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LETTER

Common and rare plant species respond differently to fertilisation and competition, whether they are alien or native

Wayne Dawson,[1,2] Markus Fischer[1] and Mark van Kleunen[1,2]

Abstract

Plant traits associated with alien invasiveness may also distinguish rare from common native species. To test this, we grew 23 native (9 common, 14 rare) and 18 alien (8 common, 10 rare) herbaceous species in Switzerland from six plant families under nutrient addition and competition treatments. Alien and common species achieved greater biomass than native and rare species did overall respectively. Across alien and native origins, common species increased total biomass more strongly in response to nutrient addition than rare species did and this difference was not confounded by habitat dissimilarities. There was a weak tendency for common species to survive competition better than rare species, which was also independent of origin. Overall, our study suggests that common alien and native plant species are not fundamentally different in their responses to nutrient addition and competition.

Keywords

Exotic plant, fitness, mortality, naturalisation, non indigenous, rarity.

INTRODUCTION

The commonness and rarity of native plant species (Preston 1948) and the occurrence of alien plant invasions (Elton 1958) are two extensively considered phenomena within ecology. The fundamental questions 'what makes some native species common?' and 'what makes some alien species invasive?' are parallel questions which are usually asked separately in ecology, but can yield similar answers. For example, invasive species are often considered to be larger in size (van Kleunen *et al.* 2010a), have smaller seeds and greater reproductive output (Rejmánek & Richardson 1996), are faster growing (Dawson *et al.* 2011) and have higher values for resource capture traits (Hamilton *et al.* 2005; van Kleunen *et al.* 2010a) than non invasive alien plant species. Similarly, common native plant species can be larger (Lavergne *et al.* 2004; Farnsworth 2007; Cornwell & Ackerly 2010) and may invest more in reproduction than restricted rare species do (Lavergne *et al.* 2004). Traits conferring greater resource capture ability, such as high specific leaf area, may typify common more than rare species (Lavergne *et al.* 2004). Because of these similar patterns, it has been hypothesised that traits explaining alien plant invasiveness are the same as those related to native plant commonness (van Kleunen & Richardson 2007; Thompson & Davis 2011). Although this hypothesis is appealing, it remains to be tested experimentally, using rare and common native, and invasive and non invasive alien plant species (van Kleunen *et al.* 2011).

As a component of global change, eutrophication of terrestrial habitats might increase the rate of invasion events if high nutrient availability favours invasive species that are fast growing and nutrient demanding (Dukes & Mooney 1999; Bradley *et al.* 2010; Dostal *et al.* 2012). The success of both invasive alien and common native plant species may result from their possession of a suite of attributes that enables them to take advantage of increasing human made novel environments with increased resource availability (Thompson & Davis 2011). In the context of human induced increases in nutrient availability, if invasive aliens and common native species do not differ ecologically then we would expect common native species to also benefit most from increased nutrient levels, by increasing growth and biomass more than rare native species.

Both invasive alien and common native plant species are often speculated to be competitively superior compared to non invasive aliens and rare natives respectively (Medail & Verlaque 1997; Lloyd *et al.* 2002). Rare plant species are hypothesised to have adaptations suited for resource conservation rather than acquisition (Reich *et al.* 1999), and are thus believed to be limited to resource poor habitats as they cannot compete with strong resource acquiring common species in nutrient rich habitats (Drury 1974; Grime 1977). Higher nutrient levels increase plant productivity and aboveground biomass, thus increasing interspecific competition aboveground (Hautier *et al.* 2009). Thus, common species should be those with higher rates of survival under competition compared with rare species, and as competition is exacerbated by increased nutrient levels, this difference in survival rates should be more pronounced than when plants are under competition with lower nutrient availability. However, multi species experiments comparing competition and nutrient responses of rare versus common plant species remain scarce (Lloyd *et al.* 2002).

In this study, we test the expectations that both common alien and native plant species are better at responding to increased nutrient availability and at surviving competition in a grassland sward, particularly at higher nutrient levels, compared to rare aliens and natives. To increase generality, we established a large, multi species experiment including 41 plant species from six plant families, including common and rare native species, and common (i.e. invasive) and rare (i.e. non invasive) alien species.

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[1]*Institute for Plant Sciences, University of Bern, Altenbergrain 21, Bern, CH 3013, Switzerland*

[2]*Ecology, Department of Biology, University of Konstanz, Universitätsstrasse 10, Konstanz, D 78464, Germany*

**Correspondence: E mail: wayne.dawson@uni konstanz.de*

MATERIAL AND METHODS

Study species

Because plant traits are often likely to be phylogenetically correlated among species (Felsenstein 1985), we selected species within confamilial groups for comparison, from a total of six families, including the Apiaceae, Asteraceae, Brassicaceae, Poaceae, Polygonaceae and Scrophulariaceae (also including Plantaginaceae and Phrymaceae). We aimed at including at least one common native species, one rare native species, one common alien species and one rare alien species per family. However, due to difficulties in obtaining seeds and incomplete germination our final set of species was less balanced (Table 1) In the Apiaceae, a common native species was missing, whereas in the Polygonaceae, a common alien species was missing (Table 1). In the Asteraceae, we had three sub groups. One group comprised solely of species in the genus *Bidens*, a second group included native species in the Anthemidae/Gnaphaliae clade and alien species from different Asteraceae tribes (Table 1). The third group included one common native and one common alien species in the genus *Solidago*, whereas the remaining species were from other Asteraceae genera (Table 1). Seeds of most species were collected in the wild in 2008 2009, and seeds from individual plants were kept separate, representing individual maternal seed families. We obtained seeds from commercial sources only, for *Polygonum orientale* and *Artemisia vulgaris* (B and T World Seeds, Perpignan, France and Rieger Hofmann GmBH, Blaufelden Raboldshausen, Germany, respectively).

Native species were classified as 'common' or 'rare' *a priori*. Rare species were listed as vulnerable, endangered or critically endangered according to the International Union for Conservation of Nature (IUCN) red list criteria applied to Switzerland (Moser *et al.* 2002), whereas common native species were listed as being of least concern or near threatened. Expert opinion from the Swiss Flora Database Centre (ZDSF Zentrum des Datenverbundnetzes der Schweizer Flora, http://www.crsf.ch/) was used to distinguish common alien from rare alien species (Table 1). According to the Swiss Flora Database Centre, the 14 rare native species had significantly fewer 5 × 5 km grid square incidences (median = 7) than the 9 common natives (median = 265; $\chi^2 = 12.057$, $P < 0.001$, Kruskal Wallis test). Similarly, the 10 rare alien species had significantly fewer grid square incidences (median = 11) than the 8 common aliens (median = 138; $\chi^2 = 14.634$, $P < 0.001$).

Although we selected species according to taxonomic group to control for phylogenetic differences, habitat dissimilarities may confound results. For example, common species may respond more strongly to nutrient addition than rare species, if common species come from more nutrient rich habitats than rare species. To address this, we recorded the broad habitat categories our species occur in according to the Swiss Flora Indicativa (Landolt *et al.* 2010). We then created a Jaccard dissimilarity matrix from the presence absence of species in the nine listed habitats. Non metric multidimensional scaling (NMDS) analysis was then applied to the dissimilarity matrix, using three NMDS axes (for details, see Appendix S1). Plotting species on these three axes indicated that alien species tended to have more similar habitats as a group, whereas native species habitats were more variable (Fig. S1 in Appendix S1). Alien species had greater values for NMDS axis 2 and lower values for NMDS 3 compared with native species (Fig. S2 & Table S1 in Appendix S1). However, common and rare species did not significantly differ on average in values on any NMDS axis, suggesting there is no clear dissimilarity in habitats between common and rare species (Fig. S2 & Table S1 in Appendix S1).

We also extracted five environmental index scores per species, relating to hemeroby (level of human impact), temperature, soil moisture, soil nutrient and light requirements from Landolt *et al.* (2010). Each index ranges from 1 to 5, with either whole integer (soil nutrient, light, hemeroby) or half integer (soil moisture, temperature) intervals (see Appendix S1). Alien species had greater hemeroby, temperature and nutrient index scores than native species (Table S2; Figs S3 and S4 in Appendix S1). The nutrient and hemeroby index scores were also positively correlated with NMDS axis 2 (Table S3 in Appendix S1). Common and rare species only differed in hemeroby within native species, with common natives occurring in more human modified habitats than rare species (Table S2, Fig. S4 in Appendix S1).

Finally, common species in our dataset may be common because their suitable habitats are common, whereas rare species may be restricted to habitats that are rare. To test this, we first extracted the vegetation types in which each species occurs in Switzerland, from Landolt *et al.* (2010) and Delarze & Gonseth (2008). 'Vegetation type' refers to a phyto sociologically defined plant community (Ellenberg & Klötzli 1972; Aeschimann *et al.* 2004). We then calculated the potential maximum distribution of each species in Switzerland, as the number of km^2 grid cells known to contain at least one of the vegetation types in which the species has been observed, using the atlas of Hegg *et al.* (1993). Values were obtained for 39 of the 41 species (no data were available for the alien species *Rudbeckia hirta* and *Eryngium giganteum*). Both alien and common species had a greater number of km^2 grid cells containing at least one of the vegetation types typical for the species than did native and rare species respectively (Appendix S2). Only nutrient and hemeroby index scores (and none of the NMDS habitat axes) were positively correlated with the number of km^2 grid cells (Appendix S2).

Experimental set-up

The experiment was conducted on the grounds of the municipal nursery of the city of Bern, Switzerland, situated in Elfenau, a public park (46°56′00″ N, 7°28′03″ E, 542 m above sea level). First, seeds of the 41 species were germinated in 1 : 1 sand compost substrate, in a greenhouse from the beginning of May 2010. A maximum of eight seed families were sown per species. The seeds were allowed to germinate and grow for 3 weeks, after which individual seedlings were pricked out and planted individually into separated compartments of trays containing a 1 : 1 mixed substrate of coarse sand and topsoil from local arable agricultural land (Ricoter Erdaufbereitung AG, Aarberg, Switzerland). The substrate had a high clay content, and a nitrogen concentration of 1.79 g kg^{-1} of dry weight substrate.

After 3 weeks, in the last week of June and the first week of July 2010, individual plants from the same seed families were planted out into the centre of 3 L pots (one plant per pot) filled with the same substrate used for the seedlings. Half of the pots received a nutrient addition treatment in the form of 12 g slow release fertiliser pellets (N:P:K 16 : 19 : 12 + 2 MgO + trace elements, Osmocote® Exact Standard, Everris International B.V., Geldermalsen, NL), which increased the nitrogen content by 33% compared with the control pots. In addition, half of the pots at each nutrient level contained a mixed species mesotrophic grassland sward as a

Table 1 The 41 study species alien and native to Switzerland

	Native		Alien	
	Rare	Common	Rare	Common
Apiaceae	*Oenanthe lachenalii* C.C. Gmel† CR (8)		*Eryngium giganteum* M. Bieb.* (4)	*Heracleum mantegazzianum* Sommier & Levier*† (420)
Asteraceae (Bidens)	*Bidens cernua* L.* EN (25) *Bidens radiata* Thuill.* CR (3)	*Bidens tripartita* L.*† NT (57)	*Bidens connata* H. L. Mühl. ex Willd.* (3) *Bidens bipinnata* L.*† (4)	*Bidens frondosa* L.*† (45)
Asteraceae 2	*Artemisia borealis* Pall. VU (6) *Pseudognaphalium luteo-album* (L.) Hilliard & B.L. Burtt*† VU (29)	*Artemisia vulgaris* L.* LC (253)	*Aster lanceolatus* Willd.*† (17)	*Erigeron canadensis* L.* (140) *Senecio inaequidens* DC.*† (121)
Asteraceae 3	*Cirsium montanum* (Willd.) Spreng. EN (1) *Inula helvetica* Weber* VU (40)	*Solidago virgaurea* L. LC (207)	*Rudbeckia hirta* L.* (27)	*Solidago canadensis* L.*† (491)
Brassicaceae	*Cochlearia pyrenaica* DC.† VU (6) *Erysimum ochroleucum* (Schleich.) DC. VU (5)	*Arabis alpina** LC (198) *Biscutella laevigata* L. LC (277)	*Lepidium neglectum* Thell.* (5)	*Lepidium virginicum* L.*† (90)
Poaceae	*Melica transsilvanica* Schur VU (4) *Kengia serotina* (L.) Packer† VU (8)	*Brachypodium sylvaticum* (Huds.) P. Beauv. LC (494)	*Eleusine indica* (L.) Gaertn.*† (21)	*Panicum capillare* L.*† (136)
Polygonaceae	*Rumex hydrolapathum* Huds EN (24) *Rumex maritimus* L.*† CR (1)	*Rumex obtusifolius* L.*† LC (602)	*Persicaria orientalis* (L.) Spach*† (4)	
Scrophulariaceae/ Plantaginaceae/ Phrymaceae	*Linaria alpina* subsp. *petraea* (Jord.) Rouy* VU (14)	*Scrophularia nodosa* (L)*† LC (358) *Veronica anagallis-aquatica* L. *† LC (131)	*Veronica peregrina* L.*† (57) *Mimulus guttatus* DC.*† (23)	*Veronica persica* Poir.*† (458)

For all species, numbers in parentheses represent the number of 5 × 5 km square cell occurrences per species within Switzerland.

*Species occur in nitrophilous communities.

†Species were included in the analysis of aboveground biomass under competition.

For native species, the letter abbreviations represent IUCN Red list species status within Switzerland- LC Least Concern, NT Near Threatened, VU Vulnerable, EN Endangered, CR Critically endangered.

competition treatment grown from 0.6 g of seed mixture per pot (Rieger Hoffmann GmbH 'Fettwiese', see Appendix S3 in Supporting Information for list of species). The grassland sward had been sown in mid April, 6 weeks before adding the target plants. At sowing, a central patch of each competition pot was left bare, so that target seedlings could be easily planted once the grassland sward had established 6 weeks later.

Each of the eight seed families per species was planted into pots in one block, giving eight blocks, and each block was subdivided into eight sub blocks. Each sub block contained all four nutrient and competition treatments for the species of one randomly assigned confamilial group. Due to low rates of germination, *Linaria alpina* subsp. *petraea*, *P. orientale*, *Arabis alpina* and *Bidens connata* were only planted in four blocks, *R. hirta*, *Bidens radiata* and *Bidens cernua* were planted in six blocks and *Gnaphalium luteo album* and *Solidago virgaurea* in seven blocks. Thus, a total of 1,195 plants were planted.

The initial height (cm) of all plants was measured within 1 week after planting. After 12 weeks, in the third week of September 2010, all aboveground biomass was harvested, dried at 70 85 °C for at least 72 h and weighed. Roots and rhizomes of all non competition plants were washed to remove all soil, dried as just described and weighed. To test the effect of the nutrient treatment on the sward of grassland plants in the competition treatment, we also analysed differences in the aboveground biomass of the grassland sward in a sub sample of pots treated with no nutrients ($n = 34$) and with nutrients added ($n = 33$). The aboveground biomass of the grassland sward under high nutrient levels (97.853 g) was twice the amount of mean biomass under the low nutrient level (mean = 48.996 g) [estimate = 48.526 (least square mean difference), 95% CIs = 39.814 57.238; $t = 11.146$, $P < 0.001$; linear mixed effects model).

Analysis

Plant survival

We used a generalised linear mixed effects model, using the R package 'lme4', in the R program version 2.12.2 (R Development Core Team 2011), with a binomial error distribution to analyse survival of individual plants. Family group, species and block were included as random effects. Because initial plant height could affect the probability of surviving competition, the initial height of each plant was included in the model (natural log transformed and scaled to a mean of zero and standard deviation of one). Species origin (native versus alien), commonness (common versus rare), nutrient treatment (no addition, addition) and competition (alone, competition) were included as main and interacting fixed effects, giving a four way interaction model. Likelihood ratio tests were used to assess the significance of interactions, and to obtain a minimum adequate model. To account for habitat dissimilarity across all species, we ran two models including the two treatments plus either (1) only the three NMDS axes or (2) the level of hemeroby (as common and rare native species differed significantly in habitat hemeroby levels). Two way and three way interactions between each habitat variable and the two treatments were also included. We used likelihood ratio tests to assess which interactions and main effects were significant.

We then added either the significant NMDS axes, or hemeroby, and their significant interactions with treatments as variables in analyses with origin, commonness, nutrient and competition and all interactions between these four variables as previously. Likelihood ratio tests were then used again to assess the significance of interactions as before, and to obtain minimum adequate models. In addition, according to Landolt *et al.* (2010), 30 species (all 18 alien species, plus 6 native common and 6 native rare species, Table 1) are recorded in nitrophilous communities in Switzerland. To test if occurrence in nitrophilous communities may have confounded differences in responses to competition and nutrient addition among species, we re analysed plant survival for the subset of nitrophilous community species. If interactions between nutrient addition or competition and origin or commonness were no longer significant after accounting for habitat differences, then this would indicate that previous significant interactions were confounded by habitat dissimilarities between native and alien or common and rare species.

Biomass responses to nutrient addition

Due to high mortality of plants in the competition treatment and the impossibility of obtaining roots for plants under competition, we analysed the biomass responses to nutrient addition separately for plants planted alone and those planted under competition. This also allowed us to use total biomass of plants grown without competition for a maximum number of species. Due to the high mortality of *B. connata*, *Erysimum ochroleucum* and *L. alpina* even without competition, these species were excluded from subsequent analysis of total biomass responses. Among the remaining 38 species, a total of 518 plants survived.

We used a linear mixed effects model in the R package 'nlme' to analyse total biomass responses of 38 species to increased nutrient availability without competition, in relation to origin (native or alien) and commonness (common or rare). Biomass data were square root transformed to meet the assumption of normality. We included family group, species and block as random effects. A variance structure was included to account for variance heterogeneity in biomass according to species (Zuur *et al.* 2009). Species origin, commonness and nutrient treatment were all fitted as fixed effects, and all two way and three way interactions were included. Because initial plant height could affect the biomass eventually attained by a plant, initial plant height was added as a scaled natural log transformed covariate. As in the survival analysis, likelihood ratio tests were used to assess the significance of interactions, and to obtain a minimum adequate model.

We analysed differences in aboveground biomass of plants under competition among a subset of 22 species (271 plants) for which at least three individuals had survived the competition treatment (Table 1) also with origin, commonness and nutrient treatment included as main and interacting fixed effects. Initial plant height was added as a scaled natural log transformed covariate. Biomass was square root transformed prior to analysis. An identity variance structure per species and an exponential variance structure for initial plant height were also included, accounting for variance heterogeneity among species, and an increasing variance with increasing plant height (Zuur *et al.* 2009). Likelihood ratio tests were used in the same way as for previous analyses, to assess the significance of interactions and to obtain a minimum adequate model. We included family group, species and block as random effects.

In the same way as for plant survival, total biomass without competition and aboveground biomass of plants under competition were re analysed using models with (1) NMDS axes and (2) hemeroby levels, plus interactions between these and nutrient treatment included as explanatory variables. Significant habitat variables and interactions were then included in models with origin, commonness and nutrient treatment, and significance of the interactions and were re assessed using likelihood ratio tests to obtain minimum adequate models. Analyses were also re conducted for the subset of species occurring in nitrophilous communities but only for total biomass of plants not exposed to competition because insufficient data were available to analyse aboveground biomass of plants under competition for this subset of species.

RESULTS

Survival

The minimum adequate model for plant survival retained the interaction between nutrient addition and competition, the interaction between commonness and competition and origin as significant variables (Table S1, Appendix S4). Survival was reduced by competition, and this was more pronounced with nutrient addition than without nutrient addition (Fig. 1; $P = 0.006$). On average, survival was higher for alien species (89.3%) than for native species (67.2%; $P < 0.001$). Regardless of origin, survival was higher for common species (86.4%) than for rare species (72.4%; $P = 0.025$). Moreover, common species suffered a smaller reduction in survival in response to competition (98.6% alone to 72.3% under competition) compared with rare species (91.9% alone versus 51.0% under competition; Fig. 1). However, this interaction between commonness and competition was only of borderline significance ($P = 0.05$).

The addition of the significant NMDS axis 2, representing habitat dissimilarity among species, and its interaction with competition treatment weakened the significance of the interaction between competition and commonness ($P = 0.147$), (Table S2 in Appendix S4). When accounting for hemeroby, the interaction between commonness and competition was retained (Table S3, Appendix S4). The Akaike Information Criterion (AIC) value for the hemeroby model (936) was greater than for the NMDS model (933), indicating

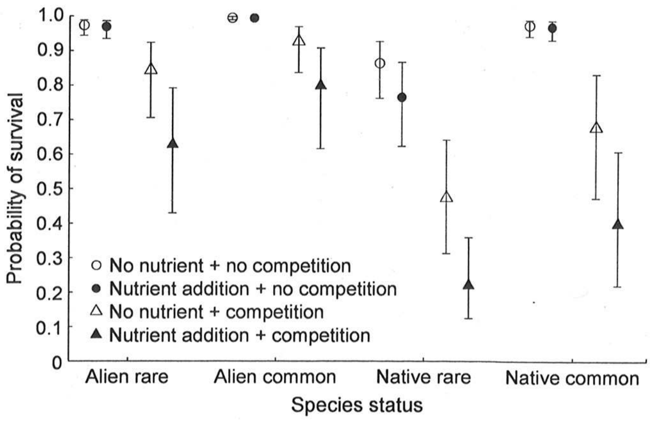

Figure 1 Mean survival probabilities of the 17 alien (8 common and 9 rare) and 23 native (9 common and 14 rare) plant species growing alone or under competition in a grassland sward, without or with nutrient addition. Error bars are 95% confidence intervals (calculated using species as a replicate).

that accounting for overall habitat dissimilarity rather than hemeroby alone provided a better fit to the survival data. For the subset of 30 nitrophilous species, only main effects of origin, commonness, nutrient and competition remained as significant parameters in the minimum model, with significantly greater survival of alien compared with native, and of common compared with rare species across treatments (Table S4, Appendix S4).

Biomass

The minimum model best explaining total biomass of plants in the absence of competition retained the interaction between commonness and nutrient addition and the main effect of origin (Table S5, Appendix S4). Total biomass production was higher for alien species (mean biomass = 23.87 g, 95% CI = 17.86 30.74 g) than for native species (mean biomass = 14.53 g, 95% CI = 9.41 20.76 g; $P = 0.024$). Regardless of origin, total biomass production was higher for common species (mean = 23.78 g, 95% CI = 17.09 31.57 g) than for rare species (mean = 14.69 g, 95% CI = 10.09 20.16 g; $P = 0.034$). The only significant interaction for total biomass was between species commonness and nutrient treatment ($P < 0.001$). On average, common species increased total biomass by 117% with nutrient addition compared with an increase of only 78% for rare species (Fig. 2).

The interaction between commonness and nutrient addition remained significant after inclusion of NMDS axes and interactions with nutrient addition in the model, as did the difference in biomass across treatments between alien and native species (Table S6, Appendix S4). When accounting for hemeroby, the interaction between commonness and nutrient addition also remained significant, as did the three way interaction between origin, commonness and nutrient addition (Table S7, Appendix S4). The AIC value for the NMDS model (1576.1) was lower than that of the hemeroby model (1609.6), indicating the NMDS model gave a better fit to the biomass data. Using the subset of nitrophilous species, the significant interaction between commonness and nutrient addition, as well as an interaction between origin and nutrient addition were retained in the minimum model (Table S8, Appendix S4). Native species tended to increase biomass more strongly in response to nutrient addition than alien species (Table S8, Appendix S4).

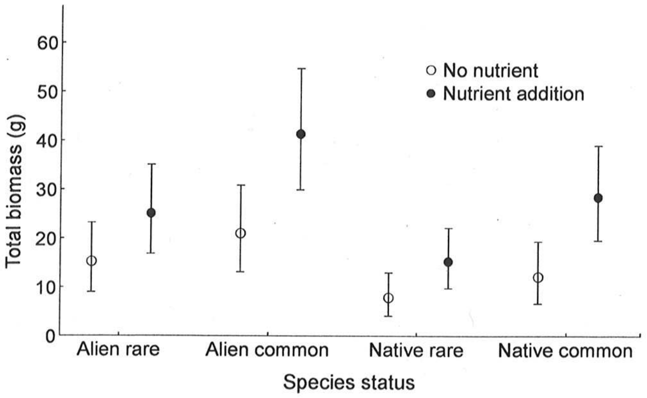

Figure 2 Mean total biomass of the 17 alien (8 common and 9 rare) and 21 native (9 common and 12 rare) plant species without and with nutrient addition. Error bars are 95% confidence intervals (calculated using species as a replicate).

In the presence of competition, there was a significant three way interaction between origin, commonness and nutrient addition which explained aboveground biomass of 22 plant species ($P = 0.02$; Table S9, Appendix S4). Common native species had 137% more biomass than rare natives under nutrient addition compared to only 37% more biomass than rare native species without nutrient addition (Fig. 3). No such differences in biomass between alien common and alien rare species with nutrient versus without nutrient addition were observed (Fig. 3). However, this three way interaction was not significant in a model including a significant NMDS axis (Table S10, Appendix S4), or in a model including hemeroby levels (Table S11, Appendix S4).

DISCUSSION

It has recently been suggested that common native and invasive alien plant species should share similar attributes (Leishman *et al.* 2010; Tecco *et al.* 2010; Thompson & Davis 2011). Our experimental evidence suggests this may indeed be the case, regarding plant biomass responses to nutrient addition and survival under competition.

Total biomass of common plant species increased to a greater degree with nutrient addition than it did for rare species, regardless of whether they were native or alien, even after accounting for habitat dissimilarities. It has been suggested that increases in resource availability may facilitate invasion because alien plant species may be better at responding to increased availability of a limiting resource than species in resident native communities (Leishman & Thomson 2005; Funk 2008). Recent meta analyses show support for (Davidson *et al.* 2011) and evidence against (Palacio Lopez & Gianoli 2011) this possibility. Our results corroborate those of Godoy *et al.* (2011), who found that invasive alien plant species in Spain did not differ in their responses to nutrient addition from taxonomically related, widespread native species. Therefore, when comparing invasive to native species, it is important to consider whether the latter are common or rare.

Habitat dissimilarity may have confounded the different nutrient responses observed for common and rare species. For example, range expanding native and alien plant species may be more likely to occur in similar nutrient rich habitats (Thompson *et al.* 1995),

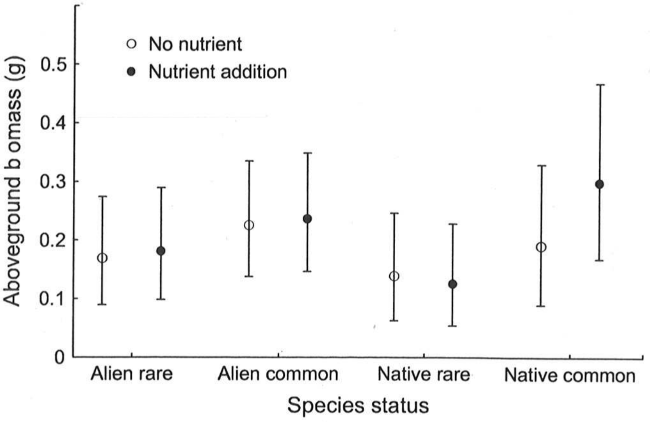

Figure 3 Mean aboveground biomass of alien rare (6) and common (7), and native rare (5) and common (4) plant species, growing under competition from a grassland sward, without and with nutrients added. Error bars are 95% confidence intervals (calculated using species as a replicate).

whereas rare native and rare alien species may have different habitat requirements. Differences in species attributes are more likely to occur when the species compared occur in different habitat types (Leishman *et al.* 2010). However, we found that the main dissimilarities in habitats were not between rare and common species, but between alien and native species. Alien species as a group occupy warmer and more nutrient rich, human modified habitats, and show tighter habitat similarity as a group, compared with the more variable native species (see Appendix S1). The difference in the level of habitat similarity within alien and native species groups may reflect introduction bias among aliens (Chrobock *et al.* 2011), or post introduction restrictions on habitats alien species can establish in, due to high propagule pressure in certain habitats or traits constraining the habitats suitable. Accounting for habitat dissimilarity in our analyses revealed that the difference between rare and common species in response to nutrient addition was robust to any underlying variation in habitat preferences.

Common species may also be widespread because the habitats which they typically occupy are also widespread, whereas rare species might be restricted in distribution because their habitats are also rare (Thompson *et al.* 1998). For species with data available, we did find that common species had a greater number of km^2 grid cells containing at least one vegetation type occupied by the species than did rare species (Appendix S2). If common species are more widespread because their habitats are more common, and those common habitats tend to be nutrient rich and altered by humans, then common species may simply be responding more strongly to nutrient addition because they occur in widespread, nutrient rich and human modified habitats. Indeed, species with more widespread vegetation types also had higher nutrient and hemeroby index scores than species with more restricted vegetation types. However, although differences in habitat requirements were evident between aliens and natives, differences between common and rare species were only evident for native ones with respect to hemeroby. This indicates that common and rare plant species in this study do not simply occur in widespread nutrient rich and restricted nutrient poor habitats respectively. Rather, common species may be widespread as they are better able to take advantage of increased nutrient availability when it occurs compared with rare species. Common native species thus may have become more common compared with rare species due to their ability to exploit increasingly human altered habitats.

As well as differing in response to nutrient addition, there was also a tendency for common species to achieve a greater total biomass than rare species, across nutrient treatments. Greater biomass has been reported as a correlate of both alien plant invasiveness (Schlaepfer *et al.* 2010; van Kleunen *et al.* 2010a; Godoy *et al.* 2011) and native plant abundance (Kelly 1996; Murray *et al.* 2002; Lavergne *et al.* 2004; Cornwell & Ackerly 2010). However, patterns of biomass differences between alien and native species are likely to be sensitive to comparator choice (van Kleunen *et al.* 2010b). Godoy *et al.* (2011) recently found that invasive species had greater carbon gain capacity and performance than widespread native relatives, including greater invasive alien biomass, suggesting that common aliens differ from common natives. Our study indicates that overall, common native and alien plants tend to have a greater biomass than their rare counterparts.

Greater biomass of common species may be a product of faster growth rates in the duration of our experiment. Positive relationships between relative growth rate and invasion success have been reported recently (Grotkopp & Rejmánek 2007; Grotkopp *et al.* 2010; van Kleunen *et al.* 2010a; Dawson *et al.* 2011). Furthermore, faster growth rates of common versus rare species could explain differences in nutrient responses, if faster growth rates allow a species to respond more strongly to increased resource availability (Grime 1977). However, we should be cautious in making comparisons of biomass between groups of species, as the experimental period may not have been long enough to establish the maximum biomass attainable for all species, thus exaggerating differences between species. Notwithstanding this, fast growth rates and greater biomass will obviously give both alien and native plant species colonising open spaces with higher resource levels, an advantage over those species unable to attain a larger biomass, through asymmetric competition for light (Weiner 1990).

On average, common species survived only marginally better under competition than rare species did, again regardless of whether they were native or alien. The higher ability of common species to survive under strong competition may indicate that competition exerted by established plants imposes an environmental filter, through which only certain species are able to pass and survive in the community. Short, stress tolerating native species with slow growth and typical of open habitats, may be more vulnerable to loss under competition and eutrophication (Walker & Preston 2006). The addition of an NMDS axis describing nutrient habitat differences led to a lack of significance of survival difference between common and rare species, and this was also true when only nitrophilous species were considered. The marginally greater survival of common species under competition may have been due to common species coming from more nutrient rich habitats (which may be more competitive) and rare species from nutrient poor habitats (which may be less competitive). In any case, survival decreased strongly under competition with nutrient addition for all species, probably due to greater competition for light and water exerted by the grassland sward, which doubled its aboveground biomass in the nutrient addition treatment. Thus, increased resource availability will not always facilitate invasion if the resident community is able to respond strongly to the increase, leading to limitation of other critical resources (Davis *et al.* 2000; Hautier *et al.* 2009). Our results suggest that survival of common and rare species under competition is likely to be impacted similarly by increased nutrient levels.

Rare and common species appeared not to differ strongly in responses of aboveground biomass to nutrient addition when grown under competition. Rather, only native common species showed a slight increase in aboveground biomass with nutrient addition, and a greater aboveground biomass than native rare species under nutrient addition. Moreover, this difference was no longer significant once habitat differences between species were accounted for. The advantage of common species being able to respond more strongly to nutrient increase compared to rare species may only be clearly expressed in more open habitats. Given the large increase in biomass of the grassland sward with nutrient addition, however, competition may have been too intense for clear differences in performance between species to be obtained.

In summary, we find little evidence that common native and invasive alien plant species fundamentally differ in their responses to nutrient increase and survival under competition. Whereas common native and invasive alien species increased biomass in response to nutrient addition more strongly than rare native and non invasive alien species, this was only expressed in the absence of competition. Increased nutrient availability alone may not lead to successful invasion or losses of rare natives and gains in common native species. Rather, effects of nutrient increases will be dependent on the level of competition at the time of nutrient increase, and the relative response to nutrient addition of the native community compared with incoming species.

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AUTHORSHIP

WD, MvK and MF planned the experiment, WD conducted the experiment and analysis and WD, Mvk and MF wrote the article.

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