

A proposed unified framework for biological invasions

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There has been a dramatic growth in research on biological invasions over the past 20 years, but a mature understanding of the field has been hampered because invasion biologists concerned with different taxa and different environments have largely adopted different model frameworks for the invasion process, resulting in a confusing range of concepts, terms and definitions. In this review, we propose a unified framework for biological invasions that reconciles and integrates the key features of the most commonly used invasion frameworks into a single conceptual model that can be applied to all human-mediated invasions. The unified framework combines previous stage-based and barrier models, and provides a terminology and categorisation for populations at different points in the invasion process.

An allopatric model for the diversification of invasion biology

The past two decades have seen an explosion of research interest on human-mediated invasions; that is, invasions by species that are not naturally present in a native assemblage, but have been moved beyond the limits of their normal geographic ranges by human actions. This explosion has, in turn, resulted in substantial development of understanding of the invasion process (e.g. [1–5]). Nevertheless, as the science of invasion biology has grown, some significant anomalies have hindered the development of robust generalisations. Perhaps the most damaging is that invasion biologists have pursued their research using a variety of terminologies, using synonymous terms for the same process, different definitions of the same term, and dissecting and pursuing the invasion process in different ways (see [5]). This starts from the basic level of defining a native species [6], and what to call a species that has been transported beyond the limits of its native

geographic range and that has established a population in an area where it was not known to occur previously [2,5,7–9]. It carries on through when species should be termed invasive or an invader [6,8,10], what are the key processes and traits that determine the transformation of a species from a native to an invader [2,11,12] and how these processes should be analysed [13–17]. This is problematic because it hinders comparison of patterns and processes in invasions, and leads to the reinvention of concepts and hypotheses.

One significant driver of this plethora of approaches is that the science of invasion biology has developed along largely independent but parallel taxonomic and environmental lines. Differences in the vectors of translocation, the challenges faced by introduced species and the consequences of invasions, have resulted in biologists concerned with different taxa and different environments adopting different frameworks and definitions for the invasion process. This acts to complicate the already significant challenges faced by biologists in accessing, absorbing and integrating the vast literature on invasions being generated from terrestrial, freshwater and marine studies, often without cross-reference (J.T. Carlton and A.M.H. Blakeslee, personal communication). Perhaps the clearest expression of these differences is the divide between studies of terrestrial plant and animal invasions. Explicitly or implicitly, most plant ecologists adopt the invasion framework set out by Richardson *et al.* [8] (e.g. [18–20]), which views invasions as a series of barriers that a species negotiates to become either naturalised or invasive (Figure S1 in the supplementary material online). This scheme was adopted in the Global Strategy on Invasive Alien Species of the Global Invasive Species Programme [21], in various management and strategy documents for invasive plants and vertebrates (e.g. [22,23]), and is the standard source for definitions in regional and national catalogues of alien plant species (e.g. [24,25]). Most animal ecologists, by contrast, adopt invasion

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frameworks that are modifications of one first proposed by Williamson [26,27] (e.g. [2,3,5,11,28–30]), which views invasions as a series of stages that a species must pass through on the pathway from native to invasive alien (e.g. Figure S2 in the supplementary material online).

At first glance, the Richardson and Williamson frameworks appear rather different, and we believe that there are indeed key differences between them. However, we also believe that the similarities outweigh the differences, and that with some clarifications and alterations, the two can sensibly be merged. Here, we discuss how and why the Richardson and Williamson frameworks differ, and then propose a merger of the two, additionally incorporating key features of other frameworks proposed for some or all of the invasion process [31,32], as a single, unified framework for invasion biology. We believe that such a merger is necessary to help unite a research field that has largely diverged on taxonomic grounds. This will be particularly important to help understand the probable consequences of the ever-increasing movements of species around the world as a result of growing volumes of international trade, environmental change, and calls for assisted migration.

Similarities and differences

For it to be possible to merge the Richardson and Williamson frameworks, they must describe the same process. Given that all species, regardless of taxon, have the potential to progress from native to alien invader (although most never reach that endpoint), with the definitions of native and alien invader being applicable to all species, this is certainly true. It follows that the main difference between the two schemes resides in how this common process is described. In essence, the Williamson framework focuses on the status a species attains, whereas the Richardson framework focuses on the barriers to progress from one state to the next: thus, this is essentially a difference in focus on outcome versus obstacles.

Although the primary difference between the Richardson and Williamson frameworks is one of focus rather than substance, there are nevertheless two areas where clarification is required to align the schemes. First, under the Richardson framework, once a species has overcome the barrier of geography, it is faced with the barrier of being able to survive and grow in the new environment (Figure S1 in the supplementary material online). This focus is understandable in a botanical context, because plants that are introduced are often 'released' directly into the environment via planting. There is less of a functional distinction between whether introduction to the environment involves individuals that have been deliberately introduced, accidentally introduced, or are cultivated, although there might be a practical distinction in terms of the potential for subsequent establishment and invasion. By contrast, the early stages of the invasion process in Williamson-based schemes are more discrete and, being animal focused, introduction is more often dependent on an act of liberation or escape (Figure S2 in the supplementary material online). That said, these differences between animal and plant invasions dissolve on closer inspection. It is clear that plants are frequently translocated beyond

their native range without making it out into the environment at all (e.g. most house plants), that some animals exist in cultivation (e.g. Pacific oysters; [33]) and that vast numbers of animal species are, similar to plants, transported and accidentally introduced, and are neither escapes nor intentional releases [34]. Thus, many terrestrial animals (e.g. earthworms and terrestrial arthropods) were and are transported and released directly, bypassing captivity and cultivation altogether, and thousands of marine animals are transported hourly around the world in ballast water [35]. Thus, the concepts, issues and challenges relating to captivity and cultivation can equally apply to plants and animals.

Second, the stage between the arrival of a species in a new environment and its spread across that environment (i.e. post-introduction but pre-spread) tends to be considered differently in the two frameworks. The Williamson framework defines this as the establishment stage (Figure S2 in the supplementary material online), and generally considers success at this stage in terms of factors that allow introduced populations to become self-sustaining. Increasingly, these factors are divided into characteristics of the species introduced, of the novel location, or that are unique to the specific introduction event (e.g. the number of individuals released, known as propagule pressure) [2,11]. The Richardson framework identifies environmental and reproductive barriers that must be overcome (Figure S1 in the supplementary material online), with the former focused on conditions that allow growth and survival. It is difficult to align the Richardson barriers with the Williamson framework, when success is linked to variation in propagule pressure (i.e. not obviously an environmental or a reproductive barrier), and when environmental barriers represent only one of the three types of factor influencing progress (see also [36]).

These difficulties might reflect biases towards different levels of organisation in the two frameworks. The Richardson scheme is individual based, focusing on the barriers that would prevent an individual from arriving at a new location, growing and reproducing, as the major impediment to naturalisation in plants is whether individuals can survive, set viable seed or persist by vegetative means (but see [37]). Williamson-based schemes are implicitly population based, with the establishment stage focusing on the problems of small population viability. Here, the focus is on advancing from one stage to the next, particularly given that the barriers to population survival are more complex than the barriers to individual survival.

Unifying the frameworks

Figure 1 proposes a unified framework for invasion biology that combines the key elements of the Williamson and Richardson schemes, as well as new insights that arise from the process of combining the two. This framework is designed to apply to all human-mediated invasions. As such, the framework includes elements that we would not expect to apply to natural dispersal, or to range expansions occurring indirectly as a result of human activities, such as habitat modification. However, it can help to provide insights into all types of dispersal, in particular special

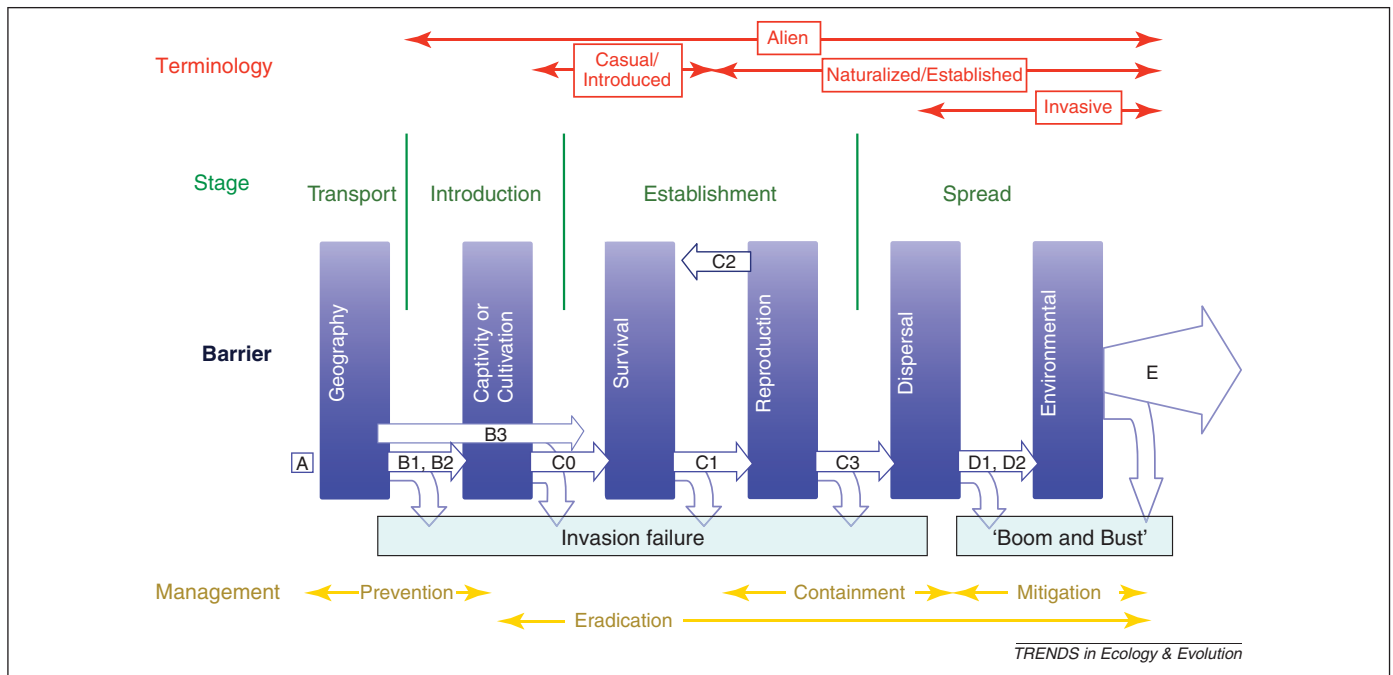


Figure 1. The proposed unified framework for biological invasions. The proposed framework recognises that the invasion process can be divided into a series of stages, that in each stage there are barriers that need to be overcome for a species or population to pass on to the next stage, that species are referred to by different terms in the terminology depending on where in the invasion process they have reached, and that different management interventions apply at different stages. Different parts of this framework emphasise views of invasions that focus on individual, population, process, or species. The unfilled block arrows describe the movement of species along the invasion framework with respect to the barriers, and the alphanumeric codes associated with the arrows relate to the categorisation of species with respect to the invasion pathway given in Table 1 (main text).

cases of biological invasions, such as managed relocation (assisted colonisation) or biological control.

The proposed unified framework is an advance on the previous frameworks in invasion biology for at least nine reasons.

Reason 1: combination of stages and barriers

The unified framework recognises that the invasion process can be divided into a series of stages and that, in each stage, there are barriers that need to be overcome for a species or population to pass on to the next stage. Although this structure was implicit in both the Richardson and Williamson frameworks, and recognised in some previous treatments of invasions (e.g. [2,37]), the unified framework makes explicit that the stages are separated by barriers, and how.

Reason 2: the barrier of captivity or cultivation

The unified framework identifies an additional barrier to invasion after the geographical barrier, which explicitly recognises that a species can be prevented from becoming an invader by a human-imposed barrier. Many animal and plant species exist in captivity and/or cultivation beyond the limits of their native ranges, but fail to cross the physical barriers of a fence or hedge. This barrier is probably lower for species in cultivation than for those in captivity. The unified framework also includes an arrow (B3) from Geography to Survival to recognise the fact that this barrier is skipped by many aliens, especially plants, fungi, protists, invertebrates, smaller fish and other taxa, which are introduced unintentionally by humans directly into the new environment. Indeed, there is a variety of mechanisms and routes by which alien

species breach the barriers of Geography and Captivity [34,38].

Reason 3: a barrier to survival

The environmental barrier in Richardson’s framework is replaced with a Survival barrier in the unified framework, which together with the Reproduction barrier lies within the establishment stage. This clarifies that an introduced population can fail to establish because individuals in the population either fail to survive, or survive but fail to reproduce. Failure to establish can result from factors associated with the species (e.g. reproductive rate or specialism), the location (e.g. presence of enemies or mutualists), apparently stochastic features of the individual introduction event (especially propagule pressure) or, often, their interaction (e.g. species × location, such as climate matching); these factors can act on survival or reproduction, or both. This clarifies that the failure of individuals or populations to survive is not just a consequence of the environment, and indeed the failure of a population of a given species to establish at a given location does not preclude the possibility that a subsequent introduction of the same species at that location will succeed (e.g. starlings in New York [39] or pines in the South African fynbos [40]).

Reason 4: establishment is a population process

Individuals in an introduced population might be able to survive and to reproduce in the exotic environment, but the population can still fail to establish because the long-term population growth rate is negative (geometric mean $r < 0$). The unified framework includes an arrow from Reproduction to Survival in recognition of the fact that several cycles

of survival and reproduction are likely to be necessary to ensure that a viable population is established. In fact, both botanists (e.g. [6,8]) and zoologists (e.g. [41]) tend to include a temporal qualifier in definitions of naturalisation or establishment, in explicit recognition of the fact that this is dependent on the existence of a self-sustaining population over a period of time corresponding to multiple generations.

Reason 5: the environmental barrier to spread

The proposed unified framework clarifies that barriers to dispersal need to be overcome if a naturalised species is to spread. Once these dispersal barriers are overcome, the alien population can spread into locations away from the point of introduction, where individuals must survive and reproduce. The more an alien spreads, the more dissimilar from the point of introduction the environment at these locations will be, because of spatial autocorrelation. Thus, a spreading population essentially faces multiple, sequential establishment events, under an ever-greater range of environmental conditions. This process is represented by the Environmental barrier in the unified framework (Figure 1). Unlike the Richardson framework [8], we make no distinction between disturbed or undisturbed habitats, because different species react differently to differential levels of environmental modification, and because disturbance is not a unitary concept, but can happen in a variety of ways (natural or anthropogenic). The invasive range is determined by the extent of suitable environment, and the Environmental barrier sets the limits to this.

Reason 6: impacts fall outside the proposed framework

The unified framework says nothing about the economic or environmental pest status of an alien species in this range, as it is possible that species can have impacts in the novel environment even if their populations are not established (e.g. the single fox gaining access to Garden Island, Western Australia: [42]) or are said to be benign when established and widespread (e.g. [43,44]; although in most cases, lack of impact might denote absence of evidence rather than evidence of absence).

Reason 7: failure at any barrier is a failure

The proposed unified framework explicitly recognises that a native species can fail to become an invader because it fails to pass any one of the barriers at any stage of the invasion process. Here, it is worth reiterating the point (see [2,14,16,17]) that to understand the cause(s) of success in passing any given barrier or stage, it is important that the characteristics of successes be contrasted with those of failures at the same stage only. Moreover, the unified framework recognises that invasions can fail even after the alien has spread, as reflected in the 'boom and bust' dynamics that are a feature of an increasing number of biological invasions (e.g. [2,26,45]); 'bust' here can refer to contraction to small population sizes or complete population extinction.

Reason 8: mapping management options

The unified framework allows different management measures to be mapped on to the invasion process. This helps to

clarify the responses to invasions that are most likely to be relevant or successful at different stages and, hence, where the responsibility for different management interventions is likely to lie [32,34,46]. However, unlike the Convention on Biological Diversity or American Federal Law (Executive Order 13112), the unified framework makes no comment about the impact or harm that such species might cause, as these are subsidiary issues to the process of invasion.

Reason 9: a framework for terminology

The proposed unified framework shows how a terminology for invasion biology maps onto both stages and barriers on the invasion pathway (although which terms are appropriate is open to subsequent debate). This helps to clarify to which stages in the invasion process different terms refer, and helps to consolidate invasion terminology. This has important implications for streamlining the transfer of research results to management [9].

Further advantages of the proposed framework

A significant advantage of the proposed framework presented in Figure 1 is that it also incorporates important elements of other frameworks that previously have not been integrated with the Williamson and/or Richardson schemes. Thus, the unified framework includes the framework for management interventions proposed by Pyšek and Richardson [32], and (with minor alterations) the terminological framework proposed by Richardson *et al.* [8]. Inclusion of the latter should help to eliminate much of the synonymy and confusion in describing invasions noted by Lockwood *et al.* [5].

In addition, most other published frameworks comprise subsets of the unified framework and can be mapped onto the structure in Figure 1. For example, stages 0–V in Colautti and MacIsaac's framework [31] correspond with the unified framework, with stage 0 being equivalent to native species, stage I to transport, II to introduction, III to establishment, and stages IV and V to elements of spread towards undisturbed environments and community dominance. Heger and Trepl's [18] chronological discrimination of an idealised invasion process identifies four stages, including transport and spread, missing out the introduction stage, but including two establishment stages (spontaneous and permanent), which the unified framework incorporates as a feedback loop between barriers to survival and reproduction. Heger and Trepl [18] include four steps between these stages (immigration; individual growth and reproduction; population growth to minimum viable population; and colonisation of new localities) that are equivalent to crossing barriers of Geography, Survival and Reproduction (which the unified framework loops to achieve a viable population), and Dispersal (Figure 1). Henderson *et al.* [47] (modified from [48]) consider invasions in a landscape context. They identify six invasion stages, starting with introduction, then establishment and naturalisation, distinguished on the basis of sustained reproduction, and then dividing spread into dispersal, population distribution (i.e. second-order establishment) and invasive spread. These are

Table 1. A categorisation scheme for populations in the unified framework^a

Category	Definition
A	Not transported beyond limits of native range
B1	Individuals transported beyond limits of native range, and in captivity or quarantine (i.e. individuals provided with conditions suitable for them, but explicit measures of containment are in place)
B2	Individuals transported beyond limits of native range, and in cultivation (i.e. individuals provided with conditions suitable for them but explicit measures to prevent dispersal are limited at best)
B3	Individuals transported beyond limits of native range, and directly released into novel environment
C0	Individuals released into the wild (i.e. outside of captivity or cultivation) in location where introduced, but incapable of surviving for a significant period
C1	Individuals surviving in the wild (i.e. outside of captivity or cultivation) in location where introduced, no reproduction
C2	Individuals surviving in the wild in location where introduced, reproduction occurring, but population not self-sustaining
C3	Individuals surviving in the wild in location where introduced, reproduction occurring, and population self-sustaining
D1	Self-sustaining population in the wild, with individuals surviving a significant distance from the original point of introduction
D2	Self-sustaining population in the wild, with individuals surviving and reproducing a significant distance from the original point of introduction
E	Fully invasive species, with individuals dispersing, surviving and reproducing at multiple sites across a greater or lesser spectrum of habitats and extent of occurrence

^aHuman-mediated dispersal has created several novel categories of dispersal pathway (i.e. B1 and B2) [38], and human intervention has also significantly increased the frequency and duration that populations can persist in other categories (C0, C1 and C2).

equivalent to the seven barriers in the unified framework, although Henderson *et al.* [47] fail to distinguish between the barriers of Geography and Captivity or Cultivation. Carlton's [49] "sequence of events in the dispersal and introduction of exotic invertebrates by ships' ballast water" consists of a series of five 'filters' (I, donor area community; II, entrained ballast tank assemblage; III, assemblage upon arrival and release in the recipient region; IV, species surviving and reproducing, and V, established introductions) separated at each stage by four 'bottlenecks' (between I and II, a selection of species that actually enter the vessel; between II and III, the species that survive the voyage; between III and IV, the species that actually survive, and between IV and V, the species that continue to reproduce and become permanently introduced). The unified framework, which commences at Carlton's stage II, accommodates each of these bottlenecks and filters through our combined 'stage' and 'barrier' approaches.

Clearly, species are not static within the unified framework, but can (and are expected to) cross barriers, transit between stages, and/or stumble to invasion failure. A species can also have several alien populations at different locations at different points on the framework. Therefore, reference to position on the invasion framework in respect of any given species should be temporally and spatially explicit. In Table 1, we provide a categorisation scheme for populations that can be used in parallel with the framework, and which allows the invasion stage reached by any given population to be easily identified and compared. The categories align with the arrows that describe where species are with respect to the various barriers in the framework. The individuals within any given alien population can be distributed across a variety of stages on the unified framework, but we anticipate that the categorisation applied to any given alien population would be determined by those individuals in the population furthest along the invasion pathway (Box 1).

Box 1. Aliens placed on the unified framework

The scheme in Table 1 (main text) allows alien populations to be simply categorised and compared based on how far along the unified framework the most advanced individuals sit. It can be used to compare populations regardless of species or location. For example, the budgerigar *Melopsittacus undulatus* (Figure 1a) is an Australian native that has been introduced to several locations around the world. It is currently a common cage bird in the UK, where individuals occasionally escape from captivity but do not survive long in the wild (C0). However, there was formerly a small, free-flying budgerigar population on the island of Tresco in the Isles of Scilly that survived and reproduced between 1972 and 1975, but apparently only because of the provision of supplemental food and shelter (C2). The population in Florida initially increased and spread quite widely (D2), but subsequently declined for unknown reasons, and is a classic example of a 'boom and bust' species [45,51,52].

Australia is home to 1012 taxa in the *Acacia* subgenus *Phyllodineae*, many of which have been introduced to South Africa. Black wattle, *Acacia mearnsii* (Figure 1b) is highly invasive over large parts of South Africa (E), and is listed as one of the 100 worst invasive alien species

in the Global Invasive Species Database. The Bacchus marsh wattle, *Acacia rostriformis* (formerly *A. verniciflua*; Figure 1c) is known to have been introduced and cultivated, but no records exist of naturalisation or invasion (B2). Finally, the curry wattle, *Acacia spondylophylla* (Figure 1d) is not known to have been introduced to South Africa, or indeed to anywhere else (A)

At least 45 species have been formally assessed for the biological control of the invasive legume *Mimosa pigra* in Australia, of which 32 have been tested in quarantine in Australia, and 14 released into the environment [53–55]. *Temnocerus debilis* (Figure 1e) was imported and tested in quarantine. An application for release was, however, rejected (B1). *Sibinia fastigiata* (Figure 1f) was repeatedly imported and released into the environment after host-range tests suggested the agent posed a negligible risk of feeding on other plants; however, it consistently failed to establish, perhaps owing to differences in the flower phenology between its native and invasive ranges (C0). *Carmentia mimosa* (Figure 1g) causes significant damage to *Mimosa pigra*, and although it is generally a slow disperser, natural dispersal augmented by redistribution means that it had almost reached the limit of the distribution of the weed by 2004 (E).

(a) Budgerigar



(b) Black wattle



(c) Bacchus Marsh Wattle



(d) Curry Wattle



(e) *Temnocerus debilis*



(f) *Sibinia fastigiata*



(g) *Carmenta mimosa*



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Figure 1. Examples of aliens placed on the unified framework. (a) budgerigar, *Melopsittacus undulatus*; (b) black wattle, *Acacia mearnsii*; (c) Bacchus marsh wattle, *Acacia rostriformis*; (d) curry wattle, *Acacia spondylophylla*; (e) *Temnocerus debilis*; (f) *Sibinia fastigiata*; and (g) *Carmenta mimosa*. Reproduced, with permission, from Rohan Clarke (a), David Richardson (b), Daniel J. Murphy, Royal Botanic Gardens Melbourne (c,d) and CSIRO (e–g).

Conclusion

The exponential growth of interest in biological invasions has been driven by independent growth in parallel research programs, divided largely along taxonomic [50] and habitat lines (J.T. Carlton and A.M.H. Blakeslee, personal communication). Yet, these different programs share common issues, in terms of the process of invasion, and common consequences, in terms of the ecological and economic impacts of a failure to stem the tide of invaders. There is thus a clear need in invasion biology for a model whereby the key research findings from all its branches can be integrated. We believe that the unified framework proposed here is a significant step towards that goal. It can be applied to all invasions, regardless of taxon, location or realm, recognising that species can fail to become invasive at any of the stages identified because of a failure to breach any of the barriers to progress between stages. We

hope that adopting, refining and elaborating the unified framework will help to clarify how and why invasions occur, and where, when and how invasions can be stopped.

Acknowledgements

TMB thanks the Centre for Invasion Biology, University of Stellenbosch, for hospitality and travel costs. PP and VJ were supported by the projects no. 206/09/0563 (Czech Science Foundation), AV0Z60050516 (Academy of Sciences of the Czech Republic), MSM0021620828 and LC06073 (Ministry of Education of the Czech Republic). PP also acknowledges support from the Praemium Academiae award from the Academy of Sciences of the Czech Republic. JR UW and DMR acknowledge support from the DST-NRF Centre of Excellence for Invasion Biology and the Working for Water Programme.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.tree.2011.03.023.

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