands of *P. abies* are particularly susceptible to disturbances such as storm, drought, insect outbreaks and forest fire (e.g. Lindner, 1999; Albrecht et al., 2009; Kölling et al., 2009). *P. sylvestris*, which is more drought-tolerant than *P. abies*, might be limited by warmth in some regions (Bolte et al., 2009). Friedrichs et al. (2009) identified an increase in drought sensitivity for *P. sylvestris* (as well as *F. sylvatica* and *Q. petraea*) in central Germany. While some authors predict a reduction in stands of *P. sylvestris* due to elevated temperatures and nitrogen deposition, others propose high adaptive capacity of *P. sylvestris* in mixed forests (Roloff and Grundmann, 2008).

Seven papers refer to *Betula* spp. One of these papers reports an expected lower susceptibility to climate change in Germany (Bolte et al., 2009). This is supported by Kätzel (2008) who suggests that pioneer species might benefit due to their regeneration strategy if environmental conditions change rapidly. For the Netherlands, Van der Meer et al. (2002) model a reduced regeneration of *B. pendula* and *B. pubescens* under climate change. They conclude that although production of early successional forests is stimulated, replacement of early-successional species by late-successional ones is accelerated.

The few papers mentioning thermophile broadleaved species attribute an increasing importance to them in the context of climate change (Lindner, 1999; Hemery, 2008; Roloff and Grundmann, 2008). For suitable areas of temperate Europe, these might be species such as *Juglans regia*, *Castanea sativa*, *Prunus avium*, or *Sorbus* spp. (Hemery, 2008; Roloff and Grundmann, 2008). To date, they are only competitive at sites with specific microclimatic and edaphic conditions respectively azonal and extrazonal sites, or in the context of historical silvicultural systems, creating more open forest structures. Some species may not at present be native but could be considered as “near-native” according to Hemery (2008). He points to the fact that, besides climatic suitability, non-native species need to be considered with regards to their implications

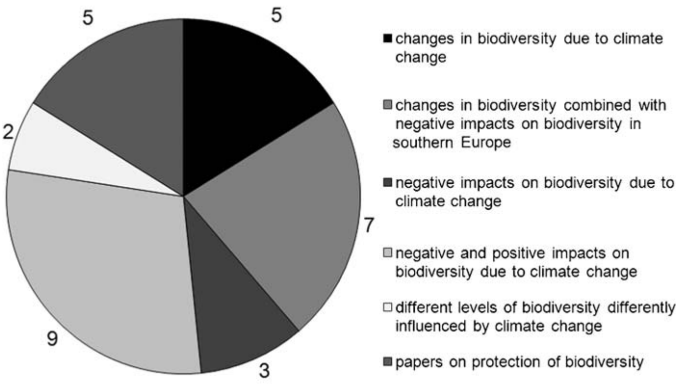

Fig. 5. Shares of different issues and statements on biodiversity in the context of climate change.

for biodiversity and ecosystem functions such as soil and water protection function, wood production and cultural aspects.

3.3.2. *Aspects of diversity*

Thirty-one of the papers reviewed address the issue of biodiversity, some of them also considering impacts other than climate change (Morgan et al., 2001). Most authors out of this sample expect negative impacts on biodiversity or an increase in vulnerability of species on a European level (Fig. 5) (Thuiller et al., 2005; Verboom et al., 2007; Vos et al., 2008). Negative impacts on biodiversity are caused by reductions or losses in ranges due to climatic changes aggravated by fragmented habitats and regional changes in land use and nitrogen deposition (Sala et al., 2000; Verboom et al., 2007). Sala et al. (2000) consider land-use changes to be the most important driver of future global biodiversity changes, followed by climate change as the second most important driver. In particular, the loss of key species has strong impacts on ecosystems. Dale et al. (2001) point out that the loss of a single tree species might significantly reduce overall biodiversity as most tree species sustain a community of other organisms. Another large proportion of the 30 papers identifies both potential positive and negative impacts of climate change on biodiversity depending, amongst other factors, on the intensity of changes or disturbances, the individual tolerance of species, their migration potential and existing migration barriers. Five papers regarding biodiversity mention biodiversity changes without interpreting them as positive or negative. Several papers refer to biodiversity conservation including biodiversity in protected areas. Hemery (2008) points to the fact that measures to mitigate climate change, such as managing forests for carbon sequestration, can counteract objectives of biodiversity conservation.

Eight out of the 30 papers concerning biodiversity mention different levels of diversity, whereas two papers explicitly analyse different levels. Lasch et al. (2002) model a decrease in species diversity in forest stands of eastern Germany, whereas structural diversity increases. The decrease is caused by the change of simulated forest type towards rather uniform stands (*Tilia* or *Betula* spp., depending on site fertility). Higher structural diversity is caused by an increase in shrubs and herbaceous species. The authors conclude that despite modelled changes in species composition, species diversity and groundwater recharge, further development may depend strongly on sites, stand composition and management strategies (Lasch et al., 2002). Jurasinski and Kreyling (2007) describe an increase in species diversity attended by decreasing diversity between habitats. This is reflected in an increasing similarity of studied Alpine summits in Switzerland due to an upward shift of plant species in the time period from 1907 to 2003. According to Nitschke and Innes (2006), changes in ecosystem structure due to changes in composition will alter biodiversity through both gains and losses of species. Referring to the Austrian Alpine region, Lexer and Seidl (2009) suggest that niches and species diversity will be increased due to the influence of altered disturbance regimes, given the existence of propagules. Accordingly, windthrow events may also contribute to increasing biodiversity through a pattern of cleared and uncleared patches (Lässig, 2000 cited by Schelhaas et al., 2003). Tree damages can further favour species adapted to dead wood as well as understory plant diversity by enhancing light conditions (Dale et al., 2001; Archaux and Wolters, 2006). Though Jentsch and Beierkuhnlein (2008) conclude that positive effects on biodiversity as a result of climate change are conceivable, they emphasize the fact that there is insufficient knowledge on extreme weather events and reactions of ecosystems or biodiversity. Modelling biodiversity changes in Europe, Metzger et al. (2008b) suggest that impacts of climate change might be strongest for plant and tree species due to their comparatively narrow climate envelopes. They expect an increase in biodiversity in northern Europe and a strong decrease in southern Europe.

3.3.3. *Azonal, extrazonal forest stands and ecotones*

Twenty-seven papers refer to azonal or extrazonal forest vegetation or ecotones. Several of these papers deal with the adaptive capability of these forest ecosystems due to small-scale site differences or refugial function. Current populations may already include genotypes with high adaptive capacity or adapted to specific microhabitat conditions. This could be of particular importance with regard to short-term weather-extremes (Kätzel, 2008) as well as long-term changes, when pre-adapted genotypes could expand into adequate habitats (Hamrick, 2004). Many rare or endemic species distributions are primarily constrained by edaphic attributes or microclimatic specifics. Bioclimatic models do not take such parameters into account and species might persist locally at lower abundances in refugial-type populations even though they are modelled as absent on higher spatial levels (Millar et al., 2007; Nitschke and Innes, 2008a). Hence, bioclimatic models may be inadequate for application in nature conservation (Schwartz et al., 2006; Nitschke and Innes, 2008a). For instance, habitats providing microclimatic conditions of higher humidity during drier periods, e.g. riparian forests, could act as a form of climatic refugia where communities moving in a changing climate may survive (Nitschke and Innes, 2006). However, the remaining individuals might be very vulnerable to any further disturbances, as concluded for Swiss alpine plants by Engler et al. (2009).

Especially at the margins of their ranges, species with disjunct or limited distributions are likely to be more prone to extinction due to climate change because gene flow between populations and colonisation rates can be low (Travis, 2003; Hamrick, 2004). Additionally, a study from Switzerland states the susceptibility of sites with low water retention capacity as well as sites bound to ground-water or strata water at slopes to increasing drought and heat waves. Plants on nutrient-poor sites are also likely to suffer from drought as nutrient uptake is highly correlated with water availability (Rigling et al., 2008).

The thirteen papers concerning ecotones refer to tree line shifts in alpine or boreal environments. Kappelle et al. (1999) expect natural ecotones to be particularly sensitive to climate change. Brzeziecki et al. (1995) suggest that recent ecotones could become dominant forest communities in a changing climate in Switzerland. Some authors attribute specifically to climate change, shifts to higher latitudes and altitudes as well as changes in the composition and structure of tree line ecotones (Bertin, 2008; Rigling et al., 2008; Lindner et al., 2010) whereas others also take further influences, such as land-use change, into account (Bolli et al., 2007; Gehrig-Fasel et al., 2007). Bolli et al. (2007) found tree establishment at their study site in the Swiss Alps to be restricted by the availability

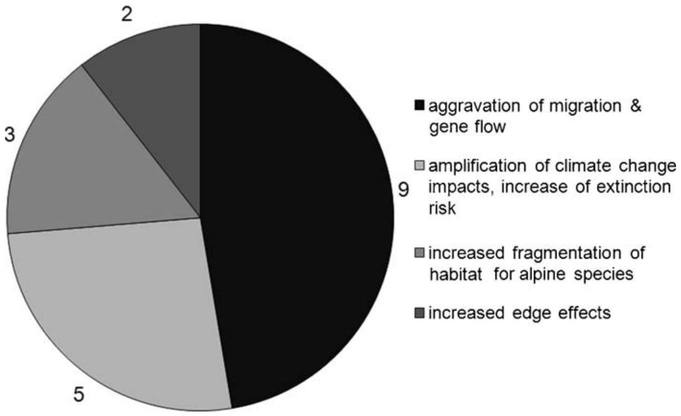

Fig. 6. Conclusions made about fragmentation with regards to forest and plant species in the context of climate change (numbers of articles).

of suitable microsites, which is likely to delay tree line dynamics in response to climate change.

3.3.4. Coherence of forest areas

Nineteen papers analyse interdependencies between climate change and ecosystem fragmentation. Most of these papers refer to the fact that fragmentation is likely to exacerbate climate change impacts on individual species or biodiversity, by hampering species migration and gene flow between populations, consequently increasing the risk of extinction (Fig. 6) (e.g. Kappelle et al., 1999; Kirschbaum, 2000; Davis and Shaw, 2001; Noss, 2001; Jump and Penuelas, 2005; Hemery, 2008; Lindner et al., 2010). Kappelle et al. (1999) assume that, besides species migration potential, size, quality and distribution (connectivity) of habitat fragments as well as the quality of the matrix will be crucial for the survival of species or populations. A strongly negative impact of currently fragmented European forests on forest herb colonisation is identified (Honnay et al., 2002). For alpine species, three papers predict a proceeding fragmentation of habitat with rising temperature (Theurillat and Guisan, 2001; Verboom et al., 2007; Bertin, 2008). Furthermore, fragmentation increases climatic edge effects on individual fragments (Kappelle et al., 1999; Noss, 2001). Promoting connectivity of forest landscapes is considered to be a substantial measure in nature conservation and adaptation to climate change (Millar et al., 2007; Vos et al., 2008; Keith et al., 2009; Smulders et al., 2009).

3.3.5. Natural regeneration

Fifteen of the reviewed papers deal with influences of climate change on the natural regeneration of tree species, another three papers with effects on plant species regeneration in general. Natural selection processes and site-specific competition likely support the establishment of better adapted individuals to altered environmental conditions (Roloff and Grundmann, 2008; Wohlgemuth et al., 2008). However, they will only be adapted if site conditions do not change dramatically during their life-span. There may be situations when natural regeneration may lead to maladaptation and increased site-specific risk in the light of climatic changes, for example if *P. abies* regenerates on dry sites, as suggested for a forest district in north-eastern Germany (Lindner, 1999). Some disturbances, such as storms, have the ability to facilitate regeneration, whereas others, such as drought or heat, are likely to change or reduce regeneration success (Jentsch and Beierkuhnlein, 2008; Nitschke and Innes, 2008a; Seidl et al., 2008; Wohlgemuth et al., 2008; Bolte et al., 2009). Tree seedlings are particularly susceptible to drought and heat (Dale et al., 2001; Rigling et al., 2008; Saccone et al., 2009). According to Gessler et al. (2007), increased frequency and duration of summer droughts in the southern part of Central Europe may possibly impede the natural regeneration of *F. sylvatica*. In Northern Europe, climate change and increasing concentrations of carbon dioxide may enhance the regeneration capacity of forests (Maracchi et al., 2005). McCarty (2001) states that nature conservation needs to take influences of climatic changes on species reproduction and survival into account. He therefore emphasises the need for conserving microclimatic diversity in habitat types. Three papers note the impact of game, which has the ability to affect regeneration in both positive and negative ways. Thus, adjusted game populations are still, or even more, considered as an essential precondition for the success of natural regeneration (Roloff and Grundmann, 2008; Kölling et al., 2009).

3.3.6. Natural succession stages

Fourteen papers concern different stages of forest succession in the face of climate change. Modelled responses in forest basal area to climate induced changes in growth, phenology and seed production decreased with an increase of the successional status of a forest in the Netherlands (Van der Meer et al., 2002). The predicted increase in disturbances facilitates successional change, providing possibilities for ecosystem readjustment to changing conditions (Easterling and Apps, 2005). Nitschke and Innes (2008a) conclude that the integrity and quality of ecosystems may be altered if the existing climax species are not resilient. Formation of new ecosystem conditions due to altered disturbance regimes can mean either an increase in diversity or homogenization of ecosystems, depending on the range of created habitat structures (Nitschke and Innes, 2006). It is expected that rapid climate change and more frequent disturbances involving geomorphologic instability and habitat heterogeneity will facilitate early successional species that is generalistic, short-lived *R-strategists* (Dukes and Mooney, 1999; Kirschbaum, 2000; Gillson and Willis, 2004; Nitschke and Innes, 2006; Aitken et al., 2008). Accordingly, Moser et al. (2010) found that recruitment of pioneer tree species was promoted after a stand replacing wildfire in Rhone valley, Switzerland, compared to *P. abies*, *P. sylvestris* and *Larix decidua*.

Consequently, in frequently disturbed areas habitat for species that require late-successional forest states is missing (Nitschke and Innes, 2006).

3.3.7. Ancient woodlands and historical silvicultural systems

Five of the papers reviewed raise the issue of historical silvicultural systems or ancient woodlands in the context of climate change. Forests formed through anthropogenic use, for instance through historical forest management, can be valuable from a nature conservation perspective, such as pastoral forests providing particular open stand structures. Grant and Edwards (2008) suggest that climate change may challenge future management strategies for ancient woodlands as it adds to the stresses associated with altered or abandoned management practices. As conditions for the dominant tree species will worsen due to increased rates of environmental change, concepts focussing on maintaining key species in specific habitats may not be effective. Hence, flexible management strategies and concepts promoting resilience or sustainability of the ecosystem are recommended (Grant and Edwards, 2008). Studying plant assemblages in British beech woodlands (*F. sylvatica*), Wesche et al. (2006) conclude that many plants that are highly competitive in ancient woodlands are very sensitive to rapid climate change. This is caused by their fragmented location and rather low migration rates. Rackham (2008) asserts that an increase in hot periods is likely to imperil the eastern outliers of oceanic ancient woodland plants such as *Hyacinthoides nonscriptus* or *Primula vulgaris* in parts of England. Wohlgemuth et al. (2008) allude to the utility of maintaining wood pasture in traditional areas of Switzerland for reducing combustible material, thereby decreasing the risk of forest fires.

3.3.8. Dead wood

Only four papers approach the issue of dead wood in the context of climate change and only one paper refers to dead wood in the context of biodiversity in forests (Lexer and Seidl, 2009). Another paper briefly refers to an increase in dead wood due to storms in connection with bark-beetle outbreaks (Schelhaas et al., 2003). Modelling for a region in eastern Germany shows that availability of dead wood depends more on management parameters than on climate change (Fürstenau et al., 2007). Even though a higher accumulation of dead wood can be expected with increasing disturbances, salvage prescriptions will probably lead to decreasing levels (Lexer and Seidl, 2009). This is probably true for large-scale formation of dead wood, for instance after storm calamities.

3.3.9. Protected areas

Though none of the papers explicitly refers to protected areas in forests, impacts of climate change on nature reserves in general (15 papers) as well as on the nature reserve network Natura 2000 (3 papers) are discussed. Climate change is likely to change the quality of reserves by changing species ranges and species composition (Skov and Svenning, 2004). While in some protected areas species representation may decline, in others it could increase (Hannah et al., 2007). The loss of a single species may have significant impacts on a protected area, particularly if the species was one or the main reason for the designation of the reserve (Hossell et al., 2003). Araujo et al. (2004) predict a climate change driven loss over 50 years of 6–11% of modelled plant species out of currently optimal reserve systems across a large part of Europe. Losses would be even greater under limited dispersal and clustered reserve design. Normand et al. (2007) model a decrease in bioclimatic suitability for 75–85% and 69–99% for plant species characteristic of the Danish habitat types (until 2100 under scenarios B2 and A2 for Denmark and Europe). Vos et al. (2008) also observe a reduction in ranges and habitats protected under Natura 2000 for nine bird species in Northwest Europe by 2050.

Protected areas including environmental heterogeneity increase species survival chance as they may escape or evade changing conditions in favour of more suitable habitat (Noss, 2001; Gillson and Willis, 2004). It is supposed that the area required globally for achieving a specific species representation level will be greater under future climatic conditions and that an early implementation of new protected areas would be supportive (Hannah et al., 2007; Hannah, 2008).

4. Future challenges for nature conservation in forests

In this review it becomes apparent that climate change could, and already does, affect forest ecosystems and forest functions in complex ways. Challenges will arise for research as well as for forest and conservation management regarding nature conservation concepts and objectives. However, these challenges are not satisfactorily reflected in the reviewed literature. The application of our categories of nature conservation in forests revealed that essential questions are referred to rather generally and particular issues are still missing.

4.1. Species and habitats: what do we want to protect and how?

4.1.1. What is natural? The problem of reference systems

Regarding the protection of species and habitats, new challenges will arise based on an accelerating revision of what might be defined as natural at a particular site. As a result of changing site conditions, the fact that local or native species can be considered to be well adapted to particular site conditions loses its validity (Harris et al., 2006). Nature conservation concepts referring to native species composition need to be reassessed given that past states are not stable and will not always be a practical basis for evaluation.

However, planting of tree species on unsuitable sites in the past might be the explanation for earlier responses of trees to climate change in some regions. For example, Rackham (2008) describes mortality of *F. sylvatica* on thin chalk soils after extremely hot summers in Great Britain. He stresses that *F. sylvatica* has been planted there and tree species such as *Fraxinus* or *Tilia* would naturally dominate these sites. In Germany, *P. abies* has also been planted on shallow sites with low water retention capacity, where warmer and drier conditions become noticeable in increasing calamities and reduced productivity to date. Decisions about appropriate tree species will be especially difficult if climatic conditions at a given site change rapidly (Peters, 1990). Traditionally, nature conservationists have been mostly reluctant regarding non-native tree species due to their limited interactions with native plant and animal species, their potential for unknown pests and diseases or their invasive characteristics (Kowarik, 2003). If forest managers increasingly favoured non-native but productive tree species in the face of climate change, conflicts between economical and ecological orientated stakeholders would result. In consideration of tree species which are not native today but might play an important role under a changing climate, field studies would be helpful to assess possible consequences for nature conservation and the provision of ecosystem functions. Locally, stands of such tree species may already exist for historical or cultural reasons, such as *C. sativa* in parts of Germany or northern France.

In a transitioning climate, species holding invasive potential could become more competitive due to characteristics such as short regeneration times and high migration rates (Dukes and Mooney, 1999; Maracchi et al., 2005). Currently neutral tree species might also become invasive. Additionally, in a warmer climate a greater proportion of introduced species or species escaping from cultivation will be able to survive (Dukes and Mooney, 1999; Dale et al., 2001). This will raise the question of whether a species is invasive or non-invasive and just migrating in a changing climate. Invasive species could affect ecosystems for example by competition, hybridisation, diseases or altering habitats, culminating in extinction of some species and losses in biodiversity (Dale et al., 2001; Hamrick, 2004). In light of climate change, preventing or combating measures might not always be efficient. It must be analysed if particular neobiotic species need to be integrated and accepted in forest ecosystems.

4.1.2. Altered habitat structures: the example of dead wood

Even though changes in volume and quality of dead wood due to increasing disturbances can be expected, this issue is discussed only briefly in the reviewed literature. Different disturbance types will create dead wood of different size and quality, standing or lying dead wood. From a nature conservation perspective, this is beneficial as a wide variety of dead wood qualities favours different plant and animal species (e.g. Christensen et al., 2005; Lindhe et al., 2005). Disturbances may further lead to altered sun-exposure, which may be of high importance, e.g. for saproxylic beetles (Lindhe et al., 2005). Decay processes are also influenced if altered disturbance regimes provoke a change in humidity and radiation intensity. As rare saproxylic beetle species (characteristically for primeval forests) require continuity in dead wood supply and old growth structures (Müller et al., 2005), the alteration of dead wood quality due to climate change should be an object of further research. In combination with intensified drought periods, higher volumes of dead wood might also increase the risk of forest fires.

4.1.3. How to protect species in a world of changes?

Approaches adapting existing protected areas to climate change may be especially challenging in the long-term. Efforts to conserve species or populations in a specific habitat could become obsolete if species change their ranges due to climate change (Huntley, 1995; McCarty, 2001). This could create dilemmas regarding traditional nature conservation objectives. However, maintaining partial or minimum populations of rare species as sources for dispersal and migration under a changing climate will be valuable even if local extinctions are likely in the long-term (Hannah et al., 2002). Protected areas and reserve networks will still be an important instrument for achieving nature conservation targets as they can provide refugial habitat and facilitate migration. However, it is noted that, in light of predicted environmental changes, concepts such as maintaining states of current specific habitat types in particular locations might be unrealistic and need to be reinterpreted (Wesche et al., 2006; Normand et al., 2007). As static and more flexible protection objectives will most likely require different strategies, design and management of protected areas need to be adjusted to changing conditions (Halpin, 1997; Hossell et al., 2003; Pearson and Dawson, 2005; Hannah et al., 2007; Normand et al., 2007; McNeely, 2008). This includes allowing for changes in species composition, placing protected areas strategically to facilitate species movement and establishment (Halpin, 1997; Hossell et al., 2003) or increasing connectivity, mainly within and adjacent to existing reserves (Hannah, 2008). The importance of habitat heterogeneity for providing high species diversity as well as changes in species composition or populations in protected areas has been highlighted (Halpin, 1997; Noss, 2001; Gillson and Willis, 2004). Conservation of individual species also needs to consider range changes on higher spatial scales (national, international) to assess the relevance of local conservation efforts. The protection of additional forest areas will involve difficulties due to competing requirements on the forest resource as well as established forest ownership structures. For instance, calls for further protection of beech forests (*F. sylvatica*) in Germany by nature conservationists meet with refusal on the part of many forest owners. The problem is further aggravated by a lack of financial compensation for conservation requirements. Additionally, in many Central European countries, forests are highly fragmented and landscapes are used intensively. Against this background, more mobile forms of protected areas, for example by rotating closures (Hannah, 2008), might be impractical. Another option is to maintain or establish (flexible) buffer zones around core zones of current reserves which could facilitate adaptation at least in the mid-term (Halpin, 1997; Van Dyke, 2008). Halpin (1997) points to the fact that any changes in land use that increase flexibility will require ecological evidence for conservation benefits to be effective.

Improving the coherence of forest ecosystems will probably facilitate migration of species following their climate envelopes in a changing climate. Certainly, migration of species which are not desirable from a nature conservation perspective, such as invasive species, would also be assisted. Given the currently highly fragmented status of many ecosystems in Central Europe, maximising the permeability of landscapes through corridors or stepping stone habitat is of great conservation value but at the same time especially challenging. In addition to protected area networks, integrative conservation measures enabling species migration will certainly be essential in light of climate change.

4.2. Allowing for natural processes while maintaining forest functions

4.2.1. Natural development stages in the context of increasing disturbances

In the context of increasing disturbances such as drought periods, natural regeneration of particular tree species may fail on some sites. If conservation perspectives allow for natural dynamics this is not inevitably harmful. However, if losses in tree species regeneration mean a loss of particularly desired forest functions, planting of more tolerant tree species or provenances may become necessary according to the site specific objectives. To maintain ecosystem resilience, enrichment planting could also be an opportunity in forest reserves, at least in the short-term (Nitschke and Innes, 2008b). For the purposes of nature conservation, a temporal and spatial coexistence of earlier and late succession stages (and related species) is particularly valuable, providing a variety of habitat and increasing ecosystem resilience. It is suggested that an increase in disturbances will facilitate early-successional species. However, Kuparinen et al. (2010) conclude that populations exposed to regular disturbances, such as storms or forest fire, might display higher rates of evolutionary adaptation due to higher mortality.

Given that uncertainties about ecosystem reactions to altered disturbance regimes persist, the call of Halpin (1997) for more detailed analyses of key species and changes in local disturbances to better understand ecosystem responses to climate change remains valid today (Lindner, 1999; Lindner et al., 2000; Jentsch and Beierkuhnlein, 2008; O'Neill et al., 2008).

As water balance and soil state seem to be key factors in mediating ecosystem responses to climate change, forestry should especially emphasise careful management which minimises soil compaction, degradation, runoff and erosion (Ehrlich, 1996; Noss, 2001; Roloff and Grundmann, 2008; Nortcliff, 2009). To adapt managed forests to the impacts of climate change, reductions in rotation periods are a measure sometimes taken into consideration (Lindner, 1999; Maracchi et al., 2005). As commercial forestry already reduces natural lifetimes of trees by harvesting before trees reach biological maturity, a further reduction could be particularly harmful to nature conservation objectives. Many rare bird, mammal, insect or lichen species depend on old trees in late successional forest states and on related structural diversity (e.g. *Dendrocopos medius*, *Ciconia nigra* or *Myotis bechsteinii*) (Scherzinger, 1996). However, measures need to be considered in relation to the adaptive capacity of the existent tree species and the particular ecosystem. If they lead to advanced conversion of unsuitable monocultures into mixed forests they may have positive effects on nature conservation purposes as well.

4.2.2. Resilience and adaptation by high levels of diversity?

As adverse disturbances caused by anthropogenic climate change cannot be excluded from forest ecosystems the importance of adaptive measures such as increasing ecosystem resilience in addition to the mitigation of anthropogenic climate change becomes clear. Even though a quarter of the reviewed literature addresses the issue of biodiversity in a changing climate, several papers focus on plant or tree species diversity rather than on other levels of diversity. As climate change will add to already existent stresses, preserving forest biodiversity in order to halt global losses will become even more challenging. To analyse impacts of climate change on biodiversity comprehensively, other levels of diversity beyond species richness, such as habitat and genetic diversity must also be considered. It is supposed that high species and genetic diversity will facilitate natural adaptation processes and increase resilience of forest ecosystems (Noss, 2001). Habitat diversity will additionally facilitate species migration by providing refugial habitats or stepping stones. Several authors suggest that approaches such as maintaining high diversity should be applied not only within stands but also at higher spatial levels (e.g. region, landscape) (Lindner, 1999; Lindner et al., 2000; Hemery, 2008; Rigling et al., 2008). Achieving high levels of diversity will surely be a key measure regarding both integrative and segregative approaches of nature conservation. In light of the great uncertainty associated with climate change, concepts of near-natural forestry orientated on natural processes and focussing on less susceptible, mixed stands in forest management is again forcefully promoted (Hemery, 2008).

4.2.3. *Adaptive capability – a great unknown?*

There is still a lack of knowledge about the responses of zonal, azonal and extrazonal forest stands and related species in a changing climate. Besides those papers regarding tree line ecotones, no paper refers to the meaning of forest edges in a changing climate. Natural forest edges are rare and will only be found at ecological transition zones (Scherzinger, 1996). But also anthropogenic generated forest edges may include a great diversity of species and structures. The assumption seems likely that they could also latently include genotypes or species which might be pre-adapted to climatic change, as individuals are exposed to stronger climatic effects (compared to the more stable climate in the bordering forest ecosystem). They could additionally act as a corridor for several species.

Ancient woodlands are characterised by continuity in forest existence (Westphal et al., 2004). If increasing disturbances and changing climatic conditions disrupt this permanence, will there be adequate conservation measures to protect ancient woodland indicator species? Will there be refugial sites for such species at all and if so, will they be able to reach them? However, forests shaped by historical use could include genotypes or species with high demands for light and warmth, which might benefit from elevated temperatures. Coppice forests, for instance, include plant species adapted to disturbances such as periodical felling and burning (Rackham, 2008). Historical silvicultural systems could also create flexibility, for example by shorter rotation periods in the under storey or selected parts of the forest (e.g. coppice-with-standard) or by increasing diversity. Hence, the management of ancient woodlands and historical silvicultural systems might be a valuable part of an integrative nature conservation concept in the context of climate change and should be an object of further research.

On a regional scale, nature conservation should take adaptive capabilities due to small-scale differences in sites and structures into account. Further research, e.g. genetic studies would be particularly helpful to assess possible adaptation capabilities due to already existent pre-adapted individuals. Studying tree species populations along a climate and site gradient across Europe in the long-term could additionally increase knowledge about possible responses and potentials.

5. Conclusions

Nature conservation in forests is challenged both practically and conceptually (Bertin, 2008). In part, difficulties are associated with the setting of specific conservation objectives. Depending on whether objectives allow for ecosystem dynamics or not will lead to different perceptions of risk. Different time frames of studies may lead to varying considerations of the importance of particular climate events. In the light of climate change, static approaches of nature conservation focussing on the protection of species and habitats need to be reassessed and refined. They will not lose their meaning at all but should be part of a comprehensive concept allowing for dynamics and considering large-scale interrelations. There will be a need for conservation concepts which either permanently evaluate and adjust objectives, according to the idea of adaptive management, or include further changes *a priori* (Hannah et al., 2002; Millar et al., 2007; Nitschke and Innes, 2008b; Rigling et al., 2008). Management frameworks, which are regularly advanced by testing specific measures with scenarios, can offer opportunities in managing for nature conservation in forests. Existing general principles of nature conservation in forests should be evaluated and adjusted against the background of climate change. Challenges such as species migration in a changing climate or the need to maintain functional forest ecosystems for present and future generations reveal that neither segregative nor integrative approaches alone will meet these requirements. Thus, future principles need to include both integrative and segregative, concerted components.

New protected areas in forests should be selected for the purpose of coping with climate change and to fill in gaps in existing reserve networks (Hannah, 2008). Both within and outside protected areas, high levels of habitat heterogeneity are likely to promote species survival, as well as changes in species composition (Halpin, 1997; Gillson and Willis, 2004). Forest management should emphasize the idea of managing the matrix surrounding forest reserves, which at the same time allows for increasing permeability on a larger, landscape scale. There might also be possibilities for win–win situations between nature conservation objectives and managing forests for ecosystem services, such as water quality.

Influences other than climate change, such as habitat destruction, intensified and altered land-use, fragmentation and deposition might also be important driving forces for ecosystem change and should be minimised to increase the resilience of forest ecosystems. The reviewed papers attach differing importance to the individual driving forces and still there are great uncertainties about the interrelations between them. Here, further research should be conducted, allowing for the identification of vulnerable areas and adjusted conservation strategies.

Whether emphasis is placed on economical, ecological or social objectives in forests will in large part depend on societal decisions and values (Ehrlich, 1996; Bollmann et al., 2009). In light of partially antagonistic ways to adapt forest ecosystems to climate change, implementation of conservation measures will require awareness raising and a high level of information on part of all stakeholders.

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