Alien plants can be associated with a decrease in local and regional native richness even when at low abundance

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1. The impacts of alien plants on native richness are usually assessed at small spatial scales and in locations where the alien is at high abundance. But this raises two questions: to what extent do impacts occur where alien species are at low abundance, and do local impacts translate to effects at the landscape scale?

2. In an analysis of 47 widespread alien plant species occurring across a 1,000 km² landscape, we examined the relationship between their local abundance and native plant species richness in 594 grassland plots. We first defined the critical abundance at which these focal alien species were associated with a decline in native \(\alpha\)-richness (plot-scale species numbers), and then assessed how this local decline was translated into declines in native species \(\gamma\)-richness (landscape-scale species numbers).

3. After controlling for sampling biases and environmental gradients that might lead to spurious relationships, we found that 8 out of 47 focal alien species were associated with a significant decline in in native \(\alpha\)-richness as their local abundance increased. Most of these significant declines started at low to intermediate classes of abundance. For these eight species, declines in native \(\gamma\)-richness were, on average, an order of magnitude (32.0 vs. 2.2 species) greater than those found for native \(\alpha\)-richness, mostly due to spatial homogenisation of native communities. The magnitude of the decrease at the landscape scale was best explained by the number of plots where an alien species was found above its critical abundance.

Synthesis: Even at low abundance, alien plants may impact native plant richness at both local and landscape scales. Local impacts may result in much greater declines in native richness at larger spatial scales. Quantifying impact at the landscape scale requires consideration of not only the prevalence of an alien plant, but also its critical abundance and its effect on native community homogenisation. This suggests that management approaches targeting only those locations dominated by alien plants might not mitigate impacts
effectively. Our integrated approach will improve the ranking of alien species risks at a spatial scale appropriate for prioritizing management and designing conservation policies.

Introduction

How do we integrate alien plant impacts on native biodiversity across large spatial scales? Most studies quantifying the impacts of alien plants are undertaken at small spatial scales, usually experimental plots (Powell, Chase & Knight 2011; Hulme et al. 2013; Stricker, Hagan & Flory 2015), but the implications for conservation require assessments of impacts at larger spatial scales. The traditional view has been that to scale up impacts from plot to landscape will simply require calculating the product of the per capita effect of an alien species, its local abundance and its geographic distribution (Parker, Simberloff & Lonsdale 1999; Thomsen et al. 2011; Barney et al. 2013). However, there is increasing evidence that simply scaling up impacts from the local to the landscape scale ignores the importance of spatial heterogeneity in determining the effects of alien species (Thiele et al. 2010; Ricciardi et al. 2013; Latzka et al. 2016). In particular, even for a single alien species, the magnitude of impacts varies with the study location (Hulme et al. 2013), does not always scale linearly with abundance (Gooden, French & Turner 2009; Hulme et al. 2014) and is dependent on the spatial scale of assessment (Powell, Chase & Knight 2013). There is therefore a requirement that impacts of alien plants are studied across multiple sites, over a range of abundances and at different spatial scales. Most ecological studies have quantified impacts only where alien species are at high abundance (Hulme et al. 2013; but see Pearson et al. 2016), yet within any landscape the abundance of a particular alien species will vary spatially. Although theoretical approaches have explored the consequences of different relationships between alien abundance and subsequent impacts (Yokomizo et al. 2009; Latzka et al. 2016), as yet no study has attempted to quantify critical abundances – defined as the abundance at which a species starts to be associated with a
consistent detectable change in native plant richness (Figure 1A), i.e. an apparent impact (sensu Pearson 2016).

A further concern is whether impacts observed at plot scales have any bearing on the magnitude of impacts at the landscape scale. The translation between apparent impact at the local scale (e.g. decline in native $\alpha$-richness with increasing abundance of an alien species) and apparent impact on the native species pool at the landscape scale (e.g. decline in native $\gamma$-richness) depends on spatial turnover in native species composition and the consistency or randomness of species loss across communities (Figure 1B). Across a landscape, high spatial turnover in resident community composition may buffer the local loss of native species, resulting in a limited decrease in the regional pool of native species. This may occur where alien species reduce the occupancy of common native species to a greater degree than rare species (Powell et al. 2011). Alternatively, plant invasions have been shown to drive biotic homogenisation of resident communities (Lambdon, Lloret & Hulme 2008), in which case $\gamma$-richness may decrease significantly, even without necessarily being associated with a large change in species number at the local scale (Hulme & Bremner 2006). It is important to distinguish between these two scenarios. An alien species may never reach high local abundance, but, if it has a low critical abundance and is widespread, it may have an overall impact higher than a more regionally restricted species found at much higher abundance. Thus, it is essential to know how impacts associated with critical abundances actually translate to declines in species richness at the regional scale.

To address this issue, we investigated the relationship between the local abundance of alien plant species and apparent declines in both native $\alpha$-richness (assessed at a 6 x 6 m plot scale) and native $\gamma$-richness (assessed across a 1,000 km$^2$ landscape) in semi-natural grasslands. Using data from a detailed phytosociological survey of Banks Peninsula, New Zealand, a total of 47 focal alien species that were examined to answer:
1. How frequently do significant declines in native plant species richness occur at low critical abundances of an alien plant?

2. What is the relationship between local scale declines in native $\alpha$-richness and regional changes in native $\gamma$-richness?

3. Are declines in native $\alpha$-richness found at low rather than high critical abundances more likely to translate to shifts in $\gamma$-richness?

We expected to observe declines in native species richness mostly at high abundances of the alien species, consistent with mechanisms of invader impact via resource competition (Gross et al. 2015). We also hypothesised that in these grassland systems, the apparent impact of aliens would be driving the homogenisation of grassland communities, therefore creating a greater decrease in native $\gamma$-richness than expected by chance.

**Methods**

**Vegetation data**

We used floristic data from a comprehensive vegetation survey of Banks Peninsula (c. 1,000 km$^2$), New Zealand (43°33’ - 43°54’ S, 172°37’ - 173°07’ E) conducted between 1983 to 1988 (Wilson 1992). Species abundance was recorded once over the 5 years in each 6 x 6 m quadrats distributed along a regular 915 x 915 m grid covering the entire Peninsula (1224 plots). The same individual surveyor scored species abundance along a seven-point scale based on both species cover and density, similar to the widely used DAFOR scale (Hill et al. 2005): Occasional, Common-Occasional, Common, Abundant-Common, Abundant, Abundant-Dominant, Dominant. We merged the two highest abundance classes to ensure a sufficiently large sample size, deriving a six-point scale which was renamed for convenience: 1-Rare, 2-Occasional, 3-Frequent, 4-Common, 5-Abundant, 6-Dominant. Plant species were classified
as native or alien to New Zealand following standard definitions (New Zealand Plant Names

Prior to human colonisation, Banks Peninsula was largely forested but the major land use today
is a mix of improved and unimproved grasslands. Thus, to ensure comparability in land-use
across plant communities, we restricted our analysis to unimproved grassland plots. We used
the New Zealand land-use classification for 1990 (LUCAS database from the Ministry for
Environment – available at https://data.mfe.govt.nz/layer/2375-lucas-new-zealand-land-use-
map-1990-2008-2012-v011/) to exclude all plots located in high-producing grassland (c. 28% of
plots) as these corresponded to improved pastures with a history of fertilisation and sowing
of alien pasture grasses. We then applied a further filter to exclude mixed woodland/grassland
(c. 27% of plots), only including plots for which the most abundant species was herbaceous.
We ended up with 594 plots of unimproved grassland. The total pool of species across these
594 plots was 431 vascular plant species (242 natives and 189 aliens). To ensure a sufficient
sample size for our analyses, we selected the subset of focal alien species that were recorded
more than five times in at least three or more abundance classes, thereby describing an
abundance gradient of at least three levels. This resulted in a total of 47 focal alien species, all
of which included observations at the lowest abundance class (i.e. Rare), which served as the
baseline against which we measured apparent impact.

Previous studies using data from the Banks Peninsula vegetation surveys have identified
elevation, slope and north-facing aspect to be the main environmental parameters associated
with native and alien plant species distribution (Tomasetto, Duncan & Hulme 2013; Pouteau,
Hulme & Duncan 2015). These gradients capture the major anthropogenic and climatic drivers
shaping the vegetation of Banks Peninsula, particularly moisture, grazing and fire. Using
environmental data from Pouteau, Hulme & Duncan (2015), we observed that our subset of the
Banks Peninsula dataset also showed native $\alpha$-richness to increase and alien $\alpha$-richness to
decrease towards higher elevations as well as steeper and more south-facing slopes (Table S1a).
In addition, we detected a temporal sampling bias towards less steep slopes (decreasing average slope of plots) over the 6 years of the survey, which, given the distribution of species across environmental factors mentioned above, resulted in a slight decrease in the mean native and alien richness recorded over the years (Supplementary material S1).

If the abundance of a focal alien species was associated with these environmental and temporal gradients in an opposite direction to native richness, it would point to a typical “passenger effect”, i.e. a decline in native richness driven by environmental gradients that happen to favour alien species (MacDougall & Turkington 2005). This would create spurious negative correlations between focal alien species abundance and native species richness. Preliminary tests revealed that a quarter of the focal alien species did show such negative correlations with the environmental gradients (Table S1b). We chose to account for these underlying gradients by including them as covariates in the following analyses to disentangle potential spurious associations. Nevertheless, the correlative nature of the analyses imply the significant trends observed should only be interpreted as apparent impact (*sensu* Pearson *et al.* 2016).

*Trends in native α-richness along abundance gradients*

We aimed to detect the critical abundance of an alien species, defined as the abundance of the alien species at which we start detecting an apparent impact on native α-richness (Figure 1A). This apparent impact was measured as a change in native α-richness relative to where the alien focal species was Rare (i.e. the lowest observed abundance class). For each focal alien species *i*, we fitted a generalized linear model (GLM) with a Poisson error distribution using maximum likelihood to examine the extent to which variation in native α-richness co-varied with the abundance of the focal alien species. We added elevation, slope, aspect, year of sampling and alien plant species richness as co-factors in all the GLMs. Aspect was decomposed into northness (cos[aspect]) and eastness (sin[aspect]), but only northness was kept in the models since eastness has been shown to play only a minor role in explaining native richness in these grasslands (Pouteau *et al.* 2015).
We set up explicit *a priori* contrasts between mean native $\alpha$-richness at the lowest abundance class (i.e. *Rare*) and each subsequent abundance class (i.e. *Occasional* < *Frequent* < *Common* < *Abundant* < *Dominant*). Thus, a negative coefficient for a given abundance class indicated a decrease in average native $\alpha$-richness compared to plots where the focal alien species was *Rare*. Coefficients were expressed in terms of percent change in mean native richness at each abundance class by calculating $[\exp(coef) \times 100 - 100]$. We then bootstrapped these coefficients to account for unequal sample sizes between abundance classes. The bootstrapping procedure resampled 9999 times with replacement the 594 grassland plots and refitted all GLM models at each run. For each abundance class and each focal alien species, we built 95% confidence intervals using bootstrap percentiles to determine the robustness of the observed coefficients. Only coefficients whose confidence interval did not overlap zero were considered as robust.

To identify a critical abundance class at which there was a significant difference in native $\alpha$-richness, we not only required statistical significance of the coefficient but also that subsequent coefficients for all higher abundance classes be consistently in the same direction (either positive or negative). Such an approach allowed us to be confident that the critical abundance class was associated with a consistent shift in native $\alpha$-richness along the abundance gradient. Our analyses permitted us to detect positive shifts in native $\alpha$-richness, but this was observed for only one focal alien species (*Supplementary material S2*), which might be expected simply by chance given such a large dataset (Bernard-Verdier & Hulme 2015). We chose to focus our study on declines in native species richness as these are the main concern in conservation and management of alien species. Thus, the following analyses only examine those focal alien species associated with negative trends in native $\alpha$-richness.

**Spatial distribution of apparent impact across the landscape**

We assessed the distribution of apparent impact at the landscape scale for each significant focal alien species based on the spatial distribution of its abundance. Three metrics were used to
describe the spatial distribution of a focal alien species: prevalence (frequency of occurrences), dominance (number of plots where the alien abundance is recorded as Dominant), and apparent impact (number of plots where the focal alien species abundance is equal or superior to its critical abundance).

Variation in native $\gamma$-richness along abundance gradients

For all focal alien species associated with a consistent decline in native $\alpha$-richness, we investigated if this local loss of species translated into a reduction in the total native species pool across the entire study area (native $\gamma$-richness). Similarly to our analyses of $\alpha$-richness, we examined trends in native $\gamma$-richness along gradients of increasing focal alien species abundance. For a given focal alien species $i$, native $\gamma$-richness at abundance class $j$ was calculated as the total number of unique native species present across all plots where the species was recorded at abundance $j$. Since $\gamma$-richness necessarily increases with the number of plots sampled, we compared the observed native $\gamma$-richness to a null expectation (null model 1). For a given focal alien species $i$ and for a given abundance class $j$, the null model shuffled 9999 times the identity of plots where the focal alien species was either Rare or at abundance $j$, and recalculated a null value of $\gamma$-richness at abundance $j$. We considered native $\gamma$-richness to be lower than expected by chance when the observed value of $\gamma$-richness was in the lower 2.5th quantile of the null distribution. We subsequently calculated an effect size corresponding to the difference between the observed native $\gamma$-richness and the mean expectation of the null model.

Comparing local vs. regional impact sizes

To estimate the consequences for total loss of species at the landscape scale we quantified the difference ($\Delta \gamma$) between the native $\gamma$-richness above and below a focal alien species’ critical abundance. Observed differences in native $\gamma$-richness above critical abundances may be driven...
by three parameters: differences in sample size (i.e. number of plots), differences in $\alpha$-richness;
and differences in spatial turnover in species composition (i.e. spatial $\beta$-diversity).

We corrected for the sampling variation above and below critical abundances by using another
null model (null model 2) that shuffled the abundance of a focal alien species across all plots
where the species occurred. This null model allowed us to calculate a sample-size corrected
change in native $\gamma$-richness ($\Delta \gamma_c$), obtained by subtracting the mean expected difference in
native $\gamma$-richness above critical abundances given sample size ($\Delta \gamma_{null}$) from the observed
difference ($\Delta \gamma_{obs}$). Significance of $\Delta \gamma_{obs}$ was assessed based on quantiles of the null distribution
as described above. We then compared this corrected change in native $\gamma$-richness ($\Delta \gamma_c$) to the
observed mean loss in native $\alpha$-richness above critical abundances across significant focal alien
species.

**Estimating native community homogenisation above critical abundances**

We also tested for a change in native $\beta$-diversity above critical abundances. One common
hypothesis is that plant invasions tend to homogenize communities, i.e. reduce the spatial
turnover in species composition. We estimated overall turnover in native species across sites
using the multi-site Simpson dissimilarity index ($\beta_{sim}$; Baselga 2010) calculated by the function
“nestedbetasor” in R package vegan (Oksanen et al. 2016). We computed $\beta_{sim}$ across plots
above and below the critical abundance of each focal alien species and calculated the difference
in native $\beta$-diversity: $\Delta \beta = \beta_{sim}$ (above) – $\beta_{sim}$ (below). Negative values of $\Delta \beta$ correspond to a
decrease in turnover in natives above critical abundance, i.e. a tendency for communities to
have more similar, or homogenous, native species composition in plots where the focal alien
species is at or above its critical abundance. To test the robustness of a positive or negative
difference, we bootstrapped observed $\Delta \beta$ values by resampling with replacement 999 times the
plots above and the plots below the critical abundance. To test for significant differences in
native turnover given the differences in numbers of plots above and below the critical
abundance, we used the same null model as before (*null model 2*) to compare the observed
difference ($\Delta \beta_{obs}$) to its null expectation (distribution of $\Delta \beta_{null}$). We calculated the standardized
effect size $\Delta \beta_c = [ \Delta \beta_{obs} - \text{mean}(\Delta \beta_{null}) ] / \text{sd}(\Delta \beta_{null})$ and assessed significance of $\Delta \beta_c$ based on
quantiles of the null distribution as described above.

**Results**

**Trends and critical abundances for native $\alpha$-richness**

Almost one quarter (11/47) of focal alien species were associated with a significant decrease
in native $\alpha$-richness (Figure 2; Table 1 & S2), while only two focal alien species were
associated with an increase. However, once environmental and sampling covariates were taken
into account, three species initially negatively associated (*Critesium murinum* L., *Phleum
pratense* L., *Rytidospermum racemosum* Edgar and Connor; Table S2) and one positively
associated (*Cynosurus echinatus* L.) with native $\alpha$-richness were no longer significant and
therefore dropped from the analysis. For these four species, associated trends in native $\alpha$-
richness may have reflected passenger effects as a result of covariation between alien
abundance and either elevation (*R. racemosum*), year of sampling (*P. pratense*), or slope (*C.
murinum*, *C. echinatus*; Table S1b). For the eight remaining focal alien species with negative
trends, and one with a positive trend, the relationships remained robust even when accounting
for environmental gradients. Since it is difficult to generalise trends based on a single species,
we chose to focus on apparent negative impacts. Results for the one positive relationship are
not discussed further but reported in *supplementary material S2*.

The critical abundances detected ranged across all five abundance classes, with a peak in
frequency at intermediate classes of abundance. Indeed, all but one significant focal alien
species were associated with lower native $\alpha$-richness as soon as, or even before, they were
*Common* within a plot (Figure 2). While these trends often started at low abundances, effect
sizes on native \( \alpha \)-richness tended to become larger with increasing abundance of a focal alien species, and the largest effect size tended to be associated with the highest abundance class recorded for a focal alien species (Figure 3). The relationship between effect size and species abundance was approximately linear for most focal alien species, with the exception of *Anthoxanthum odoratum* which appeared to exhibit marked threshold effects upon becoming dominant in a plot. Plots at or above the critical abundance had on average 2.01 ± 0.94 (mean ± SD) fewer species than plots with lower abundance (Table 1). The magnitude of this difference varied among species, being highest for *A. odoratum* (3.6 species), *Trifolium repens* (2.7 species) and *Dactylis glomerata* (2.4 species), but was not significantly correlated with the critical abundance class \((r = 0.63, \text{df} = 6, P = 0.092)\).

**Spatial distribution of apparent negative impact across the landscape**

Focal alien species with significant critical abundances followed a variety of spatial distributions in the landscape (Table 2) and ranged from species found in less than 28% of plots (e.g. *Achillea millefolium*) to those found in almost 88% of plots (e.g. *Lolium perenne*). Only five of the eight species ever reached the *Dominant* abundance class. In fact, focal alien species were found to be *Dominant* in less than 10% of all plots and no focal alien species was found to be *Dominant* in more than 5% of the plots where it occurred (Table 2). The spatial distribution of apparent impact (i.e. plots where the focal alien species is above its critical abundance) varied broadly among focal alien species (Table 2) and was not correlated with the total number of occurrences \((\rho = 0.59, P = 0.13)\), nor with the total number of plots where a species was *Dominant* \((\rho = 0.04, P = 0.93)\).

**Variations in native \( \gamma \)-richness along abundance gradients**

In general, native \( \gamma \)-richness declined with focal alien species abundance in a similar fashion to that observed for \( \alpha \)-richness (Figure 4). Statistically significant differences in native \( \gamma \)-richness mostly coincided with the same critical abundance detected for \( \alpha \)-richness or were one
or two abundance classes higher, except for one species (*H. lanatus*) whose small effect sizes never supported a significant decrease in $\gamma$-richness compared to *null model 2. 

*Relationship between decreases in native $\alpha$, $\beta$ and $\gamma$-diversity*

Using the critical abundances identified for native $\alpha$-richness, we compared the relative magnitude of changes in native $\gamma$-richness and native $\alpha$-richness above critical abundances (Table 2). As expected, differences in mean $\alpha$-richness above vs. below critical abundances were always significant (all Student tests: $P<0.01$). This decrease in $\alpha$-richness was not higher for more widespread species (Spearman’s $\rho = -0.02$, $P = 0.97$), nor for species with a wider spatial distributions of apparent impact ($\rho = 0.42$, $P = 0.30$). For instance, *A. millefolium* had a much larger apparent impact on native $\alpha$-richness (72% decline in native $\alpha$-richness) than *A. odoratum* (~2%) although the latter species was found in almost three times as many plots.

Based on values corrected for sample size by *null model 2*, declines in native $\gamma$-richness above critical abundances were on average an order of magnitude higher ($32.2 \pm 15.4$) than declines in native $\alpha$-richness ($2.02 \pm 0.94$). Only one species (*A. millefolium*) showed no significant decrease in native $\gamma$-richness above critical abundances (Table 2). Across all species, declines in native $\gamma$-richness ($\Delta \gamma_c$) were not correlated with average declines in native $\alpha$-richness above critical abundances (Figure 5a). Contrary to our expectations, lower critical abundances were not associated with larger declines in native $\gamma$-richness ($\rho = -0.05$, $P = 0.91$). Moreover, larger declines in $\gamma$-richness were not associated with more widespread focal alien species (correlation with total number of occurrences; $\rho = -0.61$, $P = 0.11$), nor focal alien species that were more often *Dominant* (correlation with number of plots where *Dominant*: $\rho = -0.11$, $P = 0.79$), but tended to be correlated with the number of occurrences above critical abundances (i.e. spatial spread of apparent impact; Figure 5b).
Overall, a decrease in native $\gamma$-richness above critical abundance tended to be associated with a decrease in spatial turnover of native species (Simpson index of $\beta$-dissimilarity; Table 1), except for two focal alien species $H. lanatus$ and $T. repens$ which revealed a significant increase in turnover (positive and significant $\Delta\beta$; Table 1). Larger decreases in native $\beta$-dissimilarity above critical abundance were associated with higher critical abundances ($\rho = -0.80$, $P = 0.017$), but appeared unrelated to the magnitude of change in native $\alpha$-richness ($\rho = 0.43$, $P = 0.30$) or $\gamma$-richness ($\rho = -0.019$, $P = 0.66$).

**Discussion**

In this study, we found that apparent local impacts of alien plant species on native species richness frequently start at low to intermediate abundance. We proposed the concept of critical abundance as a method to quantify apparent impact across a landscape, and found that there was no correlation between the size of apparent impact on native richness at the local scale ($\alpha$-richness) and at the landscape scale ($\gamma$-richness). Ranking species in terms of their impact across a landscape by simply assessing how frequently they are found at high abundance would therefore be misleading. Thus a knowledge of critical abundances appeared to be a key tool to determine large-scale losses in native $\gamma$-richness.

Almost one fifth of alien plant species examined were associated with declines in native $\alpha$-richness. This is a large proportion considering that we did not measure apparent impact in comparison to uninvaded plots, but only to plots where the alien species was Rare. Thus it is conceivable that apparent declines in $\alpha$-richness of native plants are even greater or more frequent than observed, especially given the likelihood of effects at low alien abundance. While survey data can only ever provide correlative evidence of apparent impact (HilleRisLambers et al. 2010), the progressive declines in native species richness with increasing focal alien species abundance are certainly consistent with cause and effect (Pearson et al. 2016). Some
significant correlations are expected to arise by chance in such a large dataset, at a frequency which depends on sample size, species abundance distributions and co-occurrence across the landscape. We have previously shown that for alien plant species on Banks Peninsula apparent negative impacts of alien species on native $\alpha$-richness do occur more frequently than expected by chance (Bernard-Verdier & Hulme 2015).

Furthermore, in contrast to many correlative studies examining impacts of alien plants, we attempted to account for underlying environmental gradients that might result in spurious correlations. Four environmental covariates accounted for between 20% and 30% of the variation in native $\alpha$-richness and thus the likelihood of covariation with alien abundance was high. Slope, aspect and elevation determine the intensity of sheep grazing as well as likelihood of fire on Banks Peninsula (Tomasetto et al. 2013; Pouteau et al. 2015) and thus we feel we have captured not only abiotic gradients but also the main biotic gradient (grazing) with our covariates. Indeed, approximately one third (3/11) of focal alien species exhibiting negative relationships with native $\alpha$-richness were found to become non-significant when accounting for environmental covariates and sampling bias, which pointed to typical passenger effects. It is of course possible that we failed to capture other undocumented gradients (e.g. legacy effects of historic land management) that might lead to spurious correlations between alien abundance and native richness but these would be difficult to capture quantitatively. In most cases, native richness declines were found to occur when the alien species were at low to intermediate abundance. Cases where apparent impacts were observed at low abundance of the focal alien species may point to mechanisms other than resource competition as the primary means for community change. For example, there might be indirect effects on the native plant community through increasing soil nitrogen, in the case of $T. repens$ (Elgersma & Hassink 1997) as well as allelopathy which has been postulated for $A. millefolium$ (Alipour, Farshadfar & Binesh 2012). Several focal alien species found associated with reductions in native richness at higher abundance have been shown experimentally to suppress native species through resource
competition, in particular: *L. perenne* (Groves, Austin & Kaye 2003), *H. lanatus* (Bennett, Thomsen & Strauss 2011), and *D. glomerata* (MacDougall & Turkington 2004). Nevertheless, even in cases where apparent impacts on native richness occurred at low abundances of the focal alien species, the magnitude of the impact tended to increase and be maximal at higher abundances, suggesting that actions to limit the local abundance of alien weeds should nevertheless remain a priority to minimize their impact on native communities.

Putative impacts of alien species on native plant species richness have largely focused on changes in *α*-richness (Hulme *et al.* 2013). However, the few studies which have also assessed the response in *γ*-richness have found it to decrease more markedly than *α*-richness (Hulme & Bremner 2006; Fukami *et al.* 2013). Powell et al. (2011) propose that *γ*-richness would only be more markedly reduced than *α*-richness in communities where there was high spatial turnover in native species composition and alien species resulted in the loss of rare rather than common species. However, if native plant communities have low *α*-richness but high spatial turnover (β-diversity) then even if losses of native species occur at random this would result in the declines in *γ*-richness being greater than for *α*-richness. Such a scenario may explain why on Banks Peninsula the decrease in *γ*-richness was at least an order of magnitude greater than that observed for *α*-richness since the mean number of native species per plot was rarely more than 10 but the total pool of natives was over 240, thus providing much greater scope for declines in *γ*-richness. In contrast to the view that greater impacts on *γ*-richness should be uncommon (Powell *et al.* 2011), increasing impact at larger spatial scales appears to be a consistent finding among the few studies to date. This may reflect that other studies have also examined locations with high β-diversity (Hulme & Bremner 2006). Consistent with studies in North American grasslands (Martin & Wilsey 2015), our results provide further evidence that alien species can significantly reduce the spatial turnover in species richness and sizeable
apparent impacts of alien species on $\gamma$-richness may be fairly common in these ecosystems. It is therefore quite likely that most studies examining alien impacts on species richness have underestimated the larger scale consequences of alien species. This is of particular concern in grasslands that appear to be increasingly dominated by alien species worldwide (Seabloom et al. 2015).

Attempts to scale-up apparent impacts from plot to landscape by calculating the product of the per capita effect of an alien species, its local abundance and its geographic distribution (Parker et al. 1999; Thomsen et al. 2011; Barney et al. 2013) will not adequately capture changes in $\gamma$-richness. Recent efforts to include spatial heterogeneity of impact have also combined abundance-impact curves and abundance distributions to estimate the probability distribution of impacts across the landscape (Latzka et al. 2016). However these approaches may still not be enough, as only in the case where there is low spatial turnover in native species richness would $\gamma$-richness be a straightforward function of local per capita effects on $\alpha$-richness (Powell et al. 2011). Thus, important additional parameters required to scale-up per capita apparent impacts on $\alpha$-richness would be a measure of the plant community spatial turnover and the relative impact of the focal alien on rare versus common native species.

Managers face a challenging problem when prioritising species for management in the context of conserving native species richness across a landscape. Although many of the alien species may be valuable for livestock (Driscoll et al. 2014), several of them ($L. perenne$, $D. glomerata$, $H. lanatus$) are acknowledged as significant environmental weeds, while two others ($T. repens$, $A. odoratum$) are viewed as potential environmental weeds in New Zealand (Howell 2008). Depending on the criteria chosen for species selection, the target can differ quite considerably. For example, on Banks Peninsula, if the most widespread species were to be prioritised it would be $L. perenne$, while if the species that had the strongest local apparent effect on species richness was to be targeted this would be $A. odoratum$. Yet to maximise conservation of species...
At the landscape scale, the focus should be on *T. repens* since it had the largest apparent impact on \( \gamma \)-richness.

Neither species local dominance nor its distribution provide adequate information to prioritise management but these can often be the primary criteria for decision-making rather than quantitative evidence regarding impacts. Furthermore, national listings of invasive species status may provide inadequate criteria to rank species risks within a region, as illustrated by the fact that a recognized environmental weed such as *H. radicata* showed the only positive apparent impact on native \( \alpha \)-richness in our study area.

Given the considerable effort and budget expended in using herbicides against alien weeds in conservation grasslands (Wagner et al. 2016), the case needs to be made that quantitative data on impacts may be a cost-effective investment in ensuring management resources are targeted effectively (Pearson et al. 2016). If the goal is to limit impacts on native \( \gamma \)-richness on Banks Peninsula, then management of only nine plots dominated by *A. odoratum* may deliver equivalent native richness benefits as targeting 75 plots invaded by *D. glomerata*. Providing the evidence-base need not be expensive but would require sampling native richness along suitable gradients of target species abundance in order to identify potential abundance thresholds above which impacts become significant and assess the relative contributions of \( \alpha \)-richness and \( \beta \)-diversity to \( \gamma \)-richness. Armed with this information, managers may be empowered to make more informed decisions and target alien plant species more cost-effectively.

**Authors’ contributions**

Both authors jointly developed the ideas. MBV led the analysis and elaborated conceptual figures, while PEH obtained the funding and led the writing. Both authors contributed critically to the drafts and gave final approval for publication.
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Data accessibility

The datasets supporting this article are available for download from the Landcare Research Datastore (https://doi.org/10.25898/4DG9-F570). These data represent a subset of the original survey which is publicly available on the New Zealand National Vegetation Survey Databank (https://nvs.landcareresearch.co.nz/Data/DatasetDetails/2424/13248).

References


Table 1. Generalized linear models of native α-richness declines for the eight alien species showing significant apparent impacts. Five environmental co-variates known to influence native α-richness were included (Elevation, Slope, Northness, Alien α-richness, Year of survey) before adding the abundance of the focal alien species as a final independent variable. When a species abundance contributed significantly to the GLM (ΔAIC > 2), we tested for the existence of a decreasing trend starting at a critical abundance (Acrit; cf. Methods). Only species contributing significantly to the GLM and showing a critical abundance were considered to have a significant apparent impact. Percent deviance (%dev) explained by the full model and by each additional variable are calculated as (total.dev – residual.dev)/total.dev. All GLMs are built with a Poisson link function, and coefficients for co-variables are transformed as $\exp(\text{GLM.coef}) \times 100$ to represent % variation in native richness per unit increase.

<table>
<thead>
<tr>
<th>Focal alien species</th>
<th>Full model df</th>
<th>Elevation %dev</th>
<th>Slope %dev</th>
<th>Northness %dev</th>
<th>Alien richness %dev</th>
<th>Year %dev</th>
<th>Focal abundance %dev</th>
<th>ΔAIC</th>
<th>Acrit</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Achillea millefolium</em> L.</td>
<td>157 34.0%</td>
<td>0.2</td>
<td>7.7%</td>
<td>3.3</td>
<td>3.3</td>
<td>0.2</td>
<td>0.2%</td>
<td>12.1%</td>
<td>59.2</td>
</tr>
<tr>
<td><em>Holcus lanatus</em> L.</td>
<td>492 27.9%</td>
<td>0.2</td>
<td>13.0%</td>
<td>1.7</td>
<td>6.4%</td>
<td>2.1</td>
<td>0.2%</td>
<td>1.4%</td>
<td>25.5</td>
</tr>
<tr>
<td><em>Lolium perenne</em> L.</td>
<td>511 25.9%</td>
<td>0.1</td>
<td>3.9%</td>
<td>1.6</td>
<td>8.3%</td>
<td>4.5</td>
<td>0.0%</td>
<td>5.6%</td>
<td>101</td>
</tr>
<tr>
<td><em>Trifolium repens</em> L.</td>
<td>511 34.1%</td>
<td>0.2</td>
<td>15.5%</td>
<td>1.5</td>
<td>6.7%</td>
<td>2.1</td>
<td>0.8%</td>
<td>3.6%</td>
<td>86.2</td>
</tr>
<tr>
<td><em>Cynosurus cristatus</em> L.</td>
<td>429 27.4%</td>
<td>0.2</td>
<td>11.5%</td>
<td>1.7</td>
<td>6.0%</td>
<td>2.9</td>
<td>0.0%</td>
<td>2.1%</td>
<td>32.6</td>
</tr>
<tr>
<td><em>Dactylis glomerata</em> L.</td>
<td>496 28.8%</td>
<td>0.1</td>
<td>10.2%</td>
<td>2.0</td>
<td>7.9%</td>
<td>2.1</td>
<td>0.9%</td>
<td>3.3%</td>
<td>66</td>
</tr>
<tr>
<td><em>Trifolium striatum</em> L.</td>
<td>173 20.3%</td>
<td>0.0</td>
<td>2.7%</td>
<td>2.3</td>
<td>11.2%</td>
<td>2.3</td>
<td>0.0%</td>
<td>2.6%</td>
<td>5.8</td>
</tr>
<tr>
<td><em>Anthoxanthum odoratum</em> L.</td>
<td>484 30.5%</td>
<td>0.2</td>
<td>14.8%</td>
<td>1.8</td>
<td>5.9%</td>
<td>2.1</td>
<td>0.8%</td>
<td>1.8%</td>
<td>33.7</td>
</tr>
</tbody>
</table>
Table 2. Change in native $\alpha$- and $\gamma$-richness and $\beta$-diversity above critical abundances for the eight alien species with significant apparent impacts on native $\alpha$-richness. Critical abundance ($A_{\text{crit}}$) corresponds to the lowest abundance class of a given focal alien species at which a decrease in native $\alpha$-richness is detected. The frequency of species across the landscape is represented as the number of plots where the focal alien species is either present, above (or equal) to $A_{\text{crit}}$, or dominant. Mean (± SD) $\alpha$- and total $\gamma$-richness are calculated both below and above $A_{\text{crit}}$. Decrease above $A_{\text{crit}}$ in mean $\alpha$-richness is expressed in number of species ($\Delta \alpha$) and percent decrease ($%\Delta \alpha$) in richness. Corrected differences in $\gamma$-richness above critical abundance ($\Delta \gamma_c$) were calculated using a null model to account for unequal sample sizes (i.e. number of plots in each abundance class). Decrease in $\beta$-diversity above $A_{\text{crit}}$ ($\Delta \beta_c$) is calculated as the difference in multi-site Simpson index of species turnover above vs. below critical abundance, standardized against the same null model. Significant (P<0.05) decreases compared to the null expectation are indicated in bold.

<table>
<thead>
<tr>
<th>Focal alien species</th>
<th>$A_{\text{crit}}$</th>
<th>Frequency in landscape</th>
<th>$\alpha$-richness</th>
<th>$\gamma$-richness</th>
<th>$\beta$-diversity</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Presence</td>
<td>$\geq A_{\text{crit}}$</td>
<td>Dominant</td>
<td>$\alpha &lt; A_{\text{crit}}$</td>
</tr>
<tr>
<td>Achillea millefolium L.</td>
<td>2 occasional</td>
<td>166</td>
<td>120</td>
<td>0</td>
<td>4.1 ± 3.4</td>
</tr>
<tr>
<td>Holcus lanatus L.</td>
<td>3 frequent</td>
<td>502</td>
<td>341</td>
<td>3</td>
<td>5.3 ± 5.6</td>
</tr>
<tr>
<td>Lolium perenne L.</td>
<td>3 frequent</td>
<td>521</td>
<td>352</td>
<td>23</td>
<td>5.6 ± 4.4</td>
</tr>
<tr>
<td>Trifolium repens L.</td>
<td>3 frequent</td>
<td>520</td>
<td>429</td>
<td>0</td>
<td>7.1 ± 6.9</td>
</tr>
<tr>
<td>Cynosurus cristatus L.</td>
<td>4 common</td>
<td>439</td>
<td>125</td>
<td>3</td>
<td>5.5 ± 5.3</td>
</tr>
<tr>
<td>Dactylis glomerata L.</td>
<td>4 common</td>
<td>506</td>
<td>75</td>
<td>11</td>
<td>5.5 ± 5.2</td>
</tr>
<tr>
<td>Trifolium striatum L.</td>
<td>4 common</td>
<td>182</td>
<td>21</td>
<td>0</td>
<td>5.7 ± 4.3</td>
</tr>
<tr>
<td>Anthoxanthum odoratum L.</td>
<td>6 dominant</td>
<td>494</td>
<td>9</td>
<td>9</td>
<td>5.6 ± 5.4</td>
</tr>
</tbody>
</table>
Figure 1. Scaling-up apparent impact of alien plants on native richness from the local community to the landscape using the concept of critical abundances. A) At the local community scale, apparent impact is detected \((d)\) at a certain critical abundance \((A_i)\) for each focal alien species. Different impact curves yield different critical abundances; B) Scaling-up from apparent local impact on native richness (loss in \(\alpha\)-richness above critical abundance) to loss of native species at the landscape scale (loss in \(\gamma\)-richness) remains a challenge. If native species were always lost randomly from local communities, we could expect a positive relationship (dotted black line) between losses in \(\alpha\)- and \(\gamma\)-richness for a given set of initial communities. However, the commonness or rarity of the species lost, along with the accompanying changes in \(\beta\)-diversity, will also influence apparent impact size at the landscape scale, and observed values are likely to fall outside of this line. Systematic local exclusion of infrequent species and/or loss of \(\beta\)-diversity above critical abundances will lead to a higher decrease in \(\gamma\)-richness than expected (observed values above the dotted line). On the other hand, high levels of \(\beta\)-diversity and/or loss of common species may buffer impacts at larger spatial scales (values below the dotted line).
Figure 2. Frequency of apparent impacts on native $\alpha$-richness across abundance classes for 47 focal alien species. Light grey bars represent the total number of focal alien species observed at a given abundance class. Dark grey bars correspond to species associated to a significant decrease in native richness above an initial critical abundance, i.e. apparent impact. Black bars represent species for which that abundance class is the critical abundance. Most focal alien species did not show any negative association with native $\alpha$-richness. Eight out of 47 species were found to be associated with declines in native plant species richness, with critical abundances occurring mostly when the species were at low to intermediate abundances. Note that not all 47 focal alien species reach the highest abundance class, and that our method could not test for declines in native plant species richness at the lowest abundance class (Rare) since it served as the reference.
Figure 3. Decrease in native $\alpha$-richness with increasing abundance of the 8 focal alien species associated with significant declines in native plant species richness. Effect sizes (ES) are calculated from the Poisson regression coefficients (ES = exp(coef) x 100 – 100) and express the percent change in mean native richness compared to where the focal alien species was Rare. The dotted line represents no change compared to Rare, i.e. ES = 0. Error bars represent the 95% bootstrap confidence intervals and determine significantly negative coefficients (black filled circles). Arrows identify the critical abundance at which $\alpha$-richness starts to decrease consistently (cf. definition in Methods). For each focal alien species, points are represented only if sample sizes per class were at least 5 plots.
Figure 4. Variation in native γ-richness with increasing abundance of the 8 focal alien species associated with significant declines in native plant species richness. For each abundance class, γ richness is the total number of species present across all plots where the focal alien species was recorded at a given abundance. Effect size for γ-richness is defined as the difference in number of species between the observed γ richness and its null expectation based on where the focal species is rare (null model 1). Filled symbols indicate a significantly different value than expected, i.e. outside the 95% confidence intervals of the null model controlling for sample size (grey area). The grey arrow points to the critical abundance value detected for α-richness (see Figure 3).
Figure 5. Loss in native γ-richness with a) increasing mean change in native α-richness and b) prevalence of plots above critical abundances of the 8 focal alien species associated with significant declines in native plant species richness. Differences in γ-richness (Δγ-richness) correspond to the difference in total number of unique native species above vs. below critical abundances, corrected for sample size (null model 2). Differences in native α-richness (Δα-richness) correspond to the difference in mean α-richness of plots above vs. below the critical abundance class. More negative values indicate greater losses in richness. Loss in native γ-richness was not correlated with mean loss in native α-richness above critical abundances. However, it was correlated with the number of plots where the focal alien species was recorded above critical abundances. A regression line was added to visualize the decreasing trend, although we tested for rank correlation. Species names are abbreviated by the three first letters of genus and species. Statistics for Spearman’s rank correlation are indicated above the panels (ns: $P > 0.05$; *: $P < 0.05$).