

APPLIED ISSUE

Using space-for-time substitution and time sequence approaches in invasion ecology

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SUMMARY

1. Invasion biologists use two main approaches to evaluate the effects of non-native species (NNS) on diversity of native species (DNS), namely space-for-time and time approaches. These approaches have pitfalls related to lack of controls: the former lacks pre-invasion data, while the latter often lacks data from non-invaded sites.

2. We propose a framework that combines space-for-time and time approaches and which should result in more focused mechanistic hypotheses and experiments to test the causes of invasibility and the effects of NNS on DNS. We illustrate the usefulness of our framework using two case studies: one with the submersed macrophyte, *Hydrilla verticillata*, in reservoir and the other with the fish, *Geophagus proximus*, in a large river–floodplain system.

3. *Hydrilla verticillata* invaded sites with DNS similar to that found in non-invaded sites, indicating that biotic and/or abiotic factors did not influence invasion success; however, DNS increased over time in invaded sites compared with non-invaded sites, suggesting that *H. verticillata* facilitated natives. In contrast, *G. proximus* invaded sites with higher DNS than non-invaded sites, suggesting that biotic and/or abiotic factors favouring natives were important for invasion success, but DNS increased in invaded and non-invaded sites over time, indicating that an independent factor contributed to DNS increases.

4. Conclusions from both studies would have been inaccurate or incomplete if the space-for-time and time approaches had not been used in combination as proposed in our framework.

Keywords: alien species, community invasibility, exotic species, facilitation, impact of invaders

Introduction

The effect of non-native species (NNS) on natural communities and ecosystems and the factors that make an ecosystem invulnerable are two of the main issues addressed in invasion biology (Elton, 1958; Levine, Adler & Yelenik, 2004; Rejmánek *et al.*, 2005; Agostinho *et al.*, 2010; Thiele *et al.*, 2010; Powell, Chase & Knight, 2011; Vilà *et al.*, 2011). The diversity of native species (DNS) can play a double role. On the one hand, it can be the response variable, indicating the effects of NNS on a specific community; on the other hand, it can be a predictor of the fate of NNS (Meiners & Cadenasso, 2005). Understanding the effects

of NNS on DNS and DNS on NNS has become a central issue in ecology.

Several studies that measure the effects of NNS on DNS use a “space-for-time” approach, that is, comparing invaded with non-invaded sites to infer the effects of the presence of one (or several) NNS on DNS (Sax, Kinlan & Smith, 2005). Studies using this approach have concluded that the effects of NNS are scale dependent (Powell *et al.*, 2011) and can be negative (Gaertner *et al.*, 2009; Hejda, Pyšek & Jarošík, 2009; Flory & Clay, 2010; Rolon, Rocha & Maltchik, 2011; Vilà *et al.*, 2011; Wahl *et al.*, 2011), positive (Strayer *et al.*, 2003; Rodriguez, 2006; Barrientos & Allen, 2008) or non-significant (Aday, 2007; Hoyer *et al.*, 2008;

Cunha *et al.*, 2011). It is very likely that positive and non-significant results are under reported (Schlaepfer, Sax & Olden, 2011). However, without pre-invasion data from invaded and non-invaded sites, conclusions may be erroneous (see other criticisms of this approach in Sax *et al.*, 2005). For example, invaded sites that have lower richness than non-invaded sites in the post-invasion condition may suggest that NNS negatively affected DNS. However, an alternative conclusion is that invaded sites could have had lower species richness than the non-invaded ones prior to invasion (Fig. 1). This is possible if, for example, invaded sites had lower habitat heterogeneity and/or other environmental conditions that limit numbers of both native species and NNS (Byers & Noonburg, 2003; Davies *et al.*, 2005; Davis, 2009). Another possibility is that NNS invaded less rich sites because of lower biotic resistance (Elton, 1958; Kennedy *et al.*, 2002). Thus, one cannot determine whether NNS really had a negative impact on DNS. In a more extreme case, invaded sites could have had much lower richness than the non-invaded ones before the invasion occurred and NNS

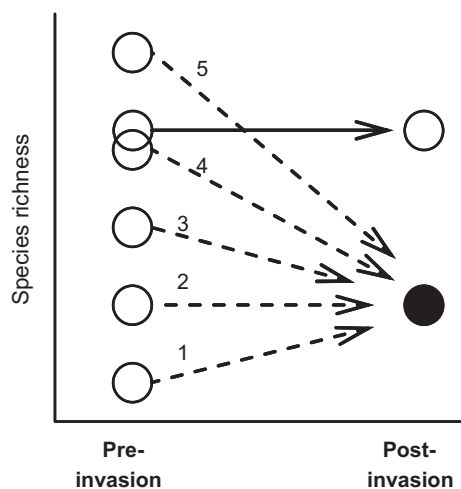


Fig. 1 A hypothetical example where species richness of a non-invaded site (empty circle) remains constant while native richness of an invaded site (black circle) increases (trajectory 1), remains constant (trajectory 2) or decreases (3–5) over time. Trajectory 1 shows that non-native species (NNS) increased the richness of invaded sites, while trajectory 2 shows that NNS had no effect on native richness. Note that both conclusions differ from that reached using the space-for-time approach (i.e. using post-invasion data only). Trajectory 3 is in accordance with the finding that NNS negatively affected native species richness according to the space-for-time approach, but this approach overestimated the impact (post-invasion difference between richness in invaded and non-invaded sites). Trajectories 3–5 are the only ones that agree with the conclusions obtained by the time approach, namely that NNS decreased DNS, but the magnitude of the effects remains unknown when data from non-invaded sites are lacking.

could have increased the richness of these sites through facilitation but not enough to match the diversity of non-invaded sites (trajectory 1 in Fig. 1). In this case, the real conclusion (positive impact of NNS on DNS; e.g. Rodriguez, 2006; Altieri *et al.*, 2010) would be contrary to the one reached with the space-for-time approach. Thus, it is clear that by using only the space-for-time approach, (i) it is not possible to tease apart impacts of NNS on DNS from other factors and (ii) the apparent effects of NNS on DNS may be misinterpreted. Unfortunately, these drawbacks may translate even into meta-analyses of species invasion impacts (e.g. Gaertner *et al.*, 2009; Powell *et al.*, 2011; Vilà *et al.*, 2011).

Although the time approach (comparisons of sites in pre- and post-invasion situations) is apparently the only one to resolve the above-mentioned limitations and serves the purpose of measuring the real impact of NNS on DNS, it can also produce erroneous conclusions. For example, using only the time approach trajectories 3, 4 and 5 of Fig. 1 indicates negative effects of NNS on DNS, but without knowing diversity in non-invaded sites, one cannot assess the real magnitude of this impact. In an even more complex example, suppose that invaded and non-invaded sites suffer a reduction in the number of species over time, as observed in systems where anthropogenic impacts have reduced diversity (e.g. when invasive species are “passengers”; Didham *et al.*, 2005; MacDougall & Turkington, 2005). Several outcomes are possible, despite the apparent but erroneous indication of impacts of NNS on DNS. For example, the decrease in native richness in invaded sites over time could be of the same order, lower or higher than those of the non-invaded sites, but the time approach would indicate only negative effects of NNS on DNS. Without data from non-invaded sites in pre- and post-invasion situations, it is not possible to estimate the direction of the effects of NNS on DNS or the magnitudes.

These sources of confusion, recognised by some (e.g. Flory & Clay, 2010; Thiele *et al.*, 2010), could be resolved by testing invasibility and the effects of NNS on DNS using experiments (e.g. Kennedy *et al.*, 2002; Stachowicz *et al.*, 2002; Lanta & Lepš, 2008; Flory & Clay, 2010; Scherber *et al.*, 2010). However, in addition to several logistical difficulties and high costs, invasion time lags of some NNS make such experiments less appealing (Rejmánek, 2000). Additionally, experiments in the field which introduce NNS into sites that do not contain them could be unethical (Levine *et al.*, 2004). Data from long-term monitoring are now commonly collected by non-official management programmes as well as by formal LTER programmes (some initiated at Darwin’s time;

Magurran *et al.*, 2010), for example, currently, there are 15 LTERP sites in Brazil. Thus, for selected sites, it is now relatively easy to obtain pre- and post-invasion data, allowing researchers to better disentangle the factors influencing invasibility and the effects of NNS on DNS.

In this paper, we first propose a conceptual framework that aims to separate the factors influencing invasion (pre-invasion state) from the impacts derived from invasion (post-invasion state). Combining data from non-invaded sites (lacking in the temporal approach) with data from pre-invasion sites (lacking in the space-for-time approach) into a single conceptual framework will improve our understanding of invasions. Secondly, we use one macrophyte and one fish example, obtained in man-made and natural ecosystems, to illustrate the utility of our conceptual approach. There are similarities between our conceptual framework and the one proposed by Sax *et al.* (2005); however, their framework differs by seeking to assess impacts of NNS by comparing multiple taxa in the native and exotic habitats, whereas ours uses data about species richness in invaded and non-invaded sites obtained in the same ecosystem. Our framework therefore makes disentangling of effects simpler and more cost effective in many ecosystems. Although our conceptual framework does not

resolve all potential problems with field (observational) data, it organises the main ideas and provides guidance for formulating hypotheses about mechanisms influencing invasibility and the effects of NNS on natives, and it supplements the framework by Sax *et al.* (2005) by helping to address more specific and focused hypotheses and experiments. Furthermore, we highlight the potential for misinterpretation posed by studies limited to either the temporal or the space-for-time approach.

The conceptual framework

Our framework (shown as a graphical schema) compares data obtained in invaded and non-invaded sites, in pre- (time *t*) and post-invasion (time *t* + 1) situations (Fig. 2). In this way, it parallels the proposal of Levine *et al.* (2004) to conduct experiments in advance of an expanding invader population to test whether biotic resistance repels invasion.

For simplicity, we assumed that the DNS of non-invaded sites is constant over time. A reservoir is an example of an invasion area, while discrete sites (or sampling units) could be permanent plots or patches of macrophytes (if these plants are the target organism – see

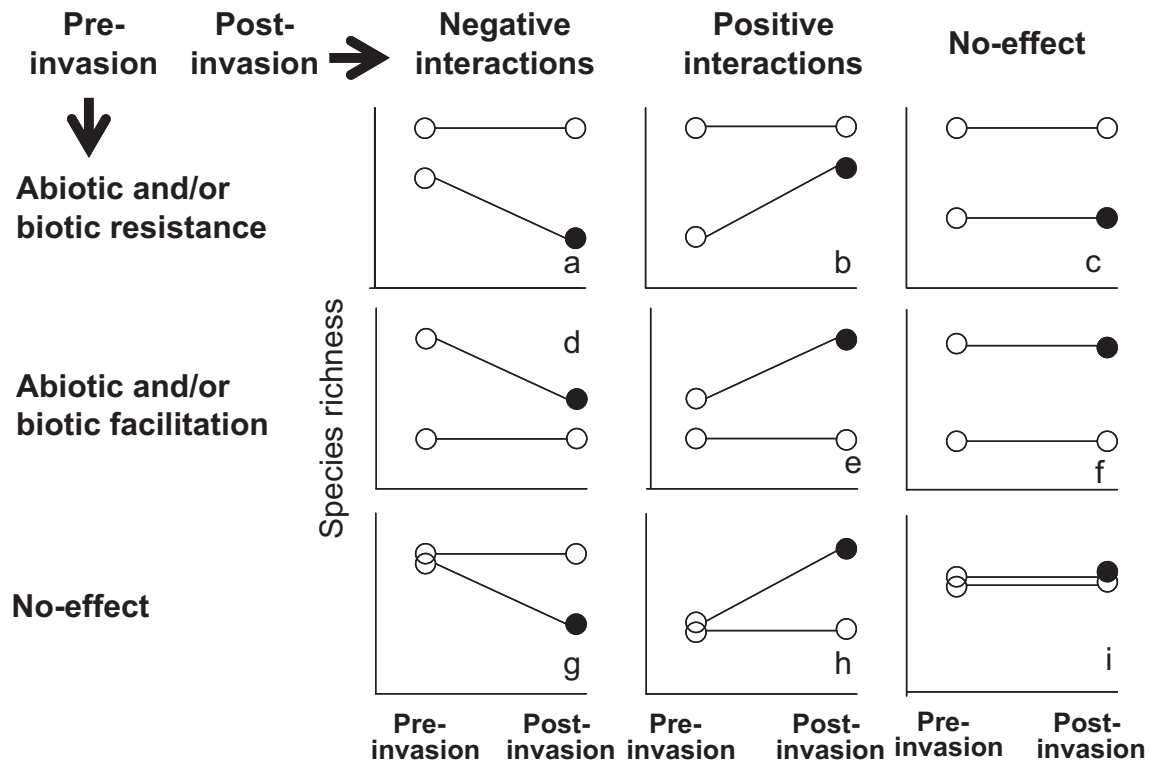


Fig. 2 A framework to separate factors explaining invasion success (abiotic and biotic resistance, abiotic and/or biotic facilitation and no effect) and effects of negative interactions, positive interactions or no effects. Empty circles: non-invaded sites; black circles: invaded sites.

our first case study) within each area. A floodplain is another example of invasion area, and in this case, individual ponds could be considered discrete sites (see our second case study). As colonisation is dependent on organism mobility, the most appropriate choice of favourable sites for animals is more difficult (although also possible – see our second case study) compared with plants. A NNS usually does not invade all sites in an ecosystem and thus, having samples in the same sites post-invasion, it is possible to compare native community attributes (in our example DNS) in the same sites in pre- and post-invasion states. Assuming that non-NNS stressors are uniform across the invasion area, by collecting data from the same non-invaded sites in pre- and post-invasion states, the pre-invasion sites are “real controls” in the space-for-time approach, while the non-invaded sites are “real controls” in the time approach. Accordingly, this rationale results in nine possible outcomes (Fig. 2):

- Invaded sites originally had fewer native species than non-invaded ones (Fig. 2a–c), indicating that abiotic and/or biotic resistance are important for invasion, and DNS decreases (indicating negative effects of NNS on DNS; Fig. 2a), increases (indicating positive effects of NNS on DNS; Fig. 2b) or does not change (indicating non-effects; Fig. 2c) post-invasion;

- Invaded sites originally had more native species than non-invaded ones (Fig. 2d–f), indicating that abiotic and/or biotic facilitation is important for invasion, and richness decreases (negative effects of NNS on DNS; Fig. 2d), increases (positive effects of NNS on DNS; Fig. 2e) or does not change (no effect; Fig. 2f) post-invasion;

- Invaded sites originally had the same species richness as non-invaded ones (Fig. 2g–i), indicating no effects of environmental factors or biotic resistance or facilitation on invasion, and richness decreases (negative effects of NNS on DNS; Fig. 2g), increases (positive effects of NNS on DNS; Fig. 2h) or does not change (no effect; Fig. 2i) post-invasion.

Testing these outputs would require statistics that could test for the effects of each factor (time – years of the study; and sites – invaded and non-invaded sites) independently as well as their interactions (e.g. two-way ANOVA; or Repeated Measures ANOVA if samples are collected in short intervals and generation time of the organism is short). Significant effects of the interaction between the factors on DNS would corroborate the cases in Fig. 2a,b,d,e,g,h. Significant effect of only sites would corroborate Fig. 2c,f, while non-significant effects on DNS would corroborate no pre- and post-invasion differences (Fig. 2i).

Variations in these potential outcomes could occur and are expected due to the complexity of interactions in real ecosystems (Callaway, 1997; Sax *et al.*, 2005). For example, diversity of non-invaded sites could increase along with time, in response to management practices aiming at biodiversity conservation or decrease in response to impacts acting at large scales (e.g. pollution). However, despite these variations, the general rationale we applied in our framework is likely to apply, and we believe that these nine responses summarise most of the possible outcomes expected to occur in pre- and post-invasion situations.

Our approach applies to NNS of plants and animals, and it can be used in ecosystems that have been successfully invaded and where pre-invasion data exist. However, the first, important assumption of the model is that the target NNS has dispersed over the entire ecosystem (or area) under investigation, so that non-invaded sites are not the result of dispersal limitation and/or propagule pressure, which are important drivers of invasion success (Simberloff, 2009).

A second assumption is that adequate time has passed to allow assessment of the potential impacts of NNS on DNS. Although this is difficult to assess, one can suppose that months to years would be necessary for short-lived (e.g. planktonic) and mobile organisms (e.g. fish), especially in small ecosystems. By contrast, decades would be necessary for dispersal-limited plants or animals in large areas.

Using the framework: case studies

The introduced macrophyte Hydrilla verticillata (L.f.) Royle. *Hydrilla verticillata* was recorded in the Paraná basin for the first time in July 2005 and has since spread quickly in several natural and artificial (reservoirs) ecosystems (Souza, 2011). We used data on *H. verticillata* from the Rosana Reservoir, a large Brazilian man-made lake. The Rosana Reservoir is located in the Paranapanema River (Upper Paraná Basin) and is 350 km² in area. Macrophytes (including *H. verticillata*) occur in small arms, but also in the main axis of the reservoir, despite its long fetch. Data were collected in February 2004 (pre-invasion) and November 2010 (post-invasion) at 87 sampling stations (53 were invaded). All sites were geo-referenced with a GPS and located along the main axis of the reservoir. At each sampling point, the presence/absence of *H. verticillata* and of other submersed species were recorded from a boat moving at a constant slow speed along transects placed perpendicular to the shore, to the maximum depth of colonisation by *H. verticillata* or any other submersed macrophyte. Where macrophytes were not found by visual inspection, we used a rake on a 4-m-long pipe and a grapple

to ensure that macrophytes would be recorded if they were present at deeper sites. Details about this reservoir and the sampling protocol can be found in Pierini & Thomaz (2009).

The cichlid fish *Geophagus proximus* (Castelnau, 1855). We chose this cichlid invader to evaluate our framework because it is a territorial omnivore and occupies the littoral zone, where species richness and thus biological interactions are usually high. Thus, we expected a clear effect of the invader on DNS. *Geophagus proximus* was detected in the Upper Paraná River in early 2000 (reservoirs of Tietê River; Vidotto & Carvalho, 2007; Moretto *et al.*, 2008). Shortly after discovery, it dispersed to other artificial (reservoirs) and natural (floodplain) environments in the region, reaching the studied stretch of this basin in 2005 (K. S. Goes and A. A. Agostinho, unpubl. data).

Fish were collected at 12 sites of the Baía River (nine floodplain lakes and three channels) located in the upper Paraná floodplain, where a Long Term Ecological Research Project has been ongoing since 2000. The main functioning force in the floodplain is still the flood pulse (Junk, Bayley & Sparks, 1989; Agostinho *et al.*, 2008), which is also considered a homogenisation factor, dispersing species and increasing similarity among the distinct environments of the floodplain. Sampling was conducted in 2001 and 2010 (three samples in each year – March, June and September, at six invaded and six non-invaded sites). Fish were collected with 20-m-long gillnets with different mesh sizes (2.4-, 3-, 4-, 5-, 6-, 7-, 8-, 9-, 10-cm opposite knots), which remained for 24 h and were checked for fish at every 8 h.

Data analyses

Two-way ANOVA was used to test for factor effects on species richness (time – levels were years; sites – levels were invaded and non-invaded) and their interaction. This test was chosen due to its simplicity and because it is well known to biologists.

Results

In the Rosana Reservoir, macrophyte species richness did not differ between invaded and non-invaded sites in 2004. In 2010, invaded sites had higher species richness than non-invaded sites, while the values of the non-invaded sites in both years were similar (Fig. 3a). The ANOVA detected a significant interaction effect ($F_{1,170} = 19.39$; $P < 0.0001$), suggesting that the NNS contributed to increased DNS (Fig. 3a).

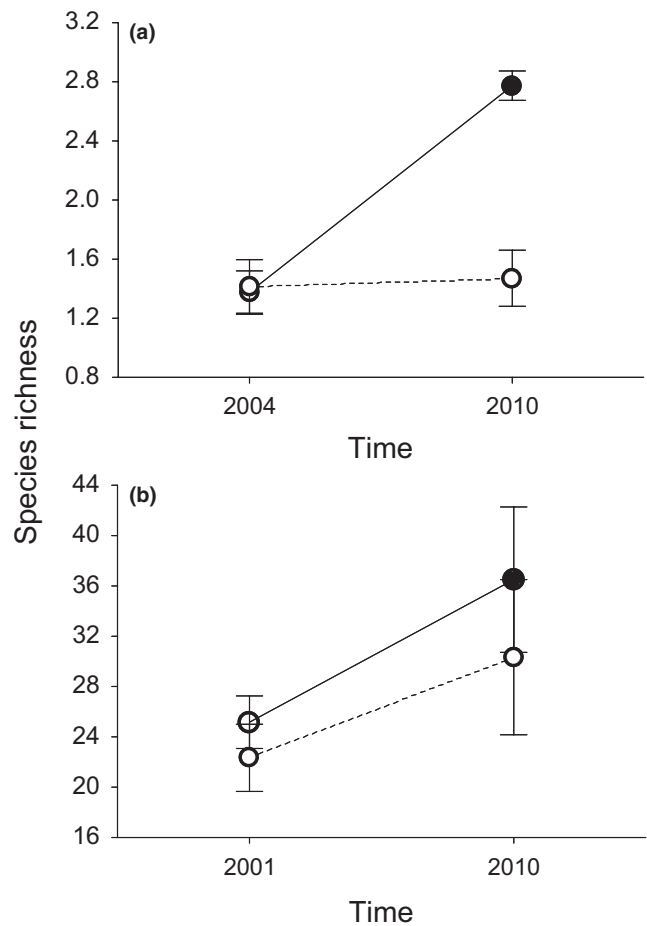


Fig. 3 Species richness of (a) native macrophytes (number of species per sampling station) in the Rosana reservoir during pre- and post-invasions by *Hydrilla verticillata*; and (b) native fish (number of species per 1000 m² of gillnet per 24 h) in the Upper Paraná River during pre- and post-invasions by *Geophagus proximus*. Mean values ± SD are shown. Empty circles: non-invaded sites; black circles: invaded sites.

For *G. proximus*, sites without invaded species had a slightly lower diversity of non-native species (DNS) compared with sites with invaded species in 2001 and 2010. However, in 2010, species richness was high irrespective of invasion state (Fig. 3b). ANOVA revealed a significant effect of time ($F_{1,20} = 4.51$; $P = 0.04$), that is, on average, mean species richness did not vary statistically between invaded and non-invaded sites, indicating that some other factor contributed to the increased DNS in the region. These patterns suggest that *G. proximus* was a successful invader in environments with high species richness.

Discussion

The case studies we used to illustrate the framework's utility showed its potential to guide research. Using the

framework, we were able to form more detailed hypotheses and, consequently, to describe more realistic processes. In our studies, the existence of long-term data sets was essential for the application of the framework.

The Rosana Reservoir case study showed that *H. verticillata* invaded sites independently of the sites' DNS. These results did not support the pre-emption hypothesis (i.e. invasion is prevented by DNS; e.g. Elton, 1958; Capers *et al.*, 2007) or biotic facilitation (i.e. invasion is enhanced by DNS; e.g. Levine & D'Antonio, 1999). Because DNS did not differ between invaded and non-invaded sites in the pre-invasion condition, abiotic conditions operating simultaneously on *H. verticillata* and DNS were not sufficient to explain differences in DNS between invaded and non-invaded sites post-invasion. Thus, it seems that *H. verticillata* invaded sites independently of their abiotic or biotic features. Similarly, in a study of Connecticut lakes (U.S.A.), there was no indication that native richness prevented invasion; the density of natives (an attribute that we did not consider) was more important (Capers *et al.*, 2007). On the other hand, a negative effect of at least one native species (*Vallisneria americana* Michx.) prevented *H. verticillata* invasion in a North American creek (Chadwell & Engelhardt, 2008). Thus, it seems that *H. verticillata* invasion responses to native species vary among ecosystems.

Findings from the Rosana Reservoir case study clearly illustrate the usefulness of the proposed framework. Using only post-invasion data, it would not have been possible to determine whether *H. verticillata* colonised species rich sites or increased DNS after invading. Similarly, if only invaded sites had been analysed (time approach), it would not have been possible to determine whether *H. verticillata* facilitated natives (as suggested by DNS increase) or not, given that we would not have data on non-invaded sites in the post-invasion situation. DNS increased steadily in the reservoir following *H. verticillata* invasion. Considering that controls (non-invaded sites) did not change compared with the invaded sites post-invasion, it seems that *H. verticillata* changed the environment so that it was more favourable for the growth of native species. In fact, habitat modification is likely the most important mechanism by which NNS facilitate natives (Rodríguez, 2006). For example, local diversity of native macrophytes has been enhanced by at least one exotic submersed macrophyte (*Myriophyllum spicatum* L.); facilitation was attributed to habitat changes mediated by this exotic, including a reduction in water velocity and an increase in water clarity (Rybicki & Landwehr, 2007). Although the Rosana Reservoir is a lentic water body, its shores are intensively affected by wave action making it

difficult for macrophytes to establish (see Pierini & Thomaz, 2009). However, intense growth from tubers (Bianchini *et al.*, 2010), abundant root development and resistance to water movement are typical of *H. verticillata*, and these attributes allow this plant to colonise such disturbed habitats (Sousa, 2011), which in turn become more prone to colonisation by natives.

In our study, two native taxa, *Chara guairensis* R. Bicudo and *Nitella furcata* (Roxb. ex Bruz.) Ag. emend. R.D. Wood, were often recorded at sites colonised by *H. verticillata*. However, we caution that increasing DNS does not mean that *H. verticillata* does not outcompete other native species. Competitiveness and undesirable environmental/economic impacts of *H. verticillata* have been the foci of many studies over the last 40 years (e.g. Haller & Sutton, 1975; Spencer & Rejmánek, 1989; Hofstra, Champion & Clayton, 2010). Experiments have shown that *H. verticillata* has strong competitive ability compared with other submersed species (Spencer & Ksander, 2000), including Neotropical native Hydrocharitacea (M. J. Silveira, unpubl. data). Data from the field are less conclusive. In the Upper Paraná River, for example, *H. verticillata* reduced *Egeria najas* biomass but did not result in exclusion (Sousa, 2011). Thus, while enhancing DNS, *H. verticillata* may facilitate species assemblages with a different composition from those found in uncolonised sites, with potentially complex environmental impacts. Even in such complex cases, our framework may be highly revelatory: use of different metrics of diversity in the framework, for example, might yield different results and help generate even greater understanding of shifts in species composition and evenness.

Similar to *H. verticillata*, studies of *G. proximus* in the Baía River also showed the usefulness of our framework. Analysis of invaded sites alone resulted in a sharp increase in DNS (from *c.* 24 to 36 species). However, applying the framework, we noticed a concomitant increase in species richness of non-invaded sites (*c.* 23–30 species). This finding implies the importance of large-scale factor(s) affecting the overall increase in DNS. For *G. proximus* in the upper Paraná River floodplain, flood pulse and connectivity seem to be important. In 2001, the floodplain experienced an intense drought that negatively affected fish diversity (Petry, Agostinho & Gomes, 2003), while intense flood pulses in 2007 and 2010 likely contributed to an increase in species richness (Agostinho *et al.*, 2007; Fernandes *et al.*, 2009).

The success of invasive species at sites with high diversity is well known in the literature, with the main causes attributed to high resource availability and/or greater habitat heterogeneity and facilitation by natives

(Levine & D'Antonio, 1999; Byers & Noonburg, 2003; Fridley *et al.*, 2007; Davis, 2009; Stohlgren, 2011). In the case of *G. proximus*, high resource availability seems to be the most feasible, as invaded sites are channels or connected floodplain lakes that usually support high species richness. Therefore, the high diversity sites occupied by *G. proximus* are also related to the dispersion of the species in the region: the species first occupies the Paraná River (from the floodplain upstream) and then disperses laterally to the floodplain and downwards in the direction of the Itaipu Reservoir (K. S. Goes and A. A. Agostinho, unpubl. data).

The mechanism described previously does not indicate that invasion by *G. proximus* resulted in no impact. This invader may compete with other species, especially with species having similar life history strategies and those within the same family, such as *Satanoperca pappaterra* (Heckel 1840). In fact, *G. proximus* appears to be replacing *S. pappaterra* in several environments of the upper Paraná River (K. S. Goes and A. A. Agostinho, unpubl. data). However, our framework's key utility lies in evaluation of broad patterns in the ecology of invasions. In the case of the floodplain, the ability of the flood pulse to favour an increase in DNS may have masked other invasion effects. Knowledge of the putative importance of flood pulse effects can be used to inform and guide future research to evaluate potential impacts of *G. proximus* in this ecosystem.

It should be stressed, however, that while we have observed increases in DNS in the two case studies, decreases associated with biological invasions might be more common (e.g. Flory & Clay, 2010). For example, in New Jersey old-fields, *Lonicera japonica* Thunb. was more likely to invade sites with high species richness (Meiners, Cadenasso & Pickett, 2004). However, after 5–15 years, a significant negative relationship between change of species richness and change of *L. japonica* cover was noted (Yurkonis & Meiners, 2004). Regardless of initial species richness, species were disproportionately lost from sites that were heavily invaded. In this case, the space-for-time snapshot (Fig. 4 in Meiners & Cadenasso, 2005) correctly indicated the negative dependence of species richness on invader cover. Interestingly, declines in species richness associated with *L. japonica* invasion resulted from negative effects on local colonisation rates and not from the competitive displacement of established species (Yurkonis & Meiners, 2004).

Finally, for the sake of simplicity, we used just two points in time throughout all our examples. Needless to say, observations over longer time intervals should result in a better understanding of invasion phenomena (see

Clarke, Latz & Albrecht, 2005). For example, it is conceivable that effects on DNS will change over time. An invasive species may initially facilitate establishment of some native species. Later, however, when the invader's density or cover increases, competition and elimination of native species may prevail. This has apparently been the case for some mobile Californian coastal dunes stabilised by introduced "phalanx" European beach grass (*Ammophila arenaria*) (Aptekar, 1999). Our understanding of the dependence of species establishment on the abundance of dominant species is still rather rudimentary (Gilbert, Turkington & Srivastava, 2009).

Conclusions and perspectives

Our framework demonstrates how combining data from pre- and post-invasions (time approach) with data obtained from invaded and non-invaded sites (space-for-time approach) can provide insights about factors related to invasibility and about the effects of NNS on DNS that would be difficult to ascertain whether these approaches were used individually. We note that it is very likely that many of the published results based just on only one of these approaches are still, at least qualitatively, valid. When comparing invaded and non-invaded sites, for example, ecologists usually consider many environmental factors so that sites are comparable (Brown, Scatena & Gurevitch, 2006). Nevertheless, conclusions from studies using space-for-time or temporal approaches alone should be regarded with caution. The importance of synthesising information of invasion biology has been recently acknowledged, and this field is experiencing advances with other frameworks that combine approaches that are generally used separately (Foxcroft, Pickett & Cadenasso, 2011; Gurevitch *et al.*, 2011). For example, van Kleunen *et al.* (2010) showed that combining invasive alien species versus native species comparisons and invasive versus non-invasive alien species comparisons in the same framework could provide insights that were not possible when analysed separately.

We anticipate that our framework will help to focus hypotheses and experiments (e.g. MacDougall & Turkington, 2005), ultimately bettering our understanding of the mechanisms behind invasions, as well as complement the interpretation of observational data. For example, indications of biological resistance provided by diversity (i.e. invasion of sites with low DNS; Fig. 2a–c) suggest that further experiments, manipulating native richness and measuring the output of NNS, are needed. Moreover, experiments that manipulate habitat heterogeneity and/or resource availability should be conducted

if these factors are implicated as important determinants of invasion success (i.e. invasion of sites with high DNS; Fig. 2d–f). In fact, it has been advocated that invasion biology would improve if a combination of approaches including quantitative empirical data, experimentation and structural equation modelling were used together (Didham *et al.*, 2005). Our framework is tailored to the first approach but could also be used with the other two approaches.

Although our conceptual framework is based on species richness, other population, community and ecosystem properties could easily be addressed. For example, functional diversity, food-web structure (number of links) and taxonomic composition (e.g. calculated ordination scores) could be used as response variables. It is important to note, however, that interpretation would differ when other parameters are used.

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