Predicting invasion success: a basic framework using plant functional traits

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Summary Looking for important traits that could predict species invasions is a major goal in ecology. Universal traits, i.e. traits uniquely related to invasion are rare. The relative importance of particular traits can change depending on the local context. Recent advances in functional community ecology have shown that simple morphological or eco-physiological plant functional traits (PFTs) can be successfully related to species success along large ecological gradients. PFTs usually co-vary along axes of specialisation and independent axes define an *n* dimensional trait space describing species trait niche. Based on this theory, we hypothesised that the identification of axes of specialisation among traits for invasive species might be the key to explain their success in new environments. Traits related to these axes can be used as functional markers to predict invasion patterns. We tested this basic framework for 12 exotic grass species found on Banks Peninsula, New Zealand, using a large data set (1340 botanical records).

Keywords Invasion, plant functional traits, axis of specialisation, plant height, nitrate/ammonium trade-off, elevation gradient, dominant grasses, Banks Peninsula, New Zealand.

INTRODUCTION

Biological invasions are one of the main biodiversity threats worldwide (Millennium Ecosystem assessment 2005). It is urgent to find efficient tools to predict invasive success and their impacts on native ecosystems (Funk *et al.* 2008). The search for universal traits that can explain invasion success has been relatively unfruitful. The relative importance of particular traits for invasion is likely to change among environments and is strongly context-dependent (Dawson *et al.* 2009). Recently, the use of plant functional traits (PFTs) has been proposed as a mean to predict invasion patterns (Tecco *et al.* 2010). PFTs are any morphological or eco-physiological plant attribute that is directly or indirectly linked to a function enabling a plant to persist in its environment. Because, they are related to one or more components of plant fitness (Violle *et al.* 2007), they are good candidates to study the causes of invasion across a wide range of ecological conditions (Tecco *et al.* 2010). The central hypothesis is that species with similar traits attributes are likely to respond in a similar way to the same environmental factors (response-traits) (Lavorel and Garnier 2002).

In the past decade, several studies have attempted to describe the spectrum of PFTs observed across the plant kingdom (e.g. Wright *et al.* 2004). Traits have been shown to co-vary along axes of specialisation defining major trade-offs among traits. For instance, plant species worldwide have been shown to fall along one major axis of specialisation separating conservative from exploitative plant types based on their leaf trait attributes (Wright *et al.* 2004). However, this global pattern may not be sufficient to predict local patterns of abundance at the community scale. At this scale, other independent axes of specialisation have been described (Ackerly 2004, Maire *et al.* 2009) (related for instance with plant stature, roots or seed traits). Independent axes can define an *n* dimensional trait space (species niche traits) within a particular community (Gross *et al.* 2007) and can explain species coexistence and community assembly (Ackerly 2004).

Here, we propose a framework that aims to identify particular PFTs that are likely to explain species invasion success depending on the local ecological context. The main idea is to identify axes of specialisation among particular groups of invasive species that could explain their relative success in their new environment. These axes are likely to be different from the trade-offs observed in global comparisons. Invasive species may have been selected through complex naturalisation processes and some functional strategies can be over- or under-represented in the new environment compared to their native range (Lambdon *et al.* 2008). As such, functional diversity in the new environment might be truncated and functional differentiation among invasive plants in their new environment needs to be reassessed.

In this paper, we apply this idea to examine invasion success in New Zealand grasslands. Most of the invasive grasses have been widely studied in Europe and trait databases are available to support our framework. Invasive grasses are one of the most successful taxa in New Zealand and can establish in grasslands from lowlands to alpine areas (Knox 1969). We hypothesised here that (i) axes of specialisation occur across the dominant invasive grass species in New Zealand grasslands; (ii) traits that differentiate these species the most are likely to explain their success in the new environment; and (iii) traits that are important

in explaining local abundance may change depending on local environmental conditions.

MATERIALS AND METHODS

We investigated 12 invasive grass species that are among the most dominant in New Zealand grasslands (Knox 1969), namely *Agrostis capillaris*, *Agrostis canina*, *Anthoxanthum odoratum*, *Arrhenatherum elatius*, *Dactylis glomerata*, *Festuca arundinacea*, *Festuca rubra*, *Holcus lanatus*, *Lolium perenne*, *Poa pratensis*, *Poa trivialis* and *Trisetum flavescens*. These species co-exist in productive European meadows. They have been introduced to New Zealand during the past 150 years for agriculture, and are found across a wide range of ecological conditions. The distribution and local abundance of species across Banks Peninsula, New Zealand, was recorded during a field survey conducted by H. Wilson (1988; data available at Landcare Research's online National Vegetation Survey database: nvs.landcareresearch.co.nz, and used with permission of H. Wilson). This survey, conducted between 1983 and 1988, recorded the abundance of all vascular plant species found in 1340 36 m^2 plots

systematically located across the 100,500 ha area of Banks Peninsula. Species rank abundance was recorded visually in each plot (species abundance). The twelve grass species studied are present in 93% of the recorded plots and are among the dominant species in 75% of them. Species traits have been drawn from a previous study (Maire *et al.* 2009), where a wide range of root, leaf and plant stature traits have been measured on the 12 species in an experiment undertaken in the French Massif Central (see legend to Figure 1).

A principal component analysis (PCA) was first conducted to identify major axes of differentiation across the 12 species (Gross *et al.* 2007). Then, we identified two traits that differentiated the 12 species the most along the first two PCA axes. Linear and stepwise regressions were conducted to test whether these two traits were able to predict average species abundance on Banks Peninsula. To test the existence of trait-environment interactions, we then integrated the effect of traits and elevation in a full factorial model. Models with the lowest Akaike information criterion (AIC) were selected. For this last analysis, we calculated within each 100 m altitudinal belt the average abundance of each species. All statistical analyses were performed using the statistical software JMP 5.01 (SAS Institute, Cary, NC, USA).
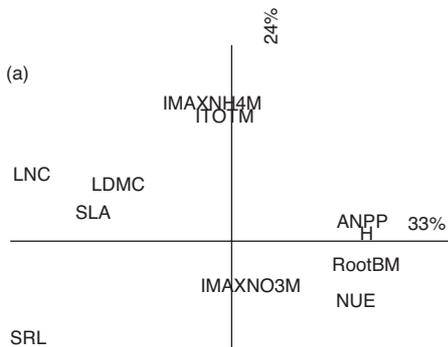
Figure 1. Axes of specialisation and average invasive grass species abundances on Banks Peninsula. (a) Principal component analysis (PCA) of plant traits measured under controlled conditions (see below for abbreviations); (b) Linear regression between nitrate preference and average species abundance (log transformed); (c) Linear regression between plant height and average species abundance (log transformed) on Banks Peninsula. Traits selected were: leaf nitrogen content (LNC), specific leaf area (SLA), leaf dry mater content (LDMC); specific root length (SRL); annual net productivity (ANPP); root biomass (rootBM); nutrient use efficiency (NUE); root maximal uptake capacity for total nitrogen, NO_3^- or NH_4^+ (IMAXTOT, IMAXNO$_3^-$, IMAXNH$_4^+$). A higher nitrate preference is shown for higher value of IMAXNO$_3^-$. Regression parameters are shown: ** = P <0.001.
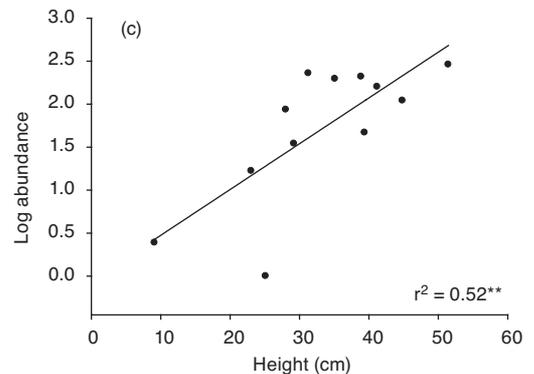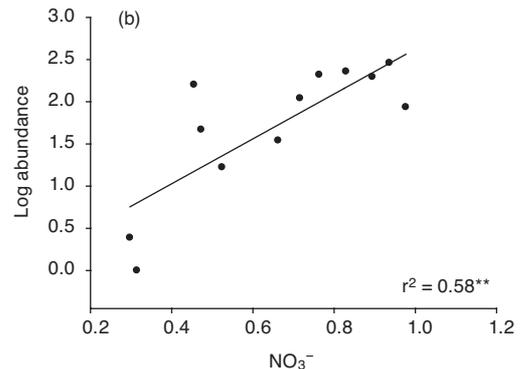
RESULTS

The 12 species were segregated along two axes of specialisation (Figure 1a). The first axis of speciali-sation (Axis 1) explained 33% of the variance. This axis separated species based on their stature (plant height, productivity), which was negatively correlated with leaf traits and root morphological traits (SLA, LNC, SRL, see Figure 1 for abbreviations). Axis 1 discriminated tall and conservative plants from small exploitative grasses. A second independent axis of specialisation (Axis 2), which explained 24% of the variance, separated species based on their mineral N affinity and maximum N uptake capacity, i.e. ammo-nium/nitrate trade-off.

Plant height (H) and plant preference for nitrate (NO_3^-) were selected as two uncorrelated traits for each axis of specialisation. Across all Banks Peninsula, each trait was strongly related with average species abun-dance on Banks Peninsula ($r^2 = 0.79$***, Figure 1). Tall species with nitrate preference tended to be more abundant on Banks Peninsula (Table 1). However, the importance of traits changed along the elevation gradient (Table 1, significant interaction between H × NO_3^- × Elevation: P = 0.002) (Figure 2). Tall plants

Table 1. Relation between PFTs and alien species abundance on Banks Peninsula analysed with a step-wise regression. Selected models exhibited the lowest AIC. (A) Species abundance across Banks Peninsula explained by PFTs: nitrate preferences (NO_3^-) and plant height (H); (B) Interaction between traits and elevation.

A		r^2	AIC	P
Model		0.79	−19.02	0.0009
	df	*Estimate*	*Fratio*	*P*
NO_3^-	1	1.86	9.75	0.01
H	1	0.03	7.23	0.02
Error	9			
B		r^2	AIC	P
Model		0.18	−364	<0.0001
	df	*Estimate*	*Fratio*	*P*
Elevation	1	−0.0002	1.47	ns
NO_3^-	1	0.71	23.35	<0.0001
Elevation × NO_3^-	1	−0.001	1.99	ns
H	1	0.01	6.49	0.01
Elevation × H	1	−0.00002	0.78	ns
NO_3^- × H	1	−0.03	2.09	ns
Elevation × NO_3^- × H	1	−0.0003	9.67	0.002
Error	264			

with nitrate preference were more abundant at low elevation (200 m). In contrast, in the subalpine area (above 700 m high) plants of intermediate size with both nitrate and ammonium preferences were able to coexist. Tall plants with high nitrate preference were in low abundance at high elevation (Figure 2).

DISCUSSION

The identification of axes of specialisation within a group of invasive grass species was sufficient to
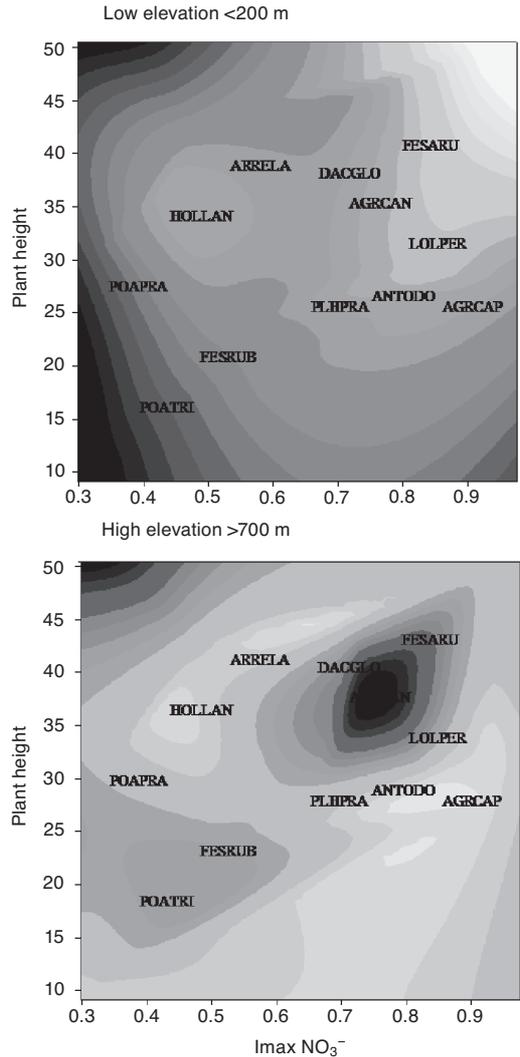
Figure 2. Relationship between traits and abundance along the elevation gradient on Banks Peninsula. Dark colours indicate a low level of abundance, light colours indicate high dominance. Species location is indicated in the trait space.

detect two functional traits linked with invasion. The 12 grass species were segregated along two main axes of differentiation. The first axis separated tall and slow-growing species from small, fast-growing ones. The second axis discriminated species based on their N preference. Consistent with our main hypothesis, traits (H and NO_3^-) related with the major axes of specialisation in the new environment were able to predict invasive species abundance.

The tallest species that specialised in NO_3^- uptake were the most abundant across Banks Peninsula. This trait syndrome typically corresponds to highly competitive species in productive grasslands where N cycling is generally fast (Maire *et al.* 2009). On Banks Peninsula, this outcome might be linked to habitat availability, with low elevation productive grasslands dominated by *D. glomerata* and *L. perenne* representing over 70% of the land cover (F. Tomasetto, Lincoln University, unpublished data). However, we found a significant interaction between traits and elevation, indicating the occurrence of a functional shift along the elevation gradient. This observed shift is typical of those generally observed along elevation gradients. Alpine plants tend to be smaller with a preference for an ammonium N source (Ozenda 1985). Our results are also in accordance with a recent study conducted in European subalpine grasslands (Pornon *et al.* 2007), which found complementarity in mineral nitrogen use among dominant species.

This study provides a simple theoretical framework to identify traits related to invasion success. Traits linked to the observed axes of specialisation in the new environment were those most likely to predict invasion success. Trait-environment relationships observed within our group of species were also consistent with general patterns observed along large ecological gradients and for a greater number of species in other places (Ozenda 1985, Pornon *et al.* 2007).

It is clear that trait identification is only a first step to understand the dynamics of invasive species in their new environment. For example, our approach did not take into account mechanisms that may drive functional change along the elevation gradients (e.g. biotic interactions). In addition, evolutionary trait shift between the native and the introduced range could be important. Despite these limitations, our approach was able to predict the local abundance of invasive grass species across a large ecological gradient. Finally, as the traits identified in this study may also impact ecosystem functioning (Lavorel and Garnier 2002) (i.e. height may modify competition intensity; N uptake strategies may affect N cycling), our approach can also help to assess invasive species impact on native ecosystems.

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