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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

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Vol. 43:365-383 (Volume publication date December 2012)

First published as a Review in Advance on September 04, 2012

© Annual Reviews

ABSTRACT

Changes in climate, land use, fire incidence, and ecological connections all may contribute to current species' range shifts. Species shift range individually, a new ranges. In terrestrial ecosystems, range shifts alter aboveground-belowground interactions, influencing species abundance, community composition, e analog communities where foundation species and community genetics play unprecedented roles, possibly leading to novel ecosystems. Long-distance dismutualists, and decomposer organisms. These effects are most likely stronger for latitudinal than for altitudinal range shifts. Disrupted aboveground-below 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="multitrophic interactions"), no-analog communities (/search?option1=pub_keyword&value1="no-analog communities (/search?option1=pub_keyword&value1="no-a

INTRODUCTION

A range, or distribution, is the geographical area where a species can be found. The range is determined by numerous environmental factors, including clim 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, many reports on current massive range shifts of species toward higher altitudes and latitudes suggest that climate warming is a key driving factor (**Grabher** 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

adaptation to climate change suggested that many species were failing to shift range fast enough to keep up with climate warming (Warren et al. 2001, Tho 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 (Warren et al. 2011) independent of species interactions, and the question is whether including species interactions may change the outcomes of the model predictions (Laverge Species abundance can be influenced by resource availability, predation, propagule availability, symbioses, competition, and facilitation. As all these factors for establishment, growth, and reproduction. Moreover, these factors may also vary after a species has been introduced to a new range, which can affect conspecialized pollination or parasitism patterns or in other symbiotic mutualisms. Climate change may disrupt those evolutionary processes as well as initiated. Besides range shifts, species may also respond to climate warming and other environmental changes by adapting to them. For example, there is scope for general constants are species as a support of the constants.

Peñuelas 2005). Climate warming is highly multidimensional. Local effects of climate warming may result from changes in temperature, precipitation, or le 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 belowground subsystems, and interactions belowground can, directly or indirectly, influence interactions aboveground (and vice versa). Species in abovegree temporarily—new species combinations in the new range. As aboveground-belowground interactions have the potential to impose selection on plants (**Sch** subject of aboveground-belowground interactions, the effects of climate warming–induced range shifts have been poorly studied thus far (**Bardgett & Ward** 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 direct 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 a **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 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 gradient aboveground-belowground interactions more severely, owing to larger dispersal distances and differences in dispersal rates. I also provide a brief paleoecol periods. In the next sections, community and ecosystem consequences of range shifts are reviewed from the perspective of aboveground-belowground interactions more severely, owing to larger dispersal distances and differences in dispersal rates. I also provide a brief paleoecol periods. In the next sections, community and ecosystem consequences of range shifts are reviewed from the perspective of aboveground-belowground interactions more severely, owing to larger dispersal distances and differences in dispersal rates. I also provide a brief paleoecol periods. In the next sections, community and ecosystem consequences of range shifts are reviewed from the perspective of aboveground-belowground interactions.

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 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 precipitation and permafrost degradation (**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 second a second a such as the Jura, only a subset of plant species responded to climate warming. Remarkably, although the species that detected on the rate of warming (**Le Roux & McGeoch 2008**). Such species-specific range shift responses may result in no-analog communities at higher elevate example in California, where the water deficit at higher elevations increased over time (**Crimmins et al. 2011**).

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

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 than by competitive ones (Callaway et al. 2002). However, plant facilitation could also be influenced by aboveground and belowground multitrophic interactions altitude habitats. Because range shift distances are relatively short in altitudinal gradients, dispersal is less limited than along latitudinal gradients, but about bare soil surface at higher altitudes (Walther et al. 2002) considerably influences belowground decomposition processes (Wardle et al. 1999). In contrast, symbiotic (arbuscular) mycorrhizal fungi toward soil-borne pathogens being the most important soil biota influencing plant community composition (Kard interactive consequences of climate warming, such as altered frost incidence, rainfall patterns, plant types, and plant cover, may complicate predictions of states.

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

Patterns along Latitudinal Gradients

et al. 2008).

account for dispersal limitations that may arise from, for example, poor dispersal capacity, effects of habitat fragmentation, or limitations of vector organism 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 is following climate warming because the specific habitats lacked connections. Only habitat generalists could keep up with climate warming because their dispersal capacities of certain soil biota, especially soil fauna, have been mentioned in several studies. For example, the highest nematode diversity of lower in Antarctic than in Arctic zones, which suggests that dispersal limitations are, at least in part, causing the latitudinal zonation of nematodes (Procter richness. For example, in a comparison of nematodes and microbial assemblages among 30 chalk grasslands in the United Kingdom roughly scattered across Therefore, soil communities may vary with distance, irrespective of orientation (Fierer et al. 2009). Hence, range shifts in any direction can expose that plan Applications of findings from altitudinal shifts to range shift predictions in lowlands may also be complicated for other reasons. In a 44-year study (1965–200 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 fore 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 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 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 cont wildfires, which selectively omit competitors and reset succession. Fire incidence can be altered by climate warming. Because southern tree spec

new climate conditions (Colwell et al. 2008). Range shifts of species from tropical lowlands to tropical highlands are possible, but they may result in depau

Researchers have investigated aboveground-belowground interactions in relation to latitudinal range shifts. A comparison of range-expanding plant species that both types of range expanders develop less pathogenic activity in their soils than related natives do. Moreover, the range expanders on average were m coincided with induced levels of phenolic compounds, which are general secondary metabolites used for plant defense (**Engelkes et al. 2008**). Therefore, so belowground and aboveground effect sizes were additive, there was no correlation between aboveground and belowground effect strengths (**Morriën et al** 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 enabled the plants to escape their original soil pathogens, although successful range shifters defended themselves well against unknown and cosmopolitar based on growth trials in greenhouse mesocosms. The next step should be to determine the consequences of altered belowground and aboveground biotic

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 (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 constructed at the level of formations. As these vegetation maps are not analogous with contemporary vegetation, **Huntley (1990a)** concluded that the macomparing paleobiology data with contemporary ecosystems is that current vegetation in Europe has been strongly influenced by human activities and the 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 period 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 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 specialize 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 host-specific pathogens to the model resulted in dispersal distances equal to the ones that have been reported by paleoecologists based on pollen patterns to range shifts and relationships with aboveground and belowground natural enemies and their antagonists. This might also provide a different view on evolution 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 dispersal) that accelerates range expansion capacity. Thus, the feedback between ecology and evolution is strongest at range boundaries where selection is translate to present-day range shifts because of the unprecedented rate of the current warming. Moreover, modern landscapes are much more fragmented 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 type (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 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 contra 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 response to warming and drier conditions, which could have had a much stronger effect on soil community composition and the resulting ecosystem function Another example concerns the last postglacial period in Europe, during which mixed deciduous forests received their current distribution around 8,000 years 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 intervals of 1,000 years (Huntley 1990a). Nevertheless, litter composition is known to influence decomposition (Hättenschwiler & Gasser 2005), and it also 2009). These examples show that responses of plant communities to climate changes and consequences for ecosystem processes in the (late) Quaternary mature 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 fi influences the frequency and extent of wildfires, which in turn influence tree stand composition in the southern United States (**Swetnam et al. 1999**). Further 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 (**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 malimited range shifts in postglacial periods under specific conditions. In Finland, recolonization of former islands after land-ice retreat during the Holocene modetermine 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.

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-re 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 such as habitat fragmentation at high elevations. Lowland tropical systems may be highly sensitive to warming because temperatures are already higher the mountain areas where uphill range shifts are possible. Range contractions are less well studied than range expansions, and in some cases downhill range shifts are possible to over the contractions are less well studied than range expansions.

Aboveground, plants may also be released from their natural enemies, especially in the case of long-distance dispersal. This phenomenon is supposed to have subject, disassembly of aboveground-belowground interactions during range shifts may influence ecology and evolution during climate warming-induced aboveground and belowground interactions have the potential of influencing community assemblage processes as well as the evolution of the species invo

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 disdominated by reports on species extinctions due to climate warming (**Warren et al. 2001**, **Thuiller et al. 2005**), whereas later the emphasis also included conumber 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 h

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 environment disperse and the time needed by other species to be lost from communities, sensitivity to habitat fragmentation, habitat specialization, dispersal mode, etc 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 across the world, in the same climatic zones, will appear more similar because of an increasing number of shared

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 influe dealing with those compounds (**Callaway & Ridenour 2004**). Phylogenetic nonrelatedness with other species that are native in these communities can play species should have more impact on ecosystem processes (**Grime 1998**), although some low-abundant species may have disproportional effects. For exam composition (**Clay & Holah 1999**) and therefore ecosystem functioning.

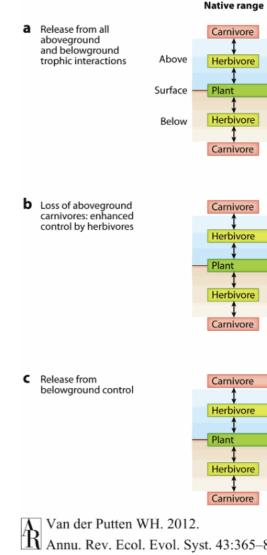
In general, new species most likely will have characteristics of early successionals because such species have good dispersal abilities. Long-distance dispersal ab. 2006). For example, the range shift of *T. dubius* has not yet led to the establishment of specific soil-borne pathogens in the new range (**Van Grunsven et** 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 & Vil 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. 20 properties with respect to aboveground and belowground enemy effects, that are similar to intercontinental exotic invaders (Engelkes et al. 2008). Figure 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 fast 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 abovegrowth 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, where



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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 contrasting degrees of enemy exposure in the new range (Mitchell & Power 2003, Van Kleunen & Fischer 2009), whereas ecological responses are not necessary explain plant invasiveness in a new range. Long-term experiments and studies along latitudinal or elevation gradients (Sundqvist et al. performance under field conditions. Transplantation studies, for example, may reveal the extent to which specificity in litter decomposition exists along latitical 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 lit is important to include negative controls in experiments when testing species' responses to climate warming. For example, in aboveground-belowground belowground interaction effects (Morriën et al. 2011) and consequences for plant abundance (Klironomos 2002). Besides effects of species gains, consequences that are under threat of extinction by climate warming, their ecological relationships, and the number of generalist and specialist relationships with conceptualizations of species loss and gain (Jackson & Sax 2010) from a multitrophic perspective. Ultimately, these approaches will show how food webs a restructuring.

Long-Term Perspectives on Range Shifts

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 real without their naturally coevolved insects, microbes, and nematodes may or may not establish interactions with species from the new range. Provided that sexample, when exposure to natural enemies diminishes, selection against the production of costly defenses is to be expected (Müller-Schärer et al. 2004), cross-continental introductions of exotic plant species, although these costs are difficult to quantify and experimental tests sometimes show opposite result

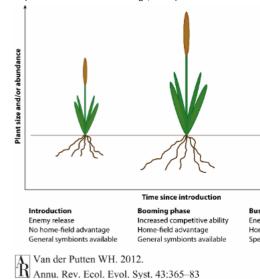
Aboveground and belowground interactions of range-shifting plants will not be static over time, as has been demonstrated for host-parasite interactions (PI

There are spectacular studies of introduced exotic species that lose their capability to produce high defense levels. For example, in a chronosequence representation increased (Lankau et al. 2009). Variation in allelochemical concentrations also influenced soil microbes, including fungi that had mutualistic in 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 magnetic plants).

stronger the pathogenic effects from the soil community (**Diez et al. 2010**). These studies suggest that introduced exotic species may become less invasive of from the new habitat. These temporal processes may contribute to the sudden population crashes that have been observed for a number of introduced specific processes.

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 energing 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 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 become



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Conclusions on Altered Aboveground-Belowground Interactions

about whether this also applies to plant species that have shifted range intracontinentally.

Thus far, most work on pattern analyses of range shifts has been dedicated to understanding the consequences of species loss due to climate warming. Effective, and the ecological consequences, as well as temporary developments of range-shifting species, are only beginning to be explored. However, we can exploit belowground organisms expand their range subsequently, but at lower and variable rates. In the meantime, aboveground and belowground organisms from biotic interactions established in the new range will in return also impose natural selection on the range-shifting species, and this natural selection may red natural enemies become cointroduced as well: Will they recognize their original host (**Menéndez et al. 2008**), will they overexploit their former host, or will 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 cospecies' novel community composition and functioning, or they may enable a soft landing for the range-shifting species in their novel habitats following restored to the range-shifting species in their novel habitats following restored to the range-shifting species in their novel habitats following restored to the range-shifting species in their novel habitats following restored to the range-shifting species in their novel habitats following restored to the range-shifting species in their novel habitats following restored to the range-shifting species in the range shifting species in the range shifting species in the ra

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 of consequences. These consequences may be expressed as altered ecosystem processes (nutrient cycles), resilience, and stability, and these may in turn influent control of pests and pathogens) (Naeem et al. 2009). Few analyses have been made of ecosystem consequences of range shifts in comparison to the numer 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 plant origin. This is analogous to work done on intercontinental invasive plant species, showing that some, but clearly not all exotics will enhance nutrient of interestingly, plant origin affected sensitivity to aboveground polyphagous insects (Engelkes et al. 2008) and feedback effects from the soil community (Vacycling-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 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

Another ecosystem consequence of range shifts is related to the question of whether diversity begets diversity (**Whittaker 1972**, **Janz et al. 2006**). Some plate foundation species (**Ellison et al. 2005**) strongly influence aboveground and belowground community composition and species interactions, which can be species assemblages aboveground and belowground in the new range may be as extended as in the native range. Non-foundation species may have less fair

The altered community composition of range-shifted plant species potentially influences community genetics (Hersch-Green et al. 2011). When range-shift genetics and evolutionary processes can be completely different. These changes at the genetic level may have consequences at the level of ecosystem processes approaches by testing how microevolutionary processes may play a role during disintegration and (re)assemblage of multitrophic interactions und 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).

individual aboveground (Bukovinszky et al. 2008) and belowground (Bezemer et al. 2010) food webs that could be altered by differential range shift capa

Investigators have proposed that assisted migration and colonization (Hoegh-Guldberg et al. 2008) may help solve problems of species that cannot shift rawell as functioning of ecosystems of the new range. Successful range-expanding plant species have invasive properties similar to intercontinental invaders of 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: whow to assess ecological consequences in case the assisted species does disproportionally well in its new range. There are already too many examples from resulted in enemy release (Keane & Crawley 2002). Therefore, before considering assisted migration and other climate warming-mitigation activities, come aboveground or belowground enemy release (Engelkes et al. 2008), symbiont availability (Hegland et al. 2009), and loss of the home-field advantage of decentary and the consider this context when discussing emerging ecosystems (Milton 2003) and novel ecosystems (Hobbs et al. 2006). As in restoration, Kardol & Wardle 2010), ecosystem-level consequences of aboveground-belowground interactions influenced by range shifts need to be considered as belowground interactions, rather than of the presence or absence of species in isolation. However, ecological novelty may change over time because of the and the resident species will be exposed. Therefore, ecosystem consequences of (climate warming-induced) range shifts may be predicted better by including this work could also help us better understand historical range shifts during glaciation-deglaciation cycles, the way those processes might have shaped cur 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
- 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
- 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.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

ACKNOWLEDGMENTS

I thank Tadashi Fukami for proposing that I write this review and for providing helpful comments; Pella Brinkman for helping me throughout the writing prosuggestions on previous versions of the manuscript. This is NIOO publication 5266.

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