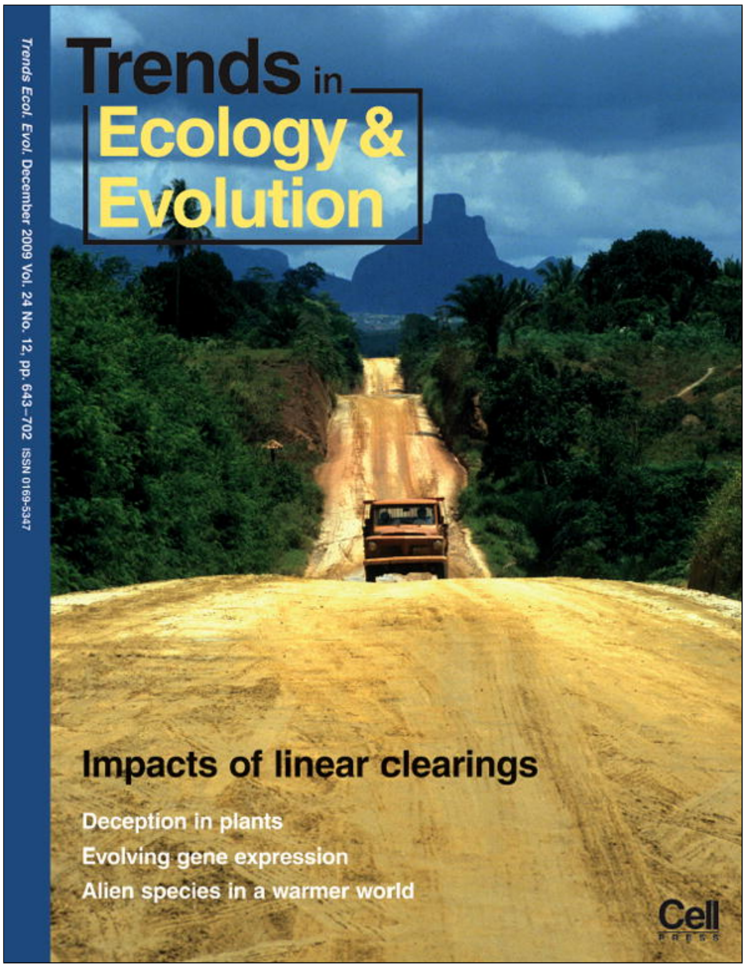
Trends Ecol. Evol. December 2009 Vol. 24 No. 12, pp. 643–702 ISSN 0169-5347
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Alien species in a warmer world: risks and opportunities

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Climate change and biological invasions are key processes affecting global biodiversity, yet their effects have usually been considered separately. Here, we emphasise that global warming has enabled alien species to expand into regions in which they previously could not survive and reproduce. Based on a review of climate-mediated biological invasions of plants, invertebrates, fishes and birds, we discuss the ways in which climate change influences biological invasions. We emphasise the role of alien species in a more dynamic context of shifting species' ranges and changing communities. Under these circumstances, management practices regarding the occurrence of 'new' species could range from complete eradication to tolerance and even consideration of the 'new' species as an enrichment of local biodiversity and key elements to maintain ecosystem services.

Does climate change affect biological invasions?

Climate change and biological invasions are two important drivers affecting biodiversity and ecosystem services [1,2]. However, their effect on biodiversity has usually been assessed independently, despite good scientific reasons to expect the rate and extent of biological invasions to be influenced by climate change [3–5]. The various pressures from global change in general, and climate change and biological invasions in particular, should therefore be considered in a more integrated manner.

The changes in climatic conditions that have occurred over recent decades have resulted in altered population dynamics of native species and, thus, also their geographic ranges, the structure and composition of communities and functioning of ecosystems [6,7]. Similarly to these observed responses of native species, climate change might also directly influence the likelihood of alien species being introduced into a territory and also affect their chances of naturalization (see Glossary). Furthermore, an indirect effect of climate change might occur as some ecosystems

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Glossary

Alien: an organism occurring outside its natural past or present range and dispersal potential, whose presence and dispersal is due to intentional or unintentional human action.
Apomictic/parthenogenic: asexual form of reproduction without fertilization.
Casual: refers to organisms that do not form self-replacing populations and rely on repeated introductions for their persistence.
Cryptogenic: a term used for species of unknown origin or means of arrival, which cannot be ascribed as being native or alien [62].
Naturalization: refers to aliens that form free-living, self-sustaining (reproducing) and durable populations persisting in the wild.
Founder population: a new population in a region, usually consisting of a small number of (here: introduced) individuals.
Introduction/introduced: direct or indirect movement by human agency, of an organism outside its past or present natural range.
Invasion/invasive: refers to established alien organisms that are rapidly extending their range in the new region. (This is usually associated, although not necessarily for an organism to qualify as invasive, with causing significant harm to biological diversity, ecosystem functioning, socio-economic values and human health in invaded regions).
Native: an organism that has originated in a given area without human involvement or that has arrived there without intentional or unintentional intervention of humans.
Trailing edge: the boundary of distribution where a species is retreating; opposite to the expanding range margin.
Voltinism: the number of broods or generations of an organism in one year.

become less resistant to invasive species or more resilient to their impacts under future climates. In extreme cases, climate-driven invasions could lead to completely transformed ecosystems where alien species dominate function or richness or both, leading to reduced diversity of native species [8,9].

Based on these theoretical and conceptual aspects, we present here a compilation and synthesis of the evidence for observed changes in biological invasions arising from recent climate change. We evaluate the relative importance of the direct and indirect effects of climate change on the invasion process, and compare these findings with studies on climate-induced changes in native species. We reason that, with continued climate change, existing definitions and crucial distinguishing factors of native and alien species become increasingly blurred. The role of alien species should therefore be assessed in a more integrated and dynamic context of shifting species' ranges and changing compositions and structures of communities. Resident species can become increasingly poorly adapted to the local environment, whereas newcomers might be better adapted and, thus, more competitive under the new conditions. Hence, irrespective of the mode of original introduction, the 'new' species might become acceptable or even necessary at some sites to assure local ecosystem function continuity and service provision.

Most of the available literature on climate-induced biological invasions deals with warming effects. Therefore, we focus primarily on temperature and less so on the effects of changing precipitation patterns. The geographical coverage of reported examples of climate-induced biological invasions is uneven among continents, with most of the examples reported from Europe, followed by Asia, with fewer from other continents. Thus, although our study focus is more an effect of availability of, and accessibility to, reported case studies, there is a global dimension to the issue.

We follow the sequential stages of an invasion process (Figure 1), starting from the introduction of a few precursor individuals, which only temporarily occur in a site during short favourable climatic periods or are spatially restricted to favourable micro-habitats. Continued climatic warming might then prolong the duration of these occasional occurrences of initial introductions, increase their frequency or enlarge the range and area of suitable habitats, making it more likely for these species to persist, to occur more frequently and to develop larger populations. With further global warming, alien species originating from warmer regions could build up numerically and spatially larger populations that might spread to wider areas. This is true for casual (i.e. temporary) occurrences as well as naturalizations. Hence, a climate-mediated invasion process follows the classic pathway of several sequential transitions [10] but with climatic parameters (here: temperature) as major determinants for at least some of the transitions (Figure 1).

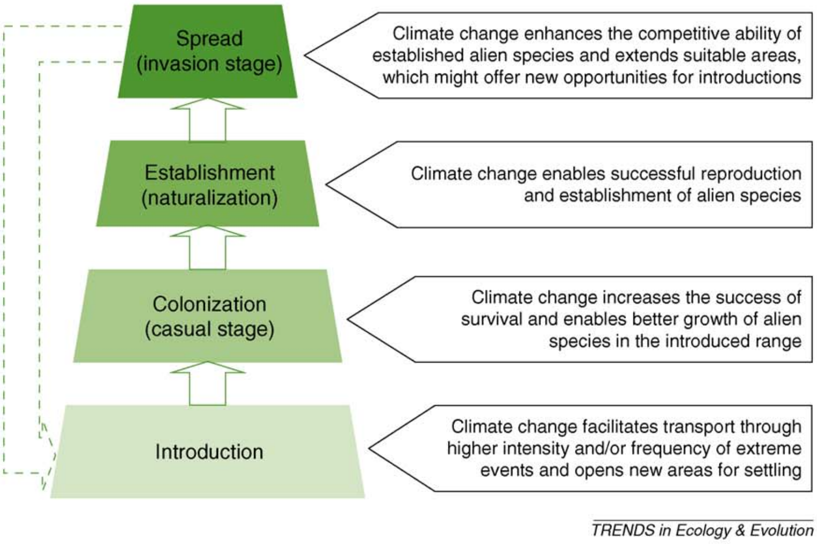

Figure 1. Influence of climate change on all the sequential transitions of a successful invasion process. Based on the scheme of Ref. [10], with their terms indicated in parentheses. For examples, see text and Online Supplementary Material.

Interplay of global warming and biological invasions

There is increasing evidence that global warming has enabled alien species to expand into regions where previously they were not able to survive and reproduce. Based on case studies of climate-mediated biological invasions that have been reported for plants, invertebrates, fishes and birds (see also Online Supplementary Material), we discuss the ways in which climate change influences the sequential stages of an invasion process.

Offering new opportunities for introductions

Populations of alien plants and animals are considered more likely to survive if they are introduced to areas with climatic conditions that are similar to those in their native distribution range. Temperature is a key factor limiting survival, growth and reproduction in plants and many animals [11,12]. Hence, the survival of alien species introduced from habitats in warmer regions to new areas with colder conditions depend on locally heated 'islands', such as thermal effluents for aquatic species [13], urban areas [14] or anthropogenic habitats (especially buildings) [15]. Otherwise, ecological adaptation is needed; for example, the tropical seaweed *Caulerpa taxifolia* evolved tolerance for colder temperatures in aquaria in Europe before being released and spreading widely in the Mediterranean Sea [8].

Global warming could provide new opportunities for introductions to areas where, until recently, introduced species were not able to survive. In temperate regions, many introduced ornamental plants from warmer regions required overwintering indoors for survival. However, in recent years, palms such as *Trachycarpus fortunei* are prominent examples that have successfully been planted outdoors and survive all year unprotected owing to generally milder winter conditions [16,17]. Furthermore, a recent analysis of commercial plant nurseries in Europe has shown that many garden species are already planted and survive 1000 km further north than their known natural range limits [18].

In addition to the removal of physiological constraints, climate change can also affect the dispersal pattern of species in various ways. For example, warmer nocturnal temperatures increase flight activity of winter pine processionary moth *Thaumetopoea pityocampa* females, and thereby enable them to disperse over greater distances [19]. A recent survey showed that the phenology of native and alien aphids largely depends on climatic variables [20]. It has also been calculated by using selected climate change scenarios that, on average, the first aphid occurrence is expected to occur 2–3 days earlier every decade.

Furthermore, the long-range dispersal of organisms by air is controlled, to a large extent, by atmospheric circulation patterns and often depends on extreme climatic events [21]. Increases in greenhouse gases and the associated general warming are likely to lead to more extreme climate events [22] such as floods, resulting in escapes of previously confined aquatic species [23], and the removal of existing vegetation and creation of bare soil, which is then easier to colonize.

Global warming also modifies human activities in a way that might increase the chances of invasion. For example, climatic warming is likely to result in the receding of summer Arctic ice cover to provide a seasonal trading route through the northern oceans. This link between the North Atlantic and North Pacific oceans would provide access for cold-water species to either ocean [24]. Likewise, the connection of geographically distant basins through waterways to overcome water consumption shortages as a result of climate change or increased irrigation of agricultural lands could also increase the distribution range of present and new invaders [25].

Facilitating colonization and successful reproduction

The presence of a 'new' species does not automatically lead to successful establishment. Unless invaders reproduce clonally, are self-compatible, apomictic or parthenogenic, being present in sufficient numbers is one of the key prerequisites for establishing a founder population [26,27]. In this regard, climatic factors might also have an important role if they can increase the per-capita reproductive output for any given population density. Species introduced from warmer regions to temperate areas have, until recently, been constrained by too short a growing season, which prevented several species from becoming naturalized; for example, by being unable to set fruit [28,29] or to compete successfully with resident species [17,30], as was the case for the cherry laurel *Prunus laurocerasus* in temperate areas of central Europe [31]. This could be about to change with warmer temperatures extending the growing season of plants and reproductive period of animals. There is evidence of a strong association between patterns of the emergence of gypsy moths *Lymantria dispar* and climatic suitability in Ontario, Canada [32]. Pheromone trap records indicated a significant increase in the distribution of this alien moth in this region since 1980. However, between 1992 and 1997, a temporary decline in climatic suitability occurred and resulted in a pronounced reduction in the area of defoliation by this species. Since 1998, the trend has reversed, with the consequent resurgence in defoliation and increased frequency of moths in pheromone traps further north and west in Ontario and other Canadian provinces. In the northern Mediterranean Sea, higher water temperatures have enabled former sterile pseudopopulations of the ornate wrasse *Thalassoma pavo* to reproduce and establish fertile populations [33]. Former greenhouse inhabitants such as the three scale species *Diaspidiotus distinctus*, *Coccus hesperidum* and *Icerya purchasi* have recently been found outdoors in Switzerland [34]. Also, non-native biological control agents of greenhouse pests, such as the predatory bug *Macrolophus caliginosus* [35] and the predatory mite *Neoseiulus californicus* [36] in the UK, have begun to establish outside the greenhouse environment. A recent survey listed >400 insect species of Australasian, African and Central and South American origin that have established in Europe, with most occurring in the Mediterranean region [37].

Enabling population persistence and spread

Global warming might also be responsible for the sudden spread of established alien insects and diseases, often causing serious economic or ecological hazards. The southern green stink bug *Nezara viridula*, formerly a sub-tropical species, has been expanding its range northward in temperate regions of Japan and Europe since the 1960s, probably because of reduced mortality resulting from milder winters. In the newly invaded regions in Japan, it has become a major pest and out-competes the indigenous *Nezara antennata* [38]. Similarly, the main invasion of the buffelgrass *Pennisetum ciliare* into the Lower Sonoran Desert of southern Arizona coincided with warmer winters since the 1980s. As with other neotropical species, buffelgrass is sensitive to low winter temperatures; thus, its range is expected to further expand north and upslope as minimum temperatures continue to increase [39].

Furthermore, in organisms for which population dynamics are mainly controlled by temperature, global warming could increase rates of dispersal and development. For example, increasing temperatures could lead to the production of an additional yearly generation [40,41]. In Japan, the American fall webworm *Hyphantria cunea* shifted from having two generations per year to three in at least a part of its range; in addition, important changes in some life-history traits, such as the crucial photoperiod for diapause induction, have occurred, enabling the species to expand its range, mainly towards the north of Japan [42]. Similarly, in European mountain forests, the native spruce bark beetle *Ips typographus* is changing voltinism as a consequence of the disproportionately large warming at high elevations [43], which could result in unprecedented outbreaks, as seen with the mountain pine beetle *Dendroctonus ponderosae* in British Columbia, Canada [44]. The same might also affect coniferous plantations in areas outside the native range, where conifers had been introduced for commercial purposes.

Mechanisms underlying invasion success in the context of climate change

All these aforementioned examples (and for more case studies see Online Supplementary Material) suggest that changing climatic conditions, and warming in particular, appear to have had an increasingly important role in triggering increases in population abundance and distribution not only of native but also of alien species since the 1970s, when climatic conditions began to change. For many cases, an in-depth understanding of their ecological limits and how these have changed during the recent past supports this hypothesis. Such changes are particularly obvious at higher latitudes and altitudes, where previously there were thermal constraints. For example, the range distribution of the pine processionary moth *Thaumetopoea pityocampa* is no longer limited by unfavourable larval feeding conditions (i.e. night air temperature $<0\ ^{\circ}\mathrm{C}$ and temperature inside the nest $<9\ ^{\circ}\mathrm{C}$ on the preceding day) [45], enabling the species to expand its existing range, but also to colonize new areas that are disconnected from its present distribution. Plants such as the palm *Trachycarpus fortunei* have also benefited from milder winter conditions; mean temperatures of the coldest month $>2.2\ ^{\circ}\mathrm{C}$ in the past few decades have enabled this species to establish fertile populations in the wild [17]. Changes in climatic conditions that result in a prolonged growing and reproductive period often provide alien species with exploitable opportunities [46]. As a consequence, global warming can shift or breach barriers that previously limited spread and thus enable expansion into areas where the species were previously kept in check by climate ([47,48], but see [49]).

These examples show that some alien species benefit from ameliorated conditions, mainly owing to warmer temperatures. Less is known about introductions that failed or species that show range contractions or reduced impacts as a consequence of climate change, as suggested for tropical ectotherms [50,51]. Moreover, as well as temperature, other aspects of climate change, such as changes in precipitation regimes [52], are also likely to influence invasion processes. There is observational evidence from long-term monitoring data gathered since 1993 suggesting that increase in rainfall promotes a wider distribution of the introduced Argentine ant *Linepithema humile* into new areas in California, USA [53]. A snow addition experiment in North American mixed-grass prairie showed that increases in snowfall would enhance the recruitment, and therefore abundance, of alien forbs [54]. By contrast, there are also scenarios where native species might regain competitive advantage over the alien invader, depending on the potential seasonal increase in precipitation [55]. As in the case of climate change impacts on native species, the data on impacts of changing rainfall regimes on alien species is less readily available than for temperature, and it remains to be seen if general, predictable patterns will arise.

Climate change blurs migration and invasion

The increasing number of colonization events and subsequent establishment of species originating from regions with a warmer climate than in the area of establishment and spread is remarkable (our (non-exhaustive) list provided in the Online Supplementary Material includes >100 taxa). Such species appear to have responded to the changed climatic conditions of the recent past, which enabled them to reproduce and establish in the presence of resident species. Simultaneously, native species have also exhibited marked natural poleward movements from warmer regions, sometimes at the expense of local resident species that are adapted to colder climates [56–59]. For example, the annual numbers of migratory lepidopteran species in southern Britain are increasing, and are linked to positive temperature anomalies in spring and summer. They are considered to represent a competitive threat to resident species which typically have lower mobility and are more specialized in habitat requirements [60]. Similarly, the rapid increase in the establishment of migrant butterflies on the Nansei Islands (Japan) during the twentieth century was correlated with increasing surface temperatures [40]. There has been a general increase in the number of Mediterranean dragonfly species in middle and northern European countries, and African species are expanding their range to southern Europe, whereas Eurosiberian species are showing range contractions [61]. However, it is not known for every event whether the species arrived autonomously at the new location or profited from anthropogenic assistance, thus, the term ‘cryptogenic’ has been suggested for a species that is not demonstrably native or introduced [62].

It is often difficult to disentangle human-mediated movements and natural migration processes. For example, the present northward expansion of the native moth *Thaumetopoea pityocampa* probably results from a combination of a natural short-range expansion triggered by climate warming and of long-distance events where moth pupae are carried with the soil accompanying large pine trees translocated by humans as ornamentals (A. Roques, personal observation). Mediterranean insects such as the praying mantis *Mantis religiosa* and the bush cricket *Meconema meridionale* are expanding their native range in southern Germany, but they are also found further north, far away from their natural range; these populations are considered to be the result of accidental transport by humans [61].

With continued climate change, native species are forced to shift their ranges over ever-larger distances and/or depend on human assistance to reach suitable habitats. In times of human domination of ecosystems of the Earth, their transfer to the new habitat might have occurred directly with human assistance [18,63,64] or indirectly profiting from human infrastructures linking previously unconnected areas [25]. Hence, it becomes increasingly difficult to assess the role of humans in the observed range expansion [65,66], especially if species originate from the same continent or adjacent regions, but human assistance in their transfer cannot be excluded. This increases the risk of being perceived in the new habitat as an alien invader. Thus, a crucial distinguishing factor between native and alien species for the actual definition [67] and also for international agreements [68] becomes increasingly blurred with continued climate change.

Consequences of climate-mediated invasions

Alien species can be viewed as drivers and passengers of change in biological communities [69,70]. Many invasive species exert strong impacts on invaded communities and ecosystems [71] and transform ecosystem properties [10], which inevitably leads to changes in biological communities. The consequences of climate-mediated biological invasions are far-reaching and more controversial than those of past invasions not affected by climate change, where species typically originate from habitats with similar climatic conditions [72,73]. In climate-mediated invasions, the occurrence of an alien species depends on a change in site conditions that might push the system to a different location in environmental space. For example, milder winters changed the environmental space of deciduous forests to conditions that are now more suitable for evergreen broad-leaved species [31]. As a consequence, resident species can become increasingly poorly adapted to the local environment, which will then provide opportunities for newcomers that are better adapted and, thus, more competitive under the new conditions. Expanding native and alien species sharing similar traits and site preferences could establish mixed communities, such as a new assemblage of evergreen broad-leaved plants establishing in former deciduous broad-leaved forests at the southern foot of the European Alps [74]. Likewise, combinations of the invasion of alien species and climate change have resulted in the reorganization of marine ecosystems, as shown for example in the Atlantic waters off the coast of the USA [75] and Europe [76], and in the Mediterranean Sea [77]. Such mixed assemblages and the resulting 'novel ecosystems' [78] raise important questions in an applied context; for example, which factors enable native species to persist with invaders once the latter have established [79]? Which invasive species should be targeted for control and which ones can be ignored [80]?

Environmental changes, producing expanding or shifting species' ranges, respect neither political borders nor those of nature reserves. Hence, some species that increase their range as a result of climate change might be perceived in a new administrative region as alien and could be subject to varying forms of control to prevent their spread [60]. From this perspective, conservation strategies should also respect and consider dynamic ecological processes to preserve biodiversity [81,82], otherwise well-intentioned control measures against invasion might result in unexpected outcomes [83,84].

Lack of knowledge and research needs

Most of the current information about range shifts and invasions comes from the plant and animal kingdoms, whereas little is known about invasions of alien microorganisms [85]. For example, modern forestry practice uses commercial mixtures of symbiotic ectomycorrhizal fungi for successful establishment of trees in silviculture [86], transporting them away from their native distribution range. The impacts of these alien fungi on local ecosystems are unknown, not to mention the impacts of the interaction with climate change. What is known, however, is that the introduction of symbionts can trigger the invasion of alien trees, such as pines, in parts of the southern hemisphere [87].

Another gap in our knowledge is that there is an obvious unbalanced coverage of evidence for climate-induced invasions. Most of the existing knowledge focuses on changes in temperature because pattern and trend in temperature are less heterogeneous than expected for precipitation regime [22], which makes it easier to derive general trends. Nonetheless, changing patterns of rainfall and water availability are a major component of global climate change and could impact large parts of the world, such as Australia, Africa, as well as parts of Asia and the Americas, where water is the major limiting factor. Hence, future research should provide a more balanced picture of climate-induced changes, both geographically and in terms of factors other than temperature. There is also more evidence of expanding range margins than retreats and, as in the case of climate-induced range shifts in native species, the trailing edge of alien species' ranges remains poorly studied [88].

The interactions of the various pressures involved in global change (e.g. changes in climate, atmospheric composition in terms of CO_2 and nitrogen compounds, changing land use) and the associated feedback effects are likely to represent one of the largest uncertainties in projections of future biodiversity change [89,90] and will have profound impacts on research into global change and ecosystem management. The same applies for indirect impacts, as for example for aquatic environments the effects of changing temperatures on water column stratification, changes in ocean currents, pH, or upwelling, adding further question marks to the longer-term development of ecosystems under climate change [91].

The simultaneous action of all these intervening pressures are expected to result in synergistic effects, meaning that, in combination, they have a greater total effect than the sum of individual effects alone [92]. In this framework, the role of alien species should be assessed in a more integrated and dynamic context involving shifting species' ranges and changing compositions and structures of communities under changing environmental conditions.

Conclusions

In a changing world, it will be increasingly difficult to evaluate the impacts of alien species and prioritising species for removal, and it is likely that the increasing presence of 'new' species and the decline of 'old' ones will change successional patterns and ecosystem functioning [93,94]. With continued climate change and the resulting increasing discrepancy between the requirements of resident species and altered environmental conditions, one should take into account that some of the alien species that are earmarked for control today might become acceptable or even desired species at some sites tomorrow to assure the functions and services of local ecosystem [95]. Although this cannot be an excuse to ignore current threats from alien species, plans to control them should consider the potential consequences that such control might also have for native species and ecosystems under climate change scenarios.

These changes pose complex challenges for the management of biodiversity as well as of wild and cultivated resources and could include implications for ecosystem functioning, especially with the addition or loss of ecosystem engineers [96]. Hence, management practices with regard to the occurrence of 'new' species will require comprehensive evaluation of changing habitat conditions and will depend on the individual case. They could range from complete eradication to toleration and consideration of the 'new' species as an enrichment of the local biodiversity as a means to facilitate ecosystem restoration or to maintain ecosystem function as native communities re-assemble and establish under a new climate regime.

Acknowledgements

This contribution results from the Integrated Project 'ALARM: Assessing large-scale environmental risks for biodiversity with tested methods' [97] funded by the European Commission (GOCE-CT-2003-506675). P.P. and V.J. were supported by grant numbers AV0Z60050516 and MSM0021620828; Z.B-D. and B.C. by grant number NKFP6/013/2005; W.T. by the ANR Biodiversité DIVERSITALP; A.R. and C.R. by the ANR Biodiversité URTICLIM; M.V. by CONSOLIDER CSD2008-00040 and M.Z. and M.M. were supported by the European Regional Development Fund (Center of Excellence FIBIR). The comments of four anonymous referees on earlier versions of the manuscript are acknowledged.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.tree.2009.06.008.

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