

Plants in a warmer world

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Abstract

Climate is a major determinant for the phenology, physiology, distribution and interactions of plants. The world's recent climate has shown a substantial increase in average temperature which is changing these processes in a perceptible way. The following review compiles and discusses studies reporting recently observed changes in the behaviour, ranges and interactions of species which are thought to be associated with climate change. The multitude of recently published studies providing evidence for the ecological impacts of climate change on many different continents strongly suggests that the last 30 years of warmer temperatures have had a substantial influence on both seasonal patterns, and altitudinal and poleward shifts in vegetation. Common features of change, but also some discrepancies in the response of plants to climate change, are discussed, as well as implications for biodiversity, higher level impacts on community structure and trophic interactions, and some ecosystem consequences.

Key words: climate change, global warming, invasion, phenology, range shifts, treeline

Introduction

In recent years, an unusual series of warm temperature anomalies has been recorded. The ten warmest years since the beginning of meteorological measurements have all occurred from 1987 onwards, nine since 1990, with 1998 the warmest record, followed by 2002 and 2001 (WMO 2002). The global mean surface temperature has increased over the last century by approximately 0.6 K (Houghton et al. 2001) and is projected to continue to rise at a rapid rate in the coming decades (e.g. Zwiers 2002). The trend over the course of the last century has been uneven, but in the period since 1976 the warming trend is roughly three times that for the past 100 years as a whole (WMO 2002).

It is generally agreed that in many areas climatic conditions shape the physiological behaviour and pro-

ductivity of species (e.g. Lieth 1975; Long & Woodward 1988; Cramer et al. 1999; Shaver et al. 2000; Geider et al. 2001) as well as their ranges and thus the composition and distribution of biomes (e.g. Holdridge 1947, 1967; Box 1981, 1996; Walter & Breckle 1983ff.; Emanuel et al. 1985; Woodward 1987; Prentice et al. 1992). With a changing climate, these parameters are also likely to change and a subsequent reaction of climate sensitive species and ecosystems is expected (e.g. Huntley et al. 1995; Sykes et al. 1996; Iverson & Prasad 1998; Kappelle et al. 1999; Saxe et al. 2001; Theurillat & Guisan 2001).

The following review compiles studies, which are mostly based on quantitative 'ground truth' (Billings 1997) data, reporting observed changes in the behaviour, ranges and interactions of species, so called ecological 'fingerprints' of climate change impacts

(Walther et al. 2001a; Parmesan & Yohe 2003; Root et al. 2003). A selection of studies is presented spanning a period of at least 10 years and examining species whose physiology, phenology and/or ecology is known to be largely determined by climatic parameters. Results from experimental or modelling studies have only been regarded when they provide a better insight into the climatic dependency of the considered species or ecosystem. The review focuses first on phenological studies, followed by a more extended overview on shifting species' ranges, and ends with examples of ecological feedback mechanisms and ecosystem processes on higher hierarchical levels.

Changing phenology of species

Phenology is the study of the cycling of biological events throughout the year (Bradley et al. 1999), and is considered the most responsive aspect of nature to climate warming (Sparks & Menzel 2002). Phenological research has a long history, and thus, many long-term phenological data sets exist to be evaluated based upon changes over the past decades. On the basis of phenological records covering a sufficient length of time, trends in the response of living organisms to climatic changes can be tracked.

Temperature – or possibly a climate variable correlated with temperature – of the preceding months is seen as a key determinant of spring phenophases (i.e. first flowering date, time of budbreak, etc.) (Sparks et al. 2001; Fitter & Fitter 2002; Penuelas et al. 2002). Evidence that events in spring have been happening earlier in recent decades arises from a wide range of taxa and across a wide range of geographic locations (Fig. 1).

Global meta-analyses documented a mean advancement of spring events by 2.3 days per decade (Parmesan & Yohe 2003). However, the response of different

species and/or at different locations may be uneven. Such differences in the phenological response to climate warming may result from the variability of the taxa included in the studies, the season of warming and geographic distribution of data collection (Beaubien & Freeland 2000; Emberlin et al. 2002; Fitter & Fitter 2002). It is also apparent that the length, start and end date of the series of observational data are critical in determining the signal (e.g. Sparks & Menzel 2002). However, despite some inconsistencies in the numeric values of the data, the overall trend towards an earlier onset of spring in northern mid-latitudes is obvious (cf. Fig. 1). According to Sparks & Menzel (2002) changes have been most profound in those events that occur earlier in the year. They attribute this to the fact that changes in temperature experienced so far have been more pronounced in the winter and early spring period. The same conclusion is drawn by Fitter & Fitter (2002), who mention that early flowering species were most affected by warming. Furthermore, Post & Stenseth (1999) report that woody plants have shown less sensitivity to climatic variability than herbaceous plants (cf. also Arft et al. 1999). Hence, it is not surprising that a late flowering shrub species (*Buddleja davidii*) showed the most pronounced delay amongst the ten significantly later flowering species in England, whereas the full set of 385 investigated plants have advanced their flowering date by 4.5 days on average during the past decade (Fitter & Fitter 2002).

In spite of the general increase in global average temperatures in recent decades, there are some regions experiencing local cooling in the same period (see Folland & Karl 2001). In accordance with such spatial variability in climatic trends, there are also regions with no effect or even a later onset of spring phenophases, such as the Balkan (Menzel 2000); regions in the Ural Mountains (Ahas et al. 2002), in the US-states Virginia and North Carolina (Fitzjarrald et

Table 1. Change in the growing season based on phenological monitoring series.

Location	Period	Change in growing season (days)	Number of species	Reference
Germany	1951–1996	+6.6	4	Menzel et al. (2001)
Switzerland	1951–2000	+13.3	13	Defila & Clot (2001)
Cardedau field station (NE Spain)	1952–2000	+32.6 ± 2.23	24	Penuelas et al. (2002)
Japan	1953–2000	+12	1	Matsumoto et al. (2003)
Europe (International Phenological Gardens)	1959–1993/96	+10.8	16	Menzel & Fabian (1999); Menzel (2000)
Northern latitudes	1981–1991	+8 ± 3	NDVI* data	Myneni et al. (1997)
Vegetated areas north of 45 °N	1981–1994	+12	NDVI* data	Shabanov et al. (2002)
Eurasia	1981–1999	+18 ± 4	NDVI* data	Zhou et al. (2001)
North America	1981–1999	+12 ± 5	NDVI* data	Zhou et al. (2001)

*NDVI = Normalised Difference Vegetation Index



	Location	Period	Phenochange (day year ⁻¹)	Number of species	Reference
1	Hungary	1851–1994	–0.06–0.02	1	Walkovszky (1998)
2	Japan	1900–1988	–0.07–0.05	1	Yoshino & Park-Ono (1996)
3	Alberta, Canada	1900–1997	–0.26	1	Beaubien & Freeland (2000)
4	Estonia	1919–1996	–0.17–0.05	4	Ahas (1999)
5	Norway	1928–1977	–0.53–0.27	7	Post & Stenseth (1999)
6	Wisconsin	1936–1947 1976–1998	–0.12	55	Bradley et al. (1999)
7	Estonia	1948–1996	–0.5–0.3	13	Ahas et al. (2000)
8	Europe	1951–1996	–0.28–0.02	16	Menzel (2000)
9	Germany	1951–1996	–0.53–0.03	9	Menzel et al. (2001)
10	Switzerland	1951–2000	–0.23	13	Defila & Clot (2001)
11	Cardedeu, NE-Spain	1952–2000	–0.77–0.17	24	Penuelas et al. (2002)
12	South-central England	1954–2000	–1.17–+0.77	385	Fitter & Fitter (2002)
13	Western United States	1957/1968–1994	–0.38–0.2	2	Cayan et al. (2001)
14	Europe	1959–1993	–0.20	16	Menzel & Fabian (1999)
15	North America	1959–1993	–0.18–0.14	1	Schwartz & Reiter (2000)
16	China	1963–1996 excl. 1968–70	–0.13–+0.27	18	Zheng et al. (2002)
17	Washington DC	1970–1999 excl. 1984	–1.53–+0.35	100	Abu-Asad et al. (2001)
18	Europe	1984–1999	–1.1	1	Emberlin et al. (2002)

Fig. 1. Observed changes in spring phenology of plants in the northern hemisphere (for a regional analysis of changes in European spring phenology see Ahas et al. 2002).

al. 2001), and in China (Schwartz & Chen 2002) particularly the eastern part of southwestern China (Zheng et al. 2002). Further possible reasons for species not showing phenological adaptability may be that seasonal developments are regulated by photoperiod or other genetic regulatory systems rather than by climatic parameters (Bradley et al. 1999).

Fewer phenological data are available for the fall season. However, the few data sets that include phenophases in both spring and autumn reveal a trend towards a prolongation at both ends of the season and thus, an extension of the growing season (Table 1).

Whereas in spring the phenological phases in high- and mid-latitudes are considered to depend strongly on temperature conditions during winter and spring, the most important factors causing phase changes in autumn are not as clear (Menzel et al. 2001). However, the observed lengthening of the growing season based on terrestrial phenological data accords with satellite observations of leaf area index anomalies over the past two decades (e.g. Lucht et al. 2002). Furthermore, the global increase in biospheric activity inferred from the increasing amplitude of annual oscillations in the atmospheric CO₂ also suggests an extension of the growing season by about 7 days in the Northern Hemisphere since the 1960s, which is most accentuated after 1980 (Keeling et al. 1996; see also Slayback et al. 2003).

The change in phenological phases not only results in a prolonged growing season, but also affects plant fitness (see e.g. Penuelas & Filella 2001) and may contribute to changes in the distribution and abundance of species (Chuine & Beaubien 2001; see also Walther 2002). Finally, these shifts in the seasonal pattern may in the long run contribute to genetic changes across generations and thus, induce an evolutionary response to recent global warming (Réale et al. 2003; see also Bradshaw & Holzapfel 2001; Pulido et al. 2001).

Changes in species composition and shifting species ranges

On a global scale, the composition and distribution of biomes is largely determined by climatic parameters (see above). With climate change, it is predicted that the margins of species ranges or boundaries of biomes may become adjusted (e.g. Huntley et al. 1995; Sykes et al. 1996; Iverson & Prasad 1998). Indeed, there is evidence that climate change has already induced biome shifts (see Klötzli et al. 1996; Penuelas & Boada 2003). A classical example of a partial replacement of neighbouring altitudinal belts is reported by Penuelas & Boada (2003) from north-eastern Spain. Based on historical records, vegetation

maps and aerial photographs, evidence is provided for summergreen beech (*Fagus sylvatica*) forest being replaced at its lower margin by advancing evergreen oak (*Quercus ilex*) forest and other vegetation types. On the other hand, beech (*Fagus sylvatica*) claims new territories at the upper margin, invading heather (*Calluna vulgaris*) heathlands. Penuelas & Boada (2003) ascribe this upward shift of vegetation belts to the rising annual temperature of 1.2–1.4 °C during the last 50 years with the main increase in the last 30 years. In line with the Spanish case study, the comparison of historic vegetation records in lowland beech (*Fagus sylvatica*) forests in Switzerland also revealed an increase in the abundance of thermophilous species (Carraro et al. 1999; Béguin 2001; see also Walther 1997; Meduna et al. 1999) and the retreating tendency of montane species at the lower end of their distribution (Walther 1997; Carraro et al. 1999; Walther & Grundmann 2001).

Another possible vegetation shift is reported from Australian cool temperate *Nothofagus* rainforest where there is an intrusion of warm temperate and sub-tropical elements from lower altitudes (Read & Hill 1985). In New South Wales, the failure of southern beech (*Nothofagus moorei*) to regenerate within the forest is reported, while sub-tropical and warm temperate species, such as coachwood (*Ceratopetalum apetalum*), successfully regenerate under the *Nothofagus* canopy and are about to replace southern beech (*N. moorei*).

A new type of warm temperate forest is about to establish in the lake region at the borderland of northern Italy and southern Switzerland. In bioclimatic terms, this area is positioned in the transition zone from deciduous broad-leaved vegetation to evergreen broad-leaved vegetation (see Klötzli 1988; Klötzli et al. 1996). A minor climatic shift has sufficed to push the area towards conditions suitable for evergreen broad-leaved forest and opened a new ecological niche for warm temperate species. However, for historical reasons there are only a few evergreen broad-leaved species indigenous to these areas, as they did not succeed in re-immigrating after the last glaciation (cf. e.g. Mai 1995; Grabherr 1997). But, the long history of cultivation of exotic plants in gardens and parks has established a rich source of warm temperate species in cultivated areas (see e.g. Schröter 1936; Schmid 1956; cf. also Walther 1999, 2001) and recent field surveys in the area have made it clear that the newly opened ecological niche has been occupied preferably by these introduced thermophilous ornamental species (Klötzli et al. 1996; Walther 1997; Carraro et al. 1999; Walther 2000, 2003). Hence, their spread and naturalisation is facilitated by the changing climatic conditions. Within less than half a century, the lower part of

the former deciduous broad-leaved vegetation belt has been taken over by proliferating exotic evergreen broad-leaved species (Gianoni et al. 1988; Carraro et al. 1994; Klötzli et al. 1996; Walther et al. 2001b). Evidence for an ecologically effective climate shift in the area arises from the comparison of the climatic conditions from the first half of the 20th century with those of the second half. The analyses revealed that events with low temperatures (< -10 °C) have occurred significantly less frequently in the latter period (Carraro et al. 1999; see also Beniston & Rebetez 1996), and the simultaneous marked reduction (-46 days) in the number of 'frost days' (cf. also Easterling 2002) has resulted in a prolonged growing season of ~320 days, on average, in the last three decades (Walther 2002). The significance of low winter temperatures for shaping the range and distribution of species in temperate regions has been documented by Sakai & Larcher (1987), Woodward (1990), Innes (1998), Inouye (2000), Scheifinger et al. (2003) and Pither (2003) (see also Sykes et al. 1996; Woodward 1996; Shafer et al. 2001). The period of milder winter conditions since the 1970s is in temporal synchrony with the major phase of local invasions of thermophilous species, and is considered to have particularly favoured both the survival and the establishment of dense stands of evergreen broad-leaved species on sites with former deciduous forest vegetation (Walther 2000, 2001; see also Klötzli & Walther 1999).

The establishment of exotic thermophilous elements in the native flora has also been reported from Spain, with the appearance of tropical and subtropical species from South America and South Africa (Sobrino et al. 2001), and from the west coast of Ireland with the spread of the Chilean rhubarb (*Gunnera tinctoria*) (Pilcher & Hall 2001). On Tai Mo Shan, the highest mountain in Hong Kong, frost-sensitive tropical plants have spread 150–200 m up the mountain since 1991 invading communities from which they were previously excluded (Corlett 2002). Finally, a poleward shift is evident at the northern boundary of woody evergreen broad-leaved species in Europe, with holly (*Ilex aquifolium*) claiming new areas in southern Scandinavia, especially in Sweden (Berger & Walther 2003). These changes in the floral composition are thought to be related to recent climate warming.

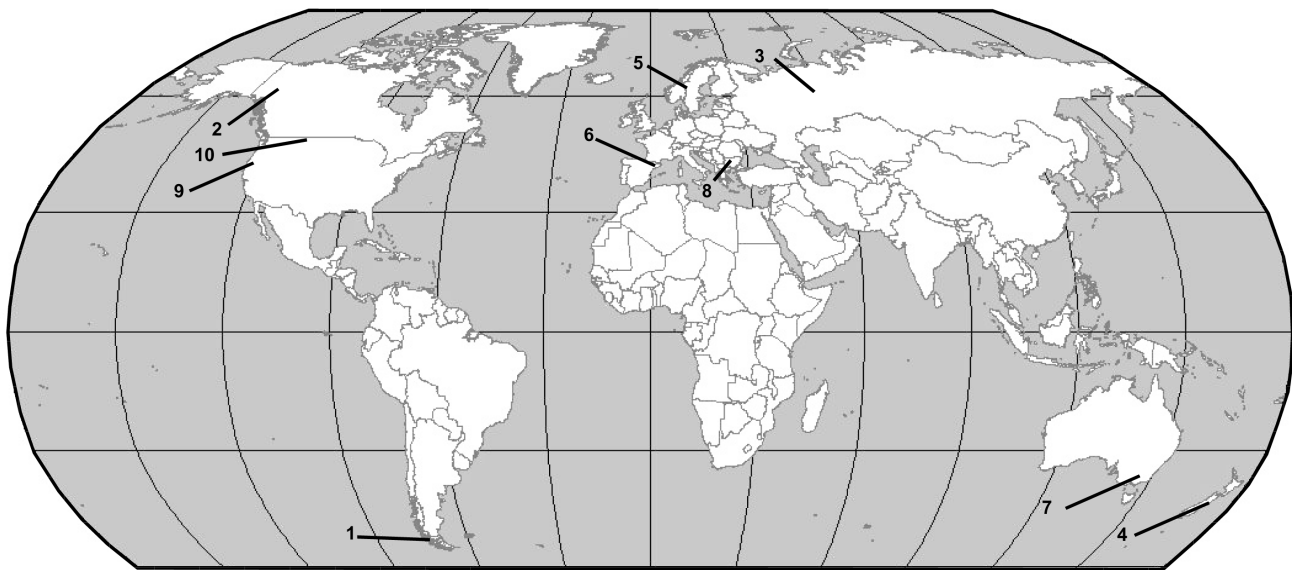
In addition to such temperature-induced changes, other case studies highlight rainfall-driven shifts in vegetation composition. Brown et al. (1997) report greater shrub numbers and increases in total cover of large woody shrubs in a region of grassland–shrubland transition of the Chihuahuan Desert in south-eastern Arizona. The changes in vegetation since the 1970s are thought to be associated with an altered climatic regime with increased winter precipitation. An exam-

ple in the opposite direction is provided by Allen & Breshears (1998) with a drought induced retreat of ponderosa pine (*Pinus ponderosa*) forest leading to the advance of pinion juniper (*Pinus edulis* and *Juniperus monosperma*) woodland in northern New Mexico. A similar process is under investigation in an inner Alpine dry valley with the die-back of Scots pine (*Pinus sylvestris*) and the increasing competitiveness of the more drought resistant downy oak (*Quercus pubescens*) (e.g. Lock et al. 2002).

Recent warming in tropical montane cloud forest has changed patterns of dry-season mist frequency. Highly mobile and thus early responding species, such as birds, reptiles and amphibians, probably anticipate the direction of future vegetation change with crashes in populations of many cloud-forest species but increases of premontane, cloud forest intolerant species, immigrating from the adjacent lower elevational belt (Pounds et al. 1999; see also Condit et al. 1996; Markham 1998; Nadkarni & Solano 2002).

The transition from woodland to grassland is visually the most striking vegetation boundary. For both latitudinal and altitudinal gradients, treelines (here defined according to Körner 1998a) have been subject to many research projects (see reviews by e.g. Hermes 1955; Wardle 1974; Tranquilini 1979; Stevens & Fox 1991; Miede & Miede 1994; Rochefort et al. 1994; Körner 1998b; Holtmeier 2000; Sveinbjörnsson 2000; Burga & Perret 2001; Malanson 2001). Although there is general agreement on the involvement of climatic determinants in this transition, the debate on the degree of relevance of the various particular climatic parameters driving the limit of tree growth remains controversial (e.g. Körner 1998b; Peterson 1998; Malanson 2001; Grace et al. 2002; see also Jobbagy & Jackson 2000). Assuming that growth and reproduction of trees at treeline stands are controlled by temperature, a rapid advance of the treeline would be predicted with global warming (Grace et al. 2002). Indeed, studies on the potential impact of climate change on the position of the treeline are reported from many regions in the world (Fig. 2).

Whereas Meshinev et al. (2000), Kullmann (2002) and Penuelas & Boada (2003) have detected significant shifts of the treeline and suggest a causal relationship between climate change and the establishment of tree seedlings beyond the forest margin, other studies describe a relatively stable treeline position in the last half century (e.g. Wardle & Coleman 1992; Butler et al. 1994; MacDonald et al. 1998; Cuevas 2000, 2002; Cullen et al. 2001; Masek 2001; Klasner & Fagre 2002). The substantial inertia or 'time lag' (cf. Malanson 2001; see also Chapin & Starfield 1997) in the response of treeline position is explained by the relatively poor availability and/or dispersal of seeds of the in-



Location	Period	Shift of treeline	Species	Reference
1 Chile	since ca. 1850	10 m	<i>Nothofagus pumilio</i>	Cuevas (2000); see also Cuevas (2002)
2 North western Canada	past 150 years	10–20 m 2–5 alt. m	<i>Picea glauca</i>	Szeicz & MacDonald (1995)
3 Northern Ural mountains, Russia	since 1920	100–500 m 20–30 alt. m	<i>Larix sibirica</i>	Shiyatov (1993, 2000) (cit. in Holtmeier 2000)
4 New Zealand (South Island)	last 60 years	7–9 m 5–8 alt. m	<i>Nothofagus menziesii</i> , <i>N. solandri</i> var. <i>cliffortioides</i> , <i>N. fusca</i> , <i>Prumnopitys ferruginea</i>	Wardle & Coleman (1992)
5 Sweden	last 50 years	120–375 alt. m	<i>Betula pubescens</i> ssp. <i>tortuosa</i> , <i>Sorbus aucuparia</i> , <i>Picea abies</i> , <i>Pinus sylvestris</i> , <i>Salix</i> div. spec., <i>Acer platanoides</i>	Kullmann (2002); see also Kullmann (2001)
6 Montseny mountains, Spain	since 1955	70 alt. m	<i>Fagus sylvatica</i>	Penuelas & Boada (2003)
7 Mount Hotham, Victoria, Australia	since 1967	<15 m	<i>Eucalyptus pauciflora</i> , <i>E. stellulata</i>	Wearne & Morgan (2001)
8 Bulgaria	since 1970	130 (–340) alt. m	<i>Pinus peuce</i>	Meshinev et al. (2000)
9 Oregon coast range Marys Peak, USA	ca. 30 years	10 m	<i>Abies procera</i>	Magee & Antos (1992)
10 Glacier Nat. Park, Montana, USA	since 1973	mentioned in text	<i>Abies lasiocarpa</i> , <i>Pinus flexilis</i> , <i>Pinus albicaulis</i> , <i>Picea engelmannii</i> , <i>Larix lyallii</i>	Butler et al. (1994)

Fig. 2. Reports on seedling establishment beyond the present treeline (According to the original literature the distance measure for shifts of treeline is differentiated between **m** = surface meters and **alt. m** = meters in altitude, respectively).

volved species (e.g. Wardle & Coleman 1992; Lescop-Sinclair & Payette 1995; Masek 2001), by particular edaphic or aeolian conditions (see e.g. Kupfer & Cairns 1996 and cit. lit.; Holtmeier 2000), and/or the importance of disturbance for tree recruitment above the treeline (e.g. Villalba & Veblen 1997; Luckman & Kavanagh 1998; Cullen et al. 2001). These factors lead to an autogenic control of treeline dynamics and make them not fully predictable from environmental conditions (Wildi & Schütz 2000). Whereas Magee & Antos (1992) and Wardle & Coleman (1992) outline the low adaptability of treeline species to spread into dense grassland vegetation (see also Hobbie & Chapin 1998; Moir et al. 1999), Germino et al. (2002) highlight the importance of an ameliorated microclimate by herbaceous ground cover for facilitating tree seedling establishment.

Instead of a spatial displacement, several studies reported other more structural features of vegetation change at the treeline, such as:

- the increase in population density (e.g. Butler et al. 1994; Luckman & Kavanagh 1998; Suarez et al. 1999; Klasner & Fagre 2002);
- an increased rate of tree growth (e.g. Villalba et al. 1997; Suarez et al. 1999), provided that the warming does not imply increased water-limitation in the regarded ecosystem (cf. Barber et al. 2000; Lloyd & Fastie 2002; see also Miehe 1996; Villalba & Veblen 1997; Moir et al. 1999; Kusnierczyk & Ettl 2002);
- and/or the development of vertical tree stems from pre-established krummholz vegetation (e.g. Lescop-Sinclair & Payette 1995; Luckman & Kavanagh 1998; see also Weisberg & Baker 1995; Hessl & Baker 1997; Dereg & Payette 1998).

Finally, there is also general agreement that recruitment patterns in treeline forests are episodic rather than gradual (Hättenschwiler & Körner 1995; Szeicz & MacDonald 1995; Kupfer & Cairns 1996; Paulsen et al. 2000; Cullen et al. 2001). Thus, treeline position may alternate between periods of relative stasis, when it is unresponsive to climate variation, and periods of rapid change during times when critical climate parameters exceed some threshold value (Lloyd & Graumlich 1997; Suarez et al. 1999; Paulsen et al. 2000). This inherent resilience of treeline forest to environmental change may result in a temporary disequilibrium relationship with climate (see Holtmeier 2000; Johnstone & Chapin 2003) and thus, argues against using the treeline as a criterion for assessing effects of rapid climate change (Körner 1999; Holtmeier 2000; see also Kupfer & Cairns 1996). Furthermore, although treeline species share the same environment, they may react to climate change in species-specific and thus, sometimes opposite way (see e.g. Carrer et

al. 1998; Luckman & Kavanagh 1998; Motta & Nola 2001; Payette et al. 2001).

Vegetation changes beyond the treeline have been reported by Sturm et al. (2001) with increases in height and diameter of individual shrubs and the expansion of shrubs into previously shrub-free areas in the Arctic during the past 50 years (cf. also Chapin et al. 1995; Serreze et al. 2000). Further north in the Arctic, Cornelissen et al. (2001) suggest a climate-induced change in species composition of arctic plant communities with declining macrolichen abundance as a consequence of the increased abundance of vascular plants (cf. also Harte & Shaw 1995). At the opposite pole, Fowbert & Smith (1994) recorded rapid population increases in the two native vascular plants on the Antarctic Peninsula. Colonies monitored on three islands of the Argentine Islands increased between 1964 and 1990 by nearly 25-fold (*Deschampsia antarctica*) and by over 5-fold (*Colobanthus quitensis*), which is considered to be a response to the increasing summer air temperatures in the region of the maritime Antarctic (see also Smith 1994). However, not only do native species claim areas newly exposed by the retreat of ice (e.g. Grobe et al. 1997; see also Crawford et al. 1993; Pockley 2001), but new species of both bryophytes and vascular plants with origins from lower latitudes have also recently been reported as successfully establishing in sub-Antarctic regions (Kennedy 1995; Convey 2001, and lit. cited therein).

An analogous process of increasing species number and frequency is found at the altitudinal margin of plant life. Hofer (1992), Grabherr et al. (1994) and Klanderud & Birks (2003) provide data on increasing species abundance and richness of plants on high mountain tops showing the overall trend of an upward shift of the alpine-nival flora (see also Grabherr et al. 1995, 2001; Keller et al. 2000; Pauli et al. 2001), which is attributed to the observed warming in climate in these areas (cf. e.g. Beniston et al. 1994; Weber et al. 1997). A recent resurvey of high mountain peaks in the Swiss Alps based on the Hofer (1992) data has revealed that the trend of increasing species numbers in the summit area still continues (G.-R. Walther, unpubl. data).

Feedback mechanisms and ecosystem processes

The aforementioned studies provide evidence that climate change is affecting vegetation in a perceptible way. In accordance with the observed changes in phenology, species composition and shifting species ranges of plant taxa (cf. also Minorsky 2002), there are also an increasing number of case studies providing evidence for changes in seasonal patterns and behaviour

as well as altitudinal and poleward shifts in the distribution of climate-sensitive animal species (see reviews by e.g. Hughes 2000; McCarty 2001; Sparks & Menzel 2002; Walther et al. 2002). An interesting fact of phenological cross-taxon studies is that the direction of change in plant and animal phenologies observed at the same location often coincides with each other (see e.g. Penuelas & Filella 2001; Walther et al. 2002). However, long-term data sets on species from different trophic levels show that individualistic responses of species follow less gradual changes in climatic averages but depend on particular, species-specific threshold values (e.g. Visser et al. 1998; Thomas et al. 2001; Visser & Holleman 2001; Voigt et al. 2003; see also Harrington et al. 1999). Hence, although the qualitative or directional response to changes in environmental conditions may be the same (e.g. earlier phenophases), discrepancies arise from differences in the quantitative response of different populations of the same species (Visser et al. 2003) or between different species and thus, may lead to a decoupling of species interactions (Penuelas & Filella 2001; Stenseth et al. 2002).

Feedback mechanisms between organisms of different trophic levels may be one reason for differences in species-specific response patterns to climatic change. An example is reported from sub-alpine forests in Italy, where Motta & Nola (2001) detected an increasing trend in the growth rate of stone pine (*Pinus cembra*), whereas at the same site the basal area increments of larch (*Larix decidua*) have oscillated substantially and no similar positive trend could be verified. The periodic strong growth reduction of larch is regarded to be a consequence of periodic outbreaks of the species-specific larch bud moth (*Zeiraphera diniana*). The effect of herbivory obviously masks any climatic signal in the growth trends of larch, but does not affect the other conifer species (cf. Davis et al. 1998; see also Briones et al. 1998; Holtmeier 2000; Cherubini et al. 2002).

There are several studies suggesting that climate warming affects the availability of resources and abundance of competitors (see e.g. Post et al. 2001, and lit. cit. therein; cf. also Ford 1982). Such effects of climate change may either be direct, as discussed for insect herbivores by Bale et al. (2002), or indirect, through changes in the species composition of plants, implying major changes in population dynamics and community composition of animals. In this regard, Brown et al. (1997) have shown that the density changes in woody shrubs were accompanied by changes in animal assemblages, with previously common animal species becoming locally extinct, while other previously rare species have increased (cf. also Cornelissen et al. 2001; Richardson et al. 2002).

Physiological differences among species and the individualistic response to environmental change may

alter the ecology and conservation of species and result in shifts in the competitive balance among species with the consequence of unpredictable impacts on community structure and ecosystem functioning. The complexity of ecological interactions renders it difficult to extend the responses of individuals or populations to that of communities or ecosystems (see e.g. Loreau et al. 2001; cf. also Moore et al. 1996). Although the components of the considered system may have undergone considerable modifications, ecosystem properties may show less sensitivity to climate change than would be predicted from extrapolations of environmental responses of single species, due to compensatory effects among species or limitations by factors other than climatic parameters (Chapin et al. 1995; see also Grime 1997; Briones et al. 1998; Press et al. 1998; Shaver et al. 2000; Rees et al. 2001; Rustad & Norby 2002).

However, there are still gaps in the knowledge of the ecological consequences of climate change. For instance, there is considerable uncertainty as to the effects of global change on soil biodiversity (Wall et al. 2001; cf. also Heal et al. 1996; Whitford 1992) as well as to the integration of aboveground and belowground processes under climate change scenarios (e.g. Norby & Jackson 2000; Wolters et al. 2000). Another important, but in advance hardly assessable aspect is the future diversity and abundance of pathogens and disease vectors. However, there is no doubt that their ecological impacts on the composition and functioning of ecosystems will be substantial (cf. e.g. Scherm & Coakley 2003; Mitchell et al. 2003; see also Chapin et al. 1997; Epstein 2001; Gilbert 2002; Harvell et al. 2002).

Furthermore, year-to-year changes due to large scale climatic phenomena such as the North Atlantic Oscillation and El Niño-Southern Oscillation are much larger in magnitude than the trend in climate change, attributing considerable noise to the long-term signal of global warming (cf. Stenseth et al. 2002; see also Blenckner & Hillebrand 2002) and imposing difficulties in disentangling the general patterns of climate change impacts from short-term fluctuations (cf. also Graetz 1996; Kaufmann 2002; van Noordwijk 2003).

Finally, climate-biota-interactions do not follow a one-way relationship of dependence. Changes in the structure and abundance of vegetation can contribute to changes in the exchange of surface energy (e.g. Sturm et al. 2001) and thus, affect hydrological processes through feedback mechanisms with the exchange of moisture between land surfaces and the lower atmosphere (Kennedy 1995; see also Shukla & Mintz 1982; Vitousek 1994; Foley et al. 1998; Hayden 1998; Pielke et al. 1998; Füssler & Gassmann 2000).

Conclusions

The biotic response to 30 years of enhanced global warming has become perceptible and substantial. An overwhelming number of studies provide evidence for climate change impacts on species, communities and ecosystems (see reviews by e.g. Hughes 2000; McCarthy 2001; Smith et al. 2001; Walther et al. 2001a, 2002; Root et al. 2003). In addition, many observational and experimental studies on the physiology, behaviour and ecology of the species considered in climate change studies provide a detailed mechanistic understanding of the underlying processes and dynamic features associated with species-specific adaptability and response mechanisms to changing climatic conditions, further supporting the credibility of a causal link between change observed in living systems and recent climate change. Although the overwhelming majority of case studies on global warming impacts reveal a consistent pattern of change (Root et al. 2003), sometimes the response of species to climate change may be variable or even contradictory (cf. e.g. Menzel 2000, Emberlin et al. 2002; see also Jensen 2003). This should not be interpreted as conflict in evidence, but rather as being in agreement with a general global warming trend for two reasons. First, a general increase in global average temperatures includes in itself spatial, temporal and in some areas directional (i.e. regional cooling or warming trend) heterogeneity (cf. Folland & Karl 2001), and second, the varying response amongst species may also be a consequence of the complexity of living systems with intra- and interspecific feedback mechanisms (cf. Davis et al. 1998). Thus, it appears difficult to combine the results of individual studies from different areas dealing with different species to educe a common, quantitatively comparable trend across different taxa, trophic levels and/or geographic regions (cf. also Watt & McFarlane 2002).

With regard to plant communities and vegetation formations, the displacement of present vegetation belts towards higher altitudinal or latitudinal areas may serve as a simplistic theoretical construct to demonstrate that climate change induces shifts in the vegetation zonation, but is unlikely to occur without major internal reorganisation in terms of both the composition and relative proportion of species (cf. Kappelle et al. 1999; see also Price & Barry 1997; Walker & Steffen 1997). Due to complex and highly species-specific feedback mechanisms, the process of shifting vegetation formations implies the rearrangement of affected assemblages with so far unknown weighting of the species involved. Rare species may become dominant, whereas previously dominant species may play a less prominent role. In the long run this

may lead to communities unknown to the present world (Scholes & van Breemen 1997; see also Chapin et al. 1993). In retrospect, paleoecologists have introduced terms like no-analogue assemblages or disharmonious assemblages for communities occurring in the past without modern analogues (see e.g. Huntley 1995); the same might be applied in the prospect with regard to novel assemblages developing under climate change modification.

It is also not assured that the migration rates of species will keep pace with the rate of global warming (e.g. Dyer 1995; Malcolm et al. 2002). The individualistic responses of species to environmental gradients depend on species-specific threshold parameters and may lag considerably behind gradual climatic change. In addition and in contrast to vegetation changes of the past, migration routes have become increasingly impassable due to human activities (cf. Pitelka et al. 1997; Kappelle et al. 1999; Dynesius & Jansson 2000; see also Peters 1992; Myers & Lester 1992). On the other hand, human activity enables the exchange of species among remote continents and subsequent intrusion of neophytic elements into the native biota (cf. e.g. Mack & Lonsdale 2001). As some case studies in this review have shown, changing environmental conditions provide new ecological niches for colonisation by introduced species and facilitate the invasion of exotics, which were previously kept in check by climatic factors (see also Cronk 1995). In the future, these species may even play an important role in post-climate change communities (Williams 1997). For these reasons, predictability is limited when attempting to derive the distribution and composition of future vegetation assemblages through a comparison with vegetation dynamics of the past (Moore 2003).

In the long-term perspective, the biotic implications of climate change and its evolutionary consequences depend on both the magnitude and rate of warming and the impact this has on patterns of climatic extremes and regimes of disturbances (see e.g. Easterling et al. 2000; Dale et al. 2000; Parmesan et al. 2000; Smith et al. 2001). There is also a dependence on the impact of other, on a temporal scale probably more imminent threatening human influences on biological systems such as habitat conversion, overexploitation and pollution (e.g. Leemans 2001; cf. also Harte et al. 1992; Myers 1992; Scholes & van Breemen 1997). The ecological consequences of the combination of these influences are considered to be extensive and substantial (see e.g. Travis 2003), and it is the future development of these threatening factors that will determine the fate and behaviour of plants in a warmer world.

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