Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate

Jonathan Lenoir, Jean-Claude Gégout, Antoine Guisan, Pascal Vittoz, Thomas Wohlgemuth, Niklaus E. Zimmermann, Stefan Dullinger, Harald Pauli, Wolfgang Willner and Jens-Christian Svenning

J. Lenoir (lenoir.john@gmail.com), The Ecoinformatics & Biodiversity Group, Dept of Biological Sciences, Aarhus Univ., Ny Munkegade 114, DK-8000 Aarhus C, Denmark and AgroParisTech, UMR1092 AgroParisTech-INRA, Laboratoire d'Etude des Ressources Forêt-Bois (LERFoB), 14 rue Girardet, FR-54000 Nancy, France. – J.-C. Gégout, AgroParisTech, UMR1092 AgroParisTech-INRA, Laboratoire d'Etude des Ressources Forêt-Bois (LERFoB), 14 rue Girardet, FR-54000 Nancy, France, and Center for Advanced Studies in Ecology and Biodiversity (CASEB), Depto de Ecologia, Pontificia Univ., Católica de Chile, Alameda 340 C.P. 6513677, Santiago, Chile. – A. Guisan, Fac. of Biology and Medicine, Dept of Ecology & Evolution, Univ. of Lausanne, Bâtiment Biophore, CH-1015 Lausanne, Switzerland. – P. Vittoz, Fac. of Biology and Medicine, Dept of Ecology & Evolution, Univ. of Lausanne, Bâtiment Biophore, CH-1015 Lausanne, Switzerland and Fac. of Geosciences and Environment, Univ. of Lausanne, Bâtiment Biophore, CH-1015 Lausanne, Switzerland. – T. Wohlgemuth and N. E. Zimmermann, Swiss Federal Research Inst. for Forest Snow and Landscape Research WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland. – S. Dullinger, Vienna Inst. for Nature Conservation and Analyses, Giessergasse 6/7, AT-1090 Vienna, Austria, and Fac. Centre for Biodiversity, Dept of Conservation Biology, Vegetation and Landscape Ecology, Univ. of Vienna, Rennweg 14, AT-1030 Vienna, Austria. – H. Pauli, Inst. of Mountain Research: Man and the Environment (IGF) of the Austrian Academy of Sciences, c/o Fac. Centre for Biodiversity, Dept of Conservation Biology, Vegetation and Landscape Ecology, Univ. of Vienna, Rennweg 14, AT-1030 Vienna, Austria. – W. Willner, Vienna Inst. for Nature Conservation and Analyses, Giessergasse 6/7, AT-1090 Vienna, Austria. – J.-C. Svenning, The Ecoinformatics & Biodiversity Group, Dept of Biological Sciences, Aarhus Univ., Ny Munkegade 114, DK-8000 Aarhus C, Denmark.

In as much as the elevation gradient in species composition is often thought to be driven by the corresponding temperature gradient, species ranges are both expected and predicted to shift upward in response to climate warming. Indeed, there are numerous reports of species moving towards higher elevations in response to the rising temperatures for both animals (Konvicka et al. 2003, Tryjanowski et al. 2005, Wilson et al. 2005, Franco et al. 2006, Hickling et al. 2006, Moritz et al. 2008, Raxworthy et al. 2008, Chen et al. 2009) and plants (Klanderud and Birks 2003, Walther et al. 2005, Pauli et al. 2007, Kelly and Goulden 2008, Lenoir et al. 2008, Parolo and Rossi 2008, Vittoz et al. 2008, Lenoir et al. 2009), and the evidence for significant upslope migrations now seems overwhelming regardless of the position along latitudinal (Klanderud and Birks 2003, Konvicka et al. 2003, Wilson et al. 2005, Raxworthy et al. 2008, Chen et al. 2009) or elevational (Walther et al. 2005, Pauli et al. 2007, Kelly and Goulden 2008, Lenoir et al. 2008, Vittoz et al. 2008, Lenoir et al. 2009) gradients. Due to this empirical evidence and, perhaps, the intuitive expectation of rising elevational ranges as a consequence of a warming climate, ecologists have primarily focused on elaborating on the mechanisms and consequences of such upslope shifts including (Colwell et al. 2008): 1) biotic attrition in the lowland tropics, 2) gaps between current and projected elevational ranges (range-shift gaps), and 3) mountaintop extinctions in the long-term.

However, most of the studies that reported expected range shifts towards higher elevations have detected species moving towards lower elevations as well. Table 1 provides an illustrative, non-comprehensive survey of such studies from the recent years: in summary they demonstrate that ca 65% of the species have shifted their mid-range positions upslope, 10% have not changed their mid-range positions, and 25% have shifted their mid-range positions downslope (Table 1). In addition, according to a global review of the literature published until the beginning of the 21st century (Parmesan and Yohe 2003) ca 20% of the species have adjusted their ranges towards lower elevations and/or southern latitudes. Hence, a considerable fraction of the investigated species has shown range shifts that are inconsistent with the forecasted effects of climate warming. These downslope movements seem very unlikely to occur as a direct consequence of rising temperatures, but the potential mechanisms involved have received little attention.

Stochastic fluctuations in the positions of individuals, or populations, together with measurement errors, represent one such potential "mechanism". However, many, though not all of the studies reporting downslope shifts have explicitly tested the observed changes in single species' ranges for significant deviation from random fluctuations. For plants, significant downslope shifts have been reported for 5 of 46 species displaying significant mid-range shifts between the periods 1905–1985 and 1986–2005 (Table S2

Table 1. Studies that have documented changes of the mid-range positions (i.e. mean, median or optimum) of species' elevational distributions in relation to current climate change. Only studies comparing at least two inventories are listed here. This list is informal and not intended to be exhaustive.

Species groups	Sampling periods	Geographic locations	Number of species	Percentage of species			Mean shift of the central position	Author references
				Upward shifts	No shifts	Downward shifts		
Moth	1965 and 2007	Mount Kinabalu, Borneo	102	59%	12%	29%	+68 m between surveys	Chen et al. (2009)
Plant	1977–1978 and 2006–2007	Santa Rosa mountains, south California	10	90%	0%	10%	+65 m between periods	Kelly and Goulden (2008)
Plant	1905–1985 and 1986–2005	The Vosges, Jura, Massif Central Pyrenees, Alps and Corsican mountains, France	171	69%	0%	31%	+65 m between periods	Lenoir et al. (2008)
Animal	1993–2003	Tsaratanana mountains, Madagascar	30	73%	7%	20%	+65 m per decade	Raxworthy et al. (2008)
Butterfly	1970–1990 and 2004–2005	England	3	67%	0%	33%	+52 m between periods	Franco et al. (2006)
Animal	1960–2000	England	329	69%	0%	31%	+10 m per decade	Hickling et al. (2006)
Butterfly	1967–1973 and 2004	Sierrade Guadarrama, central Spain	19	74%	0%	26%	+119 m between periods	Wilson et al. (2005)
Bird	1970s and 2000s	Alps, France	41	10%	76%	15%	−2 m between periods	Archaux (2004)
Butterfly	1951–1980 and 1995–2001	Czech Republic	119	76%	0%	22%	+60 m between periods	Konvicka et al. (2003)

IBS SPECIAL ISSUE

296

in Lenoir et al. (2008)). For reptiles and amphibians, Raxworthy et al. (2008) have found significant downslope shifts for 2 of 7 species displaying significant mid-range shifts between 1993 and 2003. For birds, Archaux (2004) has reported significant downslope shifts for 5 of 8 species displaying significant mid-range shifts between the 1970s and the 2000s.

However, it could be argued that starting from the near-consensual report of a general and strong upward shift signal in species mid-range positions along the elevation gradient, the relevant random distribution of species mid-range shifts for testing the occurrence of significant downslope movements should be centred around some expected upslope shift, according to the observed climatic trends, rather than around zero (i.e. a null expectation of constant distributions). Indeed, the relevant question is: which proportion of species would we expect to shift their mid-range position downslope by chance alone (i.e. due to random population fluctuations, data idiosyncrasies, and observer errors) despite an average upslope trend of z m? This proportion is highly dependent on the variation in mid-range shifts caused by such "stochastic processes" alone (Fig. 1): the narrower this variability, the lower the proportion of species likely to show such stochastic downslope shifts. However, if random fluctuations and observer errors do not fully explain the observed downslope shifts, what mechanisms might then drive these unexpected range changes?

One potential mechanism is land-use-related habitat modification, which has already been shown to cause downslope range shifts in particular settings (Hättenschwiler and Körner 1995, Archaux 2004). In addition, however, such shifts may also result from changes in species interactions (facilitation, competition, and predation) in response to climate warming (Hughes 2000). Here, we propose a conceptual and testable model that explains the observed downslope shifts of species as resulting from the effects that both climate and land use change, separately or in concert, might have on species interactions. We start from the proposition that species are often limited by physical stresses at one margin, but by biotic interactions at the other, more favourable, margin of their distribution along environmental gradient (McArthur 1972, Connell 1978, Brown et al. 1996, Brown and Lomolino 1998, Leathwick and Austin 2001, Normand et al. 2009). We then argue that both climate warming and land-use-related habitat modification may increase levels of disturbance in these ecosystems leading to: 1) a transient reduction of the importance of competition as a limiting factor on species distributions; and 2) an associated potential range expansion towards lower elevations for species whose lower elevation margin was previously strongly limited by competition.

Climate warming may cause temporary downslope range shifts due to transient competitive release at the lower margin of species distribution

Climate warming may not only affect species distributions via altering abiotic conditions but also by changing the importance or intensity of species interactions (Hughes
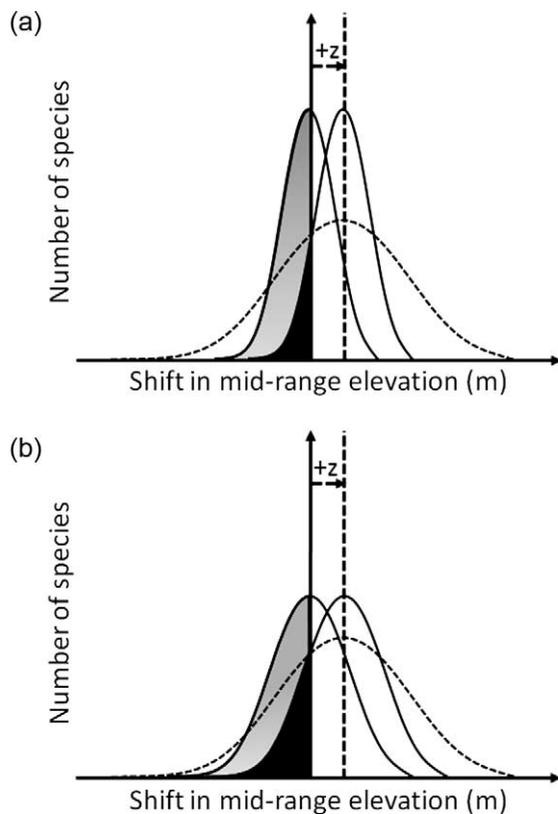
(a)

(b)

Figure 1. Null expectation of the proportion of downslope mid-range shifts despite an average upslope trend of z m for (a) narrower range of random variation and (b) wider range of random variation. Broken curves represent the observed distribution of shifts in species mid-range elevation from a colder to a warmer period. Unbroken curves represent the random distribution in species mid-range elevation within a single statistical population. The gray filling illustrates the expected proportion of random downslope shifts in mid-range positions in the absence of climate change (50%). The black filling illustrates the expected proportion of random downslope shifts in mid-range positions despite a warming-driven upslope trend of z m (<50%). The vertical broken line displays the average upslope trend of z m.

2000, Brooker 2006). Indeed, it has been demonstrated that changes in species interactions may override autecological responses to a changing climate and even reverse community trajectories (Suttle et al. 2007). Before explaining our model which is based on such changes in species interactions, we would like to pinpoint the two most important conceptual cornerstones it rests upon.

First of all, the lower-margin-competition versus higher-margin-stress limitation concept (McArthur 1972, Connell 1978, Brown and Lomolino 1998) suggests competitive effects as the major mechanism for setting the lower limit of species' elevational ranges. More generally, the importance of competition is thought to increase as environmental severity decreases, a theory known as the stress-gradient hypothesis in plant ecology (Bertness and Callaway 1994, Callaway and Walker 1997, Brooker et al. 2005, Maestre et al. 2009). This concept might be less applicable towards the lowest elevations of the lowest latitudes in subtropical to tropical areas, where temperature and water stress vary in

opposite directions, and where lower range margins may be relatively often set by drought-induced stress (Normand et al. 2009). However, the stress-gradient hypothesis appears generally valid in elevational ranges where the macroclimate does not present drought-induced stress gradients that complicate the effect of the elevational gradient (Callaway 1998, Callaway et al. 2002). Thus, this concept will apply to many mountainous regions, notably in moist temperate and tropical areas. As a corollary, many species in such systems will likely be characterized by realised climatic niches being smaller than fundamental ones (Vetaas 2002) in particular towards lower elevations (due to biotic interactions). For example, Vetaas (2002) has suggested that competition plays an important role in constraining the climatic ranges of four Himalayan *Rhododendron* species in their native habitat as compared to their climatic ranges in ornamental gardens and arboreta, three of which being able to grow there under a far wider range of climatic conditions (generally warmer). Therefore, any mechanism that alleviates competitive exclusion is likely to induce changes in species realised distributions.

Secondly, the importance of competition in structuring communities is likely reduced by increased levels of disturbance (Dayton 1971, Connell 1978, Huston 1979, McAuliffe 1984, Brooker and Callaghan 1998, Brooker 2006). Thus, if climate warming increases disturbance levels within a specific ecosystem, it is reasonable to expect that it will, to a certain degree, relax the role of competition as a selective filter for community assembly. Indeed, climate warming affects ecosystems stochastically through an increasing frequency and intensity of events such as drought-induced insect outbreaks (Allen et al. in press), heat-induced wildfires (Schumacher and Bugmann 2006), windthrows (Usbeck et al. in press), and permafrost degradations (Cannone et al. 2007). All these climatic-extremes-induced effects can be viewed as disturbances under definitions such as destruction of plant biomass (Grime 1979), cause of mortality (Huston 1979), and disruption of ecosystem, community or population structure (Pickett and White 1985). Indeed, the increasing frequency of climatic extremes, indicated by changes in the interannual variability around mean values of climate parameters, have already been reported to influence species range margins (Zimmermann et al. 2009). The interplay between the idea of disturbance-related release from competition and the above-mentioned stress-gradient hypothesis gives the key to understanding potential downslope range shifts despite climate warming.

We start outlining our conceptual model by restricting the temperature-elevation-stress relationship to elevational ranges where heat and drought have hardly any impacts, e.g. from temperate montane to alpine ecosystems (Fig. 2a). Following the stress-gradient hypothesis, the importance of competition is therefore likely to decrease upwards along the elevation gradient (Fig. 2b), from favourable abiotic conditions at low elevations (warmer conditions) to harsh abiotic conditions at high elevations (cold damage during winter, reduced energy during the growing season). To simplify matters in our conceptual model, we distinguish between two illustrative species with exactly the same realised distribution along the elevation gradient (as defined
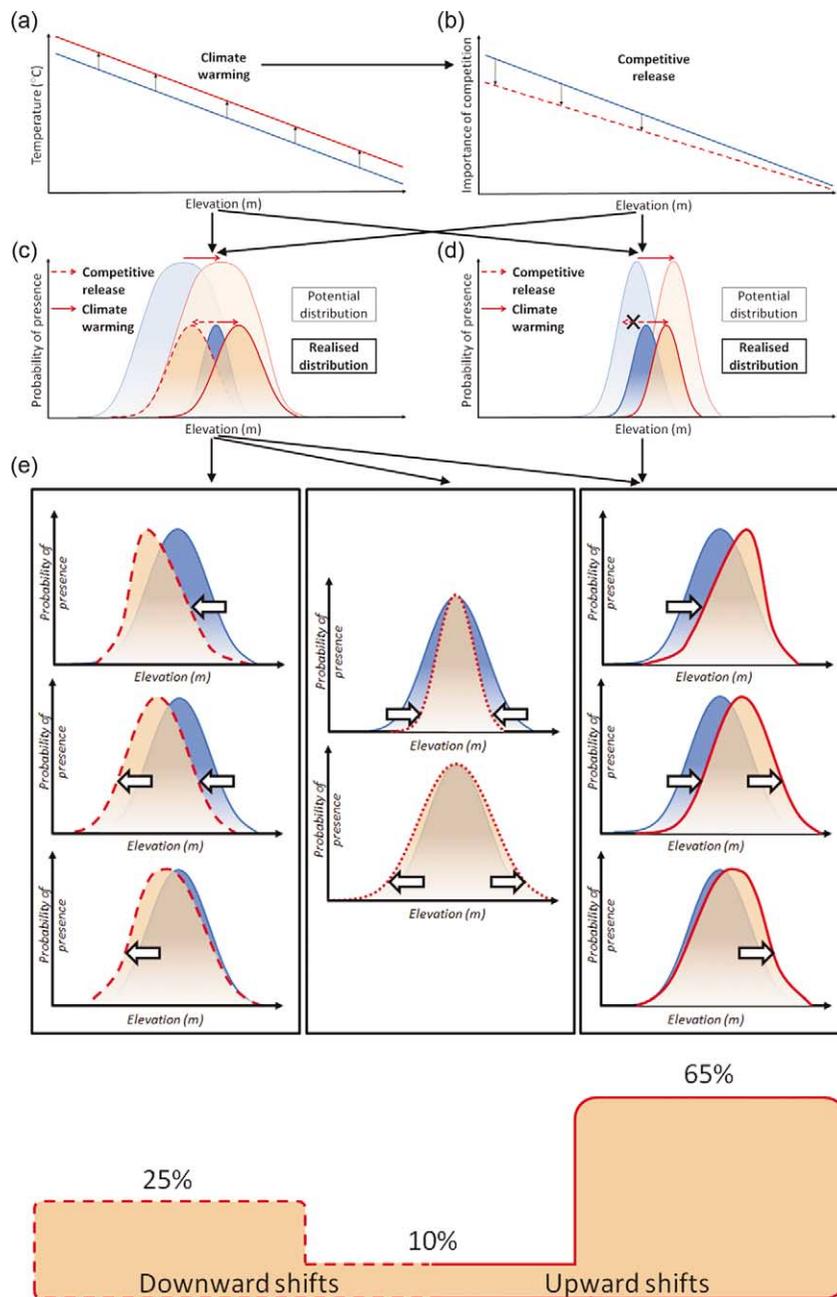
297

Figure 2. Conceptual model of changes in species' elevational distributions in response to climate warming. Panels depict: (a) the general decreasing trend in mean annual temperature along the elevation gradient, and an overall warming between two periods; (b) the general decrease in the importance of competition along a gradient of environmental severity represented by the elevation gradient, and the potential impact of warmer conditions on the relationship between elevation and the importance of competition; (c) the realised and the potential distributions along the elevation gradient for a species strongly limited by competitors from below, and the potential upslope and/or downslope range shifts of the realised distribution due to both climate warming and competitive release; (d) the realised and the potential distributions along the elevation gradient of a species less limited by competitors from below, and the resulting upslope range shift of the realised distribution due to climate warming (competitive release does not allow shifts towards lower elevations that are no longer climatically suitable); and (e) all the resulting combinations of changes in species elevational distributions involving contraction, expansions, or both simultaneously, and the observed proportions of species displaying upward, stable, and downward shifts in elevation in response to recent climate warming. Blue colours represent initial conditions before climate warming, whereas red colours represent changed conditions after an increase in temperatures. Red broken lines represent the impact of a reduction in the importance of competition after climate warming. The elevation gradient considered in our conceptual model ranges from temperate montane to alpine ecosystems where heat and drought have hardly any impact.

from their realised niche), but differing in the way they fill their potential distribution area (as defined from their fundamental ecophysiological niche) (Fig. 2c, d). Hereafter, we will consistently refer to the "potential distribution" as the range corresponding to the species' fundamental ecophysiological niche, and to the "realised distribution"

as the range corresponding to the species' realised niche. The first illustrative species is strongly limited at the lower margin of its elevational distribution by competitors from below (low ''realisation'' of the potential distribution), whereas the second one is much less limited by biotic interactions (high ''realisation'' of the potential distribution). It is difficult to infer the physiological climatic requirements of these two species from their actual range since their elevational distributions are identical. Nevertheless, they might respond differently to climate warming because of this distinct ''realisation'' of their ecophysiological range.

Let us now introduce the effect of climate warming in our conceptual model (red colours in Fig. 2). As argued above, warming-induced disturbances are likely to transiently reduce the importance of competition along the elevation gradient (Fig. 2b). Simultaneously, climate warming is likely to shift species' potential distribution along the elevation gradient towards higher elevations (Fig. 2c, d). However, the transient reduction in the importance of competition at the lower margin of a species' elevational distribution is likely to particularly benefit species that currently have a greater part of their potential distribution unfilled because of competition. For such species, climate warming allows range expansion towards lower elevations from which they had hitherto been competitively excluded (Fig. 2c). In contrast, species which are currently little limited by competition and largely fill their potential distribution areas along the elevation gradient will not be able to move downwards due to the upward shift of habitats climatically suitable to them (Fig. 2d). Figure 2e gives a full account of the climatically driven range shifts along the elevation gradient conceivable under this model.

To sum up, species with a low ''realisation'' of their potential distribution areas along the elevation gradient are especially good candidates for downslope shifts, if they additionally have good dispersal abilities and a wide fundamental climatic niche. For example, Vetaas (2002) has suggested that *Rhododendron* species with their lower margins hitherto set by competition can grow under warmer climatic conditions, i.e. expand towards lower elevations. Additionally, species mid-range shifts might result not only from expansions at range margins alone, but also from changes in species local abundance (Fig. 2e). For example, species with low competitive abilities, but a wide potential distribution along the elevation gradient associated with a high degree of plasticity (Fig. 2c) might be already present downwards as remnant populations living at environmental extreme sites where the competitive species are excluded by abiotic factors (Eriksson 2000). In this latter case, downslope mid-range shifts might simply result from an increasing abundance of the species with these outlier populations acting as ''expansion foci''. Finally, we note that downslope range shifts under this model would be likely to be temporary, as the importance of competition may become reasserted if climate change slows down or come to a halt, while species will eventually be forced upwards in elevation if climate change continues and conditions at lower elevations shift beyond the fundamental climatic niche of the species.

Habitat modification as an alternative mechanism causing downslope range shifts

Species may also shift downslope as a direct consequence of habitat modification, with or without involving competitive release, either following natural disturbances (windthrows, fires, and avalanches), human-induced disturbances or permanent habitat changes (recreational activities, land use changes, and management practices), or due to other local changes in habitat suitability. For example, in the Swiss Central Alps, Hättenschwiler and Körner (1995) have suggested that the cessation of forest cattle grazing and the high level of nitrogen deposition may have led to denser and more exuberant ground vegetation, thereby enhancing the replacement of *Pinus sylvestris* seedling populations by those of *P. cembra* below the present lower margin of *P. cembra* adult trees. Similarly, Archaux (2004) has suggested that the increase of conifer areas at the expense of broad-leaved trees due to changes in forest management might cause both coniferous- and deciduous-forest bird species to shift their mean elevation downwards. We note that habitat modification in conjunction with climate warming may explain upslope range shifts as well. As an illustration, in the Swiss Alps, Gehrig-Fasel et al. (2007) have reported that >90% of upslope shifts in the local tree line are due to ingrowth and the filling of gaps indicating that land use is the primary driver over climate warming in many instances, although the two drivers may also act in combination. In a conceptual model involving climate change and herbivory pressure, Cairns and Moen (2004) have highlighted a potential pathway for the interaction of both climate change and herbivore pressure on tree line fluctuations leading to upslope migration, a stationary state, or retrogression of tree lines. Hence, habitat modification has often been claimed to be an important driver of elevational range shifts, acting in concert with climate warming or even outweighing it (Hättenschwiler and Körner 1995, Archaux 2004, Cairns and Moen 2004, Gehrig-Fasel et al. 2007, Vittoz et al. 2009).

Nevertheless, habitat modification may well involve increased disturbance levels and thereby cause release from competition independently of climate warming, but with similar effects on species' elevational distributions. Human-induced disturbances are likely to be more frequent in lowland areas, however, given a generally increasing degree of anthropogenic habitat modification towards lower elevations of most mountainous settings (Nogués-Bravo et al. 2008). Consequently, the reduction in the importance of competition due to disturbances should be more important there, allowing range expansions of the realised distribution of species towards lower elevations as long as climatically suitable sites are available down below their lower margins. Therefore, species that fill only part of their potential distribution areas along the elevation gradient (Fig. 2c) are more likely to shift downwards in response to habitat modification alone, especially if their potential distribution areas do not shift upwards. For example, it has been suggested that unplanned vegetation destruction (burning and grazing), removing the pressure from competitive dominants from below, has enabled alpine and subalpine species in New Zealand to increase their elevational distributions downwards (Halloy and Mark 2003).

Towards a unified view of climate warming and habitat modification effects on downslope range shifts

Let us now consider a more unified point of view integrating the effects of climate warming and habitat modification. On the one hand, habitat modification may act in concert with climate warming to cause a reduction in the importance of competition at the lower margin of a species' elevational distribution and to allow a potential downslope shift in its mid-range position due to potential expansions at the competitively-released margin (Fig. 2e). This is especially true for species that fill only part of their potential distribution areas along the elevation gradient (Fig. 2c). On the other hand, habitat modification may restrict upslope range expansions due to climate warming or even cause regression patterns at the higher margin of a species' elevational distribution (Fig. 2e). For example, species may partially fail to colonise new climatically suitable areas at the higher margins of their elevational distributions if they are constrained by habitat fragmentation (Honnay et al. 2002). Additionally, other non-climatic factors such as restricted space towards mountaintops (Colwell et al. 2008), limited dispersal ability (Bossuyt et al. 1999, Hermy et al. 1999, Svenning and Skov 2006), and/or edaphic constraints may restrict, or at least delay warming-induced upslope shifts. Finally, natural habitat modification may further delay warming-induced upslope shifts through unexpected patterns of regression at the higher margins of species' elevational distributions (Fig. 2e). For example, Cannone et al. (2007) have suggested that warming-induced permafrost degradations at high elevations may trigger habitat disturbances, in the form of debris flow and landslides, causing unexpected patterns of regression in vegetation coverage above 2500 m. This constitutes another migration barrier that restricts upslope migrations to disturbance-adapted species (Cannone et al. 2007).

Such limitations to upslope migrations are coherent with observations in different species groups: extinctions at the lower margins of species distributions have been reported to be more common than colonisations at the higher margins (Wilson et al. 2005, 2007, Kelly and Goulden 2008, Moritz et al. 2008, Lenoir et al. 2009). This may sometimes result in no upslope migration, but rather in local changes in species abundance over time (Wilson and Nilsson 2009). In such cases, mortality-induced shifts may take place more rapidly than do recolonisation-induced shifts associated with both migration and establishment processes (Davis 1989). The resulting pattern is a transient ''lean'' upslope (Breshears et al. 2008). The few establishments of a given species towards higher elevations may fail to compensate for the losses at lower elevations leading to transient declines in species richness or biotic attrition not only at lower elevations (Colwell et al. 2008), but across the whole elevation gradient (Fig. 2 in Wilson et al. (2007)). This configuration is transient and, again, is likely to open a ''window of opportunity'' for highly vagile and plastic species that might shift either upslope or downslope to fill the gaps initiated either by climate warming or habitat modification. Such a process leaves biological communities with reduced numbers of species, and dominated by more

mobile and opportunistic species (Warren et al. 2001). Increased frequency of windthrows across central European forests during the last few decades (Usbeck et al. in press) is one example of disturbances that is likely to produce ''windows of opportunities'' for vagile species with a high degree of plasticity. Thus, habitat modifications strongly interact with climate warming and contribute to bias competitive release even further towards lower elevations, making downslope range shifts of some species more likely than with climate warming alone.

Other plausible causes of downslope range shifts

Of course, downslope range shifts could be driven by changes in other aspects of climate than mean temperature, e.g. precipitation regime, snow cover duration, water balance, or seasonality in climate parameters. These complex aspects of climate variability may heavily influence species range margins (Zimmermann et al. 2009), and thus more complex environment-competition interactions are likely to cause unexpected range shifts in response to climate warming. At high elevations, for example, warmer temperatures may decrease the winter snow cover duration (Beniston 2005), and thus may cause frost damage at the higher margin of a species' elevational distribution, which in turn may alleviate the competitive effect of this species on other ones potentially migrating towards lower elevations (Fig. 2c). Consequently, the competitive control that this species exerts on the distributions of the species above will likely become less tight. Additionally, the influx towards areas vacated by upslope shifting competitive species is likely to occur both from above and below. This should result in some species shifting upslope and others shifting downslope, and others even expanding towards both sides without changing in their mid-range position (Fig. 2e). Therefore, complex environment-competition interactions may also cause downslope range shifts, but temporarily before other stronger competitors invade.

A case study from French mountain forests: proportion of random downslope movements

According to our null expectation, the proportion of random downslope mid-range shifts despite an average upslope trend of z m is dependent on the range of random variation among shifts (Fig. 1). We used data from a previous study focusing on the shifts in the elevational position of plant species' maximum probability of presence (optimum) (Lenoir et al. 2008) to estimate this range of random variation among shifts and then assess the proportion of random downslope mid-range shifts despite an average upslope trend of z m. That study found an average upslope trend of 65 m, among 171 plant species, between a 1905–1985 dataset and a carefully matched 1986–2005 dataset for French mountain forests. Each dataset comprised 3991 surveys. To estimate the range of random variation among shifts, we constructed two random

datasets, each built by randomly drawing (with replacement) 3991 forest surveys from the 1905–1985 dataset described by Lenoir et al. (2008). Because the increasing trend in mean annual temperature and the warmest records have mostly occurred since the late 1980s (Jones et al. 2001), we chose to draw our two random datasets from the first period to avoid potential strong differences in climatic conditions between the two randomly-drawn datasets. Indeed, it was important that the two bootstrap samples represented an identical range of environmental conditions. We then used the same analytical method as described in Lenoir et al. (2008) to compute species elevation optimum for each of the 171 studied species in each of the two bootstrap samples. The estimated elevational optimum position was bounded between the lowest and the highest elevations in the 1905–1985 dataset. However, instead of computing the difference in each species optimum elevation between two different periods, we here computed the difference in each species optimum elevation between two bootstrap samples from the same period to get the distribution of differences in optima expected from stochasticity alone. We repeated this procedure 1000 times using the "boot" library (Canty and Ripley 2008) in R (R Development Core Team 2009). Averaging cross the 1000 iterations, we found a mean difference in species optimum elevation of −0.4 m (standard deviation: 10.5 m) and a confidence interval for mean at 95% ranging from −14.2 m (standard deviation: 10.7 m) to 13.3 m (standard deviation: 10.6 m). Finally, to assess the proportion of downslope mid-range shifts expected at random despite an average upslope trend of 65 m in French mountain forest plants, we simply repositioned, for each of the 1000 iterations, the distribution of random differences in optima 65 m upwards, i.e. to the right, by adding 65 m to the

location of each shift (Fig. 3a). We then estimated the expected proportion of random downslope shifts, despite an average upslope trend of 65 m, as the proportion of shifts in the left tail of the distribution, truncated at 0 m shift (see solid dark gray bars in Fig. 3a). Across the 1000 iterations (Fig. 3b), we found a proportion of 16% (standard deviation: 4%) of species expected to have optima below the 1905–1985 elevational mean, by chance alone, which is about half the proportion of downslope shifts we originally found (30%) between 1905–1985 and 1986–2005 (Lenoir et al. 2008). Thus, the number of species found to move downwards along the elevation gradient is approximately twice as high as expected by chance under the observed general upward trend. We note that this estimated proportion of species "going against the flow" (14%) is higher than the number of species with significant downslope shifts (5/171) found when individual species optimum elevation were tested for significant difference from a constant species optimum elevation expectation (Table S2 in Lenoir et al. (2008)). However, this probability reflects the conservative nature of the test we used for testing differences in individual species optima along the elevation gradient (Lenoir et al. 2008).

The five forest plant species displaying significant individual downslope shifts despite an average upslope trend of 65 m are *Clinopodium vugare, Dryopteris dilatata, Quercus pubescens, Rubus fructicosus* and *Saxifraga cuneifolia.* Two of these species have seeds dispersed by birds (*Quercus pubescen*s and *Rubus fructicosus*), the spores of *Dryopteris dilatata* are tiny and hence easily going with the wind, while *Clinopodium vulgare* is dispersed by epizoochory (Rameau et al. 1993). Hence, four of these five species have efficient dispersal mechanisms, most likely an important trait for allowing downslope range shifts despite climate warming.
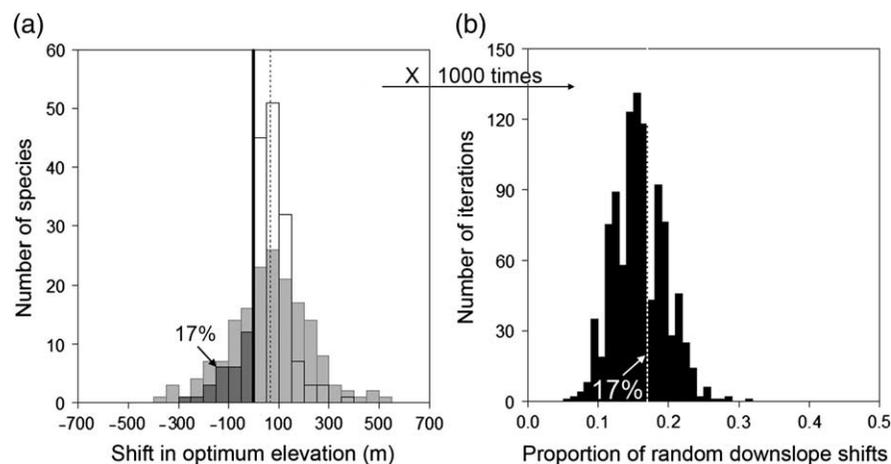

Figure 3. Distribution of (a) observed and random differences in optima along the elevation gradient for 171 plant species using published data from French mountain forests (Lenoir et al. 2008), the distribution of random differences in optima representing a single illustrative case of the 1000 bootstrap iterations, and (b) distribution of the proportion of random downslope mid-range shifts despite an average upslope trend of 65 m for the 1000 bootstrap iterations. Solid light gray bars represent the observed shifts in species optimum elevation between 1905–1985 and 1986–2005. Unfilled bars represent the distribution of random shifts in species optimum, computed by comparing two bootstrap samples drawn from the 1905–1985 dataset, after repositioning this distribution 65 m upslope, i.e. to the right (see text for details). Solid dark gray bars represent the proportion of downslope mid-range shifts expected at random, despite an average upslope trend of 65 m. The vertical dark broken line displays the average upslope trend of 65 m. The vertical white broken line displays the proportion of random downslope mid-range shifts despite an average upslope trend of 65 m for the single illustrative case of the 1000 bootstrap iterations.

Although *Saxifraga cuneifolia* has low dispersal abilities (barochory) and a distribution mainly restricted between 1500 and 2000 m, it also occurs sporadically in the lowlands, reaching down to 300 m in French mountain forests (Rameau et al. 1993). Thus, *Saxifraga cuneifolia* might represent a species strongly limited by competitors from below (Fig. 2c). Additionally, *Rubus fructicosus*, and to a lesser extent *Clinopodium vulgare*, and *Quercus pubescens* seedlings, are highly reactive to canopy opening, i.e. positively influenced by disturbance. While we do not intend to validate our conceptual model with these examples, we note that these five downslope shifting species have a series of traits making them likely to respond to climate change in a way outlined by our model. However, a much more thorough empirical testing of this model is clearly needed.

Conclusion

We suggest that downslope range shifts of species may constitute an indirect biotic response to both climate warming and habitat modification rather than representing just random effects due to stochastic fluctuations in population distributions or observer errors. The concept presented here should become part of a general framework for future studies of changes in species distributions in response to climate warming. In our conceptual model, we assume, on a timescale too short for adaptative change, that downslope shifts primarily occur for species that are strongly limited by competition at their lower elevation range margin, and therefore have a realised distribution that do no fill their potential distribution areas almost completely along the elevation gradient. To test this hypothesis, one could select two sets of species: one set of species that have significantly shifted downslope and another set of species that have significantly shifted upslope. One could then compare their realised distribution in their natural habitats with their potential distribution areas additionally assessed by experiments (common garden or ecotron). In such an experiment, we would expect larger differences between the realised and the potential distributions along the elevation gradient for the set of species that have significantly shifted downslope. Although downslope range shifts, particularly where solely driven by warming-induced competitive release, should be only transient, we underpin the necessity to take the hitherto neglected downslope range shifts of species more explicitly into consideration when making predictions of the effects of future climate change scenarios on species distributions.

References

Allen, C. D. et al. in press. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. – For. Ecol. Manage.

Archaux, F. 2004. Breeding upwards when climate is becoming warmer: no bird response in the French Alps. – Ibis 146: 138–144.

Beniston, M. 2005. Mountain climates and climatic change: an overview of processes focusing on the European Alps. – Pure Appl. Geophys. 162: 1587–1606.

Bertness, M. D. and Callaway, R. 1994. Positive interactions in communities. – Trends Ecol. Evol. 9: 191–193.

Bossuyt, B. et al. 1999. Migration of herbaceous plant species across ancient-recent forest ecotones in central Belgium. – J. Ecol. 87: 628–638.

Breshears, D. D. et al. 2008. Vegetation synchronously leans upslope as climate warms. – Science 105: 11591–11592.

Brooker, R. W. 2006. Plant–plant interactions and environmental change. – New Phytol. 171: 271–284.

Brooker, R. W. and Callaghan, T. V. 1998. The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. – Oikos 81: 196–207.

Brooker, R. W. et al. 2005. The importance of importance. – Oikos 109: 63–70.

Brown, J. H. and Lomolino, M. V. 1998. Biogeography. – Sinauer.

Brown, J. H. et al. 1996. The geographic range: size, shape, boundaries and internal structure. – Annu. Rev. Ecol. Syst. 27: 597–623.

Cairns, D. M. and Moen, J. 2004. Herbivory influences tree lines. – J. Ecol. 92: 1019–1024.

Callaway, R. M. 1998. Competition and facilitation on elevation gradients in subalpine forests of the northern Rocky Mountains, USA. – Oikos 82: 561–573.

Callaway, R. M. and Walker, L. R. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. – Ecology 78: 1958–1965.

Callaway, R. M. et al. 2002. Positive interactions among alpine plants increase with stress. – Nature 417: 844–848.

Cannone, N. et al. 2007. Unexpected impacts of climate change on alpine vegetation. – Front. Ecol. Environ. 5: 360–364.

Canty, A. and Ripley, B. 2008. Boot: Bootstrap R (S-PLUS) functions. – <www.R-project.org>.

Chen, I. C. et al. 2009. Elevation increases in moth assemblages over 42 years on a tropical mountain. – Proc. Nat. Acad. Sci. USA 106: 1479–1483.

Colwell, R. K. et al. 2008. Global warming, elevational range shifts and lowland biotic attrition in the wet tropics. – Science 322: 258–261.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. – Science 199: 1302–1310.

Davis, M. B. 1989. Lags in vegetation response to greenhouse warming. – Clim. Change 15: 75–82.

Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. – Ecol. Monogr. 41: 351–389.

Eriksson, O. 2000. Functional roles of remnant plant populations in communities and ecosystems. – Global Ecol. Biogeogr. 9: 443–449.

Franco, A. M. A. et al. 2006. Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. – Global Change Biol. 12: 1545–1553.

Gehrig-Fasel, J. et al. 2007. Tree line shifts in the Swiss Alps: climate change or land abandonment? – J. Veg. Sci. 18: 571–582.

Grime, J. P. 1979. Plant strategies and vegetation processes. – Wiley.

Halloy, S. R. P. and Mark, A. F. 2003. Climate-change effects on alpine plant biodiversity: a New Zealand perspective on quantifying the threat. – Arct. Antarct. Alp. Res. 35: 248–254.

Hättenschwiler, S. and Körner, C. 1995. Responses to recent climate warming of Pinus sylvestris and Pinus cembra within their montane transition zone in the Swiss Alps. – J. Veg. Sci. 6: 357–368.

Hermy, M. et al. 1999. An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. – Biol. Conserv. 91: 9–22.

Hickling, R. et al. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. – Global Change Biol. 12: 450–455.

Honnay, O. et al. 2002. Possible effects of habitat fragmentation and climate change on the range of forest plant species. – Ecol. Lett. 5: 525–530.

Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? – Trends Ecol. Evol. 15: 56–61.

Huston, M. 1979. A general hypothesis of species diversity. – Am. Nat. 113: 81–101.

Jones, P. D. et al. 2001. The evolution of climate over the last millennium. – Science 292: 662–667.

Kelly, A. E. and Goulden, M. L. 2008. Rapid shifts in plant distribution with recent climate change. – Proc. Nat. Acad. Sci. USA 105: 11823–11826.

Klanderud, K. and Birks, H. J. B. 2003. Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. – Holocene 13: 1–6.

Konvicka, M. et al. 2003. Uphill shifts in distribution of butterflies in the Czech Republic: effects of changing climate detected on a regional scale. – Global Ecol. Biogeogr. 12: 403–410.

Leathwick, J. R. and Austin, M. P. 2001. Competitive interactions between tree species in New Zealand's old-growth indigenous forests. – Ecology 82: 2560–2573.

Lenoir, J. et al. 2008. A significant upward shift in plant species optimum elevation during the 20th century. – Science 320: 1768–1771.

Lenoir, J. et al. 2009. Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986–2006). – Ecography 32: 765–777.

Maestre, F. T. et al. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. – J. Ecol. 97: 199–205.

McArthur, R. H. 1972. Geographycal ecology: patterns in the distribution of species. – Harper and Row.

McAuliffe, J. R. 1984. Competition for space, disturbance, and the structure of a benthic stream community. – Ecology 65: 894–908.

Moritz, C. et al. 2008. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. – Science 322: 261–264.

Nogués-Bravo, D. et al. 2008. Scale effects and human impact on the elevational species richness gradients. – Nature 453: 216–219.

Normand, S. et al. 2009. Importance of abiotic stress as a range-limit determinant for European plants: insights from species responses to climatic gradients. – Global Ecol. Biogeogr. 18: 437–449.

Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. – Nature 421: 37–42.

Parolo, G. and Rossi, G. 2008. Upward migration of vascular plants following a climate warming trend in the Alps. – Basic Appl. Ecol. 9: 100–107.

Pauli, H. et al. 2007. Signals of range expansions and contractions of vascular plants in the high Alps: observations (1994–2004) at the GLORIA* master site Schrankogel, Tyrol, Austria. – Global Change Biol. 13: 147–156.

Pickett, S. T. A. and White, P. S. 1985. The ecology of natural disturbance and patch dynamics. – Academic Press.

R Development Core Team 2009. R: a language and environment for statistical computing. – R Foundation for Statistical Computing, <www.R-project.org>.

Rameau, J. C. et al. 1993. Flore forestière française – guide écologique illustré – tome 2: montagnes. – Inst. pour le Développement Forestier.

Raxworthy, C. J. et al. 2008. Extinction vulnerability of tropical montane endemism from warming and upslope displacement: a preliminary appraisal for the highest massif in Madagascar. – Global Change Biol. 14: 1703–1720.

Schumacher, S. and Bugmann, H. 2006. The relative importance of climatic effects, wildfires and management for future forest landscape dynamics in the Swiss Alps. – Global Change Biol. 12: 1435–1450.

Suttle, K. B. et al. 2007. Species interactions reverse grassland responses to changing climate. – Science 315: 640–642.

Svenning, J. C. and Skov, F. 2006. Potential impact of climate change on the northern nemoral forest herb flora of Europe. – Biodivers. Conserv. 15: 3341–3356.

Tryjanowski, P. et al. 2005. Uphill shifts in the distribution of the white stork Ciconia ciconia in southern Poland: the importance of nest quality. – Divers. Distrib. 11: 219–223.

Usbeck, T. et al. in press. Wind speed measurements and forest damage in Canton Zurich (central Europe) from 1891 to winter 2007. – Int. J. Climatol.

Vetaas, O. R. 2002. Realized and potential climate niches: a comparison of four Rhododendron tree species. – J. Biogeogr. 29: 545–554.

Vittoz, P. et al. 2008. One century of vegetation change on Isla Persa, a nunatak in the Bernina massif in the Swiss Alps. – J. Veg. Sci. 6: 671–680.

Vittoz, P. et al. 2009. Low impact of climate change on subalpine grasslands in the Swiss northern Alps. – Global Change Biol. 15: 209–220.

Walther, G. R. et al. 2005. Trends in the upward shift of alpine plants. – J. Veg. Sci. 16: 541–548.

Warren, M. S. et al. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. – Nature 414: 65–68.

Wilson, R. J. et al. 2005. Changes to the elevational limits and extent of species ranges associated with climate change. – Ecol. Lett. 8: 1138–1146.

Wilson, R. J. et al. 2007. An elevational shift in butterfly species richness and composition accompanying recent climate change. – Global Change Biol. 13: 1873–1887.

Wilson, S. D. and Nilsson, C. 2009. Arctic alpine vegetation change over 20 years. – Global Change Biol. 15: 1676–1684.

Zimmermann, N. E. et al. 2009. Climatic extremes improve predictions of spatial patterns of tree species. – Proc. Nat. Acad. Sci. USA 106: 19723–19728.

IBS SPECIAL ISSUE