Dominant native and non-native graminoids differ in key leaf traits irrespective of nutrient availability

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Abstract

Aim

Nutrient enrichment is associated with plant invasions and biodiversity loss. Functional trait advantages may predict the ascendancy of invasive plants following nutrient enrichment but this is rarely tested. Here, we investigate 1) whether dominant native and non-native plants differ in important morphological and physiological leaf traits, 2) how their traits respond to nutrient addition, and 3) whether responses are consistent across functional groups.

Location

Australia, Europe, North America and South Africa

Time period

2007 - 2014

Major taxa studied

Graminoids and forbs

Methods

We focused on two types of leaf traits connected to resource acquisition: morphological features relating to light-foraging surfaces and investment in tissue (Specific Leaf Area, SLA) and physiological features relating to internal leaf chemistry as the basis for producing and utilizing photosynthate. We measured these traits on 503 leaves from 151 dominant species across 27 grasslands on four continents. We used an identical nutrient addition treatment of nitrogen (N), phosphorus (P) and potassium (K) at all sites. Sites represented a broad range of grasslands that varied widely in climatic and edaphic conditions.

Results

We found evidence that non-native graminoids invest in leaves with higher nutrient concentrations than native graminoids, particularly at sites where native and non-native species both dominate. We found little evidence that native and non-native forbs differed in the measured leaf traits. These results were consistent in natural soil fertility levels and nutrient enriched conditions, with dominant species responding similarly to nutrient addition regardless of whether they were native or non-native.

Main conclusions

Our work identifies the inherent physiological trait advantages that can be used to predict non-native graminoid establishment; potentially because of higher efficiency at taking up crucial nutrients into their leaves. Most importantly, these inherent advantages are already present at natural soil fertility levels and are maintained following nutrient enrichment.

Keywords

Biological invasions, functional traits, invasive species, introduced species, leaf traits, native species, nitrogen deposition, NutNet, nutrient availability, plant traits

Introduction

Inputs into global nutrient cycles from human activities are often associated with widespread plant invasions, rapid biodiversity loss and changes in ecosystem functioning (Davis *et al.*, 2000; Stevens *et al.*, 2004; Seabloom *et al.*, 2015; Harpole *et al.*, 2016). Impacts on ecosystem functioning often are predicted based on changes in leaf traits (Lavorel & Garnier, 2002; Garnier *et al.*, 2007), and recent findings confirm that some leaf traits such as leaf nutrient concentrations increase in the most dominant plant species even in response to short term nutrient inputs in global grasslands (Firn *et al.*, 2019). However, it remains unclear whether (1) non-native plant species are advantaged by nutrient inputs over native species (Davis *et al.*, 2000; Besaw *et al.*, 2011; Dawson *et al.*, 2012b; Seabloom *et al.*, 2015), or (2) whether species that dominate in the high fertility conditions typical of human-modified environments share similar traits, regardless of their biogeographic origin (i.e. native or non-native) (Thompson & Davis, 2011; van Kleunen *et al.*, 2011; Dawson *et al.*, 2012a). Resolving this uncertainty can potentially improve our ability to mitigate biodiversity loss, and predict changes in ecosystem functioning, following plant invasions and widespread nutrient enrichment (Drenovsky *et al.*, 2012). With this aim, we expand on recent findings (Firn *et al.*, 2019), using data collected across four continents, to compare whether leaf traits of the most successful or dominant native and non-native species increase in response to nutrient enrichment.

Nutrient enrichment is hypothesized to benefit plant species that are able to make a fast return on their investments in leaf production (Chapin III, 1980). Fast returns may arise from leaves that have particular morphological or physiological traits. For example, morphological traits such as SLA determine the area over which a plant can capture light versus the amount of investment they make in the infrastructure to do so, and thus can be predictive of maximum photosynthetic rates (Wright *et al.*, 2004). Similarly, higher leaf nitrogen (N), phosphorus (P) and potassium (K) concentrations can enhance a plant’s ability to produce and utilize photosynthate, since the molecular equipment needed to do so, i.e. chlorophyll, nucleic acids, adenosine triphosphate and various enzymes, all require these major nutrients (Epstein & Bloom, 2005). Nonetheless, leaves that support very high maximum photosynthetic rates often come with high costs, such as higher respiration rates, greater palatability to herbivores, higher susceptibility to drought, shorter leaf lifespan, and a greater minimum requirement for nutrients (Westoby *et al.*, 2002; Díaz *et al.*, 2004; Wright *et al.*, 2004; Kurokawa *et al.*, 2010; Nogueira *et al.*, 2018). For nutrient enrichment to benefit species that make fast returns on leaf investment, the gains of a greater supply of nutrients must exceed any potential increases in herbivory or other costs.

In spite of the importance of morphological and physiological leaf traits (Cornelissen & Thompson, 1997; Garnier *et al.*, 2004; Cornwell *et al.*, 2008; Stiegel *et al.*, 2017) and their relationship with nutrient enrichment (Garnier *et al.*, 2007; Firn *et al.*, 2019) for plant community dynamics and ecosystem functioning, it remains unclear whether the traits of dominant native and non-native species consistently differ in the field, and how nutrient enrichment affects these differences. Evidence suggests that invasive plant species build leaves that generate faster returns on investment, as they often exhibit higher SLAs (i.e. higher leaf areas versus tissue investment in the leaf) and leaf N concentrations than native species (Ordonez *et al.*, 2010; van Kleunen *et al.*, 2010; Ordonez & Olff, 2013; Funk *et al.*, 2017). This difference could arise due to pre-adaption of non-native species to higher resource availabilities in their native ranges (MacDougall *et al.*, 2018), or shifts in their functional traits after they establish in their invaded ranges due to genotypic changes or phenotypic plasticity (Parker *et al.*, 2013; Ordonez, 2014; Martinez *et al.*, 2019). Furthermore, non-native species may escape their co-evolved enemies and therefore experience lower rates of herbivory in their introduced ranges (Keane & Crawley, 2002;

Leishman *et al.*, 2014). This would allow them to benefit from the increased supply of nutrients associated with nutrient enrichment, without suffering increased costs due to higher herbivory (Blumenthal, 2005, 2006). However, evidence from other studies suggests that nutrient enrichment may act as an environmental filter that selects for similar traits in dominant species regardless of their origin (Thompson *et al.*, 1995; Leishman *et al.*, 2010; Dawson *et al.*, 2012a). As a consequence, it has been argued that in the face of widespread nutrient enrichment, differences in native and non-native species traits are not useful for understanding plant invasions (Thompson & Davis, 2011). Here, we aim to resolve this uncertainty and investigate: i) whether dominant native and non-native species differ in important morphological and physiological leaf traits, ii) how leaf traits of dominant native and non-native species respond to nutrient enrichment, iii) whether these responses are consistent across functional groups and iv) whether abiotic factors, including mean annual temperature (MAT, ^{0}C), temperature variation, mean annual precipitation (MAP, mm), MAP variation, soil N, P and K concentrations, improve the predictive power of our models.

Methods

Field sites

Our 27 grassland sites on four continents span a large range of abiotic conditions and land-use histories (Table S1). Mean annual temperature ranges from 0.3 ºC (alpine grassland in Switzerland) to 18.4 ºC (semi-arid C_4 perennial grassland in Australia); mean annual precipitation ranges from 262 mm (shrub steppe in the USA) to 1898 mm (montane grassland in the USA); elevation ranges from 50 m (Old field in Canada) to 2320 m (alpine grassland in Switzerland) and pre-treatment soil N ranges from 0.06 % (tallgrass prairie in the USA) to 1.55 % (mesic grassland in the UK) (Table S1). All sites are part of a cooperative globally distributed experiment called the Nutrient Network (Fig. 1, http://www.nutnet.org/) and their selection was unrelated to species identity. Sites also exhibited large variation in species richness (Fig. 1), which included differences in native and non-native species richness. Native richness ranged from 1 (old field in Canada) to 104 species (e.g. mesic grassland in South Africa) and non-native richness ranged from 0 (e.g. montane grassland in South Africa) to 47 (annual grassland in the USA). The biogeographic origin of each sampled species was assessed by the principal investigators at each site and checked using national flora databases (NPGS, 2016; Botantical Society of Britain and Ireland, 2019; Bundesamt fuer Umwelt BAFU, 2019; Sociedade Portuguesa de Botanica, 2019). Of the 151 species that were sampled, 39 were non-native and 116 were native to the sites from which they were sampled (this sums to 155, rather than 151, because four species occurred in both their native and non-native ranges). Of the 39 non-native species, 28 (71%) were classified as invasive (Weber, 2017) or as weeds in the countries in which they were sampled (Table S2), and 31 (79%) were native to Europe. Given that only a subset of sites (n = 11) had co-occurring dominant native and non-native species, we also analysed these sites separately to test whether our findings were consistent for co-occurring dominant native and non-native species.

Figure 1 – Global distribution of 27 sites in eight countries (AU – Australia, CA – Canada, CH – Switzerland, DE – Germany, PT – Portugal, UK – United Kingdom, US – United States and ZA – South Africa), across four continents. Percentage of dominant native (blue) and non-native (orange) species sampled at each site is shown in rings. Ring size represents the total site-level species richness (native and non-native), which ranged from 21 (old field “Cowi”, CA) to 109 (annual grassland “Hopl”, US; see also Table S1).

Experimental design

Our experiment used a randomized-block design, with the majority of sites having three replicate blocks divided into two 5 x 5 m plots. We established a nutrient addition treatment of essential plant nutrients (N, P, and K plus micronutrients) and an unfertilised control for a total of 6 plots per site (two treatments * three blocks). Leaf traits were sampled after two (n = 5 sites), three (n = 8 sites) or four (n = 14 sites) years of treatment, from three to five of the most dominant species in each plot (see Table S1 for detailed information on each site). All sites applied the following rates of nutrients: 10 g N m^{-2} yr^{-1} as time-release urea; 10 g P m^{-2} yr^{-1} as triple-super phosphate; 10 g K m^{-2} yr^{-1} as potassium sulfate and 100 g m^{-2} yr^{-1} of a micro-nutrient mix (Fe, S, Mg, Mn, Cu, Zn, B, Mo, Ca). The N, P, and K fertilizers were applied annually whereas the micro-nutrients were applied once at the start of the study to avoid toxicity and only in treatments that included K. Ammonium nitrate was used in 2007 at some sites before switching to urea because of difficulties in sourcing ammonium nitrate globally. In an additional experiment at a subset of these sites, we found that different nitrogen forms had no significant effect on the outcomes of the plant community responses (Borer *et al.*, 2014).

Sampling and measurements

LEAF TRAITS

We analysed 503 leaf samples from 151 dominant species. Following standardized protocols (Cornelissen *et al.*, 2003), we randomly selected five mature individuals of the three to five most dominant species, whether native or non-native, in each plot and randomly collected five fully developed leaves with no signs of herbivore damage. Leaves from the majority of sites were combined at the species level and scanned to measure area using a flatbed scanner

(Epson perfection V300) and image analysis software ImageJ (Abràmoff *et al.*, 2004). Some sites used leaf area machines to measure leaf area in the field. The leaves were then dried at 60ºC for 48 h, weighed (dry weight) and specific leaf area (SLA) was calculated [leaf area (mm^2)/dry weight (g)]. Following this, dried leaves were ground, bulked and analysed for total leaf nutrients. Leaf N content was determined using a LECO TruMac. Leaf P, K and a set of other trace elements (not used in this study) were determined using Laser Ablation ICPMS generally after the method of Duodu *et al.*, (2015) with two exceptions: internal standard was not added but measured C, the most abundant naturally occurring element was used, and no extra pulverizing was performed beyond that required for C and N analysis; which constituted placing the sample and a 2mm diameter tungsten carbide ball in 2 mm plastic centrifuge vials, then grinding for 15 min using the TissueLyser©. About 0.2 g of leaves was compressed in a hydraulic dye producing a pellet about 6 mm across and 2 mm tall. These pellets were glued to a plastic tray in groups of ~100 and introduced into the laser chamber. A New Wave 193 nm excimer laser with a True-line cell was connected to an Agilent 8800 ICPMS. The laser beam was 65 µm in diameter and rastered a length of ~500 µm in ~50 s, five times per sample with a 30 s washout or background between rasters. Laser fluence at laser exit was about 2 J cm^{-2} and the repetition rate was 7 Hz. Reference materials and monitoring standards were the National Institute of Standards and Technology peach leaves (USA National Institute of Standards and Technology, 2017), and National Institute of Standards and Technology spinach (USA National Institute of Standards and Technology, 2014). These were analysed every 3 samples (15 rasters) for moderately close sample-standard bracketing. The average and standard deviation for each element in each sample is reported and then quantified after the method of Longerich et al. (Longerich *et al.*, 1996) using Iolite data reduction software (Paton *et al.*, 2010).

SPECIES PERCENT COVER

Species relative cover (%) was visually estimated to the nearest 1% within one-1 m^2 sub-plot in each plot, at the same time as when leaf traits were collected. Since cover was estimated for each species independently, total summed cover often exceeded 100% due to multilayer canopies. We used the percent cover data, after two to four years of treatments, to select the top three to five (six at one site) species in each subplot to measure leaf traits. The sampled species made-up an estimated 26.9% (± 1% SE) of the total vegetation cover from the sites. By only sampling dominant species, we controlled for differences in dominance between native and non-native species. Dominant graminoids had a higher abundance (mean cover = 33% ± 1% SE) than dominant forbs (mean cover = 18% ± 1% SE), as would be expected in grasslands. Species % cover did not vary in relation to species biogeographic origin (native or non-native) or nutrient addition treatment (Fig. S1). This also meant that non-native species were abundant and dominant in the communities from which they were sampled and therefore likely functionally significant (Grime, 1998; Garnier *et al.*, 2004).

Data analysis

HIERARCHICAL BAYESIAN REGRESSION MODELS

To estimate i) whether dominant native and non-native species differ in important morphological and physiological leaf traits (SLA, leaf % N, leaf % P, leaf % K) and species percentage cover, and ii) how leaf traits of dominant native and non-native species respond to nutrient enrichment, we developed multilevel regression models in a hierarchical Bayesian framework. In these models, the fixed effects were biogeographic origin (native or non-native), the nutrient addition treatment (control or NPK), and their interaction. Random effects were block nested in site nested in species (Fig. S2 and S3). Analyses were run using the integrated-nested Laplace approximation (INLA (Rue *et al.*, 2009)) interfaced with the R statistical computing package (R Core Team, 2019). We used the default, uninformative, priors in INLA for all analyses, which include the normal distribution specified as N (mean, precision), fixed effects: intercept = N(0,0), slopes = N(0,0.001), and variances modelled as log-precision with priors of log-gamma(1, 5e-5), which is specified as log-gamma(shape, inverse-scale).

In detail, for each of the leaf traits, let y_{ijkl} denote the response and $\boldsymbol{x}_{ijkl} = (x_{1jkl}, x_{2jkl}, \ldots, x_{pjkl})$ denote the *i*th sample from the *j*th block at the *k*th site of the *l*th plant species (Fig. S3). Then the response was assumed to follow a Normal distribution, here specified as (mean, variance), as follows:

$$y_{ijkl} \sim \mathrm{N}(\mu_{jkl}, \sigma^2),$$

$$\text{where } \; y_{ijkl} = \mu_{jkl} + u_l + v_{kl} + w_{jkl} + e_{ijkl}$$

$$\mu_{jkl} = \beta_0 + \beta_1 x_{1jkl} + \beta_2 x_{2jkl} + \ldots + \beta_p x_{pjkl}$$

$$u_l \sim \mathrm{N}(0, \sigma^2_u),$$

$$v_{kl} \sim \mathrm{N}(0, \sigma^2_v),$$

$$w_{jkl} \sim \mathrm{N}(0, \sigma^2_w), \text{ and}$$

$$e_{ijkl} \sim \mathrm{N}(0, \sigma^2_e) \text{ such that } \sigma^2_u + \sigma^2_v + \sigma^2_w + \sigma^2_e = \sigma^2,$$

where μ_{jkl} is the mean response associated with block *j* at site *k* and species *l* where β_0 is the model intercept and $\beta_1, \beta_2, \ldots, \beta_p$ are slope parameters for each predictor $(x_{1jkl}, x_{2jkl}, \ldots, x_{pjkl})$. Then u_l is the random effect associated with the *l*th species, v_{kl} is the random effect associated with the *k*th site (within species *l*), w_{jkl} is the random effect associated with *j*th block (within species *l* and site *k*), and e_{ijkl} is the residual error associated with the *i*th response on block *j* at site *k* for species *l*.

Next, we determined whether our findings were consistent across functional groups. To do this, we applied the same multilevel regression model described above, but separately for forb and graminoid species, rather than all species together. Because there were only 11 legumes (seven native and four non-native), they were included with the other forb species and not analysed as a separate group.

After each model was fit, residuals were calculated as the observed value of the data minus the posterior mean prediction, and then residual plots were inspected for any potential relationships in the data that may not have been captured by the model. Plots of the cross-validated probability integral transform (PIT) (Dawid, 1984) for each model were also inspected. PIT values deliver estimates of the probability that the prediction is less than or equal to the corresponding observed data point, conditional on all other data. A histogram and normal quantile–quantile plot of these values were used to assess the calibration of out-of-sample predictions (Czado *et al.*, 2009). If the residual and PIT plots were reasonable, it was concluded that the model provided a satisfactory fit to the data, otherwise data were ln-transformed and model fit was reassessed.

MODEL SELECTION AND ABIOTIC VARIABLES

We also tested whether abiotic conditions, including climatic (mean annual temperature, mean annual precipitation, temperature variability, mean annual precipitation variability) and edaphic (pre-treatment soil N, P, K) variables improved our multilevel regression models for each individual leaf trait. To do this, we tested all fixed effects combinations of our model (i.e. null model with random effects only; biogeographic origin; nutrient addition;

biogeographic origin + nutrient addition; and biogeographic origin + nutrient addition + their interaction), and individually added each abiotic variable as a co-variate to these models. We then tested which models had the highest marginal log-likelihood (MLL; a variable selection statistic which has an inbuilt penalty for model complexity (MacKay, 2003)). A higher MLL indicates greater support for the model, given the data. This allowed us to determine whether adding information about abiotic variables helps to inform on leaf trait variation between native and non-native species, and it enabled us to identify the fixed effects that most parsimoniously explain variation in leaf traits.

Results

Non-native species had significantly higher leaf %K (x 1.1 higher) than native species ("NN" in Fig. 2j), which was explained by differences between native and non-native graminoids ("NN" in Fig. 2l), not forbs ("NN" in Fig. 2k). The nutrient addition treatment consistently increased leaf nutrient concentrations across both functional groups (Figs. 2d-l). It also increased SLA (Fig. 2a) but this was predominantly explained by the responses of graminoids (Fig. 2c), not forbs (Fig. 2b). Importantly, nutrient addition did not change the overall relationships; in particular, there was no interaction between biogeographic origin (i.e. native or non-native) and nutrient addition (NN:NPK in Fig. 2).

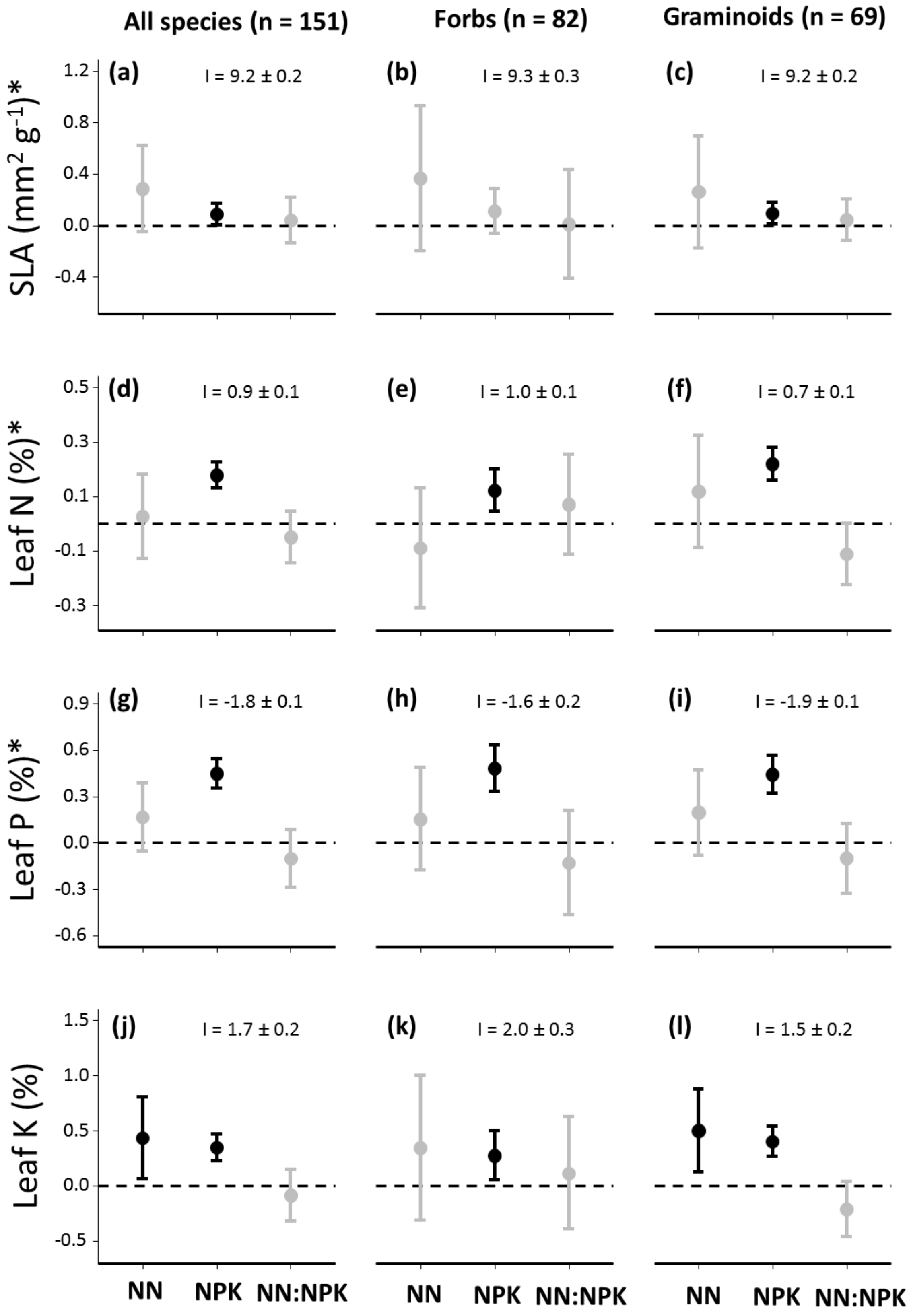
All species (n = 151)
Forbs (n = 82)
Graminoids (n = 69)
SLA (mm^2 g^{-1})*
1.2
0.8
0.4
0.0
-0.4
(a)
I = 9.2 ± 0.2
(b)
I = 9.3 ± 0.3
(c)
I = 9.2 ± 0.2
Leaf N (%)*
0.5
0.3
0.1
-0.1
-0.3
(d)
I = 0.9 ± 0.1
(e)
I = 1.0 ± 0.1
(f)
I = 0.7 ± 0.1
Leaf P (%)*
0.9
0.6
0.3
0.0
-0.3
-0.6
(g)
I = -1.8 ± 0.1
(h)
I = -1.6 ± 0.2
(i)
I = -1.9 ± 0.1
Leaf K (%)
1.5
1.0
0.5
0.0
-0.5
(j)
I = 1.7 ± 0.2
(k)
I = 2.0 ± 0.3
(l)
I = 1.5 ± 0.2
NN
NPK
NN:NPK
NN
NPK
NN:NPK
NN
NPK
NN:NPK

Figure 2 – Four leaf traits measured at all sites (n = 27). For each leaf trait, mean effect estimates (i.e. coefficients) and their 95% credible intervals (CRIs) for biogeographic origin (i.e. non-native species = NN), the nutrient addition treatment (NPK), and their interaction (NN:NPK) are shown from Bayesian hierarchical models fit with INLA and a random effects structure of species/site/block. The zero reference line represents the intercept (I) of the model (i.e. the estimate for native species in the nutrient control treatment). Mean effect estimates with 95% CRIs that do not cross zero are significant (in black). In the absence of an interaction, a significant main effect (i.e. NN or NPK) affects the response (i.e. leaf trait) across both levels of the other main effect. *SLA, leaf %N and leaf %P ln-transformed due to non-normality.

There were further differences between native and non-native species traits at the subset of sites where dominant native and non-native species co-occurred (Fig. 3). Here, dominant non-native species had significantly higher SLA (x 1.7) and leaf %P (x 1.1) than native species (Figs. 3a and g). Furthermore, non-native graminoids had significantly higher leaf %N (x 1.3), %P (x 1.1) and %K (x 1.3) than native graminoids (Figs. 3f, i and l). As with the results for all sites, these differences were consistent across the control and nutrient addition treatments; i.e. there was no interaction between biogeographic origin and nutrient addition (NN:NPK in Fig. 3). Leaf trait means for native and non-native species in the different nutrient treatments, pooled across sites and blocks, support the findings from our models (Tables 1 and 2; Figs. S4 and S5).

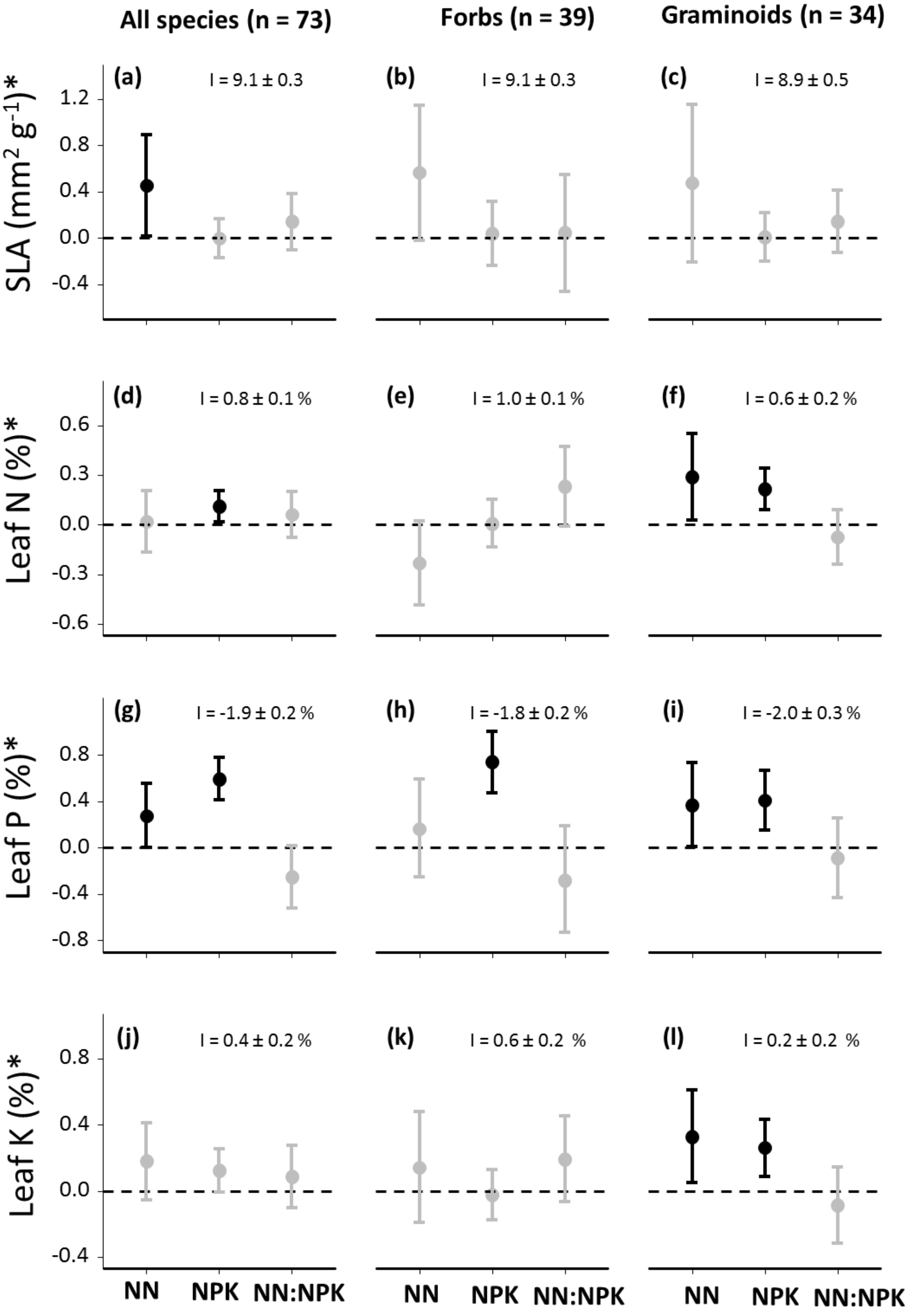
All species (n = 73)
Forbs (n = 39)
Graminoids (n = 34)
SLA (mm^2 g^{-1})*
Leaf N (%)*
Leaf P (%)*
Leaf K (%)*
(a) I = 9.1 ± 0.3
(b) I = 9.1 ± 0.3
(c) I = 8.9 ± 0.5
(d) I = 0.8 ± 0.1 %
(e) I = 1.0 ± 0.1 %
(f) I = 0.6 ± 0.2 %
(g) I = -1.9 ± 0.2 %
(h) I = -1.8 ± 0.2 %
(i) I = -2.0 ± 0.3 %
(j) I = 0.4 ± 0.2 %
(k) I = 0.6 ± 0.2 %
(l) I = 0.2 ± 0.2 %
1.2
0.8
0.4
0.0
-0.4
0.6
0.3
0.0
-0.3
-0.6
0.8
0.4
0.0
-0.4
-0.8
0.8
0.4
0.0
-0.4
NN
NPK
NN:NPK
NN
NPK
NN:NPK
NN
NPK
NN:NPK

Figure 3 – Four leaf traits measured at the subset of sites (n = 11) where dominant native and non-native species co-occur. For each leaf trait, mean effect estimates (i.e. coefficients) and their 95% credible intervals (CRIs) for biogeographic origin (i.e. non-native species = NN), the nutrient addition treatment (NPK) and their interaction (NN:NPK) are shown from Bayesian hierarchical models fit with INLA and a random effects structure of species/site/block. The zero reference line represents the intercept (I) of the model (i.e. the estimate for native species in the nutrient control treatment). Mean effect estimates with 95% CRIs that do not cross zero are significant (in black). In the absence of an interaction, a significant main effect (i.e. NN or NPK) affects the response (i.e. leaf trait) across both levels of the other main effect. *All leaf traits ln-transformed due to non-normality.

Table 1 – Leaf trait (SLA, mm^2 g^{-1}; leaf % N, leaf % P, leaf % K) means and SE for native and non-native species in the control (unfertilised) and nutrient addition (NPK) treatments at all sites (n = 27). Means are pooled across sites and blocks. Leaf traits in which native and non-native species differed significantly, based on Bayesian hierarchical models fit with INLA and a random effects structure of species/site/block, are shown in bold.

	Control treatment		NPK treatment	
Leaf Trait	Native sp.	Non-native sp.	Native sp.	Non-native sp.
All species				
SLA	15597 ± 1791	15250 ± 1329	16989 ± 1179	19869 ± 2403
Leaf % N	2.62 ± 0.1	2.55 ± 0.14	3.13 ± 0.1	2.96 ± 0.15
Leaf % P	0.21 ± 0.01	0.21 ± 0.02	0.31 ± 0.01	0.33 ± 0.03
Leaf % K	**1.83 ± 0.09**	**1.88 ± 0.1**	**2.16 ± 0.09**	**2.42 ± 0.16**
Forbs				
SLA	15526 ± 1182	15618 ± 1370	16970 ± 1331	23674 ± 5229
Leaf % N	3.07 ± 0.15	2.87 ± 0.31	3.39 ± 0.14	3.45 ± 0.34
Leaf % P	0.26 ± 0.02	0.21 ± 0.03	0.38 ± 0.03	0.41 ± 0.06
Leaf % K	2.22 ± 0.15	2.04 ± 0.16	2.47 ± 0.16	3.00 ± 0.34
Graminoids				
SLA	15650 ± 3020	15061 ± 1894	17003 ± 1792	18126 ± 2561
Leaf % N	2.26 ± 0.12	2.36 ± 0.13	2.94 ± 0.14	2.72 ± 0.14
Leaf % P	0.17 ± 0.01	0.20 ± 0.02	0.27 ± 0.01	0.29 ± 0.03
Leaf % K	**1.52 ± 0.08**	**1.79 ± 0.12**	**1.96 ± 0.1**	**2.13 ± 0.14**

Table 2 – Leaf trait (SLA, mm^2 g^{-1}; leaf % N, leaf % P, leaf % K) means and SE for native and non-native species in the control (unfertilised) and nutrient addition (NPK) treatments at the subset of sites (n = 11) where dominant native and non-native species co-occur. Means are pooled across sites and blocks. Leaf traits in which native and non-native species differed significantly, based on Bayesian hierarchical models fit with INLA and a random effects structure of species/site/block, are shown in bold.

	Control treatment		NPK treatment	
Leaf Trait	Native sp.	Non-native sp.	Native sp.	Non-native sp.
All species				
SLA	**10201 ± 1292**	**15395 ± 1797**	**11018 ± 1482**	**20791 ± 2922**
Leaf % N	2.3 ± 0.14	2.23 ± 0.13	2.63 ± 0.14	2.77 ± 0.13
Leaf % P	**0.18 ± 0.01**	**0.19 ± 0.02**	**0.33 ± 0.03**	**0.33 ± 0.03**
Leaf % K	1.86 ± 0.14	1.83 ±0.12	2 ± 0.16	2.53 ± 0.19
Forbs				
SLA	9437 ± 1209	14944 ± 1602	13108 ± 2217	24245 ± 6411
Leaf % N	2.82 ± 0.2	2.21 ± 0.27	2.85 ± 0.2	2.84 ± 0.22
Leaf % P	0.21 ± 0.02	0.18 ± 0.02	0.41 ± 0.04	0.4 ± 0.07
Leaf % K	2.46 ± 0.24	2.1 ± 0.19	2.32 ± 0.25	3.21 ± 0.41
Graminoids				
SLA	10916 ± 2245	15605 ± 2545	8000 ± 1494	19196 ± 3113
Leaf % N	**1.82 ± 0.16**	**2.25 ± 0.15**	**2.31 ± 0.19**	**2.73 ± 0.16**
Leaf % P	**0.15 ± 0.02**	**0.2 ± 0.02**	**0.23 ± 0.03**	**0.28 ± 0.03**
Leaf % K	**1.38 ± 0.11**	**1.67 ± 0.14**	**1.65 ± 0.16**	**2.18 ± 0.16**

Model selection revealed biogeographic origin was not the most important factor for predicting leaf traits. Instead, nutrient addition and mean annual temperature (MAT) were the most important predictors of leaf nutrient concentrations, and the null model was the preferred model for SLA and % cover (Table 3). In the null model there are no fixed effects and therefore all the variation is explained by the random effects (species/site/block).

Table 3 – Preferred models based on model selection using highest marginal log-likelihoods (MLLs) for each leaf trait and % cover, where the highest MLL comparatively suggests more variation is being explained in the response variable. The model with the highest MLL for each leaf trait is in bold (model 1). Models tested include the random effects only model (null model), along with all fixed effect combinations of biogeographic origin (BO), nutrient addition treatment (Trt), their interaction (Bo: Trt) and each individual abiotic variable: mean annual temperature (MAT, ^{o}C), temperature variation (Temp var), mean annual precipitation (MAP, mm), MAP variation (MAP var), Soil N (%), P and K (ppm). * SLA, leaf %N, leaf %P and % cover were ln-transformed due to non-normality.

Leaf Trait	**Model 1**	MLL	Model 2	MLL	Model 3	MLL
All species						
SLA*	**Null model**	-413.0	Trt	-416.1	BO	-417.5
Leaf % N*	**Trt+ MAT**	-95.5	BO+ Trt+ MAT	-101.1	BO* Trt+ MAT	-106.9
Leaf % P*	**Trt+ MAT**	-264.2	BO+ Trt+ MAT	-268.7	Trt	-269.6
Leaf % K	**Trt+ MAT**	-382.9	BO+ Trt+ MAT	-385.6	BO+ Trt+ Soil N	-389.9
% cover*	**Null model**	-549.9	Trt	-552.8	Soil N	-554.7
Forbs						
SLA*	**Null model**	-223.6	BO	-227.8	Soil N	-228.5
Leaf % N*	**Null model**	-64.6	MAT	-67.6	Soil N	-68.2
Leaf % P*	**Trt**	-120.4	Trt+ MAT	-124.4	Trt+ Soil N	-125.3
Leaf % K	**Soil N**	-192.1	Null model	-193.4	Trt+ Soil N	-194.2
% cover*	**Null model**	-256.5	BO	-259.5	Trt	-260.5
Graminoids						
SLA*	**Null model**	-203.4	BO	-207.3	Soil N	-208.0
Leaf % N*	**Trt+ MAT**	-55.3	BO+ Trt+ MAT	-59.5	Trt	-62.4
Leaf % P*	**Trt + MAT**	-164.0	BO+ Trt+ MAT	-167.5	Trt	-171.0
Leaf % K	**Trt**	-211.2	Trt+ MAT	-211.4	BO+ Trt+ MAT	-214.0
% cover*	**Null model**	-310.4	BO	-314.2	Trt	-314.6

Discussion

Using replicated treatments and sampling in 27 grasslands spanning four continents, our results demonstrate that dominant non-native graminoid leaf traits are physiologically different (higher leaf %K) than dominant native graminoids. Moreover, at the 11 sites where native and non-native species both dominated, non-native species invested in higher SLA and leaf %P than native species, and non-native graminoids invested in leaves with higher concentrations of all three major nutrients (N, P and K) than native graminoids. Given that these differences were consistent in natural soil fertility levels and following nutrient enrichment, our research suggests that non-native graminoid success is associated with physiological differences from native species. Our findings are likely to be conservative in regards to their implications for invasion success because i) most (71%), but not all, of the dominant non-native species in our study were classified as invasive or as weeds (Weber, 2017; table S2); and ii) some of the 116 dominant native species may be invasive elsewhere, and therefore may have similar traits to non-native species (van Kleunen *et al.*, 2010).

The ability of dominant non-native species to invest in higher SLA and leaf nutrient concentrations than co-occurring dominant native species is beneficial, particularly with nutrient enrichment. Such leaves can presumably attain higher maximum photosynthetic rates (Reich *et al.*, 2003; Wright *et al.*, 2004) and produce more chlorophyll, nucleic acids and adenosine triphosphate. These capabilities should enable more effective capture, storage and transport of energy within the plant (Epstein & Bloom, 2005; Reich *et al.*, 2009; Reich, 2014), higher stomatal conductance, and enzymatic activity (Brodribb *et al.*, 2007). Together, these benefits can lead to increased photosynthetic rates and ultimately faster plant growth (Brodribb *et al.*, 2007; Reich, 2014); thereby providing non-native graminoids with a potential growth advantage (Dawson *et al.*, 2011). This physiological advantage can be important for invasive species success even under natural soil nutrient availability, as shown in forest ecosystems (Heberling & Fridley, 2016). Nevertheless, leaves with a physiological demand for higher minimum nutrient concentrations would generally be more beneficial under relatively high nutrient availability. In many soils, this may be problematic because P has a high affinity to soil particles and is therefore less available to plants than N (Lynch & Brown, 2001). However, nutrient enrichment may increase the supply of P. This could partly explain why plant invasions and nutrient enrichment often co-occur (Davis *et al.*, 2000; Melbourne *et al.*, 2007; Seabloom *et al.*, 2015). Furthermore, litter decomposition rates tend to increase when litter has higher nutrient concentrations (Cornelissen & Thompson, 1997; Cornwell *et al.*, 2008). In addition to decomposition rates, non-native species can also alter soil inorganic N concentrations and N mineralisation rates (McLeod *et al.*, 2016; Broadbent *et al.*, 2017). Moreover, recent findings show that (1) greater dissimilarity between native and non-native species traits lead to higher impacts on N cycling in invaded ecosystems (Lee *et al.*, 2017), and (2) that dominant non-native species tend to have higher per capita impacts than dominant native species (Pearse *et al.*, 2019). Our findings therefore help to explain the strong impacts on nutrient cycling rates often observed in invaded ecosystems (Liao *et al.*, 2008; Ehrenfeld, 2010).

Higher nutrient concentrations generally make leaves more palatable to herbivores, which would be a disadvantage for non-native species. But because non-native species may be released from the specialised enemies that they co-evolved with in their native range, they also may benefit from reduced herbivory in their invaded ranges (Keane & Crawley, 2002; Leishman *et al.*, 2014), at least during the earlier stages of invasions (Verhoeven *et al.*, 2009; Diez *et al.*, 2010). Therefore non-native species may initially reap the benefits of higher SLA and leaf nutrient concentrations without suffering the costs, particularly following nutrient enrichment (Blumenthal, 2005, 2006). In a recent 20 year experiment, invasive species that were grasses and/or had higher SLA (mean values per species from a database and not measured), were more successful at spreading to new plots; whereas, invaders with lower SLA showed higher long term occupancy rates (Catford *et al.*, 2019). This suggests that higher SLA may be advantageous in the earlier stages of invasion, and lower SLA over the longer term. At least under the conditions tested in Catford et al.'s (2019) experiment at one site, which included low resource availability, a history of disturbance, and "invasive" species that were primarily non-resident native species. Under a wider range of conditions, such as those in our study (Table 1), it may be that higher SLA and leaf nutrient concentrations are advantageous for non-native species in the short and long term. Another recent study found that fast reproduction rates were associated with weedy plants in the US, regardless of their biogeographic origin (Kuester *et al.*, 2014). However, this study did not consider the ecological conditions under which species may become weedy. In contrast, our findings show that dominant non-native graminoids differ in key leaf traits regardless of nutrient availability.

Our findings suggest that non-native graminoids may potentially be pre-adapted to high fertility conditions, particularly since many invasive species, and 79% of the non-native species in our study, originated from Europe (Van Kleunen *et al.*, 2015); a region which has been exposed to cultivation since the Neolithic era (MacDougall *et al.*, 2018). Indeed, European plant species have been found to have a 300% higher probability of becoming naturalised away from home (Van Kleunen *et al.*, 2015). Moreover, human colonizers from Europe to North America and Australasia, the continents that contained all of the non-native species in our study (Fig. 1), introduced non-native graminoids as forage species to "improve" native grassland productivity (Mack *et al.*, 2000; Mack & Lonsdale, 2001; Mack & Erneberg, 2002; Seastedt & Pyšek, 2011). Given the importance of grasslands for forage, the 21% of non-native species in our grassland dataset originating from regions other than Europe likely were selected for similar traits. The European grassland species that constituted the majority of the non-native species in our study may also dominate in their native European ranges (Firn *et al.*, 2011), suggesting their trait advantages may also be relevant in their native range. However, shifts in functional strategies of non-native species in their invaded ranges may also have occurred (Parker *et al.*, 2013), and this may be related to their residence time in the non-native range. This may explain why greater differences were found at the subset of sites where dominant native and non-native species co-occur. Furthermore, given that some non-native species become more abundant in their invaded ranges, the trait differences reported here are likely to interact with other mechanisms that promote invasive species success.

Whilst native and non-native graminoids clearly differed in their leaf traits, which helps to explain the success of plant invasions in grasslands (Divíšek *et al.*, 2018), model selection showed that other factors are also important for predicting leaf traits in global grasslands. In particular, mean annual temperature and the nutrient addition treatment were the most important predictors of leaf nutrient concentrations. This supports the findings of a previous study using the same dataset, which showed that edaphic and climatic variables are important for predicting leaf traits (Firn *et al.*, 2019).

Invasion ecology is characterized by a wide number of hypotheses, relating to ecological, physiological, and evolutionary mechanisms often operating in a context of anthropogenic transformation (Fridley *et al.*, 2007; Catford *et al.*, 2009; Buckley & Catford, 2016). Although many support the idea that successful invaders perform differently than native species (Lai *et al.*, 2015), measures of how invasive species might grow differently than native plants in response to disturbances such as nutrient enrichment are often not tested experimentally across a wide ranging set of sites in the same biome like grasslands (Leifso *et al.*, 2012; Moles *et al.*, 2012; MacDougall *et al.*, 2014; Buckley & Catford, 2016; Funk *et al.*, 2017). Our study demonstrates that dominant non-native graminoids generally grow leaves with higher nutrient concentrations than co-occurring dominant native graminoids, revealing important physiological differences between these groups. Most importantly, these distinctions were consistent in natural and nutrient enriched conditions. Given that leaf nutrient concentrations are critical determinants of photosynthetic rates and ultimately plant growth, this may provide non-native graminoids with a competitive advantage over dominant native graminoids that enhances their invasion success (Divíšek *et al.*, 2018). It could also lead to strong feedbacks between faster litter decomposition and greater soil nutrient availability (Cornwell *et al.*, 2008; Hobbie, 2015), and thereby contribute to increased nutrient cycling rates often observed in invaded grasslands (Liao *et al.*, 2008; Ehrenfeld, 2010; Hobbie, 2015).

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Data accessibility

The data that support the findings of this study are available in Dryad Digital Repository with the unique identifier: doi:10.5061/dryad.tmpg4f4v8.

Supplementary Material

Figure S1 – Species % cover at all sites (a-c) and the subset of sites with co-occurring dominant native and non-native species (d-f). Mean effect estimates (i.e. coefficients) and their 95% credible intervals (CRIs) for biogeographic origin (i.e. non-native species = NN), the nutrient addition treatment (NPK) and their interaction (NN:NPK) are shown from Bayesian hierarchical models fit with INLA and a random effects structure of species/site/block. The zero reference line represents the intercept (I) of the model (i.e. the estimate for native species in the nutrient control treatment). Mean effect estimates with 95% CRIs that cross zero are not significant. *ln transformed due to non-normality

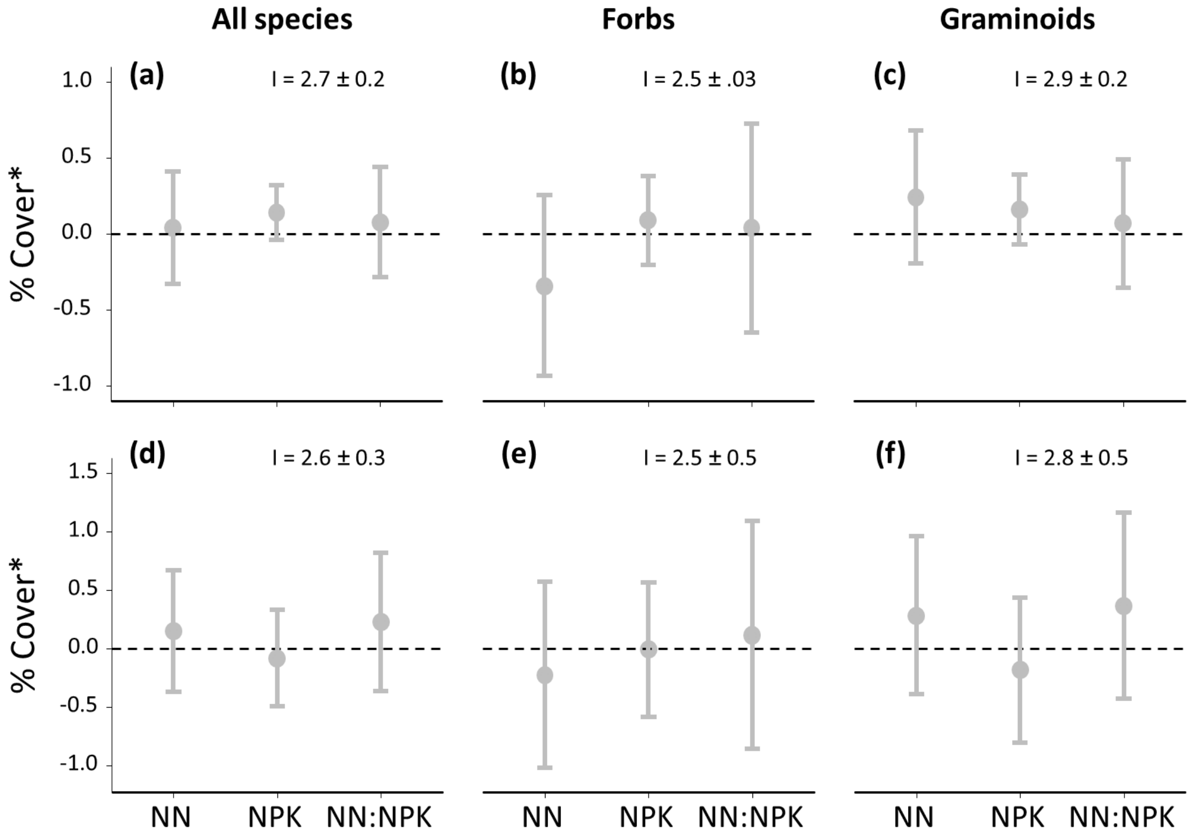

Figure S2 – Proportion of variation explained by random effects (species/ site/ block and residuals) of Bayesian hierarchical models of individual leaf traits with fixed effects of biogeographic origin, nutrient addition treatment and their interaction for all species, forbs and graminoids. *SLA, leaf %N, leaf %P and % cover were ln-transformed due to non-normality.

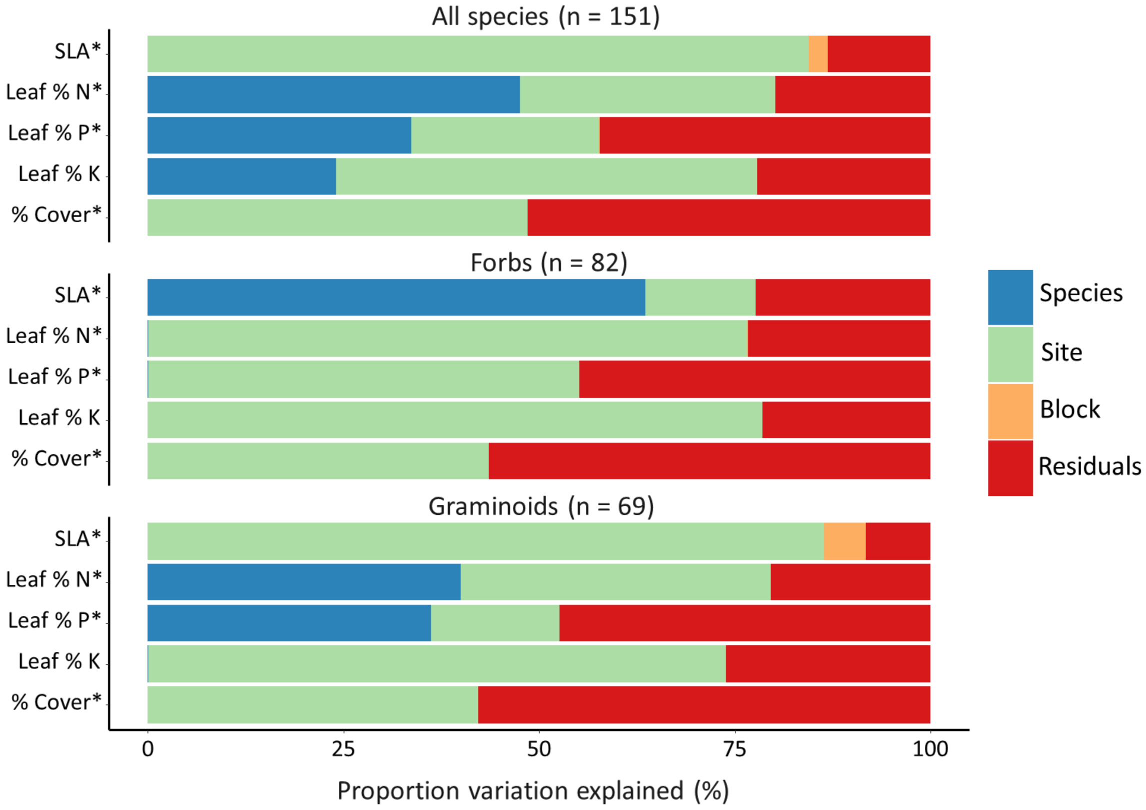

Figure S3: Directed Acyclic Graph (DAG) to represent the multilevel regression models in a hierarchical Bayesian framework that was developed to analyse leaf traits. For each of the leaf traits, y_{ijkl} denotes the response and $\mathbf{x}_{ijkl} = (x_{1jkl}, x_{2jkl}, \ldots, x_{pjkl})$ denotes the ith sample from the jth block at the kth site of the lth plant species. μ_{jkl} is the mean response associated with block j at site k and species l where β_0 is the model intercept and $\beta_1, \beta_2, \ldots, \beta_p$ are slope parameters for each predictor $(x_{1jkl}, x_{2jkl}, \ldots, x_{pjkl})$. Then u_l is the random effect associated with the lth species, v_{kl} is the random effect associated with the kth site (within species l), w_{jkl} is the random effect associated with jth block (within species l and site k), and e_{ijkl} is the residual error associated with the ith response on block j at site k for species l.

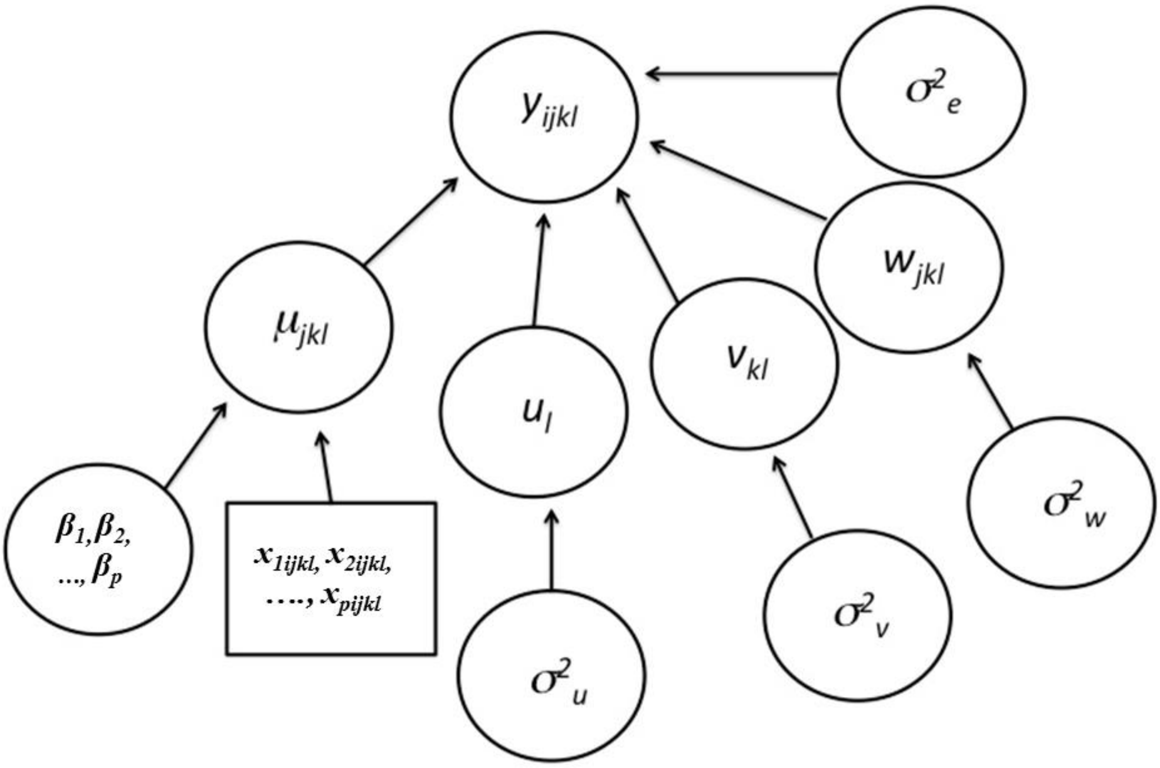

Figure S4 – Four leaf traits measured at all sites (n = 27). For each leaf trait, means and one standard error of native and non-native species in the control and nutrient addition (NPK) treatments are shown. Means are pooled across sites and blocks.

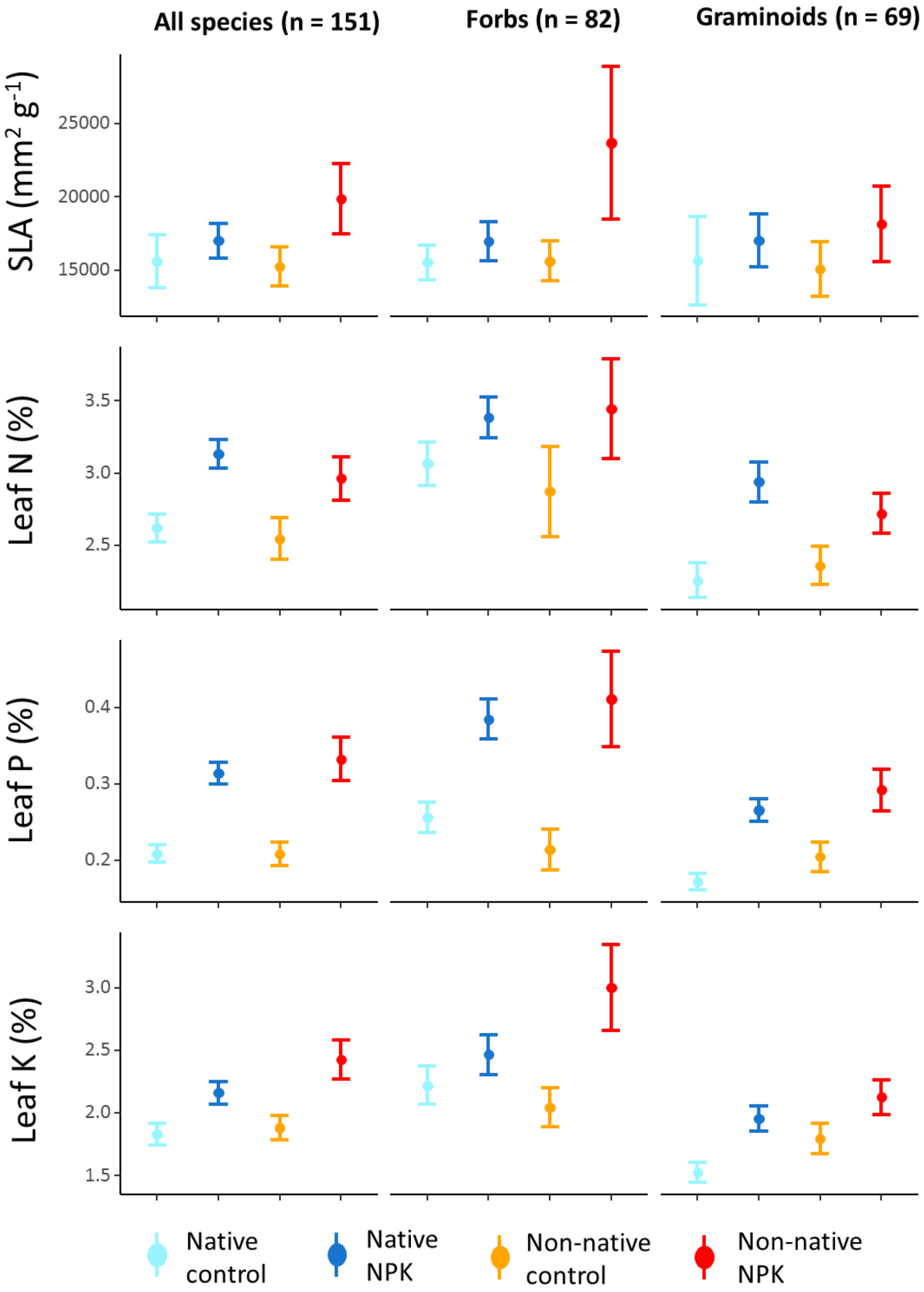

Figure S5 – Four leaf traits measured at the subset of sites (n = 11) where dominant native and non-native species co-occur. For each leaf trait, means and one standard error of native and non-native species in the control and nutrient addition (NPK) treatments are shown. Means are pooled across sites and blocks.

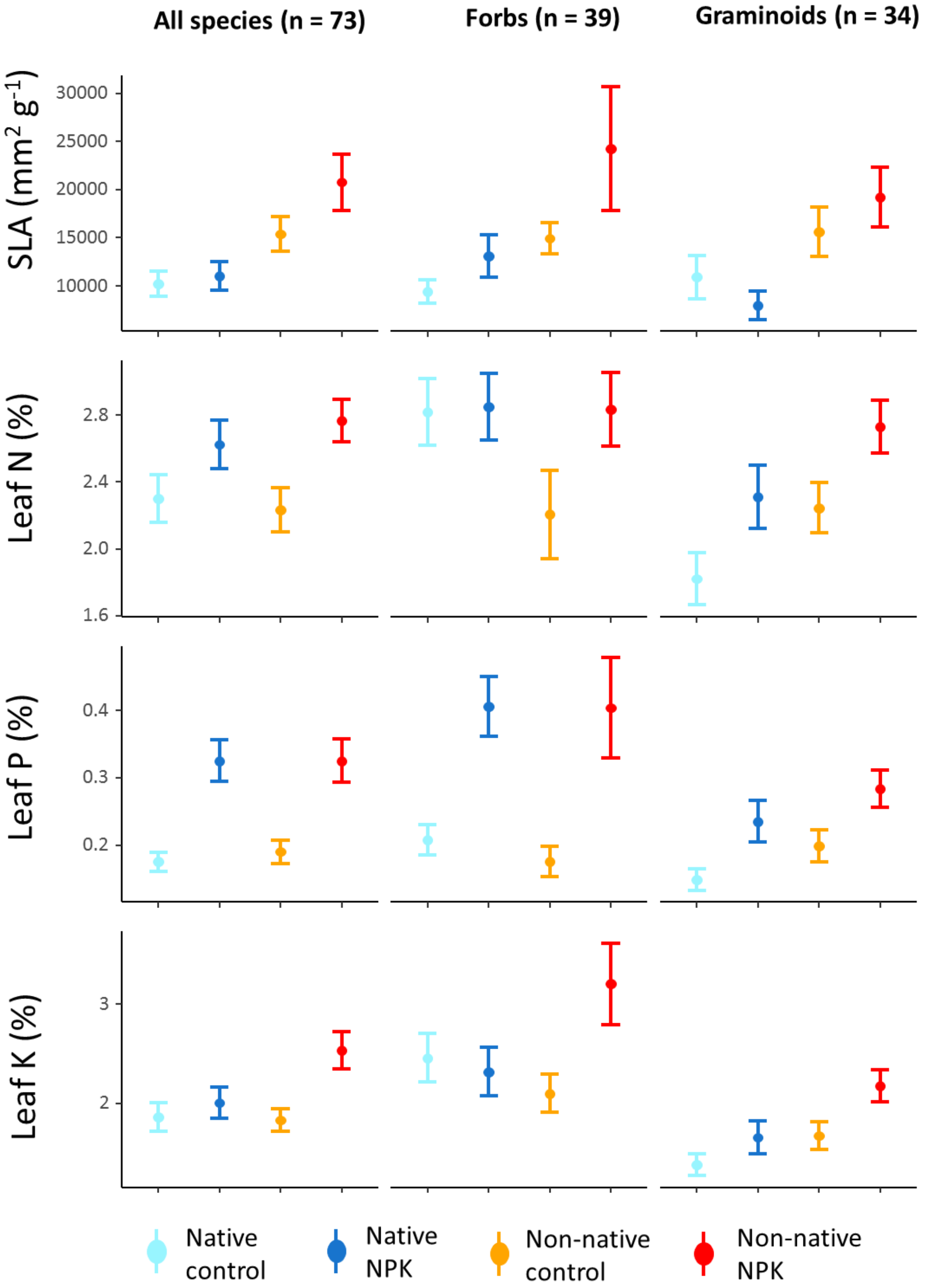

Table S1 – Abiotic and biotic site conditions, and experimental year that leaves were collected (Exp. year) for 27 sites (AU – Australia, CA – Canada, CH – Switzerland, DE – Germany, PT – Portugal, UK – United Kingdom, US – United States and ZA – South Africa).

Site	Habitat	Elevation (m)	MAT (°C)	MAP (mm)	Temp var	MAP var	Soil N (%)	Soil P (ppm)	Soil K (ppm)	Native: Non-native richness	Exp. Year
Bldr (US)	Shortgrass Prairie	1633	9.7	425	79.52	42	0.09	14	87	7:15	3
Bnch (US)	Montane Grassland	1318	5.5	1647	60.55	65	0.57	17	70	40:3	4
Bogo (AU)	Alpine Grassland	1760	5.7	1592	47.59	26	0.54	52	203	34:3	2
Burr (AU)	Semiarid Grassland	425	18.4	683	50.49	36	0.11	35	70	31:5	3
Cbgb (US)	Tallgrass Prairie	275	9	855	108.5	46	0.06	72	95	49:15	3
Com (PT)	Annual Grassland	200	16.5	554	49.77	61	0.12	44	90	54:1	2
Cowi (CA)	Old field	50	9.8	764	40.44	64	0.43	47	88	1:20	4
Duke (US)	Old field	141	14.6	1163	35.93	87	0.14	16	222	35:17	4
Elch (US)	Annual Grassland	200	17.2	331	59.89	23	0.30	55	255	16:19	3
Frue (CH)	Pasture	995	6.5	1355	76.18	11	0.13	42	144	22:3	3
Gilb (ZA)	Montane Grassland	1748	13.1	926	34.19	67	1.26	17	108	73:0	2
Hopl (US)	Annual Grassland	598	12.3	1127	52.78	87	na	na	na	62:47	4
Jena (DE)	Grassland	320	8	610	62.51	27	0.55	155	1340	33:1	2
Kiny (AU)	Semiarid Grassland	90	15.5	426	49.26	21	0.12	10	387	44:36	4
Konz (US)	Tallgrass Prairie	440	11.9	877	99.32	50	NA	NA	NA	73:3	4
Lanc (UK)	Mesic Grassland	180	8	1322	45.42	23	1.55	21	90	28:0	3
Look (US)	Montane Grassland	1500	4.8	1898	58.66	65	1.26	71	115	31:2	4
Mcla (US)	Annual Grassland	641	13.5	867	59.94	88	na	na	na	34:30	4
Mtca (AU)	Savanna	285	17.3	330	52.55	55	na	na	na	41:18	3
Sage (US)	Montane Grassland	1920	5.7	882	65.39	69	0.52	28	209	44:0	4
Sali (US)	Mixedgrass Prairie	440	11.8	607	100.3	53	na	na	na	84:12	4
Sgst (US)	Shortgrass Prairie	1650	8.4	365	84.82	59	0.09	71	255	48:4	4
Shps (US)	Shrub steppe	910	5.5	262	95.57	37	0.23	36	519	52:12	4

Sier (US)	Annual Grassland	197	15.6	935	64.7	84	0.17	20	88	39:41	4
Smit (US)	Mesic Grassland	62	9.8	597	42.14	36	0.43	82	183	4:43	4
Sum (ZA)	Mesic Grassland	679	18.2	939	25.51	55	0.29	15	97	104:0	2
Valm (CH)	Alpine Grassland	2320	0.3	1098	54.23	29	0.59	18	64	104:0	3

Table S2 – List of the dominant non-native species in our study, the number of sites and the countries in which they were sampled. Species classified as invasive by Weber (2017) are in bold. Species classified as weeds in the country in which they were sampled are indicated with an *, or (*) where only the genus was identified. Weed classification was based on The US Department of Agriculture's "Weeds of the US" list (https://plants.usda.gov/), the Canadian Food Inspection Agency's "List of pests regulated by Canada" (https://www.inspection.gc.ca/) and the Australian Government Department of the Environment and Energy's "Weeds in Australia list" (http://www.environment.gov.au).

Species name	Functional group	Number of sites and country
Alopecurus pratensis	Graminoid	1 (Canada)
Alyssum desertorum	Forb	1 (US)
Anthoxanthum odoratum	**Graminoid**	**1 (US)**
Avena barbata	Graminoid	1 (Australia)
Avena fatua	**Graminoid**	**1 (Australia)**
****Briza maxima***	**Graminoid**	**1 (US)**
**Bromus diandrus*	Graminoid	2 (US)
**Bromus hordeaceus*	Graminoid	3 (US)
****Bromus inermis***	**Graminoid**	**1 (US)**
Bromus rubens	**Graminoid**	**1 (Australia)**
(*)Bromus sp.	Graminoid	1 (US)
**Bromus sterilis*	Graminoid	1 (US)
****Carduus pycnocephalus***	**Forb**	**1 (US)**
****Chenopodium album***	**Forb**	**1 (US)**
****Cirsium arvense***	**Forb**	**1 (US)**
**Convolvulus arvensis*	Forb	1 (US)
Cynosurus echinatus	Graminoid	2 (US)
****Eragrostis curvula***	**Graminoid**	**1 (Australia)**
Erodium botrys	**Forb**	**1 (Australia); 1 (US)**
**Geranium dissectum*	Forb	1 (US)
Geranium molle	Forb	1 (US)
Glandularia aristigera	Forb	1 (Australia)
****Hordeum murinum***	**Graminoid**	**1 (US)**
Hordeum murinum ssp. leporinum	**Graminoid**	**1 (Australia)**
****Hypochaeris radicata***	**Forb**	**1 (Australia); 1 (US)**
**Lactuca serriola*	Forb	1 (US)
Lathyrus sphaericus	Forb	1 (Canada)
Lespedeza juncea var. sericea	Forb	1 (US)
**Lolium multiflorum*	Graminoid	2 (US)
****Lonicera japonica***	**Forb**	**1 (US)**
Pentaschistis airoides	Graminoid	1 (Australia)
****Plantago lanceolata***	**Forb**	**1 (US)**

Poa pratensis	**Graminoid**	**1 (Canada)**
(*)Schedonorus sp.	Graminoid	1 (US)
****Taeniatherum caput-medusae***	**Graminoid**	**2 (US)**
**Torilis arvensis*	Forb	2 (US)
Trifolium dubium	Forb	1 (Canada)
Vicia sativa	Forb	1 (Canada)
****Vulpia myuros***	**Graminoid**	**1 (Australia); 1 (US)**