Species migrations and range shifts: A synthesis of causes and consequences

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ABSTRACT

In increasingly changing environments, plant species are forced to either adapt to novel conditions or shift their ranges to track their ecological niches. Those species that can successfully track their niche may minimize extinction risks. However, establishment of new species into recipient communities will lead to species re-arrangement and novel biotic interactions. Currently, we have a limited understanding of how these processes affect communities and ecosystems. In this review we synthesize current knowledge on range-expanding species. We start with addressing the many terms used for describing different aspects of range expansions, such as native-invasive, encroachers, and intra-continental invasive species. Thereafter, we describe the factors driving range expansions, and the effects on recipient communities and at the ecosystem level. Our research indicates that, similar to the study of biological invasions, current knowledge on range expansions is highly biased, with most of the studies focusing on Europe and North America. A large part of the available research targets trees and shrubs and the most investigated habitats are grasslands, savannas and high-elevation habitats. One potential consequence of such research bias is that range expansion of many herbaceous species (especially of those species not important for agriculture) may go undetected. Another important finding is that the same factor may promote or hinder range expansion depending on habitat, life form, spatial and temporal scale at which the process is studied. Finally, while many range expansions have negative consequences on local biodiversity and community stability, some of them have positive effects (e.g. mangroves). Although an increasing number of studies investigated the effects of range expansion on recipient communities, our research indicates that we still have a limited knowledge of such processes. Future efforts should integrate both empirical and modeling approaches to disentangle the joint effects of biotic, abiotic and anthropogenic factors on range expansion. Such research should focus both on the immediate- and longer-term implications of range expansions.

1. Introduction

Species ranges are geographically dynamic boundaries encompassing the set of abiotic and biotic factors within which the presence and survival for a certain species is more likely. Such boundaries fluctuate in response to temporal variations in climatic factors, demographic variance or edge effects (Kawecki, 2008). Shifts in species' ranges can be prompted by a change in environmental conditions or management regime that result in removal of dispersal barriers (Kawecki, 2008; Nathan, 2006; Simberloff, 2011). Alternatively, range expansions can be triggered by rapid evolution of species at their habitat margins in response to changing environments (Hoffmann and Blows, 1994; Kawecki, 2008). Over the past decades, growing attention has been devoted to the role of climate change, land use and changing management practices in inducing the redistribution of species' ranges (Barger et al., 2011; Chen et al., 2011; Thomas et al., 2001). It is estimated that approximately 84% of species have shifted poleward since the 1970′s (Thomas, 2010). However, the ability of single species to respond to environmental and anthropogenic changes with range shifts is not ubiquitous, as some species can successfully track their niche while others lag behind (Lurgi et al., 2012; Pecl et al., 2017). Such asynchronous range shifts result in a reshaping of plant communities (Alexander et al., 2016; Neff et al., 2009; Parmesan and Yohe, 2003) with potential cascading effects on ecosystem processes that are not easy to predict (Pecl et al., 2017). Considerable efforts have been devoted to investigating which life-history traits are predictive of successful range expansion and what habitats may be more vulnerable to range shifts (Catling and Oldham, 2011; Fortuna et al., 2014; Iverson and Prasad, 1998; Kudo et al., 2011; Shafer et al., 2001; von Mörs and Bégin, 1993). More recently, mechanisms that favour successful range expansions have been likened to those described for successful exotic invasions, such as enemy release, biotic resistance and the evolution of increased competitive ability (Morriën et al., 2010; Simberloff, 2010; Van Grunsven et al., 2007).

In a way, range expansions can be considered a double-edged sword. On one hand, a species successfully expanding or shifting its range ensures its own survival under changing environmental conditions. On the other hand, species in the recipient community are exposed to new neighbours that may have detrimental effects and lead to competitive exclusion or local extinctions (Davis and Shaw, 2001; Hejda et al., 2009; Vila and Weiner, 2004). These two different perspectives on range expansion have lead to a wealth of terms used to describe what is essentially the same process (Heger et al., 2013). These terms include encroachment (Bond, 2008; Van Auken, 2009; Ward, 2005), species migrations (Ibanez et al 2009), species redistributions (Davis, 2009; Valery et al., 2013), intra-continental invasions (Riggins and Seigler, 2012) and invasions by natives (Simberloff, 2010). *Encroachment* refers to woody species progressively replacing grass-dominated systems (Ratajczak et al., 2014; Van Auken, 2009), often ascribed to the combination of multiple factors such as climate, fire, herbivory and fertilization (Archer et al., 1995; O'Connor et al., 2014; Ratajczak et al., 2014; Van Langevelde et al., 2003). Woody encroachment has gained particular relevance due to its negative effects on the biodiversity of grassland ecosystems, as well as on livestock ranching and consequent impacts on regional economies (Briggs et al., 2002; Limb et al., 2011). *Range shifts* are usually defined as changes of the distribution limits of a species, generally along altitudinal or latitudinal gradients (Doak and Morris, 2010). *Species migrations* have been adopted with a similar usage to range shifts. The term *intra-continental range expansions* or *intra-continental invasions* (Morriën et al., 2010) is usually adopted in the context of range expansions occurring on a large scale across adjacent countries within a same continent. In this study, we include intra-continental range expansions, but not exotic intercontinental invasions where exotic species are introduced into a new continent. Unlike exotic intercontinental invasions, range expansions are often dominated by "leading-edge dispersal" *sensu* Wilson et al. (2009) where species may be exposed to abiotic and biotic environments that are also gradually changing. This suggests that the mechanisms and the time scale of range expansions may differ from those of biological invasions. Nonetheless, the effects of the two processes may be equally negative. Indeed, Simberloff et al. (2010) defined range-expanding species that are known to have a deleterious impact on recipient communities as *native-invasive species*.

In the current review, we group all these processes under the term *range expansion*. We consider range expansions that occur as a result of changed biotic and abiotic conditions that made new habitats suitable for the range-expanding species to survive. We also consider expansions that occurred as a result of evolution of traits or phenotypic plasticity that allow for the species to colonize new areas or to expand their niche in their current range (Clements and Ditommaso, 2011). We include here both geographic range expansion and expansion of a species' fundamental niche, because these two processes may be linked. For example, hybridization of *Helianthus annuus* with its congeners resulted in a broader ecological niche, subsequently facilitating the range expansion of the species into a region with a drier climate (Heiser, 1951a, b; Lexer et al., 2003).

In this review, we aim to organize current knowledge on the causes and the drivers of species range expansion across regions and ecosystems, and to lay out the potential and known consequences of range expansion. Jointly, we highlight the strengths and weaknesses of different methodologies as well as gaps in knowledge.

We conducted a literature search using the search engines "Web of Knowledge" and "Google Scholar" using the keywords: encroachment, range expansion, range-expanding species, species redistribution, species migrations, native-invasive species, and intra-continental invasions. We selected studies on plant ecosystems and focused on native plant species spreading into new regions and habitats adjacent to their native range. We included crops and cultivars (such as switchgrass, *Panicum virgatum*) as we considered them to have become naturalized or to be added to naturalized populations with shared genetic features.

We asked the following questions:

1) What are the processes and factors that favour species range expansions and how do they differ across ecosystems?
2) What are the impacts on ecosystem processes posed by range-expanding species?
3) Are some ecosystems more vulnerable to range expansions?

Although this research does not provide an exhaustive insight on range-expanding species, it elucidates key mechanisms and consequences and, we hope, will bring focus to important questions that require immediate attention.

2. Coverage of available literature

We considered 174 papers spanning the past 20 years. For the purpose of quantitatively estimating what the habitats and life forms are that have received most attention in the framework of range expansions, we excluded reviews, theoretical papers or studies resulting from laboratory/greenhouse trials where no clear provenance of the tested plants was indicated. Studies published by the same group of authors and targeting the same species and site were treated as separate only if the predictions and the methods employed were different. This selection resulted in a collection of 109 papers (Supplementary Material, Table S1). For each study we extrapolated geographic coordinates (latitude and longitude); when not indicated, these were derived with the best precision possible. If several sites within the same region were considered, we recorded coordinates for only one of them. Locations of the studies were then reported on a map using the R package "Rworldmap" (South, 2011). We considered six geographic regions corresponding to: North America, South America, Europe, Africa, Asia, Australia and New Zealand. To estimate whether research efforts where homogenous across regions we performed χ^2 tests after correcting for area of each geographic region. For each study, we recorded the following: 1) habitat (grassland, savanna, tropical, woodland, ecotone, high elevation, tundra, disturbed, wetland), 2) the life form (tree, shrub, herbaceous), 3) the methods adopted (field or greenhouse experiment, modeling, aerial photographs), and 4) the factors considered as drivers of range expansion, indicating whether these were abiotic factors (lumping climatic and non-climatic factors such as photoperiod), biotic interactions, anthropogenic factors, or hybridization.

3. Processes and factors that favour range expansion

3.1. Climatic factors

Range expansion has been long studied in the context of species distribution and climate change (Collatz et al., 1998; Klanderud and Birks, 2003; McLachlan et al., 2005; Pauli et al., 2007; van der Putten et al., 2010). The "bioclimatic envelope hypothesis" (Sykes et al., 1996) posits that species will track their climatic envelope by shifting their distribution in order to match areas with favourable climates (Loiselle et al., 2003). This hypothesis has been the backbone of many studies investigating mechanisms and effects of climate-driven range expansions (e.g. Archer et al., 1995; Chuang and Peterson, 2016; Iverson and Prasad, 1998; Shafer et al., 2001). A well-studied example of climate-induced range-expansions is that of mangroves. These halophytic intertidal trees have expanded to their poleward limits in most continents (Lovelock et al., 2007; MacNae, 1963; Saintilan and Williams, 1999; Stokes et al., 2010). Different factors have been identified that may limit the distribution and persistence of mangroves, such as sea-level rise (McKee et al., 2007), temperature (Alongi, 2008) and rainfall (Semeniuk, 2013). Furthermore, the complex interactions between nutrient enrichment, CO_2 and biotic interactions, such as competition and herbivory, have been proposed to regulate the coexistence of

mangroves and salt-marsh species (McKee and Rooth, 2008).

3.1.1. Temperature

Temperature is considered to be the determinant of many successful range expansions along latitudinal and altitudinal gradients. An example is the altitudinal-range shift of the sub-Antarctic flora of Marion Island (Le Roux and McGeoch, 2008). Interestingly, the authors of this study found one of the highest values of upslope expansion recorded in any study (3.4 ± 0.8 m/year since 1966). However, only half of the species within the studied flora were responsible for this shift. In alpine ecosystems, increasing temperatures are considered to be largely responsible for the changes in plant range-limits along elevation gradients (Körner and Larcher, 1988). Globally, a trend of upward shifts of the treeline has been connected to changes in the composition of alpine communities (Hu et al., 2015; Kullman, 2003; Meshinev et al., 2000; Sturm et al., 2001; Urli et al., 2014). However, long-term studies indicated that upward shifts are more pronounced for low- elevation species than alpine species (Zorio et al., 2016).

3.1.2. Rainfall

Rainfall has been shown to contribute to range expansions in multiple ecosystems and several habitat types. Increased rainfall has been linked to woody encroachment (Joubert et al., 2012; Kraaij and Ward, 2006). In North America, rainy winters buffered the shrub *Cornus drummondii* against dry summers, facilitating encroachment into prairies (Nippert and Knapp, 2007). Similarly, in Namibia, the successful colonization of *Acacia mellifera* was possible only after a sequence of rainy years (Joubert et al., 2008). Positive correlations between rainfall and range expansions of mangroves were also found in coastal wetlands in Australia (Eslami-Andargoli et al., 2009; Rogers et al., 2006). A recent study showed how increasing interannual variation in precipitation (which is consistent with projected climate scenarios) favoured the encroaching shrub *Prosopis glandulosa* at the expenses of grasses at a site in New Mexico (Gherardi and Sala, 2015).

3.1.3. Snow cover

At high latitudes, warmer winters have been linked to an increase in snow cover, which has several positive effects on native shrubs (Kohler et al., 2006). Deeper snow layers provide insulation and protection from freeze–thaw cycles (Hallinger et al., 2010). Furthermore, a long-lasting snowpack allows for a larger microbial community, which supplies shrubs with a larger amount of nutrients, and eventually contributes to increased growth rates in the following growing season (Chapin et al., 2005; Mack et al., 2004). These processes have been associated with an upslope shift of the shrubline in the Scandinavian mountains since the 1970 s (Hallinger et al., 2010). Furthermore, the combination of milder winters with warmer growing seasons allowed for faster growth of several shrub species, including *Betula nana, Betula pubescens,* and *Juniperus nana* (Hallinger et al., 2010). In some cases, increased snow cover inhibits rather than promotes range expansion by shrubs. In the Taisetsu mountains (Japan), *Sasa kurilensis,* the dwarf bamboo, has long been confined to clumps in the vicinity of *Pinus pumila* that accumulate snow, sheltering dwarf bamboo from cold temperatures. The trend changed only recently when milder and shorter winters allowed for the progressive expansion of *S. kurilensis* into novel habitats distinct from those occupied by *Pinus pumila* (Kudo et al., 2011). This finding suggests that the effect of climatic factors on range expansions is not unidirectional and can change within and across habitats, as might be expected with shifts in niche margins (Kawecki, 2008).

Once a threshold is reached, the factors aiding a range expansion may hamper it. Longer winters with prolonged snow cover may facilitate shrub establishment into novel environments by procuring shelter from frost damage. However, extended winters will also shorten the growing season, limiting shrub growth and establishment (Hallinger et al., 2010). Concurrently, interactions between surface reflectance

(albedo), ground temperature and thaw depth can affect shrub expansion in tundra both positively and negatively (reviewed in Myers-Smith et al., 2011).

3.2. Photoperiod

Climatic factors promoting range expansion may be countered by other factors hindering it. For example, warmer temperatures facilitate shrub encroachment into higher elevations and latitudes, but photoperiod represents a stable abiotic filter because it affects the flowering phenology and reproductive output of many plants (Saikkonen et al., 2012). For certain life forms (e.g. annual plants), only those species that can shift their phenology and adapt to different day lengths and light quality will be able to expand their ranges to higher latitudes (Griffith and Watson, 2006). A series of recent studies have put forward some noteworthy considerations that should be addressed by future research. In a test of 173 woody species from temperate latitudes, Zohner et al. (2016) showed that only one third of them depended on photoperiod for leaf emergence; these were species from regions with short winters. Thus, photoperiod may hinder range shifts of a subset of responsive species. On the other hand, a study of two herbaceous species, *Oxyria digyna* and *Papaver radicatum*, tested the prediction that warming would confer an advantage to southern populations migrating into high latitudes (Bjorkman et al., 2016). This study found that non-climatic constraints are likely to override the fitness advantage of southern populations adapted to warm climates.

One of the most promising candidates explaining range expansions among such non-climatic factors is photoperiod (Bjorkman et al., 2016). Remarkably, the literature on the effects of photoperiod on range shifts is still scarce, and often focuses on day length, neglecting other properties of changing light environments. At higher latitudes, plants experience decreasing or no darkness at all during the growing season (Markkola et al., 2016). In addition, the intensity of light is 55% lower than at mid-latitudes (Körner, 2003), and light quality changes as well, with an increasing proportion of diffuse blue (Taulavuori et al., 2009). Such differences may affect photosynthetic efficiency and consequently carbon assimilation in plants not pre-adapted to such conditions. A potential outcome may be a diminished effectiveness of ectomycorrhizal symbioses that are critical to plant fitness in northern hemisphere soils (Markkola et al., 2016).

Climatic factors and photoperiod- Synthesis and gaps:

- Temperature, rainfall and snowfall are the most frequently investigated drivers of range expansion. Photoperiod is an understudied factor, but it may limit climate-driven range expansions toward more extreme latitudes.
- Several studies found tipping points in the beneficial effects of changing climatic variables (e.g. snowfall), suggesting there may be a threshold beyond which range expansion is hindered rather than promoted.
- Most studies focused on mean climatic factors. However, very few investigated how variability (and unpredictability) of climate may influence range expansion of a target species and its impact on the recipient communities.

3.3. Anthropogenic factors

In many cases, climate is not the sole driver of species range-expansions. Intensive habitat modification due to anthropogenic activities such as pasture creation, agriculture and urbanization have led to large-scale habitat modification. Such modifications may directly affect species range distributions or may modify regional climate-driven patterns (Parmesan and Yohe, 2003; Steinlein et al., 1996) with consequences that are hard to predict. One of the best known examples is the range expansion of trees and shrubs into prairie and grassland habitats as a

consequence of shifts in fire regime and grazing pressure (Eldridge et al., 2013b; Owensby et al., 1973; Ward et al., 2014). This process has been well studied in North America, South Africa and Australia.

In a few cases, anthropogenic factors have been suggested to interfere with climate-driven range expansions, either hindering or accelerating climatic niche tracking of certain species. For example, *Lactuca serriola,* an annual species mostly found in temperate climates in southern Europe, Asia and North Africa (Lebeda et al., 2004), has been expanding its range at higher latitudes since the 18th century (Landolt, 2001). Although climate has been historically considered the main driver of this species' range-shifts (Davis and Shaw, 2001; Thuiller et al., 2008; Walther et al., 2002), recent research suggested a decoupling of range expansion and climate patterns (Brown and Vellend, 2014; Corlett and Westcott, 2013; D'Andrea et al., 2009). We believe that this indicates that anthropogenic disturbance may have altered this correspondence between range expansion and climate.

3.3.1. Fire regime

For many centuries, fire—both natural (wildfire) and anthropogenic—has effectively maintained open grasslands and prairie habitats by removing woody seedlings and controlling the spread of shrubland and woodland species (Briggs et al., 2005; Roques et al., 2001; Spasojevic et al., 2010; Walker et al., 1981). Fire prevents woody vegetation from forming dense thickets and monospecific stands, and mobilizes nutrients that promote germination and growth of herbaceous species in prairies and grasslands (Bond, 2008). The timing and frequency of fires are crucial (Van Langevelde et al., 2003; Ward, 2005). If fires come at the beginning of the wet season (i.e. before tree seeds are produced), then it creates space in the grass sward for the tree seeds to germinate *en masse*, resulting in woody plant encroachment. However, fires occurring at the end of the wet season will kill those young tree seedlings that have managed to recruit during the wet season, and maintain open grassland or savanna (Ward, 2005). Importantly, increasing urbanization and concerns over negative effects on farming and ranching areas have led to a decreased frequency of fires, as this practice may pose a risk to human health and potentially endanger inhabited areas close to natural habitats where the fire could spread (Smit et al., 2016; Twidwell et al., 2013). As a result, in many regions, prescribed fires that should typically occur annually or biannually, have been greatly reduced by up to 20-year intervals (Ratajczak et al., 2014). Reduced fire frequency results in successful establishment of woody species, and can lead to ecosystem transitions from grassland to woodland that are difficult, if not impossible, to reverse (Ratajczak et al., 2014). As woody range-expansion progresses, individual trees become large enough to withstand fire damage. Additionally, many shrub species can reproduce clonally (e.g. Grellier et al., 2012; Twidwell et al., 2013), forming dense thickets where only the few external individuals are vulnerable to fire damage. This leads to a shift in abiotic factors (e.g. light availability) and biotic interactions (e.g. competitive dynamics between shrubs and grasses) (Lett and Knapp, 2005; Ratajczak et al., 2014; Van Auken, 2009). Although fire generally stops range expansion in grasslands and savannas (Bond, 2008; Ward, 2005), its effect is more complex in heathlands. Bartolomé et al. (2005) reported that increasing fire frequency has a positive effect on the preservation of heathlands in Spain, whereas in high-elevation heaths of northwest Italy fire enhances germination rate of *Populus tremula* and *Betula pendula* (Ascoli and Bovio, 2010) and accelerates the rate of woody encroachment at the expense of these rare habitats.

3.3.2. Grazing

In many studies of shrub and tree encroachment, grazing is an important factor that interacts with fire frequency. Concurrent with decreasing frequency of fires, livestock grazing has increased (Briggs et al., 2002; Twidwell et al., 2013). As many woody seedlings are usually unpalatable (or at least are less preferred) to grazing livestock (such as cattle and sheep, which eat grasses and herbaceous material

almost exclusively), the selective removal of herbaceous species promotes woody species establishment (Wahungu et al., 2012). A manipulative study conducted in semi-arid Mediterranean rangelands in Israel showed that absence of grazing caused a clumped distribution of shrubs (mostly the dominant *Sarcopoterium spinosum*) as opposed to a more regular distribution intermingled with annual plants (mostly the grass *Avena sterilis*) when grazing was present. Interestingly, total shrub cover did not change across grazing treatments (Seifan and Kadmon, 2006).

Increasing grazing pressure reduces standing biomass of herbaceous species, which acts as fuel for fires, and ultimately contributes to lower intensity and diminished efficacy of fires, failing to stop the spread of woody species (Accatino et al., 2016; O'Connor et al., 2014). An indirect result of increasing grazing pressure is a higher rate of encroachment of unpalatable tree species at the expense of palatable species (Gordijn et al., 2012). Therefore, an efficient way to increase species diversity in areas subject to encroachment, and halt the formation of monospecific stands, is to promote the presence of multiple grazers and browsers (eating woody material only) or mixed feeders (eating both herbaceous and woody matter, such as goats). The presence of browsers that are less selective and feed on shrubs and woody species offers an important counterbalance against grazers' removal of herbaceous species (Augustine and McNaughton, 2004; Baumgartner et al., 2015). By removing encroaching species, browsers may indirectly increase grass biomass and eventually enhance the effect of fire (Van Langevelde et al., 2003). This supports the notion that fire and grazing are both essential for preventing encroachment into grasslands and prairies, and that successful management cannot be achieved if both factors are not controlled simultaneously (Accatino et al., 2016; Hean and Ward, 2012; Staver et al., 2009).

Finally, the identity of grazers and grazing pressure have also been shown to interact with climate in determining the treeline dynamics of *Larix sibirica* in Mongolia (Sankey et al., 2006a). At this ecotone, during particularly warm years with low grazing pressure, encroachment of *Larix* was maximized. However, a similar study conducted in Montana (USA) showed no clear effect of grazing on the encroachment of quaking aspen (*Populus tremuloides*) and Douglas fir (*Pseudotsuga menziesii*) (Sankey et al., 2006b).

3.3.3. Pastoral and agricultural practices

The dynamics of many alpine–treeline ecotones is a fine example of how land-use and climate change are entwined (Ameztegui et al., 2010; Batllori and Gutierrez, 2008; Bolli et al., 2007; Diaz-Varela et al., 2010). In these habitats, disentangling the causes of encroachment is often difficult. For centuries, the tree limit in many mountain ranges was maintained at a lower elevation than the optimum to artificially create alpine pastures for ranching (Holtmeier and Broll, 2005; Treml et al., 2016). Such activities during the 19th century were largely replaced by industrial meat and milk production, resulting in substantial land abandonment (Dirnböck et al., 2003; Mather and Fairbairn, 2000). This corresponded with an upward shift of the treeline at the expense of herbaceous species typical of alpine tundra. Such a shift may have been caused by both land abandonment and climate change (Batllori and Gutierrez, 2008; Gehrig-Fasel et al., 2007; Motta and Nola, 2001). Generally, the degree to which each factor contributed to encroachment was site-specific and depended on the competitive ability of the encroaching species against the herbaceous species in the recipient community (Dullinger et al., 2003; Palombo et al., 2013).

The introduction of crop cultivars and novel crops in agricultural landscapes has been practiced both in the framework of food production and forestry (Barney and DiTomaso, 2008). Crop cultivars represent a risk to the natural biodiversity especially when introduced in areas that overlap with the distribution of native populations (Kwit and Stewart, 2012) as they may spread and hybridize with native species and in extreme cases change the genetic constitution of the native population (Andersson and de Vicente, 2010; Simberloff, 2010; Wolfenbarger and Phifer, 2000). The risk posed by crop cultivars to

native biodiversity increases as rising temperatures make regions at higher latitudes milder and thus suitable for agriculture (Saikkonen et al., 2012). One example of how range expansion can be influenced by agricultural practices is offered by switchgrass, *Panicum virgatum*, frequently used as biofuel. This species, native to North America, has historically spread along road verges and meadows (Ahrens et al., 2014; Barney and DiTomaso, 2008). Several potential mechanisms, such as propagule pressure and climate, may explain the spread. However, the introduction of cultivars that spread new genes and traits may be an additional explanation for range expansion (Ahrens et al., 2014). The introduction of *P. virgatum* crop cultivars may also be detrimental to the livelihood of small remnant switchgrass populations (Kwit et al., 2014; Mutegi et al., 2014; Vacher et al., 2004). Currently, *P. virgatum* is considered an invasive weed in certain regions and a risk to local biodiversity (Ahrens et al., 2014). Similar concerns have been raised for *Miscanthus x gigantea*, a species cultivated as biofuel (Barney and DiTomaso, 2008; Flory et al., 2012).

Agriculture, farming and logging may also interact with climate change, negatively affecting niche tracking and successful range expansion, and eventually resulting in migration failure (Bush, 2002). This scenario was described for the Peruvian Andes where logging has decimated the 'green gap', a belt of forest situated between 800 m and 1500 m asl (Bush, 2002). The 'green gap' not only retains high biodiversity but also provides a corridor for upward migration of low-elevation species tracking their climatic niche. Concurrently, at lower elevations, agriculture and farming have been claiming land at the expense of native plant communities. Therefore, habitat conversion at the rear edge and destruction of migration corridors at leading edge of such species' distribution may compromise successful range expansion of entire communities and lead to significant biodiversity loss (Bush, 2002).

Anthropogenic factors - Synthesis and gaps:

- Management by fire is gradually becoming an unfeasible option (aside from limited areas) due to its health and safety concerns. This may have effects on management strategies of woody encroachment, particularly in areas with high human population densities.
- Similar to abiotic factors, the same anthropogenic processes can have radically different effects on range expansions across countries and species (e.g. grazing in North American mountain ranges *vs.* Mongolian mountains).
- Pasture and agriculture may hinder range expansion by creating barriers to species spread and/or by restricting available habitat.
- Introduction of cultivars may increase ecological breadth and favour expansions, but it could also lead wild populations to extinction via admixture.
- Anthropogenic factors can interact with climatic factors, amplifying or hindering the magnitude of range expansions. Although many studies account for the combined influence of anthropogenic and climatic factors, we do not have a clear estimate of their relative contribution and of the outcome of their interactions on range expansion (e.g. effect of anthropogenic factors in light of climate-change scenarios).

3.4. Biotic interactions

In addition to climate and anthropogenic influence, some other factors such as biotic interactions can play a role in range expansions. Whether biotic interactions can have a direct effect on range-expansion dynamics is still debated. However, many processes such as plant-herbivore or plant-soil biota interactions may delay or accelerate range expansions. Here we present some of the most frequently studied examples:

3.4.1. Plant-herbivore interactions

Morriën and van der Putten (2013) likened facilitative biotic interactions that promote the success of invasive species to those occurring for native range-expanders. Both invasive and range-expanding species in their new range may encounter lower density of herbivores, thus experiencing reduced herbivore load compared to the species native to the community (Keane and Crawley, 2002; Maron and Vila, 2001). This may happen because in the novel range there is a lower density of specialist herbivores associated with range-expanding species (Berg et al., 2010). Indeed, experimental studies have found that range-expanding species experienced an advantage over the species of the recipient community due to higher resistance to herbivore damage (Engelkes et al., 2008; Morriën and van der Putten, 2013; Van Grunsven et al., 2010). By contrast, a study of non-native invasive, range-expanding and native species did not substantiate the notion that range-expanding species may enjoy an advantage in the novel range due to enemy release (Engelkes et al., 2008). The authors of this last-mentioned study found that non-native invasives were less vulnerable to herbivory than congeneric natives. However, this difference was not found for range-expanding species, which did not show substantially different responses from native species. Fortuna, et al. (2014) found that the intra-continental invader *Bunias orientalis* (Brassicaceae) invests fewer resources in anti-herbivore defenses in the invaded range than in the native range, which may be indicative of different herbivore pressure across ranges (see Orians and Ward, 2010 for a review of this topic). Conversely, a study of anti-herbivore defenses in *Rorippa austriaca* (Brassicaceae) did not show differences in resource allocation across native and non-native ranges (Huberty et al., 2014). A subsequent study of *R. austriaca* in Germany and the Czech Republic found that range-expanding populations produced more inducible defenses but also had more herbivore damage than populations from the core distribution in all but one study site (Macel et al., 2017).

3.4.2. Plant- soil biota interactions

Similar to plant-herbivore interactions, studies proposed that range-expanding species may cause less negative plant-soil feedback in the novel range due to dispersal limitation of harmful soil biota (Berg et al., 2010; van der Putten et al., 2010). However, the long-term benefits of enemy release on range-expanding species have been questioned because their effects on plant performance beyond the range edges may be marginal compared to abiotic factors (Katz and Ibáñez, 2017) and because the potential initial advantage for range-expanding species (Dostalek et al., 2016; Van Grunsven et al., 2010) may be lost as pathogens and herbivores accumulate over time (Morriën and van der Putten, 2013). Furthermore, the advantages resulting from reduced pathogen loads may be counteracted by the concomitant loss of symbionts (Morriën and van der Putten, 2013). Indeed, it has been shown that the abundance of ectomycorrhizal fungi declines toward the margins of the host's geographic range (Lankau and Keymer, 2016). For certain species, the negative effects of non-adapted mutualists may represent a strong barrier to colonization and establishment beyond range edges. For example, home soil advantage was found for *Vangueria infausta*, a native Botswanan fruit tree, due to differences in their endomycorrhizal-fungal communities (Bohrer et al., 2008). Analogous results were found for herbaceous plant species (*Medicago* sp. and *Chamaecrista fasciculata*), showing that the reduced abundance of symbionts at and beyond the range edges may limit successful range expansion (Bena et al., 2005; Stanton-Geddes and Anderson, 2011). These results generally highlight the need for a better understanding of the specific effects of soil biota on range expansion. For example, do range-expanding species experience enemy release, and do such positive effects (e.g. reduced abundance of soil pathogens and root-feeding nematodes) override the loss of symbionts in the novel range?

3.4.3. Plant-plant interactions

Range-expanding species can also be affected by their interactions

with other plant species. Batllori et al. (2009) showed that availability of safe sites and facilitation by trees and shrubs in the Spanish Pyrenees may override climatic factors at local and regional scale in determining treeline dynamics. Similarly, black mangroves (*Avicennia germinans*), which have been expanding their range toward higher latitudes, may experience beneficial effects from nurse plant species (e.g., *Batis maritima, Sesuvium portulacastrum, Distichlis spicata*) in the salt marsh environments they are invading (Guo et al., 2013; McKee et al., 2007; Peterson and Bell, 2012). However, such positive effects are not ubiquitous; the outcomes of these interactions were found to shift from positive to negative along a latitudinal gradient and across life stages (Guo et al., 2013). These findings are consistent with studies on the range expansion of sagebrush (*Artemisia rothrockii*) in alpine meadows in California, where the negative effect of native herbs on sagebrush recruitment was stronger in mesic than in xeric environments (Berlow et al., 2002).

3.4.4. Plant-pollinator interactions

Several studies have addressed how environmental or anthropogenic changes may modify pollinator communities (Hegland et al., 2009; Rafferty and Ives, 2010). However, less attention has been devoted to the role of pollinators in plant range-expansion. Recent studies found contradicting results; in some cases, pollinators were found to be a potential limiting factor to range expansion (Moeller et al., 2012), whereas in other cases, pollination did not affect the survival of plants beyond their range edges (Hargreaves et al., 2015). A limited amount of information is also available on zoochory (animal dispersal) and range expansions. It has been recently proposed that migrating birds could be vectors of long- and short-distance seed dispersal within and across continents (Viana et al., 2016). Several studies have shown how specialized frugivores, the nutcrackers (*Nucifraga caryocatactes, N. caryocatactes* var. *japonica, N. columbiana*), mediated seed dispersal of whitebark pines (*Pinus albicaulis*) and enhanced pioneering ability of this species (Hutchins and Lanner, 1982; Kajimoto et al., 1998; Tomback, 1982). An analogous interaction was found in mistletoes, *Plicosepalus acaciae*. This species has expanded its range within the hyper-arid Middle East as a consequence of the increase in the abundance of its main bird disperser, the yellow-vented bulbul *Pycnonotus xanthopygos* (Rödl and Ward, 2002). These birds nest in the collective farms in Israel and move up into the adjacent wadis (ephemeral rivers) to feed and disperse the mistletoe within a particular wadi system.

Biotic interactions -Synthesis and gaps

- Biotic interactions have been shown to have positive and negative effects on range expansions, depending on species-specific characteristics, type of biotic interactions and habitat.
- The notion that range-expanding species may be favoured by lower herbivore load finds little consensus in the literature, which indicates high species-specificity in such responses. In addition, such benefits are considered to be short-lived as herbivores will accumulate over time.
- The effects of reduced soil-pathogen load *vs.* lack of specialized mutualists in the novel range during range expansion are likely to be important constraints to successful range expansion, but their relative importance and persistence in time are still uncertain.
- The availability of pollinators and dispersers may change along a plant expansion gradient, as may the ranges of pollinators and seed dispersers.
- Although a growing number of studies investigate interspecific interactions of range-expanding species and plant species in the recipient community, little is known of the role of intraspecific interactions during range expansion.
- Novel and complex biotic interactions will emerge between range expanders and resident species in recipient plant communities. Understanding the outcome of such interactions is fundamental for

accurate predictions of range-expansion effects on communities.

3.5. Hybridization and rapid evolution at range margins

Populations exposed to novel environments can undergo rapid evolution, and complex evolutionary responses may be observed (Fronhofer and Altermatt, 2015; Kubisch et al., 2014). Studying the variation of relevant traits within and among populations along an expanding range may provide useful information on trait differentiation in response to different ecological factors (Brauer and Geber, 2002). Hybridization has been proposed to promote range expansion, directly or indirectly. Hybridization could either produce novel phenotypes that have an adaptive advantage in the novel habitat or it may increase population size, favouring the conditions in which mutation or gene flow may occur (Andrew et al., 2012; Pfennig et al., 2016; Rieseberg et al., 2007, 2003). The notion that hybridization may aid biological invasions has enjoyed increasing popularity over the past two decades (Bleeker et al., 2007; Ellstrand and Schierenbeck, 2000; Hovick and Whitney, 2014), although the evidence of hybridization between introduced and native conspecifics resulting in increasing spread is moderate (Hovick and Whitney, 2014). Similarly, there is still a limited, but nonetheless increasing, indication that range expansions of native species may be promoted by this hybridization mechanism (Hovick and Whitney, 2014; Pfennig et al., 2016). A widely studied species in this respect is *Helianthus annuus* (North American sunflower). According to early studies (Heiser, 1947, 1951a, b), hybridization of *H. annuus* with several congeners could have contributed to increasing its ecological amplitude, facilitating expansion into novel ranges. An analogous case is that of the intra-continental invasion by *Rorippa austriaca* (Bleeker, 2003). It has been reported that *R.* x *armoracioides*, resulting from the hybridization between *R. austriaca* and the native *Rorippa sylvestris*, is spreading through Germany (Bleeker, 2003). Although the link between hybridization and range expansion has been refuted in some cases (Rieseberg et al., 1988), hybridization can broaden the environmental tolerance of species (Lewontin and Birch, 1966; Neuffer et al., 1999). A further concern is that range shifts linked to climate change (Chen et al., 2011; Walther, 2010) could cause species that were previously separated to come into contact and hybridize, with potential species loss and unpredictable consequences at the community level (Chunco, 2014). Hybridization is not exclusively a catalyst of range expansions and may indeed have the opposite effect, reducing both fertility and survival (Arnold, 1992; Bridle and Vines, 2007; Johansen-Morris and Latta, 2006). Few studies have questioned the role of hybridization in biological invasions, suggesting that hybridization may be a "passenger of colonization success" rather than a driver insofar as being positively correlated with other factors that influence the establishment of invasive or range-expanding species (reviewed in Rius and Darling, 2014)

Numerous theoretical and experimental studies have addressed how life-history traits at leading range margins may evolve or shift in response to biotic and abiotic conditions that are radically different from those experienced by the core populations (reviewed in Chuang and Peterson, 2016). Toward the range edges, traits associated with competitive ability are expected to decline, and dispersal traits and reproductive investment selected for (Burton et al., 2010; Phillips et al., 2010). Consequently, morphological traits maximizing long-distance dispersal should be more pronounced at the range edges (Higgins et al., 2003; Schwartz, 1993), including smaller seed size and structures that extend dispersal distance such as pappus, plumes and wings (Chuang and Peterson, 2016; Huang et al., 2015; Monty and Mahy, 2010). Such shifts in seed morphology have been predicted by theoretical models as well as observed by experimental studies (Bartle et al., 2013; Cwynar and MacDonald, 1987; Huang et al., 2015; Monty and Mahy, 2010). Morphological differentiation can be accompanied by different life-history strategies: as plants cannot discriminate the environment in which a diaspore will land, bet-hedging strategies, such as seed

dormancy, may delay seed germination until favourable conditions occur (Chuang and Peterson, 2016). Most studies predict decreasing individual densities at the expanding fronts (but see Fronhofer and Altermatt, 2015), a potential consequence of which is Allee effects (Lewis and Kareiva, 1993). Allee effects - namely reduced individual growth rates in low density populations - may lead to a reduction, or even a reversal, of expansion rates (Holt et al., 2005). In such a situation where density of conspecifics gradually declines, self-compatible or clonal species are more likely to establish in new ranges and should be selected for at the expanding front (Baker, 1955).

Empirical tests of evolution of life-history traits in range expansions do not always match the predictions recorded in theoretical ecology (Hargreaves and Eckert, 2014). Importantly, many theoretical models of range expansion do not fully grasp the complexity found in natural systems. For example, several models are tailored to exotic invasions, and assume large differences between core and marginal habitats (Chuang and Peterson, 2016; Moran and Alexander, 2014). This may not be the case in climate-driven range expansions, where the environment gradually changes as species shift their distributions (Bradley et al., 2010; Chuang and Peterson, 2016; Hargreaves and Eckert, 2014). Furthermore, where entire communities (or more realistically, several species within a community) are shifting their ranges, novel biotic interactions are expected to arise that may radically affect expansion dynamics (Henry et al., 2014; Holt et al., 2005; Owensby et al., 1973; Urban et al., 2013). To date, very few studies have attempted to model entire community shifts (Peng and Zhou, 2014) and very few have incorporated the effects of increasing climatic variability and unpredictability in range-expansion models (Henry et al., 2014). Abiotic and biotic conditions of the recipient community should be considered too, as the presence of a strong competitor in the novel range may significantly curb a range-expander's dispersal (Burton et al., 2010). Finally, it is not yet clear what the relative contribution of genetic changes *vs.* phenotypic plasticity are to species trait-shifts at the expansion front (Bialozyt et al., 2006; Chuang and Peterson, 2016; Clements and Ditommaso, 2011; Ibrahim et al., 1996). A better understanding of these relationships is fundamental to building better predictions of range expansion (Holt et al., 2005).

Hybridization and rapid evolution - Synthesis and gaps:

- Hybridization can broaden a species' ecological niche and ultimately favour its range expansion. However, hybridization can also have the opposite effect by reducing fertility and survival.
- Although shifts in life-history traits and reproductive strategies at the expanding front of a species range have been shown both by theoretical and experimental studies, little is known about how such dynamics may be affected by biotic interactions with other range-expanding species or with species in the novel range.
- Most, but not all, of the theoretical models on range-expanding species focus on single species and static environmental conditions (for a notable exception see Holt et al., 2005). Such studies fail to incorporate the complexity of community-level interactions and the increased proportion of non-equilibrial changes in range dynamics, such as those proposed by extreme events predicted by climate-change scenarios.
- Disentangling the relative contribution of phenotypic plasticity *vs.* genetic change in the expanding front is fundamental for better predictions of range expansions.

3.6. Dispersal traits: benefits vs. costs

As illustrated in the previous sections, dispersal at the expansion front is predicted to be selected for during range expansions (Hargreaves and Eckert, 2014; Phillips et al., 2010; Travis and Dytham, 2002). Greater investments in dispersal can generate trade-offs among traits, such as decreased competitive ability in favour of increased

dispersal structures (Brooker et al., 2007; Burton et al., 2010; Hargreaves and Eckert, 2014; Nathan, 2006). Repeated dispersal events may reduce the occurrence of genetic bottlenecks and maintain high genetic variation (Pannell, 2015; Pluess, 2010), and this in turn may maximize a species' ability to adapt to new conditions (Pease et al., 1989). Concurrently, high dispersal between core and edge populations may maintain high gene flow and reduce trait differentiation at the expansion front (Holt et al., 2005). In cocklebur (*Xanthium strumarium*) and snow buttercup (*Ranunculus adoneus*), successful range expansion was hindered by low variation of traits linked to reproductive timing (Griffith and Watson, 2006; Stanton and Galen, 1997). This was likely due to gene flow between marginal and core populations.

Selection for increased dispersal at a range edge is influenced by multiple factors. Typically, many tree species experience strong negative soil feedback from conspecifics and thus long-distance dispersal strategies are selected for, ultimately enhancing range expansion (McCarthy-Neumann and Ibáñez, 2012). In addition, pre-adaptation (or exaptation *sensu* Gould and Vrba, 1982) to the abiotic and biotic conditions in the recipient environment may be crucial to successful dispersal. This case is illustrated by the expansion of the marsh species *Elymus athericus* along an altitudinal gradient in northwest Europe, where survival was strongly affected by the interaction between biotic factors (herbivory and competition) and pre-adaptation of parental-seed origins to environmental conditions beyond the range edges (Bockelmann et al., 2011). However, dispersal beyond a species' range may be curbed by the presence of strong competitors and antagonists (Burton et al., 2010; Clobert et al., 2009). A study of plant-herbivore interactions among different range-expanding species (Wilschut et al., 2017) showed that some species (*Rorippa austriaca* and *Geranium pyrenaicum*) attracted a significant number of root-feeding nematodes in their novel ranges, whereas *Centaurea stoebe* was less likely to be attacked. This indicates that concurrent dispersal of range expanders and their enemies can have species-specific effects, which may feed back to dispersal strategies adopted during range expansions.

Over the past decade, increasing emphasis has been placed on modeling rare long-distance dispersal processes (Bohrer et al., 2005; Nathan, 2006) and their effects on genetic diversity of range-expanding species. Bialozyt, et al. (2006) found a positive relationship between the genetic diversity of a range-expanding species and the frequency of long-distance dispersal events. These authors also found a complete loss of genetic diversity when long-distance dispersal events were rare and the area of colonization was limited. Furthermore, a study conducted by Bohrer, et al. (2005), found that the outcomes of long-distance dispersal on genetic diversity were conditional upon many properties of the expanding population.

The plethora of factors involved in determining dispersal beyond the range, and ultimately range-expansion dynamics, may be the reason why a correlation between dispersal and range size is uncertain (Gaston, 1990; Lester et al., 2007). Another fundamental drawback in assessing the role of dispersal in range expansion lies in the lack of empirical evidence on dispersal ability (Gaston, 1990), leading to a qualitative rather than quantitative estimate of dispersal (Lester et al., 2007). By virtue of this simplification, potentially important elements that factor in the dispersal process may be missed. Furthermore, dispersal and range expansion act at fundamentally different spatial and temporal scales, and the features of dispersal may change across time and space during a range expansion (Lester et al., 2007). Hargreaves and Eckert (2014) point out the need for further empirical studies that can provide strong examples and more information necessary for bettering theoretical models on dispersal processes during range expansions. Concurrently, more accurate predictions of range expansion of species and entire communities impinge on more precise estimates of the dispersal abilities of single species (Bialozyt et al., 2006; Ibrahim et al., 1996; Nathan, 2006; Shigesada and Kawasaki, 2002). A promising approach, presented in a recent study, used spatially-explicit individual-based models relying on pollen dispersal kernels to predict

the likelihood of hybridization based on pollen limitation and species heterogeneity (Klein et al., 2017). Similarly, Gerzabek, et al. (2017) investigated reproductive success at the leading edge of an expanding species, and found that success of immigrants *vs.* local recruits was dependent on founder effects and genetic drift during range expansion.

Dispersal traits - Synthesis and gaps:

- Increased dispersal ability is predicted to emerge at the range edge and to trade off with other traits such as competitive ability.
- Dispersal beyond the range edges can also be affected by pre-adaptation and presence of competitors and antagonists.
- Scarcity of empirical tests and quantitative estimates of dispersal ability significantly hinder our ability to predict future range expansions.

4. Range expansions and failure to expand: impacts on ecosystems

In the *Introduction* we defined range expansions as a double-edged sword. Although it is desirable for species to shift their ranges in response to changing environments, such successful expansions may disrupt the recipient communities (Alexander et al., 2016; Brooker et al., 2007; Macel et al., 2017; Svenning et al., 2014). In the following, we explore two contrasting scenarios: 1) the species- and ecosystem-level consequences of species not tracking their range and failing to shift their distributions (Zhu et al., 2011), and 2) the consequences of "successful" range expansions on recipient communities (Brooker et al., 2007; Nathan, 2006).

In the section titled *Dispersal traits: benefits vs. costs*, we illustrated how successful dispersal beyond a range's edge may vary across species. A consequence of this variability is that the rate of species redistribution within communities exposed to changing conditions will likely be uneven (Zhu et al., 2011). Species with high dispersal ability and/or broader niche width will be able to expand their ranges, whereas species with narrow environmental tolerance and/or low dispersal ability will maintain their original distributions (Wisz et al., 2013). This has been shown for the sub-Antarctic flora of Marion Island (Le Roux and McGeoch, 2008), where a community-level study showed that only half of the species shifted upslope in response to climate change. Le Roux and McGeoch (2008) suggested that few highly responsive species may drive the response to global warming, while the majority of the species pool is unable to successfully track their climatic niche. Even more extreme are the results of a study of the flora of the Falkland Islands indicating that upland species will undergo range retraction rather than range expansion (Upson et al., 2016). Estimates produced by this last-mentioned study suggest that by 2080 between 88% and 96% of the suitable habitats for upland species will be lost due to rising temperatures. The result of uneven migration rates in response to changing environments is the formation of "no-analog communities", where re-organization of community composition is accompanied by novel biotic interactions (Alexander et al., 2016, 2015; Le Roux and McGeoch, 2008; Le Roux et al., 2012; Lurgi et al., 2012).

4.1. Failure to expand

From a conservation standpoint, the negative impacts of failed expansions are easy to grasp: species that fail to track their niche will likely face decreased habitat availability and may also experience competition from range expanders moving into the community from an expanding front (Alexander et al., 2016; Elith et al., 2010). However, few studies offer an eco-evolutionary perspective on how this may affect community stability (Brooker et al., 2007; Holt et al., 2005). Ibáñez et al. (2009) compared montane tree species in North America with potential candidates that may replace them in the event of climate-induced range shifts. This study showed that if a decrease in the relative abundance of local species does not correspond with successful

establishment of the migrant species, the ecosystem might experience a drastic loss in biodiversity. Similar patterns were observed in Costa Rica, where global warming is predicted to cause an upward shift of species distribution into higher elevations (Colwell et al., 2008). This shift is unlikely to be matched by a redistribution of warm-adapted species into lowland communities, thus leading to "biotic attrition", i.e. a loss of species and biodiversity, in low elevation habitats. In North American tundra habitats, a slow rate of range expansion could be counterbalanced by increased rates of individual growth, known as "demographic compensation" (Doak and Morris, 2010). However, the buffer offered by this process is only temporary as its effectiveness is predicted to decrease as warming continues (Doak and Morris, 2010).

4.2. Effects of successful range expansion

Studies on range expansions into high elevations observed an increase in species richness as growing numbers of alpine species are found in nival communities (those subjected to perpetual snow) (Klanderud and Birks, 2003; Pauli et al., 2007). However, a potential consequence of rising temperatures and novel competitors is the extinction of cold-adapted species due to competitive exclusion or loss of suitable habitats (Grabherr et al., 1995; McCarty, 2001; Theurillat and Guisan, 2001). Encroaching species may disrupt recipient communities not only by means of direct competition, but also by offsetting the composition of soil biota. It has been suggested that eastern red cedar (*Juniperus virginiana*), a widespread woody encroacher in North America, may alter the composition of soil biota in a way that promotes the establishment of conspecifics, but hinders the successful growth of prairie species (Williams et al., 2013; Yannarell et al., 2014). Similarly, a recent study indicated that the range-expanding shrub *Artemisia rothrockii* (timberline or Rothrock's sagebrush) modifies soil biotic and abiotic properties. Along the same gradient, it was shown that timberline sagebrush alters the phenology of the native *Trifolium andersonii* via shading, with the effects of such interaction being comparatively greater than that of climate alone (Kopp and Cleland, 2015). Interestingly, studies on both *J. virginiana* and *A. rothrockii* indicate that after these species were removed, native plant communities were successfully restored (Collins et al., 2016; Pierce and Reich, 2009).

Several studies considered the notion that range expansion may result in landscape degradation and loss of ecosystem function. Eldridge et al. (2013a) showed that the effects of encroachment are often confounded with those of grazing. In the absence of the latter, shrub encroachment is associated with increased soil infiltrability, soil labile carbon and biocrust cover, all indicators of healthy ecosystems. Similarly, range expansion of mangroves into salt-marsh habitats (Field, 1995; Gilman et al., 2008; Woodroffe and Grindrod, 1991) has been associated with greater potential to respond to sea-level rise and to buffer against hurricanes or cyclones (Comeaux et al., 2012; Rogers et al., 2006) than other salt-marsh species (Bianchi et al., 2013; Howe et al., 2009). A particularly acute example comes from Bangladesh, where more than 700,000 people were killed by cyclones in the past 50 years, largely due to the removal of mangrove trees from coastal areas (e.g. Haque et al., 2012).

Many studies have suggested that increased colonization of novel areas by shrubs will result in higher carbon sequestration (Oechel et al., 2000; Sturm et al., 2005), although this is more likely to be the case at lower values of mean annual precipitation (Jackson et al., 2002). Combined with increased microbial activity and faster soil carbon turnover, brought about by higher soil temperatures, this increased colonization may lead to larger amounts of CO_2 released into the environment (Mack et al., 2004; Sturm et al., 2005). On a larger spatial and temporal scale, this process would cause a modification of biogeochemical cycles (Neff et al., 2009; Wheeler et al., 2007). However, such predictions are countered by empirical studies indicating that woody encroachment will not have negative consequences on recipient communities. Kammer et al. (2009) showed that treeline advancement

into tundra vegetation in the Ural mountains leads to increased nitrogen availability, which in turn increases plant biomass and eventually leads to higher carbon sequestration by vegetation.

The consequences of range expansion may also reverberate across multiple trophic levels, as was shown in Alaska, where climate-driven shrub expansion has provided more habitats for snowshoe hare (*Lepus americanus*) populations, which significantly increased in number (Tape et al., 2016). Thus, range expansions may affect trophic interactions with long-lasting consequences on ecosystem properties and biodiversity that are hard to predict *a priori*.

Synthesis and gaps:

- Aside from woody encroachment studies, the long-term effects of range expansions on recipient communities are still uncertain. More studies need to focus on such effects at the recipient community levels (where species loss may occur and novel biotic interactions may lead to non-additive indirect effects) and at the ecosystem level (e.g. nutrient cycling, water retention, carbon sequestration).
- While in some cases, the removal of a range-expanding species can return the community to its original status in a matter of years, in other cases failure to expand is expected to be even more detrimental than range expansion. It appears the latter is the case for many climate-driven species range shifts.
- Very few studies have investigated how impacts of range expansion may affect multiple trophic levels.

5. Future frontiers

Range expansions are complex processes whose impacts can affect ecosystems at multiple levels. The ability of a species to shift its range in response to climate change or anthropogenic pressure is certainly a positive feature for the species itself, as it will likely avoid extinction (Bradley et al., 2010; Shigesada and Kawasaki, 2002). However, this is just about the only certainty when it comes to range expansions. This review indicates that although there are many studies on the topic, there is still much that we do not know.

Table 1
Life forms investigated across studies of range-expanding species expressed in percentages." Multiple" refers to studies focused on two or more species, such as studies of range expanding species in ecotones or focused on entire communities.

Tree	Shrub	Multiple	Herbaceous
40.9	17.1	19.1	22.9

5.1. Continent and habitat: bias

We found that the attention to range expansion across countries ($\chi^2 = 67.91$, df = 5, p < 0.001) and habitats ($\chi^2 = 76.41$, df = 8 p < 0.001) was uneven. Proportionally, more studies were conducted in North America and Europe, and high-elevation habitats were the most frequently targeted. Conversely, tropical habitats received the least attention (Fig. 1). This is noteworthy as tropical habitats are considered cradles of biodiversity, where loss of complexity in plant communities may have long-lasting bottom-up effects. Although some studies may have been missed by our literature search, the issue of unbalanced representation of habitats and geographical regions in ecology is not new (Pyšek et al., 2008); data are often scarce for regions that are not easily accessible or that are plagued by long-standing conflicts.

5.2. Life form and species

Our review brought to light that almost 60% of the studies targeted tree and shrub species (Table 1); tree encroachment is visually immediate to detect and has important effects on regional economies. Unlike the more obvious woody plants, range expansion of many herbaceous species may be underway and may go nearly or completely undetected. There are a few notable exceptions, but even these species are recorded because they have negative effects on agriculture (e.g. thistles, *Onopordum* and *Carduus* spp.; Jongejans et al., 2006; Palmisano and Fox, 1997; Silvertown and Smith, 1989). Such detection may be further complicated by cases of hybridization between native and range
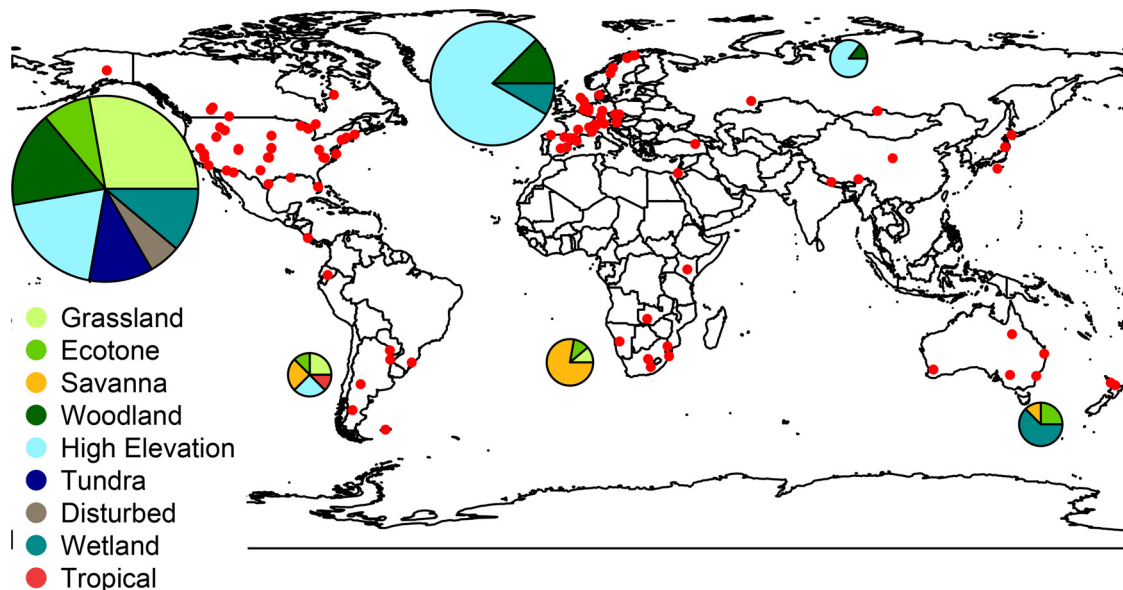
Fig. 1. Global distribution of all the reviewed field studies conducted on range-expanding species. Each red dot indicates a study. Pie charts indicate the proportion of studies focusing on each habitat type in each region, and the size of the pie chart is proportional to the number of studies for each region (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Table 2
Methods used in studies of range-expanding species reported as percentages. "Mixture" encompasses combinations of different approaches such as field experiments and photography, photography and modeling, herbarium and field data, photography and greenhouse experiments.

Modeling	Photography	Field or greenhouse	Herbarium	Mixture
10.18	4.63	66.67	0.92	17.6

expanders in which the resulting hybrids are not recognizable by distinctive morphological features (e.g. O'Hanlon et al., 1999; Saltonstall, 2011). However, the consequences of range expansions in herbaceous plant communities may be no less deleterious than those involving tree-dominated systems. In addition, there are benefits to studying herbaceous species, with their frequently shorter life cycles, due to increased ability to manipulate them in evolutionary studies. We found that 46.7% of the studies focused on multiple species and 53.3% on a single species, suggesting a fairly balanced proportion between these two different approaches. However, studies that targeted multiple species indicated an incredible species-specificity in terms of species ability to track their habitat and response to factors considered important for range expansion.

5.3. Study methods (trade-offs with spatial and temporal scales)

Field or common-garden manipulative experiments, field observations or field sampling were the dominant approaches employed (66.7%). Aerial photographs often combined with other methods, such as field surveys, modeling and/or interviews, were used in 18.5% of the studies. Fewer studies used modeling exclusively, and only one study relied exclusively on herbarium data (Table 2). Experimental (field and greenhouse) approaches were most often used to address and test specific mechanisms of range expansion. Models or aerial photographs were adopted in 15% of the studies to infer patterns of range expansion (Table 2), and only two studies used a combination of such methods. Different research methods also corresponded to a focus on different temporal and spatial scales: modeling approaches are ideal for making predictions on larger time scales, whereas aerial photos, by capturing a larger number of sites, allow for making inferences at larger spatial scales (Supplementary Material, Fig. S1). In general, most experimental studies either focused on a large number of sites (up to 50) for a relatively short time (less than 5 years), while long-term experimental studies generally focused on a limited number of sites (up to 5 sites). Two exceptions were represented by a study of herbarium records (D'Andrea et al., 2009) and field surveys repeated over a 70 year-long time span (D'Andrea et al., 2009; Klanderud and Birks, 2003), which inferred range expansions over temporal scales of over 100 years for a large number of sites. Theoretical modeling allows for long-term and large-scale predictions (e.g. Wiegand et al., 2006), while collection of data and *in situ* manipulative experiments are fundamental for acquiring a mechanistic understanding of range expansions and their impacts. We believe that, short of better understanding of biotic factors (such as the role of the recipient community in the range expansion of a species) and quantitative estimates of dispersal, the role of bioclimatic modeling (Huntley et al., 1995; Pearson and Dawson, 2003; Thuiller et al., 2008; Wisz et al., 2013) may be overestimated because such models are constrained by the assumption that current bioclimatic constraints will remain so. Empirical studies can certainly provide more data for complex models that can better approximate the reality of range expansions and ultimately lead to more accurate predictions.

5.4. Factors driving range expansion

Among the 109 papers used for this analysis, 69 studies addressed

geographic range expansion, whereas only 30 studies looked at both geographic and niche shifts (Fig. 2a). The remaining studies focused on the effects of range expansion on recipient communities and did not clearly characterize the type of range expansion. The larger proportion of the reviewed research (73%) explicitly tested cause-effect mechanisms behind range expansion, whereas the remainder (27%) either examined whether and to what extent one or more species had expanded, or investigated the effect of the expanding species on the recipient community. We found that 42.5% of these studies addressing specific cause-effect mechanisms tested abiotic factors (i.e. climatic as well as non-climatic factors, such as photoperiod) as drivers of range expansion, 17% tested biotic factors, while anthropogenic factors (4.3%) and hybridization (3.2%) were less frequently considered (Fig. 2b). We also found studies combining multiple categories of factors such as abiotic and biotic factors, abiotic and anthropogenic, and biotic and anthropogenic factors.

### 5.5. Outcome of range expansion on recipient communities

In general, studies indicated a high degree of uncertainty for plant species in recipient communities. The impact of range expansions was characterized as negative in 38.3% of the surveyed studies, while in fewer cases positive or both positive and negative effects (respectively 8.4% and 2.8%) were highlighted. However, in half of the cases (50.5%), the impact of range expansions was neither assessed nor acknowledged as a potential cause of disruption to recipient communities (Fig. 2c). Our review suggests that impacts of range expansion on recipient communities may be equally negative as those of failed range expansions. Such considerations are likely to be species- and system-specific, and should be an important criterion for future decisions in terms of land-use management and conservation strategies.

5.6. Future avenues of research

We believe that our review outlines four major avenues of research that should be addressed in the near future: 1) the direct and indirect impacts of range expansions, among multiple trophic levels, may lead to identifying community-level shifts that would otherwise go undetected. 2) Increasing climatic variability (rather than mean conditions) on range expansion and on the ability of species in the recipient community to cope with the effects of range expansion. 3) Effects of novel biotic interactions emerging in communities subject to range may reverberate across different levels of organization (species and communities) and at different spatial and temporal scales. There were very few studies assessing the effects of range expansions at different spatial and temporal scales. 4) Non-climatic factors, such as photoperiod and anthropogenic factors, may counter climate-driven range expansion with important consequences for shifting plant communities (e.g. decoupling of responses in temperature-responsive *vs.* photoperiod-responsive species). Such limits to climatic niche-tracking require further exploration.

6. Conclusions

In this review, we have shown that multiple interacting factors are responsible for range expansions (Supplementary Material, Fig. S2) and the relative importance of such factors may change across time scales, within a range and across habitats. Range expansion may be aided or countered by indirect effects or by the interaction of multiple factors with potentially synergistic effects, and may result in more aggressive expansion rates than predicted. For example, interactions between anthropogenic factors and climate are worthy of greater consideration, as their effects can be non-additive. Similarly, the effect of biotic interactions during range expansions is still highly debated (e.g. Katz and Ibanez, 2017; Tomiolo and Ward, 2018) and shows high variation
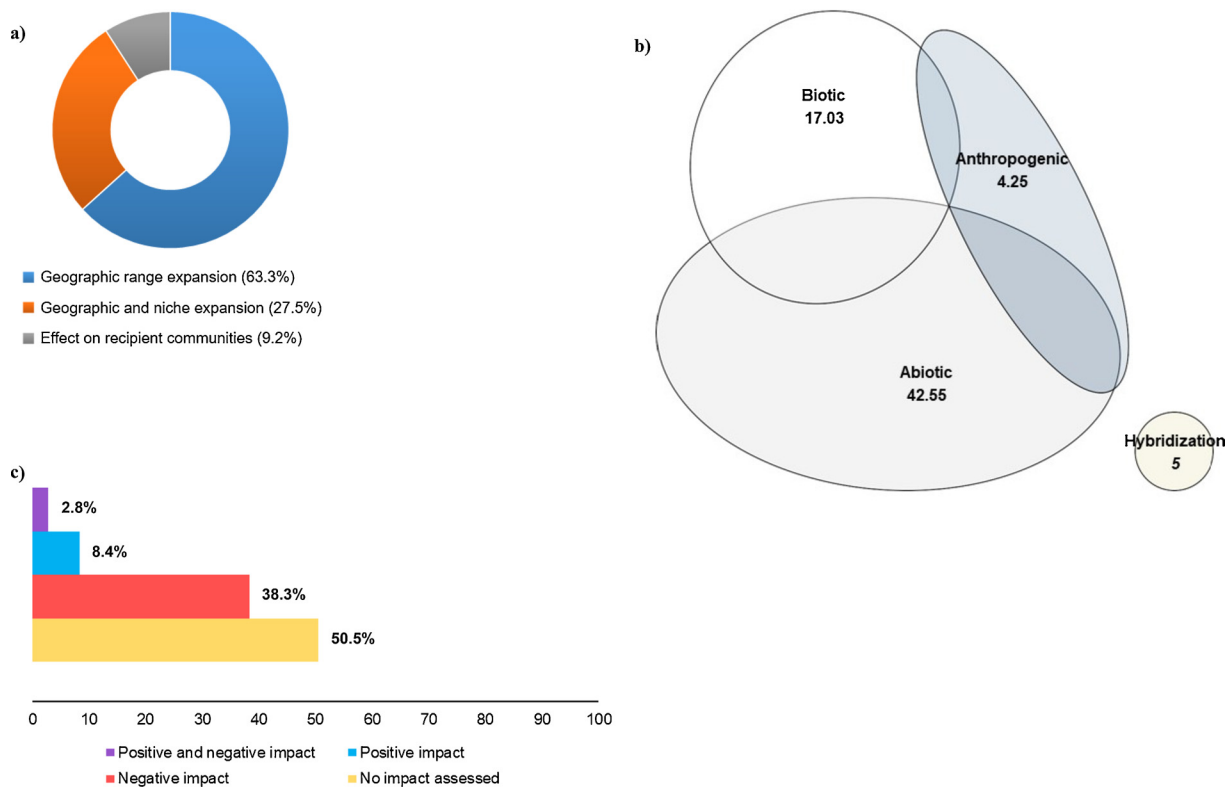
Fig. 2. a) Pie chart showing the types of range expansion addressed in the literature, most studies focus on some aspects of range expansion from a geographic and niche perspective, only a fraction of studies explicitly addresses effects of range expansion on recipient communities; b)Venn diagram representing the different factors explaining range expansion and their percentage and their combination across studies. Overlapping areas represent studies that investigated multiple types of factors, such as abiotic and biotic (17.02%), abiotic and anthropogenic (11.7%) or biotic and anthropogenic (4.25%); c) impacts of range expansions evaluated by the reviewed literature show that only half of the studies we considered assesses or acknowledges potential effects of range expansion on recipient communities.

depending on the species and the interaction considered.

Increased dispersal ability at the range edge may be determinant for of successful range expansion and may lead to admixture, with potential consequences on niche and geographic range expansion. Although, recent modeling studies have shown promising avenues in this respect (Gerzabek et al., 2017; Klein et al., 2017), quantitative estimates of single species dispersal abilities may be critical for more accurate predictions.

Because the ramifications of range expansions are so wide and far-reaching, we need to use all the available tools and integrate the strength of different approaches to evaluate the drivers and consequences of range-expansions at the single-species level (Holt et al., 2005), as well as at the level of community and ecosystems (Barger et al., 2011; Brooker et al., 2007). In addition, as suggested by Walther (2010), protection of ecological process rather than of species and communities alone, should become a focus of future studies.

Statement of authorship

ST and DW planned the review structure. ST conducted the literature search and wrote the first draft, ST and DW contributed to subsequent revisions.

Declaration of interest

All authors declare they do not have conflicts of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ppees.2018.06.001.

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