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# Double trouble: the implications of climate change for biological invasions

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## Abstract

The implications of climate change for biological invasions are multifaceted and vary along the invasion process. Changes in vectors and pathways are likely to manifest in changes in transport routes and destinations, together with altered transit times and traffic volume. Ultimately, changes in the nature of why, how, and where biota are transported and introduced will pose biosecurity challenges. These challenges will require increased human and institutional capacity, as well as proactive responses such as improved early detection, adaptation of present protocols and innovative legal instruments. Invasion success and spread are expected to be moderated by the physiological response of alien and native biota to environmental changes and the ensuing changes in biotic interactions. These in turn will likely affect management actions aimed at eradicating, containing, and mitigating invasions, necessitating an adaptive approach to management that is sensitive to potentially unanticipated outcomes.

## Keywords

biosecurity, global change, impacts, management of invasions, research needs

## Introduction

Human induced climate change is manifesting in a variety of environmental changes including alterations in global temperatures, precipitation patterns, ocean chemistry, currents, and frequency of extreme climatic events (IPCC 2019). Distribution range shifts are a widely accepted consequence of such changes (Bellard et al. 2013; Hulme 2017; Kuczynski et al. 2018), but the implications for alien biota are not straightforward as their ranges are linked not only to their physiological tolerances, but also to the processes through which they are translocated by humans. However, the invasion process is complex, moving through various stages (Blackburn et al. 2011) which may each be affected by a changing environment in different ways. Thus, it is clear that to anticipate the implications of climate change on invasions, there is a need to consider the consequences of a changing climate for how biota cross the various barriers and move through the invasion stages from transport to spread (*sensu* Blackburn et al. 2011). Importantly, as management approaches differ among these stages, an understanding of the specific implications of climate change for the various stages is needed to support management actions aimed at minimising introductions and mitigating the negative impacts of those that do occur.

## The implications of climate change along the invasion process

Climate change is likely to affect invasions via three mechanisms (Fig. 1). Firstly, by changing the nature of vectors and pathways, secondly by altering the abiotic nature of the recipient environment, and thirdly through changes to biotic interactions in recipient communities. While the first of these mechanisms acts on the transport and introduction stages, the second two act simultaneously on the stages of establishment and spread.

### Changes in the nature of pathways and the implications for the transport and introduction of alien taxa

Climate change is expected to increasingly affect the movement of people and due to the link between human movement and the introduction of alien biota, biological invasions will in turn be impacted. Notably, these changes are expected to take place as a result of changes in transport routes, destinations, altered traffic volume and changes in transit time. Presently, over 90% of the world's trade is moved by shipping (IMO 2019). This important pathway is expected to be influenced by the melting of the Arctic ice-cap, a process that will open new shipping routes. It is estimated that 5% of the world's trade could pass through these new routes, effectively increasing connectivity between Europe and Asia and decreasing transit times by up to 40% (Yumashev et al. 2017). From an invasion perspective, these changes in shipping have important implications (Miller and Ruiz 2014). For example, previously unconnected ports will act as sources and sinks for alien species and propagule pressure will increase between Europe

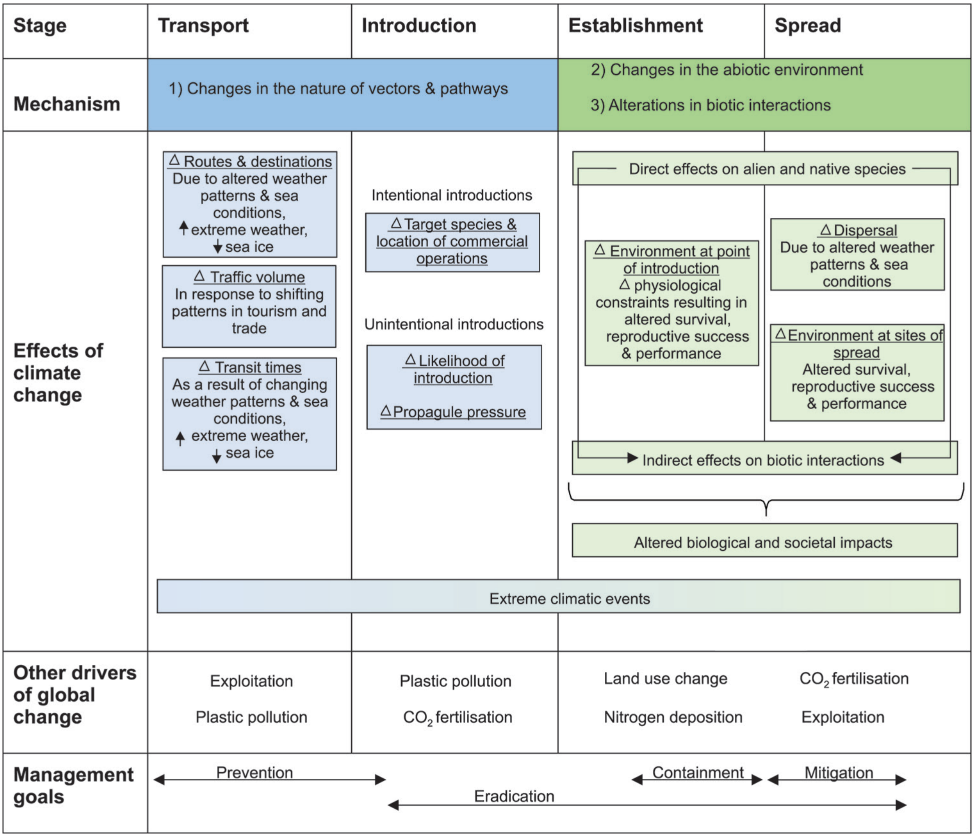


**Figure 1.** The effects of climate change on invasions and the mechanisms through which they act mapped onto the Blackburn Unified Framework for biological invasions (Blackburn et al. 2011). Examples of where other drivers of change may influence the invasion process are also indicated.

and Asia as fouling and ballast water associated species could experience increased survival due to shortened transit times (although the potential of the low water temperatures associated with the colder northern route to mitigate this effect has not yet been assessed). The shipment of goods through rivers and lakes is also expected to be affected by climate change. Lower water levels due to changes in rain patterns, droughts, and elevated temperatures might require a reduction on cargo weight, smaller vessels, and increased number of trips (Millerd 2011).

Besides direct impacts on transportation, future changes in climate are expected to alter where commodities are produced and where they are transported to. For example, salt transport in the Mediterranean Sea has revived due to decreased rainfall and increased winds raising the salinity in some regions (Raitsos et al. 2010), while the production of various fruits and vegetables is expected to shift in response to altered precipitation patterns (Parajuli et al. 2019). These sorts of shifts in agricultural production will serve to increase connectivity between presently disconnected regions and thus elevate the associated invasion risk. When accounting for changes in global trade patterns and predicted changes in climate it is anticipated that numbers of naturalised plant invasions will increase in northern-hemisphere temperate countries while declining in tropical and sub-tropical regions (Seebens et al. 2015). This pattern reflects warming in the north, increasing climate matching between dominant trade partners, while elevated temperatures in the tropics will have the opposite effect. Importantly though, increased trade volumes could offset climate driven declines in plant naturalisations (Seebens et al. 2015).

As the character of vectors and pathways change, so will the processes by which biota are introduced. Patterns in unintentional introductions are likely to closely follow changes in transport as described above. These shifts in trade, culture-based industries, and tourism (Hoogendoorn and Fitchett 2016; Yumashev et al. 2017) will see some regions become new recipients of stowaway species, while others may experience elevated propagule pressure due to increased traffic and more hospitable conditions during transit along with shorter transit times. In contrast, it is possible that some regions will experience reduced invasion risk if historically important pathways become less important.

Intentional introductions are often linked to agriculture, agroforestry, horticulture, aquaculture, and fisheries (Richardson and Rejmánek 2011; Saul et al. 2017; van Kleunen et al. 2018). Thus, as the climate shifts and regions become less optimal for growing traditional crops and target species, these industries may begin growing new taxa or varieties that are better suited to the novel conditions. This could require the importation of species for culture from other regions, thus resulting in a new invasion threat. Such implications have already been seen in response to extreme weather events. During the recent devastating drought in Cape Town, South Africa, nurseries saw an increased demand for drought-resistant garden plants (Goodness 2018). Notably, this pertained not only to native plants but also to potted cacti, despite the recognition of cacti as an invasion threat in South Africa (Novoa et al. 2015). The potential for a new wave of plant invasions has also been highlighted in in the United States where the demand for ornamental plant species that are tolerant of warmer and drier conditions has increased in response to recent climate change (Bradley et al. 2012). Notably, potted plants are an important though unintentional vector for arthropods (Nentwig 2015) and thus an increased demand for ornamental plants is likely to result in increased introductions of associated species.

Interestingly, crop choice may also change in an effort to reduce carbon emissions and address climate change. For example, Switchgrass *Panicum virgatum* has been identified as a potential carbon-negative biofuel that could be grown outside of its native range (Tilman et al. 2006), although the risk of it becoming a problematic invader has been highlighted (Hartman et al. 2011). Plant species that are introduced as biofuels could become invasive as many of the attributes that make these species suitable as biofuels also make them potentially successful invaders (Chimera et al. 2010). Management responses to climate change could result in new invasion pathways. For example, assisted migration, which is the intentional translocation of species for conservation purposes, often in response to climate change, could result in invasions (Mueller and Hellmann 2008).

For the above it is clear that climate change may completely alter the global biogeography of invasions, routes, and propagule pressure as well as redefining the species targeted for translocation due to a change in human needs.

## The implications of a changing environment for the establishment and spread of alien biota

Establishment success and ensuing spread of alien species are influenced by an interplay between the abiotic and biotic nature of the recipient environment (Soberón and Arroyo-Peña 2017). As such, climate change could have direct impacts on native and alien species that could indirectly affect native-alien species interactions, and ultimately invasion success (Hellmann et al. 2008).

For an alien species to establish it needs firstly to survive and reproduce at the point of introduction, while spread requires the same outcome at the invasion front. Because physiological processes are often regulated by environmental factors such as temperature (Levitt 1980; Charnov and Gillooly 2003), changes in climate will affect the performance and success of both native and alien species. Presently, most literature implies that alien biota will be favoured or at least not negatively affected by climate change, while native species will be disadvantaged (Vilà et al. 2007; Hellmann et al. 2008; Thuiller et al. 2008). However, this is premised on the idea that native species ranges represent optimal conditions and environmental change will represent a challenge. This assumption, however, remains largely untested. With limited knowledge held on the physiological tolerance ranges of most species, especially in relation to the interactive effects of multiple environmental changes (e.g. ocean temperature and pH), generalisations about the directionality of effects on alien vs native biota and the implications for establishment and spread cannot be made with much certainty. An added complexity comes from the fact that hybridisation within invaded regions can lead to the emergence of lineages with differential tolerances to either parental line (Donovan et al. 2010). Hybrids might not only have higher plasticity to cope with climatic changes but changes in climate can lead to higher hybridization rates (Muhlfeld et al. 2014). Nonetheless, the vulnerability to warming of some tropical groups that are already living close to their thermal optima (e.g. terrestrial ectotherms (Deutsch et al. 2008) and many plants in tropical rain forests (Corlett 2011)) cannot be denied. Warming could thus favour invasion by other tropical taxa with higher thermal tolerances as native species are lost.

Presently many alien species are casual or are restricted to artificial habitats or modified urban environments (e.g. green houses, gardens, botanical gardens) (Hulme 2017; van Kleunen et al. 2018). In the northern hemisphere, cold winter conditions currently prevent survival in the wild, but future warming could facilitate their establishment and spread. Importantly, populations in protected microclimates could serve as persistent sources of high propagule pressure that could facilitate successful establishment in the wild and spread from urban areas under future conditions. In particular, this risk has been highlighted for garden plants (Dullinger et al. 2017) and spiders (Nentwig 2015) but is likely to also apply to other taxa that presently survive with assistance (e.g. those kept as pets; Lockwood et al. 2019).

While post-establishment spread in a poleward direction by various marine alien taxa is known to have been facilitated by ocean warming (Canning-Clode and Carlton 2017), evidence of such spread in freshwater and terrestrial species is less obvious (Rahel and Olden 2008; Hulme 2017). In freshwater systems, this is likely due to the fragmented nature of lentic and lotic inland waters that limits the ability of freshwater taxa to disperse when facing environmental change (Woodward et al. 2010). Such spread restriction will likely lead to species loss more than range shift, specifically when considering the high risk of extinctions for freshwater species when compared to their terrestrial counterparts (Collen et al. 2014). Nonetheless, predictions made using bioclimatic models suggest that spread in response to warming will occur for a variety of taxa (e.g. insects (Evans and Simpson 2010), freshwater fish (Rahel and Olden 2008), and plants (Bourdot et al. 2012)). Interestingly, such models suggest that while mountainous high elevation regions may be increasingly vulnerable to plant invasions under warming conditions, this response can be context specific (Petitpierre et al. 2016; Lamsal et al. 2018). Simultaneous increases in human disturbance and propagule pressure currently limit our ability to ascribe observed increased colonisation of mountainous environments over the last two centuries solely to climate change (Pysek et al. 2011). Notably, current predictions of how environmental change may affect alien species distributions are based primarily on realised niches, as reflected by current ranges. However, existing and fundamental niches can be larger than realised niches (Soberón and Arroyo-Peña 2017) and using only the latter as a proxy for tolerance ranges in predictive models can underestimate the environmental conditions under which species can persist. Additionally, genetic admixture between previously isolated lineages may increase genetic diversity in alien populations (Krehenwinkel and Tautz 2013), potentially enabling the hybrid to occur in conditions unfavourable to either parent species (Donovan et al. 2010). This may, at least partially, explain why niche conservation is not always observed between native and alien ranges (Beaumont et al. 2009; Gallagher et al. 2010) and highlights a challenge to predicting how climate change may affect the spread of both new and established alien species. Although species distribution models may be conservative, they can still be useful in identifying groups that could invade under future climatic conditions (e.g. ornamental plants in Europe (Dullinger et al. 2017) and marine zoobenthos in the Canadian Arctic (Goldsmit et al. 2020)). With such warning, policy makers and managers can take targeted steps to prevent introductions.

By altering physiological performance and population dynamics of alien and native species, changes in climate can ultimately indirectly affect invasion success through changes to alien-native species interactions (Zarnetske et al. 2012). As the outcomes of such interactions can be highly context dependant (Lord 2017; Skein et al. 2018) and our understanding of the implications of climate change even at the species level is relatively poor, our ability to predict indirect community effects remains limited (Lord et al. 2017). While these shortcomings in foundational biodiversity knowledge have been highlighted before (Zarnetske et al. 2012), they continue to hamper our ability to anticipate and manage interactions between climate change and invasions.

## The role of extreme climatic events

An important aspect of climate change is the increasing frequency and intensity of extreme events such as droughts, floods, storms, and heat waves (Rahel and Olden 2008; Mal et al. 2018). Unlike the mechanisms described above, extreme climatic events can influence invasions in any of the stages of the invasion process (Diez et al. 2012). In terrestrial systems, storm winds have been implicated in the movement of insects and plants (Burt 2002), while flooding has spread both aquatic invertebrate and vertebrate taxa (Cohen 1994; Canonico et al. 2005). Additionally, the disturbance associated with extreme events can dampen competition for resources, ultimately facilitating establishment and spread of alien taxa (Diez et al. 2012). This process has been observed in forests where removal of tree canopy cover by hurricanes can enable invasions by understorey plants (Horvitz et al. 1998) and on rocky shores where invasive mussels have been shown to dominate primary space following storms, despite the presence of native comparators (Erlandsson et al. 2006). An additional mechanism through which extreme events affect biological invasions relates to the broad physiological tolerance of many alien taxa. This characteristic can enhance survival of alien vs native taxa during droughts and heatwaves (Larson et al. 2009; Sorte et al. 2010), facilitating establishment, spread, and potentially increasing impacts (Diez et al. 2012). It is notable that while climatic events can interact with all stages of invasions, a single event (e.g. a hurricane or flood) could introduce and aid the establishment of an alien species.

## Interactions with other drivers of change

Besides biological invasions and climate change, other drivers of global change such as land-use change, $CO_2$ enrichment, exploitation, and pollution have negative consequences for biodiversity and society (Sala et al. 2000). However, none of these drivers act in isolation and interactions among them can compound their impacts (Burgiel and Muir 2010). Thus, while the focus of this paper is on the nexus between invasions and climate change, it is important to acknowledge that invasions will also be affected by other agents of change and that these too can be plotted onto the invasion process (Fig. 1). For example, the exploitation of forest resources can facilitate the transport of alien taxa into pristine areas (Walsh et al. 2004) while plastic pollution in the oceans represents an increasingly prevalent, though unintentional vector with increasing propagule pressure of fouling biota (Avio et al. 2017). Other drivers of change are recognised to affect the establishment and spread of alien taxa by effecting native communities. In particular, elevated atmospheric $CO_2$, and nitrogen deposition tend to provide invasive plants with a competitive advantage over native comparators (Liu and van Kleunen 2017) although this advantage can be moderated by temperature and rainfall (Bradley et al 2010). In turn, changes in land-use disturb natural systems resulting in increased resource availability and invasibility by reducing competition for previously limited resources (Lear et al. 2020). In marine systems, overfishing can reduce predator driven biotic resistance by removing predators (Skein et al. 2020), leaving systems vulnerable to invasive prey. Although the above examples are illustrative of how various drivers of change may interact with invasions, it is important to acknowledge that studies simultaneously considering multiple drivers of change are not yet common place and our ability to anticipate biological responses to suites of agents of change remains limited (Bradley et al. 2010).

## Impacts of alien species in novel ranges under changing climatic conditions

Impacts can manifest at any point after introduction and are not limited to any particular stage in the invasion process. These can be biological, socio-economic, or human-health related and, in some instances, species can have impacts in more than one of these spheres (Blackburn et al. 2014; Mazza et al. 2014; Bacher et al. 2018). As the impacts associated with many alien species provide the impetus for their management, understanding how climate change may affect impacts is of scientific and practical interest.

How a changing climate might affect biological impacts of alien species can be conceptualised in terms of the relative impact potential of alien and native comparators (Dick et al. 2017). This approach posits that changes in the per capita impact and relative abundance of these biota in response to environmental changes will alter the severity of impacts. Ultimately, these responses will be governed by the direct effects of climate change on individuals at the physiological level and the indirect effects on biotic interactions described above. While the theoretical framework for understanding biological impacts is well developed, on a practical level impacts are not routinely quantified with biases among ecosystems, across taxonomic groups, and between geographic regions (Jeschke et al. 2012; Ojaveer et al. 2015; Bellard et al. 2018). While more studies are clearly needed on the impacts of alien taxa in general, there is a particularly pressing need to assess impacts on resources that are likely to become scarcer under climate change. For example, alien plants increase transpiration and evaporation losses, reducing mean annual runoff by >5% in the Western Cape, South Africa (Le Maitre et al. 2020). In the absence of remedial action, this loss is expected to double (Le Maitre et al. 2020), posing a significant risk to water security in an area predicted to face reduced precipitation in the future.

Predicting how economic impacts associated with invasions might be affected by climate change is challenging, as these effects are often linked to biological processes. It has been suggested that to estimate the future economic impact of alien species, information on current impact, future potential distribution, and the likelihood of impacts remaining similar under predicted environmental conditions is required (Hulme 2017). Considering the level of uncertainty embedded in each of these aspects, accurate predictions remain elusive for most alien taxa. However, for well-studied invasions in areas for which present environmental conditions are well understood and models of future conditions are well developed (e.g. *Drosophila suzukii* in Europe (Gutierrez et al.

2016; Shearer et al. 2016; Mazzi et al. 2017) local knowledge could provide valuable insight into expected economic impacts.

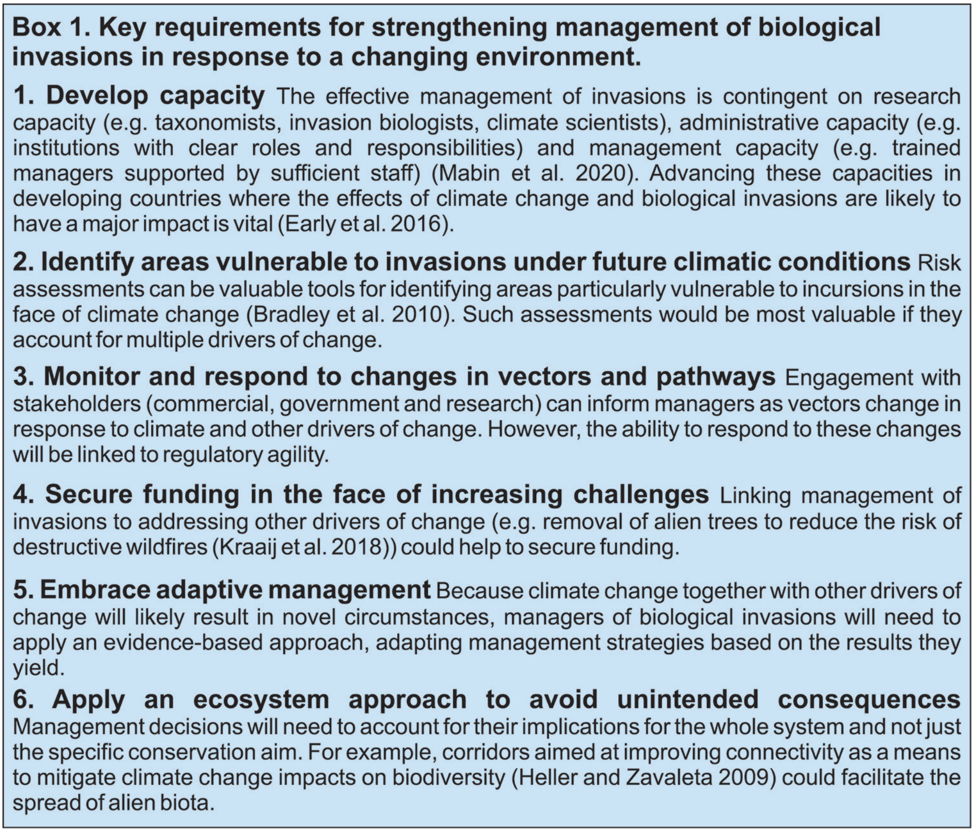
Impacts on human health under climate change are likely to be affected by shifting distribution and abundance of disease vectors (e.g. mosquitoes) and biota that are venomous or result in non-communicable diseases (e.g. allergenic reactions) (Fischer et al. 2011; Schindler et al. 2015). Although data remain scarce for many regions, in Europe alone more than 60 mammal, 70 bird, and 40 reptile species have been introduced along with their disease causing agents (Hulme 2014). Despite the obvious threat to human health and the potential implications for native taxa, the lack of dedicated risk assessment tools and the requisite data to implement them, challenges our ability to anticipate and prevent such introductions (Hulme 2014).

## What does this mean for management?

Because management approaches are linked to the various invasion stages (Fig. 1) these will face new challenges as the climate alters and other drivers of change progress. Despite much uncertainty, the prospects of successful management of incursions could be greatly improved by proactively addressing key management needs (Box 1). A major challenge will be to strengthen proactive response capabilities in countries that currently have low biosecurity capacity. The ability to meet this challenge will be intricately linked to capacity development in multiple fields including research, administration, and management (Mabin et al. 2020). Such advancements in developing nations will be particularly important, as these countries are often particularly vulnerable to multiple drivers of change, including biological invasions.

The use of risk assessments to identify areas particularly at risk to invasion (Bradley et al. 2010) can help to focus monitoring in susceptible areas. In turn monitoring in high risk areas can facilitate early detection and swift management responses, ultimately maximising the probably of management success (Genovesi 2005). This approach could be particularly important in relation to protected areas that are charged with protecting diversity and associated ecosystem services. In Europe, only a quarter of marine and terrestrial protected areas were known to support any of the "100 of the most invasive species in Europe" species (Vilà et al. 2009) between 1920 and 2015 (Gallardo et al. 2017). However, future climate facilitated species range shifts could alter this and compromise the ability of these protected areas to meet their conservation mandates (Gallardo et al. 2017). Although the invasion risk faced by protected areas remains to be considered in many regions, an increasing number of studies have highlighted an anticipated rise in risk in marine, terrestrial and freshwater systems (e.g. Markovic et al. 2014; Iacarella et al. 2020; Liu et al. 2020).

As the climate changes biosecurity will be confronted by changes in vectors and pathways that will require engagement with stakeholders, adaptation of present protocols, and potentially, new legislative tools (Seebens et al. 2015). As such measures can be slow to institute, a proactive approach is likely to be important in ensuring that



**Box 1. Key requirements for strengthening management of biological invasions in response to a changing environment.**

**1. Develop capacity** The effective management of invasions is contingent on research capacity (e.g. taxonomists, invasion biologists, climate scientists), administrative capacity (e.g. institutions with clear roles and responsibilities) and management capacity (e.g. trained managers supported by sufficient staff) (Mabin et al. 2020). Advancing these capacities in developing countries where the effects of climate change and biological invasions are likely to have a major impact is vital (Early et al. 2016).

**2. Identify areas vulnerable to invasions under future climatic conditions** Risk assessments can be valuable tools for identifying areas particularly vulnerable to incursions in the face of climate change (Bradley et al. 2010). Such assessments would be most valuable if they account for multiple drivers of change.

**3. Monitor and respond to changes in vectors and pathways** Engagement with stakeholders (commercial, government and research) can inform managers as vectors change in response to climate and other drivers of change. However, the ability to respond to these changes will be linked to regulatory agility.

**4. Secure funding in the face of increasing challenges** Linking management of invasions to addressing other drivers of change (e.g. removal of alien trees to reduce the risk of destructive wildfires (Kraaij et al. 2018)) could help to secure funding.

**5. Embrace adaptive management** Because climate change together with other drivers of change will likely result in novel circumstances, managers of biological invasions will need to apply an evidence-based approach, adapting management strategies based on the results they yield.

**6. Apply an ecosystem approach to avoid unintended consequences** Management decisions will need to account for their implications for the whole system and not just the specific conservation aim. For example, corridors aimed at improving connectivity as a means to mitigate climate change impacts on biodiversity (Heller and Zavaleta 2009) could facilitate the spread of alien biota.

**Box 1.** Key requirements for strengthening management of biological invasions in response to a changing environment.

biosecurity keeps pace with evolving vectors and pathways. Attempts to standardise pathway classification and reporting of pathway importance (CBD 2014) is promising for managing changes in pathways, but not without its challenges (Faulkner et al. 2020). It is notable that not only will managers have to contend with new introductions, but many species that have been introduced or are naturalised could become invasive under future conditions. For example, much of Europe faces a high naturalisation risk from ornamental garden plants (Dullinger et al. 2017) with future climate change expected to increase this risk for many species (Haeuser et al. 2018). This invasion debt (Essl et al. 2011) will place a further burden on management resources. In addition, competing demands from other drivers of global change are likely to place a strain on resources available for biosecurity. For example, responding to extreme events such as floods will likely mean that fewer resources will be available for management of alien taxa. However, linking management of invasions to efforts to address other drivers of change (e.g. removal of alien trees to reduce the risk of destructive wildfires (Kraaij et al. 2018)) could help to secure and efficiently use scare resources.

Importantly, eradication, containment, and mitigation efforts are likely to be affected by how environmental changes affect alien species performance and the outcomes of biotic interactions with native biota (Bellard et al. 2018). As highlighted above, these will depend on the relative physiological tolerances of the different taxa. As such, an adaptive management approach that draws on previous knowledge but responds to observed outcomes is likely to offer a sound evidence-based approach to managing invasions in a changing world. Such an approach is likely to be particularly relevant with respect to the use of biological control agents. Notably, climate change could have positive, negative, or neutral impacts on weed biocontrol agents (Sun et al. 2020). This highlights the need to account for predicted future environmental changes in pre-release trials of new biocontrol agents and the use of an adaptive approach to managing ongoing biocontrol programs.

Although management actions aim for specific outcomes, the interconnected nature of ecological systems means that targeted actions can have ecosystem level implications. For example, corridors aimed at mitigating climate change impacts on biodiversity by improving connectivity (Heller and Zavaleta 2009) could enable the spread of alien biota, while assisted migration applied as a restoration tool may facilitate invasions (Derham et al. 2018). The application of an ecosystem approach to interventions could help to avoid unintended consequences. While this and the other measures discussed above could facilitate effective management of invasions in general, they will be particularly important in helping managers to navigate challenges in the face of climate change.

## Challenges to a consolidated understanding of the implications of climate change for biological invasions

From the above it is clear that although numerous interactions between climate change and biological invasions have been recorded and we are able to make theoretical predictions about such outcomes in other instances, we do not have a consolidated understanding of the interplay between these drivers of global change (Bradley et al. 2010). This situation can be improved by addressing the following key challenges.

### Gaps in knowledge

Probably the greatest obstacle to our understanding of how climate change will affect biological invasions stems from a lack of foundational knowledge (Zarnetske et al. 2012). Such gaps are evident in biological fields spanning taxonomy (e.g. cryptic invasions often go unrecognised (Morais and Reichard 2018)), natural history (e.g. life-history traits are seldom quantified, even for taxa considered to be well studied (Swart et al. 2018)), ecology (e.g. species ranges are often not georeferenced or routinely monitored (Pereira and Cooper 2006)), and even invasion biology (e.g. the inability to assign cryptogenic species as alien or native (Mead et al. 2011)). However, just as important is the lack of foundational environmental data in many regions, even for key parameters such as temperature and ocean pH (e.g. coastal carbonate chemistry remains unknown along the South African coast). An important avenue for addressing such data deficiency is to establish long-term monitoring programs that match data on the distribution and relative abundance of native and alien biota with environmental data. Additionally, to gain a mechanistic understanding of how establishment, spread, and impacts of alien biota may be affected by a changing climate, it is vital to assess physiological tolerances of native and alien taxa and how these may be altered through adaptation. However, in recognition of the complexities of climate change it is vital that future research considers how multiple environmental stressors may interact to affect such physiological outcomes (Todgham and Stillman 2013).

Inherent in the above gaps is a geographic bias in our understanding of biological invasions (Turbelin et al. 2017) and biotic responses to recent climate change (Bellard et al. 2018). In general, few alien species are reported from Africa and Asia (Turbelin et al. 2017), and in Africa at least, this likely reflects low capacity to detect and report on invasions rather than few invasions (McGeoch et al. 2010). It is notable that studies considering the ecological and evolutionary consequences of climate change are also sparse in these regions (Parmesan 2006), highlighting that our ability to understand the confluence of invasions and climate change will remain constrained until this bias is addressed. Addressing these gaps in knowledge should be prioritised as these regions support numerous biodiversity hotspots (Myers et al. 2000).

## Transparent and reproducible taxonomy

A pillar of good science is reproducibility. While most publications uphold high standards with regards to reporting of methods, evidence of correct species identifications (e.g. citation of species descriptions used) is seldom provided (Bortolus 2008). While this issue is pervasive in ecology in general (Vink et al. 2012), it is particularly problematic in invasion biology, as the correct identification of study taxa underpins the essence of the field (Pysek et al. 2013). In order to improve the rigor of primary studies and enhance their value in terms of understanding how biological invasions may be effected by climate change, it is essential that the species descriptions used be cited (Meier 2016). This will facilitate reproducibility while also enabling researchers to track the use of species names, even when taxonomic assignments change through time.

## Context dependency

Variability in invasions is well recognised and poses a particular challenge to our understanding of the processes driving incursions and our ability to manage them (Kueffer et al. 2013). This has led to attempts to use generalisations at a broad-scale to enhance understanding (e.g. Hui et al. 2013), but this can oversimplify patterns and have many exceptions (Novoa et al. 2020). A contrasting approach has been to focus on detailed case studies that comprehensively document individual invasions, but such results can lack generality (Robinson et al. 2017). Invasion syndromes (*sensu* Novoa et al. 2020) offer an approach for identifying generalities in invasions that are evident when grouping pathways, alien species traits and ecosystem characteristics that display predictable dynamics and impacts. The implication is that specific management approaches are thus identifiable per syndrome. This conceptual leap is an important step towards accounting for context dependency of invasions in light of climate change, as pathways, species traits and recipient environments could all be affected into the future. While some invasion syndromes have been identified (Novoa et al. 2020), for this approach to be fully tested, it needs to be applied to more systems. In the context of future climate change, invasion syndromes provide a theoretical foundation for hypothesis testing research. Depending on which of the three characteristics (pathways, alien species traits, or recipient environments) are affected and the nature of the effects, syndromes may remain intact, be partially dissolved or may no longer be valid. In any event, this offers a mechanism for incorporating climate driven changes into the human, biotic, and abiotic aspects of biological invasions. Invasion syndromes that hold, even under climatic change would vastly improve our ability to manage alien taxa in a dynamic world.

## Valuable yet problematic databases

Because of the transboundary nature of both invasions and climate change, it is vital to place foundational data on well-maintained open access databases. Such broad-scale datasets could be pivotal in developing a spatial understanding of climate induced impacts on native and alien biota and providing inputs in support of environmental policy (Groom et al. 2017). To some degree this already happens through numerous international databases including GBIF, WoRMS, WRiMS, and the Encyclopaedia of Life. However, despite the value that these databases offer as expert-driven, collaborative, and centralised open-access sources of species occurrence data (Costello et al. 2018), they can face challenges in ensuring that data is accurate, up-to-date, and, importantly in the current context, georeferenced (Yesson et al. 2007). These challenges are aggravated by the fact that direct funding for the maintenance of foundational databases such as these is often limited, requiring researchers to volunteer their time. However, should these challenges be addressed, open access databases could provide a valuable source of information to researchers and managers alike.

## A problem of scale

Future climate predictions are generally made at a global spatial scale. While this approach certainly has value, it can obscure important regional trends. For example, while at a global scale the present trend of ocean warming is predicted to continue (IPCC 2019), some regions along the South African west coast are in fact cooling (Rouault et al. 2010). This highlights the need for research considering the biological implications of climate change to account for both regional and local scale changes. Although theoretically sound, this approach may pose a practical challenge, as collection of data at a regional scale is linked to scientific capacity and funding and these practical constraints are notoriously uneven among regions (Costello et al. 2010). Ultimately, this results in geographic bias in fine-scale environmental data and regional understanding of the impacts of climate change (Pasgaard et al. 2015). While the collection of remotely sensed data may offset this challenge in some instances (Pettorelli et al. 2014), some environmental variables require the collection of physical samples (e.g. alkalinity when quantifying ocean carbonate chemistry to understand ocean acidification). Thus, until the scale at which environmental data are collected matches the spatial scale at which biological impacts manifest, our ability to fully understand the repercussions of climate change for alien and native biota will remain limited.

## Caveats associated with analytical tools

The accurate forecasting of invasions, their rate of spread and potential range in novel regions are key requirements for effective management of invasions (Meyerson et al. 2019). Ecological niche models are a commonly applied predictive tool that use species traits (e.g. environmental tolerance) to map the potential range of alien species under current and predicted climates (Bellard et al. 2013). This is done by using the environmental conditions within a species known range (i.e. realised niche) as a proxy for physiological tolerances, which are then mapped onto the area of interest. While the benefit of this approach is that it enables pre-emptive assessment of invasions, it can fail to identify areas suitable for invasions as the fundamental niche may not be fully captured within the known range (de Andrade et al. 2019). Additionally, this approach assumes that processes controlling species distribution remain the same through time and space, and neglect novel interactions among biotic and abiotic variables (Elith and Leathwick 2009; Evans et al. 2015). Calibrating models with information from native and known alien ranges and reassessing niche changes as invasions progress can help to address these challenges (Pili et al. 2020). Unfortunately, models inherently become more accurate as species move towards occupying their full niche, but the predictive and applied value of models in such late stages of invasion are limited. Nonetheless, applying a mechanistic approach underpinned by a knowledge of physiology and life history traits where data allows can increase the value of predictive models (Meyerson et al. 2019).

## Interdisciplinarity

Due to the multifaceted nature of biological invasions and the human dimension at the core of the problem, it is clear that interdisciplinarity is key to improving our understanding of the intersection between climate change and biological invasions. The emergence of invasion science out of ecology has been suggested as the reason for strong interdisciplinary interactions within the natural sciences but the need for meaningful engagement with social science is increasingly being recognised (Vaz et al. 2017). In terms of climate change and invasions, resolving questions around future changes in pathways and how best to manage them are likely to benefit immensely from an interdisciplinary approach. For example, understanding how agriculture might shift in response to changes in climate will enable early engagement with stakeholders and hence better biosecurity planning.

## Conclusion

Unprecedented changes in climate will alter the nature of biological invasions and pose new challenges to their management. Changes in vectors and pathways will be largely directly human related and thus can be managed. However, the effectiveness of preventative measures and adaptive management will be greatly enhanced if they are proactive. For example, adaptation of importation permitting processes that anticipate import requests for new species or cultivars that may be better suited for culture under new environmental conditions will improve biosecurity outcomes in the face of climate change. In contrast to introduction and transport that are related to human actions, establishment and spread of alien biota are outcomes of ecological processes. Thus, our ability to effectively manage incursions through control, mitigation, and eradication will depend largely on our understanding of how climate change affects fitness at the species level and interactions among taxa. To this end, it is important that we address current knowledge gaps and invest in foundational understanding that will support informed management decisions into the future. Long-term monitoring of alien and native taxa offers an important tool for tracking invasions and gaining first insights into impacts. While context dependency in invasions already poses a notable challenge to their effective and efficient management (Novoa et al. in 2020), this is likely to be exacerbated by a changing climate. However, through proactive and adaptive management our ability to prevent and manage invasions under these challenging circumstances will be enhanced.

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