University of Groningen

Understanding plant invasions

Ordoñez Gloria, Alejandro

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2011

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):
Ordoñez Gloria, A. (2011). *Understanding plant invasions: A global scale meta-analysis*. s.n.

Copyright
Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the “Taverne” license. More information can be found on the University of Groningen website: https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment.

Take-down policy
If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): http://www.rug.nl/research/portal. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

Download date: 06-06-2022

7 Niche conservatism in invasive plants

Alejandro Ordoñez Gloria[ab], and Han Olff[a]

Abstract

Explanations for the success of alien species have frequently been based on their degree of niche overlap with native species. In order to predict and understand future invasions, we thus need to know if ecological traits/requirements of aliens remain similar [niche conservatism (NC)] or change [niche lability (NL)] in their novel habitat. Here we review the evidence for either NC or NL and the importance of these concepts for the further development of the field of invasion biology. For this we first discuss different views of the niche, and their implications for NC versus NL. Building from this, we address three key topics relevant to this discussion: evolutionary divergence vs. convergence of traits, conservation vs. adjustment of the bioclimatic niche, and the phylogenetic stasis vs. evolution of the niche. We emphasize the importance of the use of an appropriate niche concept for the accurate description and prediction of the fate of introduced aliens. In a meta–analysis, we find that NC in aliens is much more common than NL, making the concept of NC useful in predicting future invasions. In contrast, we find traits to have the possibility of being flexible, which suggests that aliens have the potential to change their traits in order to conserve their niche.

[a] Community and Conservation Ecology Group, University of Groningen
[b] Correspondence author. E–mail: A.Ordonez.Gloria@rug.nl

7.1 Introduction

The prediction, which species will establish successfully after their introduction to a non–native range, has become a priority topic in conservation biology. Scientists have therefore searched extensively for a predictive framework based on ecological mechanisms. A basic assumption in this line of research is the idea that aliens will express the same traits in both their native and introduced range. This is an important assumption, based on the idea of ”traits and niche conservatism” over space (their geographic range) and time (their evolutionary dynamics). However, a critical test of this idea is now clearly needed, especially as various *a priori* reasons can be thought of why it might not hold (as discussed in Losos 2008). Here we review the direct and indirect evidence for niche and trait conservatism in invasive species.

Niche conservatism (NC hereafter) is the idea that the niche of a species is fixed over ecological time scales (Peterson, Soberon & Sanchez-Cordero 1999, Wiens & Graham 2005) only changing very slowly over long evolutionary time spans (Ackerly 2003, Webb et al. 2002). This NC is an important implicit assumption in many population, community and macro ecological studies and has therefore major implications for conservation biology/ecology (Wiens & Graham 2005). Several factors causing it have been considered [as reviewed in Wiens et al. (2010), and Wiens & Graham (2005)] including, among others, the conservation of species–specific traits, constraints and trade–offs imposed by physiology and life history, lack of mixing between populations, absence of genetic variation for necessary traits, selection favoring a consistent choice of resources, and/or competition with species using alternative resources.

An important aspect of NC is its relevance to changes in species geographic ranges driven by global change (e.g. the case of movement of species across dispersal barriers or due to climate change). This is an issue of particular relevance in invasion ecology as the new performance–environment dynamics, generated from the rearrangement of species distribution ranges and environmental conditions, have the potential to enhance invasions (Thuiller 2007, Thuiller, Richardson, Midgley & Nentwig 2007). Specifically, if species do not ”stick to their niche” during ecological time scales, the prediction of possible invasive species before they arrive in a new environment becomes virtually impossible.

In this review we focus on three major topics concerning NC and its importance for understanding invasive plant species dynamics. We specifically review the literature on, and perform meta–analyses of: i) the importance of ecological traits for NC, ii) the idea of bioclimatic niche conservatism (BNC hereafter) and iii) the prevalence of phylogenetic niche conservatism (PNC hereafter).

7.2 The starting point: an adequate niche concept

The niche is a central concept in community ecology. It provides a the baseline for understanding many aspects of species adaptations and interactions (Chase & Leibold 2003, Hutchinson 1957, Root 1967). In order to develop a predictive framework of species invasions based on niche dynamics, it is important to first discuss which niche concept(s) is most appropriate. Across the literature, many alternative definitions for *"niche"* have been proposed based on either the geographic distribution, the functions performed, the resources a species consumes, the conditions it tolerates and/or where it is safe from enemies. Nevertheless a consistent use of those definitions is lacking. Perhaps the most commonly used of these definitions is Hutchinson's (1957), who described the niche as a *"set of biotic and abiotic conditions in which a species is able to persist and maintain stable population sizes"*. Developing from these ideas, two main (nested) niche types are currently distinguished in ecology (Chase & Leibold 2003, Pearman et al. 2008, Soberon 2007): i) the fundamental niche (or Grinnellian niche) defined as the basic conditions that allow a positive population growth rate of a particular species, in absence of any other interacting species and dispersal limitation; and ii) the realized niche (or Eltonian niche) defined by the portion of the fundamental niche in which a species can persist, accounting for constraining effects of biological interactions with other species such (e.g. competition or predation).

It is not easy to measure a species niche. Appropriate measures should include its' physiological tolerances, biotic interactions, and dispersal limitations. From all the available methods to measure a species niche, none of them has been able to incorporate all three elements simultaneously (Chase & Leibold 2003). As a result, some studies only focus on ecological and geographical properties of species on a broad scale, excluding biotic interactions between species (fundamental or Grinnellian niche). Meanwhile others include species–species interactions and biotic properties on the local scale (realized or Eltonian niche). This makes the evaluation of the conservation of niches a even harder task that already is, as one should consider not only the processes driving the conservation of niches but also the approach used to measure the niche and which type of niche the selected measure refers to (i.e. fundamental vs. realized). Additionally, niche measurements used in most studies have are strongly scale dependent. Specifically, the fundamental niche is often studied at larger scales (e.g., in relation to climatic tolerance) while realized niche processes operate more locally, adding another layer of complexity to the problem (Pearman et al. 2008, Soberon 2007).

Also for niche conservatism to play an important role in invasion ecology, it must be clear from the beginning which type of niche is addressed in a study. This will determine how niche overlap determines the success or failure of an introduced alien. Specifically, we propose that the understanding of the dynamics of species invasions depends on the conservatisms vs. lability of its fundamental niche (will it spread to areas with similar or different environmental conditions as in its native range) and its realized niche once introduced (e.g. it will ecologically outperform co–occurring species in a similar way as in its native range, or not). We expect this improves the ability to predict novel species invasions and changes in geographic range of already introduced aliens. If the fundamental niche is conservative, then invasive species should have similar climatic preferences in their native and introduced ranges(Wiens & Graham 2005). If the realized niche is conservative, then species are expected to play a similar ecological role (e.g. in the competitive hierarchy, or in relation to enemies) in their native and introduced ranges. It should be tested if this conservatism of the fundamental and realized indeed applies, or that lability is important for either of these. In the next sections, we will explore these alternative hypotheses through meta–analyses.

7.3 Trait conservatism as a driver of niche conservatism

Niche differentiation (either fundamental or realized) between aliens and natives is the mechanism most commonly invoked by the suite of hypotheses that have been proposed to explain variation in success among aliens (summarized in **Table 7.1**). It has been proposed that specific community or ecosystem properties prevent alien plants from becoming invasive (Mack et al. 2000), using explanations based on niche availability. For example, the area occupied by fundamental niches (potential habitat) for a species can be limited in a given landscape (Jackson & Overpeck 2000). Also, changes in the combinations of different environmental factors that are realized in a given landscape at a given point in time (Ackerly 2003) could allow a species to colonize previously unavailable areas. These explanations do not imply a change in the potential or realized niche of the alien. They rather suggest a limitation or change in the (spatial) availability of these niches.

Changes in fundamental or realized niche of an alien in its new range can happen when it changes key functional traits. The idea of using such traits to map the niche of species has received increased attention in recent years (McGill et al. 2006, Violle & Jiang 2009). Potentially, this approach may overcome limitations of different niche metrics, and improve the predictive and quantitative nature of community ecology. The concept is based on the assumption that some traits of species will determine under which biotic or abiotic conditions it can persist ("response traits" *sensu* Lavorel & Garnier 2002). Therefore, such traits (for example thorns, salt glands, thick leaves) can be a good proxy for the niche of a species as they tell something about the environmental conditions where can occur, so also about where it can potentially invade.

In the case of alien species, such traits can be used to better understand the invasion process. For example, by comparing the attributes of the alien between its native and introduced range, it is then possible to discriminate between niche lability vs. conservatism. This will in turn determine how extensive the invasion will be: will the alien occupy/exploit a wider or another range of biotic and abiotic conditions than would be expected from its occurrence and traits in its native range.

The majority of the studies published to date (summarized in **Fig. 7.1**) find that important ecological traits (and possibly thus the niches of alien species) are conserved between their native and alien range. This supports both the idea that important ecological traits, related to a species niche, are conserved over space and evolutionary time (Travis 1989, Wiens & Graham 2005) and that natural selection favors those traits which maximize the survival of a species, thus inhibiting niches from changing a lot (Ackerly 2003). However, it is important to state that the stabilizing effects of selection on ecological niches are the outcome of the trade–offs among traits, leading to alternative ecological strategies or life histories, causing the preservation of equilibrium values of fitness–maximizing traits within a niche. This, coupled with the low genetic variation

Table 7.1 Leading in invasion biology and their relationship to niche conservatism (**NC**) or lability (**NL**).

Hypotheses	NC	NL	References
Enemy release	+		(Blumenthal 2006, Colautti, Ricciardi, Grigorovich & Macisaac 2004, Darwin 1866, Funk & Throop 2010, Keane & Crawley 2002, Liu & Stiling 2006, Stachowicz & Tilman 2005)
Evolution of increased competitive ability		+	(Blossey & Notzold 1995, Bossdorf, Auge, Lafuma, Rogers, Siemann & Prati 2005, Callaway & Ridenour 2004)
Biotic resistance from enemies/competitors		+	(Kennedy, Naeem, Howe, Knops, Tilman & Reich 2002, Levine 2000, Levine et al. 2004, Macarthu.R & Levins 1967*a*, Maron & Vila 2001, Verhoeven, Biere, Harvey & van der Putten 2009)
New associations		+	(Colautti et al. 2004, Hokkanen & Pimentel 1989, Verhoeven et al. 2009)
Mutualist facilitation	+	+	(Richardson, Allsopp, D'Antonio, Milton & Rejmanek 2000)
Invasional meltdown	+		(Ricciardi 2001, Simberloff & Von Holle 1999)
Empty niche	+	+	(Hierro, Maron & Callaway 2005, Mwangi, Schmitz, Scherber, Roscher, Schumacher, Scherer-Lorenzen, Weisser & Schmid 2007)
Novel weapons	+		(Callaway & Aschehoug 2000, Callaway & Ridenour 2004, He, Feng, Ridenour, Thelen, Pollock, Diaconu & Callaway 2009, Vivanco et al. 2004)
Habitat filtering/ Climate matching	+		(Broennimann et al. 2007, Levine 2000)
Darwin's naturalisation hypothesis	+		(Daehler 2001, Diez et al. 2008, Duncan & Williams 2002, Jiang et al. 2010, Lambdon & Hulme 2006, Strauss et al. 2006)
Novel niches	+	+	(MacDougall, Gilbert & Levine 2009, MacDougall & Turkington 2005, Shea & Chesson 2002)

observed in some species may strongly inhibit trait evolution, which in the case of aliens restricts spreading into new niches (Case & Taper 2000).

The link between conservation of ecological traits to the idea of niche conservatism does not mean that traits will always remain fixed within a species (as shown by Albert et al. (2010) and Messier et al. (2010) in a cross-scale comparison). In fact, plants are renown for their high degree of phenotypic plasticity. In most cases, this plasticity may be required for a species to occupy its full realized or fundamental niche. Thus, a certain degree of plasticity in a trait can be viewed as the mechanism allowing a species to oc-

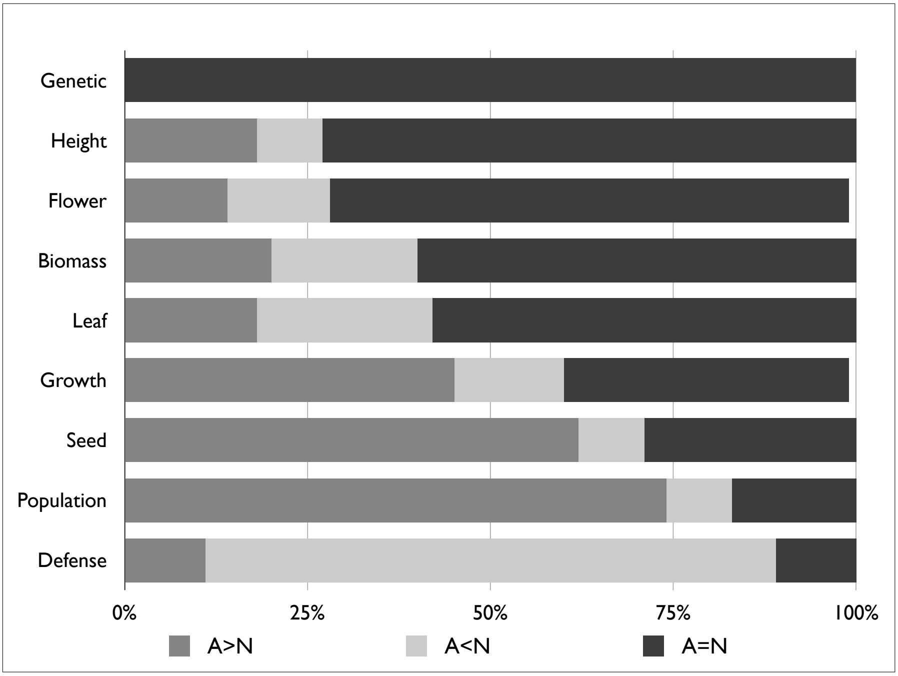

Figure 7.1 Summary of the results of 34 studies comparing ecological traits of introduced plants between its' alien (A) and native (N) range. Directionally of the contrasts are presented as: Alien higher than Native $A > N$; Alien smaller than Native $A < N$ and Alien equal to Native $A = N$). List of references used to build the figure are presented as supplementary material (***Appendix B***). Each section of the bar shows percentages of significant results showing the direction of the contrast. Used traits for each category are: *Gentic*, *Height* (Plant height, size, stem height), *Flower* (Flower size, flowering speed, number of flowers, petal width), *Biomass* (Biomass, Root mass, Root:Shoot ratio, Shoot mass), *Leaf* (Leaf Area, leaf area ratio (LAR), C13, leaf chemistry (C, N, C:N), leaf number, leaf size, leaf toughness, SLA, stomata conductance, total leaf area), (*Growth*: Growth rate, number of shoots, number of vegetative offspring, stem Number, Tillering rate), *Seed* (Fruit Mass, germination rate/speed, optimum germination temperature, reproductive output, seed bank, seed mass, Seed size, seedling establishment rates, seedling survival), *Population* (Average age, density, maximum age, population size and proportion of young stages), and *Defense* (Chemical concentration (Tannin, Hypericin, Pseudohypericin, nerolidol and viridifloral chemotypes), fruit capsule, herbivory tolerance, Trichomes).

cupy its niche (Ackerly 2003). This degree of plasticity may then be conserved between the native and alien range of a plant, leading to niche conservatism.

We have shown so far that most current evidence points towards the conservatism of key traits in invasive plants between their native and introduced ranges (**Fig. 7.1**). However, linking this trend to hypotheses based on the idea of alien–native trait similarity or dissimilarity will depend on the analyzed trait and the scale of the study (local, regional or continental). Following these results on conservatism of traits, we will discuss in the next section the conservatism of the bioclimatic niche.

7.4 Bioclimatic niche conservatism in invasive species

A large literature on species distribution models is based on the idea of the existence of a bioclimatic niche, that is specific areas where a species encounters the climatic conditions under which it can persist (e.g. as determined by its frost or drought sensitivity). These studies are often done at very large scales. Bioclimatic niches are therefore closer to a fundamental than a realized niche. Most common definitions of the bioclimatic niche explicitly exclude local environmental conditions, such as soil properties, or biotic interactions (Wiens & Graham 2005). The conservation of this climatic–space across space and time has a strong link with the idea that the fundamental niche is conserved.

This idea that bioclimatic niches are conserved over space and time (bioclimatic niche conservatism, BNC) has been intensively scrutinized in a number of studies (as reviewed in Losos 2008, Wiens et al. 2010, Wiens & Graham 2005) thanks to the increasing availability of easily accessible species distribution data, large scale and fine resolution climatic information and the development of new species distribution modeling (or SDM's) statistical techniques. However, efforts to determine the level of BNC across different species and groups (as summarized in **Fig. 7.2** and ***Appendix C***) have yielded ambiguous results; with some studies showing strong support for the conservatism of climatic niches (Buckley, Davies, Ackerly, Kraft, Harrison, Anacker, Cornell, Damschen, Grytnes, Hawkins, McCain, Stephens & Wiens 2010, Roura-Pascual, Suarez, McNyset, Gomez, Pons, Touyama, Wild, Gascon & Peterson 2006, Wiens & Donoghue 2004) while others suggest that such niches are relatively labile (Broennimann et al. 2007, Losos 2008, Losos, Leal, Glor, de Queiroz, Hertz, Schettino, Lara, Jackman & Larson 2003, Stevens 2004).

In the case of invasive alien species, BNC has large implications for the prediction of successful aliens (or areas of introduction) as it provides a framework to determine which and where alien species can become established. An example of this the work by Thuiller et al. (2005) showing (by the use of species distribution models) a close match between the climatic component, the ecological habitat suitability, and the current pattern of occurrence of South African invasive species in other parts of the world. A similar study on the waterthyme (*Hydrilla verticillata*) showed a match between the occupied realized environments in its native (Southeast Asia and the Australo–Pacific) and its invaded distributional area in North America (Peterson 2003). Additional support for BNC emerges from a study of 29 introduced reptile and amphibian species in North America (Wiens & Graham 2005) which found a strong relationship between native and introduced geographic range limits (poleward latitudinal extents); and an earlier study based on several introduced bird and mammal species (Sax 2001) showing a significant correlation between native and introduced latitudinal extents. All these works provide support to the idea that bioclimatic niches are conserved across space, constituting long–term stable constraints on the potential geographic distributions of species (Peterson et al. 1999). However, is should be noted that final conclusions on the conservation of the bioclimatic niche can only be drawn after sufficient time has passed since the introduction. Is perhaps due to this that no study to our knowledge has analyzed his-

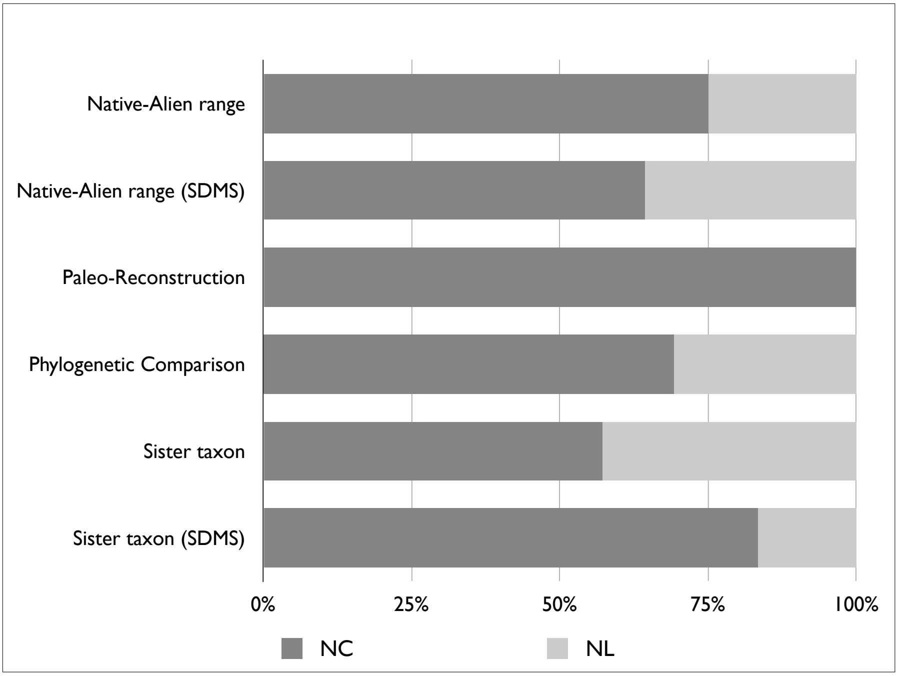

Figure 7.2 Summary of 70 studies showing direct or indirect support for or against the idea of niche conservatism (**NC**) or lability (**NL**). List of references used to build the figure are presented as supplementary material (***Appendix C***). Each section of the bar shows percentages of significant results showing support of **NC** or **NL**. Studies were summarized according to the used methodology: *Sister taxon (SDMS)* comparisons of related species using species distribution models (SDMS); *Sister taxon* performance or attributes contrast of related species; *Phylogenetic Comparison* attributes of related species/communities are compared to find a phylogenetic signal (clustered–overdispersed–random); *Paleo–reconstruction* comparisons of the range of current species to that of extinct relatives; *Native–Alien range (SDMS)* cross comparisons of SDMS form the native and introduced range of successful aliens; and *Native–Alien range* comparisons of population and eco–physiological attributes between a alien and the closest related native.

torical changes in bioclimatic niches between the native and introduced range of alien species.

Evidence for bioclimatic niche lability has however also been found, particularly for those species with broad environmental tolerances. Studies show that in some cases, successful alien species disperse to, and persist in areas which would be considered unsuitable for them based on their native range distribution (Losos 2008). An example of this is the case of the invasive spotted knapweed (*Centaurea maculosa*), which showed a significant range shift between its native (Europe) and its non–native (North America) distribution; indicating how invasive aliens are sometimes able to persist under different climatic conditions than those encountered in their native range, suggesting a lability in their fundamental niche (Broennimann et al. 2007). This could be attributed to either genetic drift/founder effects (Muller-Scharer, Schaffner & Steinger 2004), strong restrictions on gene flow between the native and introduced populations (Diamantidis, Carey & Papadopoulos 2008), hybridization and polyploidy (Blossey & Notzold 1995) or higher potential of rapid adaptive evolution of alien plants (Maron, Vila, Bommarco, Elmendorf & Beardsley 2004, Sexton, McKay & Sala 2002).

The occurrence of niche conservatism in many species, and lability in others, has important consequences for the prediction and understanding of biological invasions. This has special relevance for invasive species screening systems used today (e.g. Daehler & Carino 2000, Pheloung, Williams & Halloy 1999, Reichard & Hamilton 1997, Tucker & Richardson 1995); as these are generally based on the assumption that niches and attributes are conserved across space and time.

A last point to emphasize is the need for large–scale comparisons of climatic niches between native and introduced ranges, utilizing the available data from the hundreds of introduced animal species and thousands of introduced plants. Such studies are urgently needed to assess the ability of methods based on the BNC principle to predict the spread of invasive species.

In summary, although some studies have shown that invasive species are able to spread into novel bioclimatic niches, most of the available direct and indirect evidence leans toward the conservation of the bioclimatic niche of introduced species. As a result, invasions of non–native environments by a species are most likely if the novel climatic conditions are similar to those the species encounters in its native range.

7.5 PNC and the success of introduced aliens

Phylogenetic niche conservatism (PNC) has been defined as *”the tendency of related species to retain ancestral ecological characteristic”* (Wiens et al. 2010, Wiens & Graham 2005). Based on this idea, several studies have aimed to determine the relation between phylogenetic and ecological similarity among species, testing the hypothesis that closely related species are more likely to be ecologically similar than phylogenetically more distantly related ones. Nevertheless, as summarized in **Fig. 7.2**, the evidence is not unambiguous as studies show evidence both in support of PNC (e.g. Hadly, Spaeth & Li 2009, Swenson, Enquist, Thompson & Zimmerman 2007, Webb 2000) as against it (e.g. Losos et al. 2003, Silvertown, Dodd, Gowing, Lawson & McConway 2006).

The recent increase in interest in PNC has been the result of the better and more phylogenies for extant species, and new extensive data sets of fossil records. Additionally, the invention of phylogenetic comparative methods [Phylogenetic independent contrasts – PIC’s (Felsenstein 1985) or Phylogenetic generalized least squares –PGLS (Grafen 1992)], has facilitated the number of studies on the ”phylogenetic effect” or ”phylogenetic signal” of ecological attributes (Blomberg & Garland 2002). Overall, this merging of phylogenetics and community ecology has resulted in several studies invoking PNC as the main mechanism explaining the responses of species to anthropogenic climate change, the spread of invasive species, species biogeography patterns, or speciation and diversity trends across evolutionary times (Cavender-Bares, Kozak, Fine & Kembel 2009, Wiens et al. 2010, Wiens & Graham 2005).

Understanding and predicting the impact of invasive species is one of the central pillars of fundamental and applied ecology (Rejmanek et al. 2005, Richardson & Pyšek 2006). To address this, invasion ecologists have focused on understanding either which species traits make introduced species more likely to become invaders (Pyšek & Richardson 2007, Rejmanek et al. 2005, van Kleunen et al. 2010) or why some natural communities are more prone to invasion than others (Davis et al. 2000, Lambdon et al. 2008, Rejmanek 1999, Richardson, Rouget, Ralston, Cowling, Van Rensburg & Thuiller 2005). In an attempt to merge both of these approaches some works (Cadotte et al. 2009, Daehler 2001, Diez et al. 2008, Diez et al. 2009, Duncan & Williams 2002, Jiang et al. 2010, Lambdon & Hulme 2006, Strauss et al. 2006, Thuiller et al. 2010) have focused on the use of the relatedness (taxonomic or phylogenetic) between aliens and natives as a measurement of the likelihood of invasion. This is based on the assumption that phylogenetic similarity can be used as a surrogate to ecological or niche similarity. Therefore, several works have used the level of similarity to the native members of a community as a possible predictors of invasion success; although it should be noted that with the exception of a few works (e.g. Cadotte et al. 2009, Jiang et al. 2010, Strauss et al. 2006) the level of phylogenetic similarity has only been quantified on the basis of classic taxonomic classification rather than on newer phylogenies.

Based on the PNC idea, two very different hypotheses linking alien success and its phylogenetic relatedness to the native species pool have been formulated: i) novel genera are expected to be more successful naturalizing in those areas where there are no closely related natives (Darwin's naturalisation hypothesis *sensu* Rejmanek 1996), or ii) introduced species have a higher chance to establish in areas with phylogenetically similar species (phenotypic attraction hypothesis *sensu* Webb et al. 2002). An important assumption of both of these hypotheses is again that species niches are conserved over time, implying that closely related species tend to have more similar niches than distantly related ones (Wiens et al. 2010). However, although closely related species have a tendency to occupy ecologically similar niches, those niches are never exactly identical to each other (Peterson et al. 1999).

As more studies address the role of PNC in the success of alien species, we believe that its ubiquity cannot be assumed blindly given the increasing amount of works that do not support this idea (As shown in **Fig. 7.2** and reviewed by Losos 2008). For example, while some studies in continental North America support PNC (Mack 1996, Rejmanek 1996, Strauss et al. 2006), studies in New Zealand find evidence against it (Diez et al. 2008, Duncan & Williams 2002) while again others on Mediterranean islands have shown an idiosyncratic relation between phylogenetic relation and alien success (Lambdon & Hulme 2006, Lambdon et al. 2008). A possible reason for these heterogeneous results is that PNC strength may not be constant over different parts of the phylogenetic tree (Diez et al. 2009, Thuiller et al. 2010). As a result, certain groups of species may exhibit great evolutionary lability (as reviewed by Pearman et al. 2008) while others may express evolutionary convergence of attributes (Cavender-Bares, Ackerly, Baum & Bazzaz 2004). Based on this, it's clear that any future *"rule of thumb"* relating introduction success to phylogenetic relatedness should explicitly provide quantitative evidence for PNC (Blomberg, Garland & Ives 2003, Cadotte et al. 2009, Losos

2008) so any possible source of deviation that could likely blur this relation could be determined and controlled.

A final point to address here is the difficult task of making a link between the multidimensional nature of the niche with the simultaneous conservation and lability of attributes across the phylogeny (that is, some dimensions tend to be phylogenetic under–dispersed, while others are over–dispersed). For some authors this is not a problem, as they view the phylogenetic similarity as a conglomerate measure that merges the information of each of the dimensions defining a species niche (Strauss et al. 2006, Thuiller et al. 2010). However, it is possible that the opposite phylogenetic trends of different niche dimensions could result in random phylogenetic patterns, making the relation between phylogenetic relatedness and introduction success void, even though meaningful ecological mechanisms are currently at work.

But still it is of course true that sister species are more likely to occupy ecologically similar niches than expected from random pairwise comparisons with other species (Warren, Glor & Turelli 2008). So far, evidence from several studies in this field suggest that it is more likely for a species or a community of species to shift their range than to evolve a new niche, thus supporting PNC (Donoghue 2008). Furthermore, it should be noted that NC could not only differ across time (PNC) and space (BNC) but also differs from taxa to taxa and between spatial scales of observation. Finally, we suggest that although the level of phylogenetic similarity is a promising approach to predict successful aliens; the comparison of the patterns of phylogenetic and ecological similarity is nevertheless the most likely path to determine the ecological mechanisms that make introduced species naturalize.

7.6 Conclusion

Niche conservatism and its application in predicting invasions is still a much–debated topic in ecology with no definite answer. Evidence is found both in favor and against it. However, we conclude that most of the current evidence supports the idea of NC over space (BNC) and time (PNC) of alien species. Nevertheless, this does imply that species traits are always conserved across ranges (trait conservatism). This may result from of the interplay between environmental filtering (resulting in the conservation of the fundamental niche), competitive interactions (resulting in the shaping of the realized niche) and evolutionary patterns (making traits either evolutionary conserved or convergent).

One of the main consequences of the observed support for BNC and PNC for invasive species is that niche preferences seem mostly conserved between the native and alien ranges. As a result, this suggests that the overall likelihood of evolving and adapting to a novel niche is lower than moving to another niche with optimal or even suboptimal conditions for survival. This seems to be consistent over evolutionary time as is shown by extensive studies on fossil records and the current distribution of many taxa. Furthermore, closely related species occupy similar niches whereas distantly related species have different niche requirements; the outcome of this is that sister species are less likely to locally co–occur, reducing the competition between congenerics.

In general, NC is seen in many introduced taxa, but deviations from this trend are possible. Unfortunately, very few studies have focussed on the evaluation of the patterns of similarity or dissimilarity in the niche and/or attributes of invasive alien plants between their native and their introduced range using a large number of species. As more data become available, more studies and better comparisons should be made to determine whether or not niches of aliens are conserved between the native and alien range, what the consequences are for global change phenomena for future species invasions. This makes multi–species comparisons over a wide set of environments an important step forward in invasion ecology.

Part V

Synthesis and closing features