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Climate Change, Aboveground-Belowground Interactions, and Species' Range Shifts

Wim H. Van der Putten (/search?value1=Wim+H.+Van+der+Putten&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true)[1]

View Affiliations

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ABSTRACT

Changes in climate, land use, fire incidence, and ecological connections all may contribute to current species' range shifts. Species shift range individually, and not all species shift range at the same time and rate. This variation causes community reorganization in both the old and new ranges. In terrestrial ecosystems, range shifts alter aboveground-belowground interactions, influencing species abundance, community composition, ecosystem processes and services, and feedbacks within communities and ecosystems. Thus, range shifts may result in no-analog communities where foundation species and community genetics play unprecedented roles, possibly leading to novel ecosystems. Long-distance dispersal can enhance the disruption of aboveground-belowground interactions of plants, herbivores, pathogens, symbiotic mutualists, and decomposer organisms. These effects are most likely stronger for latitudinal than for altitudinal range shifts. Disrupted aboveground-belowground interactions may have influenced historical postglacial range shifts as well. Assisted migration without considering aboveground-belowground interactions could enhance risks of such range shift–induced invasions.

Keywords

climate warming (/search?option1=pub_keyword&value1="climate warming"), **extinction (/search?option1=pub_keyword&value1="extinction")**, **invasiveness (/search?option1=pub_keyword&value1="invasiveness")**, **geographic range (/search?option1=pub_keyword&value1="geographic range")**, **multitrophic interactions (/search?option1=pub_keyword&value1="multitrophic interactions")**, **no-analog communities (/search?option1=pub_keyword&value1="no-analog communities")**

INTRODUCTION

A range, or distribution, is the geographical area where a species can be found. The range is determined by numerous environmental factors, including climate, soil type, and species interactions. Over geological timescales, adaptive radiation, speciation, and plate tectonics can also influence the range of a species. The range of a species can shift owing to one or more changes in environmental conditions, such as climate warming, land-use change, new ecological connections, or artificial introductions of the species to a new environment. Nevertheless, many reports on current massive range shifts of species toward higher altitudes and latitudes suggest that climate warming is a key driving factor (**Grabherr et al. 1994**, **Walther et al. 2002**, **Parmesan & Yohe 2003**, **Parmesan 2006**, **Walther 2010**). If land-use change were the main driver, species' range shifts would occur in more directions.

Compared with historical geographic range shifts, such as those that have taken place during glaciation-deglaciation cycles over the past two million years (**Bush 2002**), the rate of current climate warming is unprecedented (**Walther et al. 2002**). The earliest reports on species' adaptation to climate change suggested that many species were failing to shift range fast enough to keep up with climate warming (**Warren et al. 2

001, **Thomas et al. 2004**, **Thuiller et al. 2005**). But more recent studies suggest that at least some species might respond adequately to climate warming by shifting their ranges (**Chen et al. 2011**) and that a number of species can reach enhanced dominance in the new range (**Walther et al. 2002**, **Tamis et al. 2005**, **Engelkes et al. 2008**). Thus far, most predictions on range shifts have been made independent of species interactions, and the question is whether including species interactions may change the outcomes of the model predictions (**Lavergne et al. 2010**, **Van der Putten et al. 2010**).

Species abundance can be influenced by resource availability, predation, propagule availability, symbioses, competition, and facilitation. As all these factors may vary between the old and new ranges, species that can move may not necessarily encounter suitable circumstances for establishment, growth, and reproduction. Moreover, these factors may also vary after a species has been introduced to a new range, which can affect community composition in a dynamic way. Species interactions can drive evolution or be subject to it, as seen in highly specialized pollination or parasitism patterns or in other symbiotic mutualisms. Climate change may disrupt those evolutionary processes as well as initiate new processes (**Lavergne et al. 2010**).

Besides range shifts, species may also respond to climate warming and other environmental changes by adapting to them. For example, there is scope for genetic adaptation of plants to climate warming, but there are also limitations that may contribute to diversity loss (**Jump & Peñuelas 2005**). Climate warming is highly multidimensional. Local effects of climate warming may result from changes in temperature, precipitation, or length of the growing season. Species that shift range may also be exposed to different day length (**Jump & Peñuelas 2005**). Investigators have not yet determined how adaptation and migration interact during range shifts (**Lavergne et al. 2010**).

Terrestrial ecosystems are composed of aboveground and belowground subsystems, which have been examined separately for many years even though the different subcomponents clearly interact with each other (**Wardle 2002**). Plants connect the aboveground and belowground subsystems, and interactions belowground can, directly or indirectly, influence interactions aboveground (and vice versa). Species in aboveground and belowground subsystems are differently susceptible to climate warming (**Berg et al. 2010**), leading to—at least temporarily—new species combinations in the new range. As aboveground-belowground interactions have the potential to impose selection on plants (**Schweitzer et al. 2008**), range shifts may influence selection and adaptation. In spite of rapidly increasing interest in the subject of aboveground-belowground interactions, the effects of climate warming–induced range shifts have been poorly studied thus far (**Bardgett & Wardle 2010**). In this review, I combine reported knowledge on range shifts with information on the functional role of aboveground-belowground species interactions in community organization and ecosystem processes.

Belowground subsystems include biota that interact with plants directly (herbivores, pathogens, and symbionts) or indirectly (natural enemies of the directly interacting species and components of the decomposer subsystem). The direct and indirect interactions with plant roots can influence aboveground biota and can result in effects that feed back to the soil subsystem (**Wardle et al. 2004**). Expanding from a previous review that argued that trophic interactions need to be considered when predicting consequences of climate warming (**Van der Putten et al. 2010**), I focus here on how range shifts may influence community organization and ecosystem processes. I do not pretend to be complete in my review, and a part of my conclusions are speculative, but I hope to encourage thinking about species' range shifts from a more complex (and realistic) ecological perspective.

I discuss recent work on aboveground-belowground interactions in relation to climate warming–induced species' range shifts. I compare altitudinal gradients—where dispersal distances may not be a major limitation—with latitudinal gradients—where range shifts may disrupt aboveground-belowground interactions more severely, owing to larger dispersal distances and differences in dispersal rates. I also provide a brief paleoecological view and discuss how aboveground-belowground interactions in the past might have changed during deglaciation periods. In the next sections, community and ecosystem consequences of range shifts are reviewed from the perspective of aboveground-belowground interactions. I discuss community assembly processes, including species loss and species gain, from an aboveground-belowground perspective while discussing their roles in no-analog communities (and novel ecosystems), foundation species, and assisted migration.

SPECIES' RANGE SHIFTS

Patterns along Altitudinal Gradients

The earliest signals showing that the rapid climate warming of recent decades is leading to plant range shifts resulted from work along altitudinal gradients in alpine ecosystems (**Grabherr et al. 1994**, **Walther et al. 2002**, **Parmesan & Yohe 2003**). Alpine vegetation responses to climate warming may depend on plant type and altitude. For example, along an elevation gradient of 2,400 and 2,500 m above sea level, shrubs expanded 5.6% per decade, but above 2,500 m, unexpected patterns of regression occurred that were associated with increased precipitation and permafrost degradation (**Cannone et al. 2007**).

At lower altitudes in mountains, effects of climate warming are difficult to disentangle from those of changes unrelated to climate, such as land-use change. At high altitudes, where land use does not play a major role, effects of climate warming are clearer (**Cannone et al. 2007**). Nevertheless, even in low-altitude areas such as the Jura (France), effects of warming can be detected over a 20-year period (**Lenoir et al. 2008**, **2010**). At a subarctic island, analyses of 40 years of species data revealed an average upward elevation shift of half the plant species (**Le Roux & McGeoch 2008**). Both here and in the Jura, only a subset of plant species responded to climate warming. Remarkably, although the species that determined the pattern of upslope expansion may be considered highly responsive, the response was still lower than expected based on the rate of warming (**Le Roux & McGeoch 2008**). Such species-specific range shift responses may result in no-analog communities at higher elevations, consisting of the original plant species and the range expanders. Downhill species shifts can also be observed, for example in California, where the water deficit at higher elevations increased over time (**Crimmins et al. 2011**).

Although much work has focused on patterns of altitudinal range shifts, less work has been done on the consequences of altered species interactions in relation to climate warming. In general, high-altitude plant communities may be structured more by facilitative interactions than by competitive ones (**Callaway et al. 2002**). However, plant facilitation could also be influenced by aboveground and belowground multitrophic interactions, which may need more attention for researchers to understand the consequences of climate warming in high-altitude habitats. Because range shift distances are relatively short in altitudinal gradients, dispersal is less limited than along latitudinal gradients, but aboveground-belowground interaction patterns may still be altered in highly complex ways. For example, the development of bare soil surface at higher altitudes (**Walther et al. 2002**) considerably influences belowground decomposition processes (**Wardle et al. 1999**). In contrast, ecosystem regression toward pioneer stages can affect the outcome of plant community interactions by a shift from symbiotic (arbuscular) mycorrhizal fungi toward soil-borne pathogens being the most important soil biota influencing plant community composition (**Kardol et al. 2006**). In general, global change effects on soil biota are relatively predictable (**Blankinship et al. 2011**), but interactive consequences of climate warming, such as altered frost incidence, rainfall patterns, plant types, and plant cover, may complicate predictions of soil biota responses and their feedback effects on plants and aboveground interactions.

Patterns along Latitudinal Gradients

Patterns of latitudinal range shifts have been predicted based on altitudinal shifts (**Walther et al. 2002**). Climate effects of 1 m in altitudinal range shift may be considered equal to 6.1 km in latitudinal shift (**Parmesan & Yohe 2003**). However, these conversion factors do not account for dispersal limitations that may arise from, for example, poor dispersal capacity, effects of habitat fragmentation, or limitations of vector organisms. In northwestern Europe, for example, there are clear patterns in seed dispersal limitations, as some vectors, especially large vertebrates, are much more limited in migration now than they were in the past (**Ozinga et al. 2009**). Such limitations may also apply to insect range shifts. A study in the United Kingdom showed that range expansion by habitat-specialist butterflies was constrained following climate warming because the specific habitats lacked connections. Only habitat generalists could keep up with climate warming because their dispersal was less limited by unsuitable corridors (**Warren et al. 2001**).

Poor dispersal capacities of certain soil biota, especially soil fauna, have been mentioned in several studies. For example, the highest nematode diversity occurs in temperate zones, where there are more root feeders of higher plants than exist in the tropics. Nematode diversity is lower in Antarctic than in Arctic zones, which suggests that dispersal limitations are, at least in part, causing the latitudinal zonation of nematodes (**Procter 1984**). There may also be gradients within latitudes, but these are related more to community similarity than to community richness. For example, in a comparison of nematodes and microbial assemblages among 30 chalk grasslands in the United Kingdom roughly scatter ed across a west-east gradient of 200 km, similarity in both nematodes and bacteria declined with distance (**Monroy et al. 2012**). Therefore, soil communities may vary with distance, irrespective of orientation (**Fierer et al. 2009**). Hence, range shifts in any direction can expose that plant species to novel soil biota and disconnect it from the usual biota with which it interacts.

Applications of findings from altitudinal shifts to range shift predictions in lowlands may also be complicated for other reasons. In a 44-year study (1965–2008) of climate warming in lowland and highland forests in France, latitudinal range shifts were expected in the lowland forests. However, in lowland forests, the responses of latitudinal range shifts were 3.1 times less strong than those of altitudinal range shifts in highland forests (**Bertrand et al. 2011**). There are several possible explanations: Lowland forests may have proportionally more species that are persistent in the face of warming, there may be fewer opportunities for short-distance escapes, or the greater habitat fragmentation in lowlands may prevent range shifting.

Range shifts can be limited by the availability of sites for establishment. This has been shown not only for butterflies (**Warren et al. 2001**) but also for plants. For example, **Leithead et al. (2010)** showed that range-shifting tree species from a temperate forest in Canada, such as red maple (*Acer rubrum*), can establish in a boreal red pine (*Pinus resinosa*) forest only if there are large tree-fall gaps. Native red pine forest species, in contrast, were not influenced by gap size or gap age. Interestingly, pine dominance in the red pine forest is maintained by wildfires, which selectively omit competitors and reset succession. Fire incidence can be altered by climate warming. Because southern tree species establish in tree-fall gaps too fast for the rate of wildfires to control, the combined effects may be enhanced colonization of northern forests by southern tree species. Tropical lowlands may be especially sensitive to climate warming for other reasons. The tropical climate now is warmer than at any time in the past two million years (**Bush 2002**). The spread of species from tropical forests to cooler areas may be constrained by long dispersal distances and poor colonization sites along the dispersal routes. Therefore, tropical regions may be sensitive to species loss owing to climate warming. Moreover, lowland tropics lack a species pool to provide new species that may favor the new climate conditions (**Colwell et al. 2008**). Range shifts of species from tropical lowlands to tropical highlands are possible, but they may result in depauperate lowland plant communities, which will be increasingly dominated by early successional species (**Bush 2002**, **Colwell et al. 2008**).

Researchers have investigated aboveground-belowground interactions in relation to latitudinal range shifts. A comparison of range-expanding plant species from Eurasia and other continents with species that are phylogenetically related to those from the invaded range showed that both types of range expanders develop less pathogenic activity in their soils than related natives do. Moreover, the range expanders on average were more tolerant of or were better defended against two polyphagous invertebrate aboveground herbivores. The pattern coincided with induced levels of phenolic compounds, which are general secondary metabolites used for plant defense (**Engelkes et al. 2008**). Therefore, successful range-expanding plant species may have invasive properties irrespective of their origin. Interestingly, although belowground and aboveground effect sizes were additive, there was no correlation between aboveground and belowground effect strengths (**Morriën et al. 2011**). Thus, plant species that resisted or tolerated belowground enemy effects in the new range were not necessarily well protected against generalist aboveground herbivores.

Analysis of soil samples along a latitudinal gradient of a range-expanding plant species (*Tragopogon dubius*) showed soil pathogen effects in several sites in the native range, but not in the range the species had shifted into recently (**Van Grunsven et al. 2010**). Thus, range shifts enabled the plants to escape their original soil pathogens, although successful range shifters defended themselves well against unknown and cosmopolitan aboveground polyphagous herbivorous insects (**Van Grunsven et al. 2007**, **Engelkes et al. 2008**). These results were based on growth trials in greenhouse mesocosms. The next step should be to determine the consequences of altered belowground and aboveground biotic interactions under field conditions.

Historical Patterns of Range Shifts

Species' range shifts have occurred throughout the Earth's history. For example, it is well documented that glacial cycles have caused species' range shifts (**Jackson & Overpeck 2000**, **Williams et al. 2007**, **Willis et al. 2010**). There have been approximately 20 cycles of glaciation and deglaciation during the Quaternary (the last 2.58 million years), especially in the Northern Hemisphere (**Dawson et al. 2011**). The last ice age occurred about 10,000 years ago. Based on pollen records from late Quaternary Europe, paleovegetation maps have been constructed at th e level of formations. As these vegetation maps are not analogous with contemporary vegetation, **Huntley (1990a)** concluded that the macro climate in the late Quaternary might have been completely different from the present one. But a complication of comparing paleobiology data with contemporary ecosystems is that current vegetation in Europe has been strongly influenced by human activities and the continent's heterogeneity (**Huntley 1990a**). In spite of these uncertainties, we can still surmise that communities have become reorganized over and over again during cycles of warming and cooling (**Jackson & Overpeck 2000**).

Historic range shift data still cast doubts on the rate of plant dispersal. The proposed average northward spread of 1 km per year during deglaciation periods is most likely 10 times as fast as the average dispersal capacity of individual plant species. This discrepancy in migration distances can be due to a hitherto undetected role of long-distance dispersal (**Loarie et al. 2009**). Long-distance dispersal likely played an important role in prehistoric times. In a modeling study (K.M. Meyer & M. van Oorschot, unpublished results), long-distance dispersal turned out to be crucial for enemy release, in their case from root-feeding nematodes. Long-distance dispersal of plants may also reduce their exposure to specialized aboveground enemies because these enemies may have difficulties reaching the new plant populations. Therefore, we can expect that during deglaciation range shifts, plant species might have become exposed to different aboveground-belowground interactions.

It is also possible that aboveground or belowground enemies have promoted tree range shifts (**Moorcroft et al. 2006**). In a modeling study, natural enemies were able to influence the spread of tree species into ecosystems where equally strong competitors were present. Adding host-specific pathogens to the model resulted in dispersal distances equal to the ones that have been reported by paleoecologists based on pollen patterns (**Moorcroft et al. 2006**). Obviously, research should place more emphasis on the issue of long-distance dispersal in relation to range shifts and relationships with aboveground and belowground natural enemies and their antagonists. This might also provide a different view on evolution during glaciation-deglaciation cycles.

In a review of postglacial range expansion effects on the evolution of insects, **Hill et al. (2011)** found that rapid evolution of dispersal may be promoted in the expansion zones. This suggests a positive feedback between range expansion and the evolution of traits (in this case dispersal) that accelerates range expansion capacity. Thus, the feedback between ecology and evolution is strongest at range boundaries where selection is assumed to be strongest and where population bottlenecks are common (**Hill et al. 2011**). But these data may not translate to present-day range shifts because of the unprecedented rate of the current warming. Moreover, modern landscapes are much more fragmented than the original postglacial landscapes, and this fragmentation may lead to loss of genetic variation rather than enable trait evolution (**Hill et al. 2011**).

Current insights on aboveground-belowground species interactions may be used to assess how they operated during prehistorical changes in vegetation types. For example, in a flood plain in Pakistan, isotope records reveal shifts from C3 to C4 grass-dominated ecosystems (**Barry et al. 2002**). There were also pulses in (vertebrate) fauna turnover, resulting in a loss of biodiversity and an accelerated pace of extinction in this region once C4 vegetation occurred on the flood plain. Overall, species composition was relatively steady, with brief, irregularly spaced temporal spikes of species turnover and ecological change. Time intervals of the assessment were at least 100,000 years (**Barry et al. 2002**). In contrast to these aboveground changes in vertebrate fauna, selective plant removal studies in New Zealand (**Wardle et al. 1999**) and sampling of C3 and C4 grasses in the United States (**Symstad et al. 2000**, **Porazinska et al. 2003**) suggest that conversion of C3 into C4 grasslands might have had very little effect on soil fauna or aboveground arthropod diversity. The C4 grass vegetation might have been a response to warming and drier conditions, which could have had a much stronger effect on soil community composition and the resulting ecosystem functioning (**Blankinship et al. 2011**).

Another example concerns the last postglacial period in Europe, during which mixed deciduous forests received their current distribution around 8,000 years before present. Relative tree abundance changed in those forests over the past 13,000 years, as they were dominated first by *Pinus*, then by *Tilia*, and during the past few millennia by *Fagus* species (**Huntley 1990b**). How exactly these vegetation changes have taken place and at what rate are difficult issues to explain because these data, among others, are based on chord-distance maps that have intervals of 1,000 years (**Huntley 1990a**). Nevertheless, litter composition is known to influence decomposition (**Hättenschwiler & Gasser 2005**), and it also influences soil organisms, such as earthworms (**Muys & Lust 1992**) and microbes (**Ayres et al. 2009**, **Strickland et al. 2009**). These examp les show that responses of plant communities to climate changes and consequences for ecosystem processes in the (late) Quaternary might have been quite dynamic. Over these long time periods, climate was the overarching driver. Belowground-aboveground interactions might have driven community responses at shorter spatial and temporal scales.

Other Drivers of Range Shifts

There are some, though not many, examples of range shifts caused by factors other than climate warming or cooling. For example, intensified grazing and fire regimes enabled range expansion of shrubs in Colorado (**Archer et al. 1995**), whereas the El Niño–Southern Oscillation influences the frequency and extent of wildfires, which in turn influence tree stand composition in the southern United States (**Swetnam et al. 1999**). Furthermore, there are examples of bird range expansion owing to land-use change. Improved feeding or nesting sites can drive such range shifts. For example, the Black-shouldered Kite (*Elanus caeruleus*) has shifted range northward into Spain because, during the last half of the previous century, cultivated Dehesa systems became more similar to African savannahs, where this species originated (**Balbontín et al. 2008**).

Habitat fragmentation, such as that caused by intensified land use, can limit the capacity of species' range shifts. Currently, this is considered one of the major constraints for species' responses to climate warming (**Warren et al. 2001**). Habitat fragmentation might also have limited range shifts in postglacial periods under specific conditions. In Finland, recolonization of former islands after land-ice retreat during the Holocene might have been hampered by poor connectedness to the surrounding mainland (**Heikkilä & Seppä 2003**). One possibility to determine if climate warming is the key factor leading to range shift is to determine if the pattern is one-directionally correlated with the warming gradient. But terrestrial range shifts often cause mosaiclike patterns rather than wavelike phenomena because the velocity of climate change on land is far more patchy than it is in the oceans (**Burrows et al. 2011**).

Conclusions on Species' Range Shifts

Patterns of individual species' range shifts in response to climate change are less uniform than general averages suggest because there are fast- and slow-responding species, time lags, downhill instead of uphill range shifts, and long-distance dispersal. Some range shifts are due to factors other than climate, such as changing land use or altered fire incidence. Uphill range shifts are better correlated with warming than are lowland range shifts toward the poles, probably due to shorter dispersal distances along altitudinal gradients and fewer constraints such as habitat fragmentation at high elevations. Lowland tropical systems may be highly sensitive to warming because temperatures are already higher than in the past two million years and dispersal distances to cooler areas are generally large, except in tropical lowland-mountain areas where uphill range shifts are possible. Range contractions are less well studied than range expansions, and in some cases downhill range shifts have been recorded (e.g., cases have been reported where water is more available at low elevation or where microclimate is cooler owing to forest regrowth downhill).

Aboveground, plants may also be released from their natural enemies, especially in the case of long-distance dispersal. This phenomenon is supposed to have played a role in recolonization during postglacial range shifts. Therefore, although little information exists on this subject, disassembly of aboveground-belowground interactions during range shifts may influence ecology and evolution during climate warming–induced range shifts. This may happen now, but it could also have played a role during prehistoric range shifts. Such disruptions of aboveground and belowground interactions have the potential of influencing community assemblage processes as well as the evolution of the species involved.

COMMUNITY CONSEQUENCES OF ALTERED ABOVEGROUND-BELOWGROUND INTERACTIONS DURING RANGE SHIFTS

Understanding species' range shifts requires addressing a key question in ecology: How will biodiversity and ecosystem functioning be influenced by the disappearance of existing species and the arrival of new species (**Wardle et al. 2011**)? The research on range shifts initially was dominated by reports on species extinctions due to climate warming (**Warren et al. 2001**, **Thuiller et al. 2005**), whereas later the emphasis also included consequences of climate warming for range shifts of exotic invaders (**Walther et al. 2009**). Other studies have shown that the number of species from warm climate regions in temperate areas is increasing (**Tamis et al. 2005**); thus, there is a group of species that may shift range to higher altitude or latitude in accordance with the rate of climate warming (**Chen et al. 2011**).

Patterns of Species Gains and Losses

Which species will be lost or gained following climate warming depends on a large number of aspects, including the tolerance of species to the environmental change (warming or an associated change, such as drought or extreme weather events), the time needed for species to disperse and the time needed by other species to be lost from communities, sensitivity to habitat fragmentation, habitat specialization, dispersal mode, etc. The net effect of species gains and species losses can be that total biodiversity remains constant, but biodiversity can also decrease, or even increase (**Jackson & Sax 2010**). As time proceeds, net effects of gains and losses of species may vary, and the total number of species in communities may temporarily go up or down. Although net effects of species gain and loss can be positive locally, worldwide biodiversity will decline, and communities across the world, in the same climatic zones, will appear more similar because of an increasing number of shared species.

The traits of the species coming in and going out will strongly influence that species's role in ecosystem processes. For example, novel chemistry may influence ecological relationships, as herbivores and decomposer organisms from the invaded range may not be capable of dealing with those compounds (**Callaway & Ridenour 2004**). Phylogenetic nonrelatedness with other species that are native in these communities can play an important role in predicting the success of species introductions (**Strauss et al. 2006**). Losses or gains of dominant species should have more impact on ecosystem processes (**Grime 1998**), although some low-abundant species may have disproportional effects. For example, microbial pathogens or endophytes have low abundance, but they can substantially influence plant community composition (**Clay & Holah 1999**) and therefore ecosystem functioning.

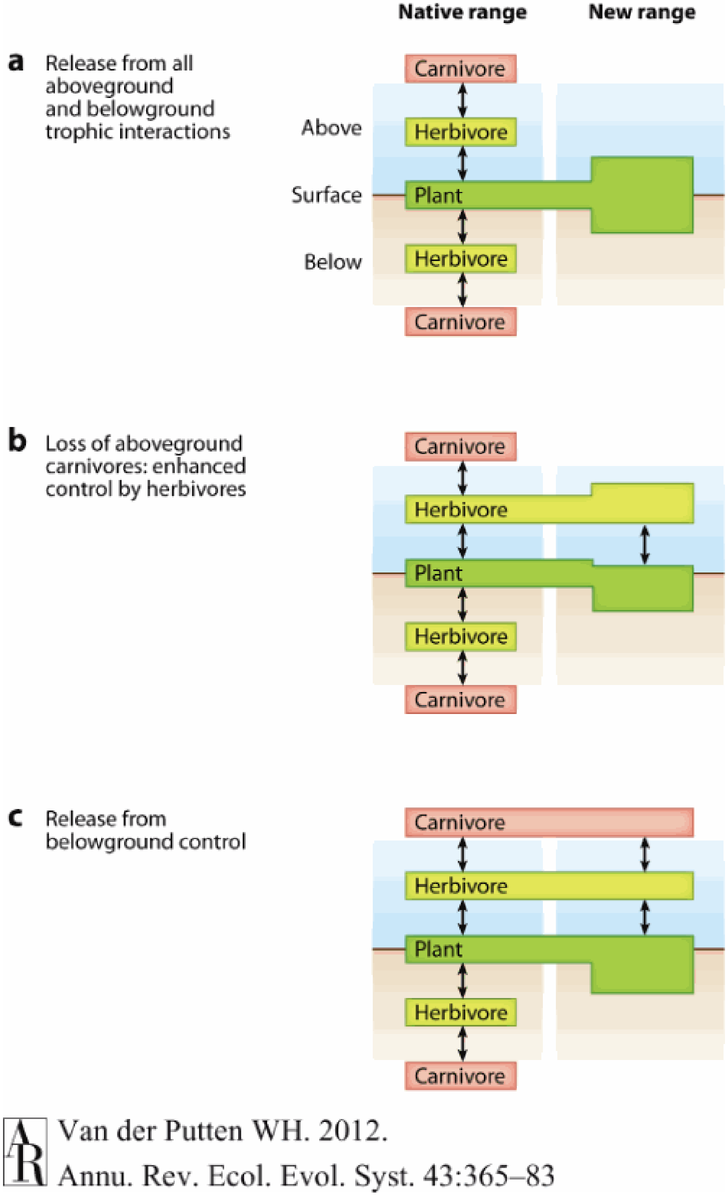
In general, new species most likely will have characteristics of early successionals because such species have good dispersal abilities. Long-distance dispersal may enable them to escape from natural enemies, to which early successional plant species can be sensitive (**Kardol et al. 2006**). For example, the range shift of *T. dubius* has not yet led to the establishment of specific soil-borne pathogens in the new range (**Van Grunsven et al. 2010**). Although not all species will respond to climate warming by range shift (**Le Roux & McGeoch 2008**), little is known about which species will stay behind, what traits they have, or what their fate will be in the long term.

Assessing Ecological Consequences

An increasing number of studies have assessed how aboveground and belowground interactions may change in relation to plant species gains (**Maron & Vilà 2001**, **Agrawal et al. 2005**, **Parker & Gilbert 2007**, **Peltzer et al. 2010**) and plant species losses (**Wardle et al. 1999**, **Scherber et al. 2010**). But few such studies have focused explicitly on plant range shifts (**Engelkes et al. 2008**, **Morriën et al. 2010**, **Van Grunsven et al. 2010**, **Meisner et al. 2012**). Interestingly, plant species that shift range and are successful in their new range have invasive properties with respect to aboveground and belowground enemy effects, that are similar to intercontinental exotic invaders (**Engelkes et al. 2008**). **Figure 1** presents different scenarios of aboveground-belowground range shifts and consequences for plant biomass. Depending on how fast plants, herbivores, and carnivores shift range, in the new range plants can produce more or less biomass than in the native range.

Figure 1

Scenarios for range shifts of plants, aboveground and belowground herbivores and their natural enemies, and consequences for plant size (or abundance). According to scenario (*a*), plants shift range faster than all aboveground and belowground biota and do not encounter biotic resistance in the new range. This leads to enhanced biomass in the new range both aboveground and belowground. In scenario (*b*), aboveground herbivores shift range as fast as plants and are released from their natural enemies. This leads to overexploitation of the plants aboveground (note that whether this also results in reduced belowground biomass that is due to a lack of photosynthesis products to support root and rhizome growth is still debated). In scenario (*c*), aboveground herbivores and carnivores shift range equally as fast as plants, resulting in unchanged aboveground biomass compared with the native range, whereas root biomass may be enhanced owing to lack of belowground herbivory (but see scenario *b*).



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Further studies using aboveground and belowground surveys and manipulations along a range expansion gradient are needed to tease apart the ecological and evolutionary consequences of individual effects. Studies of natural enemy species on invasive plants have shown contrasting degrees of enemy exposure in the new range (**Mitchell & Power 2003**, **Van Kleunen & Fischer 2009**), whereas ecological responses are not necessarily in line with the assumed enemy release effects (**Parker & Gilbert 2007**). These results call into question whether enemy release may explain plant invasiveness in a new range. Long-term experiments and studies along latitudinal or elevation gradients (**Sundqvist et al. 2011**) are needed to determine extended effects of plant range shifts on decomposition, nutrient cycling, and plant performance under field conditions. Transplantation studies, for example, may reveal the extent to which specificity in litter decomposition exists along latitudinal or altitudinal gradients. This specificity has been described as a home-field advantage (**Ayres et al. 2009**, **Strickland et al. 2009**), as the soil communities of some plant species decompose their own litter faster than soil communities for other plant species. This home-field advantage is also specific to plant genotype (**Madritch & Lindroth 2011**).

It is important to include negative controls in experiments when testing species' responses to climate warming. For example, in aboveground-belowground interaction studies, successful range expanders may be compared with unsuccessful ones to test aboveground-belowground interaction effects (**Morriën et al. 2011**) and consequences for plant abundance (**Klironomos 2002**). Besides effects of species gains, consequences of species losses due to climate warming need to be tested experimentally. This will yield information on the traits of species that are under threat of extinction by climate warming, their ecological relationships, and the number of generalist and specialist relationships with oth er plants and multitrophic organisms. These integrated and field-based approaches may help to further conceptualizations of species loss and gain (**Jackson & Sax 2010**) from a multitrophic perspective. Ultimately, these approaches will show how food webs are being influenced by global changes (**Tylianakis et al. 2008**) and how trophic networks may function under dynamic restructuring.

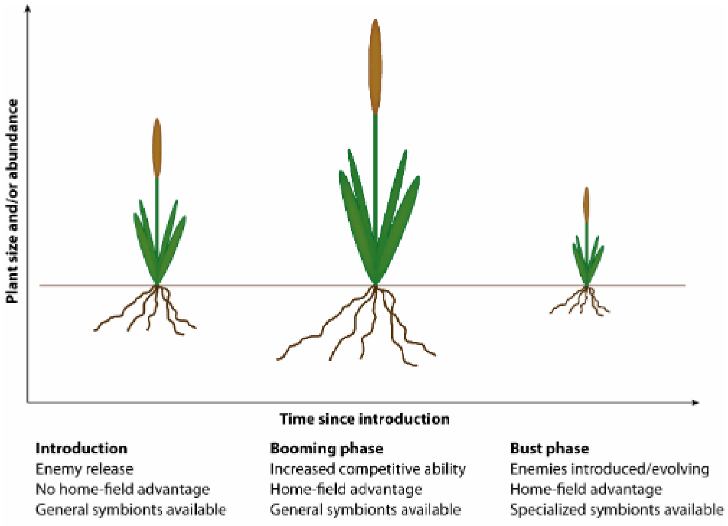
Long-Term Perspectives on Range Shifts

Aboveground and belowground interactions of range-shifting plants will not be static over time, as has been demonstrated for host-parasite interactions (**Phillips et al. 2010**). As time proceeds, the natural enemies, symbionts, and decomposer organisms and their antagonists may colonize the expanded range, but it is not yet known how fast this process may develop and how completely the original communities may become reassembled. Historical data from paleobiology do not provide such detailed information. Range-shifting plants that arrive without their naturally coevolved insects, microbes, and nematodes may or may not establish interactions with species from the new range. Provided that suitable conditions exist, natural selection may cause changes in the genetic structure of the range-shifted plants. For example, when exposure to natural enemies diminishes, selection against the production of costly defenses is to be expected (**Müller-Schärer et al. 2004**), which could lead to a trade-off between defense and growth (**Blossey & Nötzold 1995**). This process has been tested for cross-continental introductions of exotic plant species, although these costs are difficult to quantify and experimental tests sometimes show opposite results (**Wolfe et al. 2004**).

There are spectacular studies of introduced exotic species that lose their capability to produce high defense levels. For example, in a chronosequence representing over 50 years of *Alliaria petiolata* introduction to North America, phytotoxin production decreased as the time since introduction increased (**Lankau et al. 2009**). Variation in allelochemical concentrations also influenced soil microbes, including fungi that had mutualistic interactions with a native tree species (**Lankau 2011**). Over time, introduced plants may become less resistant or native biota may become more aggressive. For example, New Zealand plant species that varied in the amount of time since introduction (with 250 years as the maximum) were experimentally exposed to soil biota. This study showed that the longer the time since introduction, the stronger the pathogenic effects from the soil community (**Diez et al. 2010**). These studies suggest that introduced exotic species may become less invasive over time, owing to natural selection of the introduced species themselves or the belowground or aboveground species from the new habitat. These temporal processes may contribute to the sudden population crashes that have been observed for a number of introduced species (**Simberloff & Gibbons 2004**). A possible long-term scenario for such a boom-bust pattern has been worked out in **Figure 2** .

Figure 2

Hypothetical explanation for an introduction-boom-bust pattern of size (or abundance) of a range-shifting plant species. Following introduction, there may be benefits from (*a*) a release from native enemies, (*b*) the absence of biotic resistance in the new range, and (*c*) the presence of generalist mutualistic symbionts (pollinators, arbuscular mycorrhizal fungi) in the new range that outweigh poor home-field advantage. These benefits may further increase due to the evolution of increased competitive ability and the development of home-field advantage due to specialization of decomposer organisms from the new range. However, that benefit can turn into a major disadvantage when natural enemies from the native range migrate as well or when enemies from the new range break through plant resistance. In that case, plants are poorly defended, and despite their home-field advantage, the top-down control becomes so severe that plant size or abundance is strongly reduced, with an accompanying risk of extinction.



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Conclusions on Altered Aboveground-Belowground Interactions

Thus far, most work on pattern analyses of range shifts has been dedicated to understanding the consequences of species loss due to climate warming. Effects of species introductions by range shifts from lower to higher latitudes and altitudes have not received much attention yet, and the ecological consequences, as well as temporary developments of range-shifting species, are only beginning to be explored. However, we can expect that successful range shifting involves a gradual response of the available plant species and that aboveground and belowground organisms expand their range subsequently, but at lower and variable rates. In the meantime, aboveground and belowground organisms from the native range will establish interactions with the new species and may adapt to the new plants by natural selection. The biotic interactions established in the new range will in return also impose natural selection on the range-shifting species, and this natural selection may reduce the invasive performance as the time since introduction increases. The question is what might happen when the former natural enemies become cointroduced as well: Will they recognize their original host (**Menéndez et al. 2008**), will they overexploit their former host, or will the novel biotic interactions completely alter priority effects (**Lau 2006**)? When we consider all these possible changes, one might reasonably conclude that the original host-consumer interactions are unlikely to be restored to their state in the original range. The outcome of this complex process may contribute to boom-bust patterns of abundance that have been observed for some introduced exotic species' novel community composition and functioning, or they may enable a soft landing for the range-shifting species in their novel habitats following restoration of the original species' interactions.

ECOSYSTEM CONSEQUENCES OF CHANGED ABOVEGROUND-BELOWGROUND INTERACTIONS DURING RANGE SHIFTS

Until this point, range shifts have been considered mainly from the perspectives of species' response patterns and community interactions. The questions now are whether and how these altered species' assemblages and community interactions translate into ecosystem consequences. These consequences may be expressed as altered ecosystem processes (nutrient cycles), resilience, and stability, and these may in turn influence the provisioning of ecosystem services (for example, primary production, control of greenhouse gas emissions, and control of pests and pathogens) (**Naeem et al. 2009**). Few analyses have been made of ecosystem consequences of range shifts in comparison to the numerous studies that have been conducted recently on how climate change might result in biodiversity loss and exotic species invasions (**Wardle et al. 2011**).

In a comparative study of range-shifted plant species and phylogenetically related natives from the new range, nutrient dynamics in the root zone (**Meisner et al. 2011**) and litter decomposition (**Meisner et al. 2012**) were affected by plant (genus-related) traits, rather than by plant origin. This is analogous to work done on intercontinental invasive plant species, showing that some, but clearly not all exotics will enhance nutrient cycling (**Ehrenfeld et al. 2005**, **Vilà et al. 2011**).

Interestingly, plant origin affected sensitivity to aboveground polyphagous insects (**Engelkes et al. 2008**) and feedback effects from the soil community (**Van Grunsven et al. 2007**, **Engelkes et al. 2008**) in similar, phylogenetically controlled comparisons. Therefore, nutrient cycling–related ecosystem services may not be altered by range shifts as much as biocontrol-related services are. Failing top-down control in the new range can be due to enemy release of the range expanders (**Van Grunsven et al. 2010**), failing biotic resistance from the natural enemies present in the new range, or a combination of the two (**Keane & Crawley 2002**). In a survey of intercontinental invasive exotic plant species, exotic plants had fewer pathogen and virus species in the new range than expected (**Mitchell & Power 2003**). Little is known about whether this also applies to plant species that have shifted range intracontinentally.

Another ecosystem consequence of range shifts is related to the question of whether diversity begets diversity (**Whittaker 1972**, **Janz et al. 2006**). Some plant species can have a disproportional role in sustaining aboveground and belowground biodiversity. These so-called foundation species (**Ellison et al. 2005**) strongly influence aboveground and belowground community composition and species interactions, which can be considered extended phenotypes. Little is known about range shift potentials of such foundation species and whether species assembl ages aboveground and belowground in the new range may be as extended as in the native range. Non-foundation species may have less far-reaching effects on aboveground and belowground communities. Nevertheless, many of those species may also have individual aboveground (**Bukovinszky et al. 2008**) and belowground (**Bezemer et al. 2010**) food webs that could be altered by differential range shift capacity (**Berg et al. 2010**). Therefore, ecosystem consequences of range shifts may be that foundation species, as well as non-foundation species, lose at least part of their extended phenotypes (**Figure 1**). Consequences for ecosystem processes, resilience, and stability are as yet unknown.

The altered community composition of range-shifted plant species potentially influences community genetics (**Hersch-Green et al. 2011**). When range-shifting plant species have fewer ecological interactions in the new range than in the original range, patterns of community genetics and evolutionary processes can be completely different. These changes at the genetic level may have consequences at the level of ecosystem processes and functioning (**Whitham et al. 2006**). Therefore, range shifts will provide interesting opportunities for community genetics approaches by testing how microevolutionary processes may play a role during disintegration and (re)assemblage of multitrophic interactions under climate warming. In these studies, abiotic stress conditions should also be included, as they can change during climate warming, in both the native and new range, and they can alter composition and functioning of entire food webs belowground (**De Vries et al. 2012**).

Investigators have proposed that assisted migration and colonization (**Hoegh-Guldberg et al. 2008**) may help solve problems of species that cannot shift range under climate warming. However, assisted migration may also involve risks with consequences for the composition as well as functioning of ecosystems of the new range. Successful range-expanding plant species have invasive properties similar to intercontinental invaders (**Engelkes et al. 2008**). Whether these invasive properties are already intrinsic in the original populations, are selected during range shift, or are due to rapid evolution in the new range is unknown. All these possibilities will be relevant when preparing for assisted migration: which genotypes to select for dispersal, how to test their ecological suitability to become established in the new range, and how to assess ecological consequences in case the assisted species does disproportionally well in its new range. There are already too many examples from intentional or unintentional cross-continental invasions in which taking species out of their original community context resulted in enemy release (**Keane & Crawley 2002**). Therefore, before considering assisted migration and other climate warming–mitigation activities, community and ecosystem consequences of such actions need to be carefully assessed, including consequences of aboveground or belowground enemy release (**Engelkes et al. 2008**), symbiont availability (**Hegland et al. 2009**), and loss of the home-field advantage of decomposition (**Ayres et al. 2009**).

Researchers may need to consider this context when discussing emerging ecosystems (**Milton 2003**) and novel ecosystems (**Hobbs et al. 2006**). As in restoration ecology, where the role of soil communities and aboveground-belowground interactions are acknowledged (**Harris 2009**, **Kardol & Wardle 2010**), ecosystem-level consequences of aboveground-belowground interactions influenced by range shifts need to be considered as well. Most likely, the concept of novel ecosystems will require the consideration of species as related to aboveground-belowground interactions, rather than of the presence or absence of species in isolation. However, ecological novelty may change over time because of the temporal dynamics of the dispersal of associated species as well as the community genetics processes to which the new and the resident species will be exposed. Therefore, ecosystem consequences of (climate warming–induced) range shifts may be predicted better by including the interactions of aboveground and belowground species from a combined ecological and evolutionary perspective. This work could also help us better understand historical range shifts during glaciation-deglaciation cycles, the way those processes might have shaped current aboveground-belowground communities in terrestrial ecosystems, and the potential consequences of the current unprecedented rates of warming for future ecosystem functions and services.

SUMMARY POINTS

1. Terrestrial ecosystems consist of aboveground and belowground subsystems, and the species in these subsystems can all interact.
2. Range shifts of plant species may result in temporary release from natural enemies or symbionts, which may cause invasions or establishment failures in the new range.
3. Decomposition-related processes are supposed to be less specific, but recent work has pointed to considerable specificity in decomposer organisms, even down to the plant genetic level.

4. Latitudinal range shifts will be more sensitive to disruption of aboveground-belowground interactions than altitudinal range shifts.
5. No-analog communities have no-analog aboveground-belowground interactions, which may completely change patterns of community organization, species abundance, and biodiversity.
6. Landscape configuration may be important for range shifts, as it influences dispersal capacities of plants as well as aboveground and belowground biota.
7. Range shifts will be crucial for maintaining ecosystem functioning and ecosystem services.
8. The role of foundation species and community genetics may change substantially due to range shifts.
9. Assisted migration should be considered with care, as it may cause more problems than it solves.

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