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Interacting effects of management and environmental variability at multiple scales on invasive species distributions

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Summary

1. The distribution and abundance of invasive species can be driven by both environmental variables and land management decisions. However, understanding these relationships can be complicated by interactions between management actions and environmental variability, and differences in scale among these variables. The resulting 'context-dependence' of management actions may be well-appreciated by ecologists and land managers, but can frustrate attempts to apply general management principles.

2. In this study, we quantify the effects of land management and environmental variability at different scales on the occurrence and abundance of *Hieracium pilosella*, a major agricultural weed in New Zealand. We used a hierarchical study design and analysis to capture relevant scales of variation in management actions and environmental heterogeneity, and test hypotheses about how these factors interact.

3. We show that fertilizing and grazing interact with environmental gradients at the scale of management application (farm paddocks) to influence the establishment and local abundance of *H. pilosella*.

4. We further show that *H. pilosella*'s relationships with fine-scale abiotic and biotic factors are consistent with expected mechanisms driven by larger-scale management actions. Using data on occurrence and local abundance, we tease apart which factors are important to establishment and subsequent local spread.

5. *Synthesis and applications*. A major challenge for environmental scientists is to predict how invasive species may respond to ongoing landscape modifications and environmental change. This effort will require approaches to study design and analysis that can accommodate complexities such as interacting management and environmental variables at different scales. Management actions will be more likely to succeed when they explicitly account for variation in environmental context.

Key-words: *Hieracium pilosella*, hierarchical Bayesian, invasive species distributions, management–environment interactions, scale

Introduction

Invasive species pose significant threats to biodiversity (Sala *et al.* 2000; Bax *et al.* 2003), ecosystem function (Gomez-Aparicio & Canham 2008) and economic activity (Pimentel *et al.* 2001), lending urgency to the need to understand the factors that determine their distribution and abundance. Although many studies have identified a range of environmental and management factors that contribute to the establishment and spread of invasive species (Higgins, Richardson & Cowling 1996; Lambdon *et al.* 2008; McDonald, Motzkin & Foster 2008), there is a need to integrate this understanding into predictions of how invasive species will respond to ongoing environmental and land use change.

A major challenge is that land management and environmental factors often interact, such that the same management action may yield different results under different environmental conditions. Such interactions may explain the sometimes conflicting results derived from studies on the same invasive species. For example, the response of exotic species richness to

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fire and grazing has been shown to differ on serpentine vs. non-serpentine soils (Harrison, Inouye & Safford 2003). Controlled disturbances such as fire have been observed to both eradicate and facilitate the spread of invasive plant species depending on underlying environmental and climatic conditions (Keeley & McGinnis 2007), and elevated nutrient levels may both promote (Davis, Grime & Thompson 2000; Brooks 2003; Howard *et al.* 2004; Perry, Galatowitsch & Rosen 2004) and reduce invasion risk (Burke & Grime 1996; Sandler, Alpert & Shumaker 2007) in different situations. The resulting 'context-dependence' of management actions renders development and application of general management principles difficult.

A second challenge to teasing apart the effects of management and environmental factors on invasion patterns is to combine information from multiple spatial scales (Beever, Huso & Pyke 2006; Golubski, Gross & Mittelbach 2008). Species distributions are influenced by both large-scale environmental gradients and local environmental heterogeneity. For example, invasive plants often respond to large-scale gradients in soil nutrient availability (Gelbard & Harrison 2003; Harrison *et al.* 2003; Beever *et al.* 2006) and to finer-scale variability due to local topography or existing vegetation (Bartuszevige, Gorchov & Raab 2006). Management actions are overlaid on this environmental variability, with management units (e.g. a farm paddock or reserve) often having grain sizes and boundaries that do not coincide with the underlying environmental conditions. This 'scale asymmetry' will often lead to spatially variable outcomes of a management action. Applying fertilizer across a paddock, for example, may produce variable responses due to local heterogeneity in soil moisture availability. The effects of management actions may thus depend on both the broader-scale environmental context and local environmental heterogeneity. Therefore, understanding the interactions between management and environmental factors and their combined influence on species distributions will require explicit attention to the scales at which various underlying processes operate.

In this study, we address these challenges by integrating environmental and management data from different scales to model the distribution and abundance of *Hieracium pilosella*, a major agricultural weed in New Zealand. We use hierarchical models that reflect the nested study design and explicitly model interactions at different scales.

We show how a link between processes at different scales (Fig. 1) can be developed by identifying the likely fine-scale mechanisms by which larger-scale management actions affect species distributions.

Case study: *Hieracium pilosella* invasion in southern New Zealand tussock grasslands

Hieracium pilosella (Asteraceae) is one of four hawkweed species that have increased dramatically in abundance across New Zealand's South Island tussock grasslands over the last four decades. *Hierarcium pilosella* is capable of long-distance dispersal via wind-borne seed and, once established at a site, can spread via clonal growth to become locally abundant (Bishop & Davy 1994). The resulting extensive low-growing mats can exclude other species and are unproductive for livestock grazing, thus threatening both the pastoral industry and conservation values across more than 500 000 ha of the South Island grasslands (Hunter 1991).

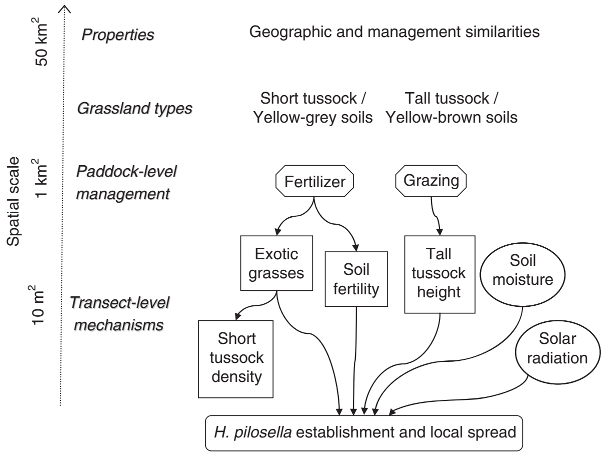

Fig. 1. Conceptual diagram of the environmental and management variables at different scales affecting *Hieracium pilosella* distribution. Management actions are carried out at the paddock level, which influence some of the abiotic and biotic variables at the transect level. Variables inside the squares are hypothesized to be directly affected by management actions, whereas the circles – soil moisture and solar radiation – are more strongly linked to underlying topographic variability. These mechanisms are hypothesized to be context-dependent and related to the grassland type the paddock is located on. Properties are also included in the models as a unit of likely covariance of such factors as the timing of management applications and unknown geographic variation. While additional dependencies are likely to exist among these variables (e.g. soil moisture is likely to affect grass cover), we have highlighted the primary pathways thought to affect *H. pilosella*.

The processes that determine the initial establishment of *H. pilosella* at a site and its subsequent spread are not well understood, and the role of management has been strongly debated. Studies of how livestock grazing and fertilizer application affect *H. pilosella* establishment and spread have produced conflicting results. For example, fertilizer application has been shown to strongly limit *H. pilosella* abundance at some sites by increasing the dominance of introduced grasses leading to competitive exclusion (Scott, Robertson & Archie 1990). In contrast, *H. pilosella* has also been shown to respond more vigorously to increased nutrient supply than a dominant native grass, *Festuca novae-zealandiae*, suggesting fertilizer may provide *H. pilosella* with a competitive advantage that facilitates its spread (Fan & Harris 1996). Livestock grazing has also shown varying effects on *H. pilosella* invasion. There is some evidence that grazing facilitates *H. pilosella* establishment by opening up the vegetation cover (Treskonova 1991), but elsewhere long-term experimental livestock exclusions have shown little difference in invasion between sites with and without livestock grazing (Rose, Platt & Frampton 1995; Duncan, Webster & Jensen 2001; Meurk *et al.* 2002). These mixed results suggest that *H. pilosella* invasion depends on both management and environmental context (Rose *et al.* 1998).

The dominant large-scale environmental gradient in the study region parallels a shift from native short-tussock (*Festuca novae-zealandiae*) or exotic grass dominated communities at lower elevation (below *c*. 800 m) to native tall-tussock (*Chionochloa* spp.) grasslands at higher elevation (up to c. 1100 m). Tall-tussocks are large and can form a dense closed canopy > 1 m tall, while short-tussocks are smaller (< 0·5 m tall) and form a more open grassland with extensive inter-tussock spaces. The shift from predominantly short- to tall-tussock grassland with increasing elevation coincides with the shift from more fertile yellow-grey to less fertile yellow-brown soils, greater rainfall, and often changes in pastoral management practices. Higher-elevation, tall-tussock grasslands are generally reserved for summer sheep grazing at low stocking rates, and have relatively low inputs of fertilizer and oversowing of pasture species. Lower elevation sites are typically open short-tussock grasslands dominated by *Festuca novae-zealandiae*, but fertilizer application and oversowing of pasture species can lead to exotic grass dominated communities that support higher stocking rates.

We tested the hypothesis that the effects of management (livestock grazing and pasture fertilization) on the establishment and spread of *H. pilosella* varied along this major vegetation/environmental gradient, and that this could account for the often conflicting reports about the factors that favour *H. pilosella* invasion. Specifically, higher elevation tall-tussock grasslands with a dense, closed canopy may resist invasion by *H. pilosella*, but we hypothesized that disturbance by livestock grazing could open up this vegetation and facilitate *H. pilosella* establishment and spread. In contrast, livestock grazing may have little impact on the establishment and spread of *H. pilosella* in lower elevation short-tussock grasslands because the open structure of these grasslands already facilitates invasion (Rose, Suisted & Frampton 2004). Similarly, fertilizer application on lower-elevation yellow-grey soils, together with the oversowing of exotic grasses, can increase the competitive dominance of exotic grasses, thereby excluding *H. pilosella* (Scott *et al.* 1990), but may not lead to the same response on higher elevation, naturally less-fertile yellow brown soils.

Materials and methods

FIELD SAMPLING AND DATA COLLECTION

Our study was carried out on six adjacent farming properties along the Knobby Range in the Roxburgh district, South Island New Zealand (*c*. S45°30′, E169°20′), chosen for unique access to information on both recent management and environmental factors. The paddocks on these properties were managed differently and ranged in elevation from 500 to 1100 m. The study area is semi-arid with a mean daily temperature of 4·5 °C in winter (July) and 16·5 °C in summer (January), and mean annual precipitation of 450–500 mm year^{-1} at lower elevations. Rainfall is greater at higher elevations, and annual rainfall variability is high with the area subject to occasional droughts.

Field sampling was carried out in the summer of 1992. The paddocks on the six properties were first stratified into tall and short-tussock grassland groups, which are readily distinguished in the field by the dominant tussock species. A series of transects were established at the intersections of a 1000 × 1000 m map grid laid over the tall-tussock paddocks, and a 500 × 500 m map grid laid over the short-tussock paddocks, with the different grid size due to paddock areas being much larger in tall-tussock grassland. Using this systematic sampling scheme, 129 transects were established across 42 paddocks on the six properties.

Each transect was 10 m long and the abundance of *H. pilosella* was measured by point-intersect sampling at 10 cm intervals along each transect (100 samples per transect), recording each point-intersect as either *H. pilosella*, exotic grass, herb, woody plant, native tussock, litter, bare ground or rock. The number of tall (*Chionochloa* sp.) and short (*Festuca novae-zelandiae*) tussocks in a 1 m strip alongside each transect were also counted. The height of the tallest *Chionochloa* and *Festuca* individual in each 1 m^2 block along the transect was also recorded. Adjacent to each transect a soil pit was dug to bedrock and the depth of the A and B soil horizons were measured. Available water capacity was determined from the soil type and depth of soil horizons, and potential solar radiation was calculated using the slope, aspect and latitude for each plot. Ten soil cores (7·5 cm depth) were taken at 1 m intervals along each transect. These were bulked and then analysed for pH, percentage organic C and chemical composition (Ca, Na, S, P, Mg, K). We then used principal components analysis (PCA) to reduce the dimensionality of these soil characteristics, using the first two axes to describe the major aspects of variation (see Results).

Management data for each paddock were obtained directly from the property owners. We focussed on stocking rate and fertilizer application because these were hypothesized to affect *H. pilosella* abundance, and because other management actions, such as burning and rabbit control, were not known in sufficient detail at the paddock or often property level. We calculated the average annual stocking rate for each paddock (in ewe equivalents per hectare per year) based on records of stock numbers over the previous 5 years. Because the rates of fertilizer application to amended paddocks were roughly similar, we treated fertilizer application to each paddock as a binary yes/no variable. Fertilizer was applied to increase levels of phosphate and sulphur in the soil, and was often accompanied by oversowing with exotic grass and legume species.

STATISTICAL MODELS

We structured the statistical analysis to account for the nested study design (transects were nested within paddocks, which were nested within properties; Fig. 1) and to address our key question: how does the effect of management on *H. pilosella* abundance vary across the large scale gradient from short to tall-tussock grassland?

We constructed two sets of hierarchical generalized linear models, each of which modelled the abundance of *H. pilosella* on the 129 transects. The first set of models (paddock-level models) tested the effect of management variables on *H. pilosella* abundance, and whether those effects varied along the environmental gradient, by including paddock-level management variables (stocking rate and fertilizer), grassland type (short or tall) and their interactions as main effects, and paddocks nested within properties as random effects. Significant main effect interactions would indicate that a management variable had a different effect on *H. pilosella* abundance in short compared with tall-tussock grassland. The second set of models (transect-level models) were designed to test the mechanisms by which paddock-level management actions were thought to change local site conditions, and in turn affect *H. pilosella* abundance. We included in these models transect-level variables that should be affected by paddock-level management and in turn should affect *H. pilosella* abundance. Thus, in short-tussock grassland, fertilizer application at a paddock level is hypothesized to increase the local dominance of exotic grasses, which in turn exclude *H. pilosella*. Across fertilized and unfertilized transects, we should therefore see a negative relationship between exotic grass cover and *H. pilosella* abundance. We included the following variables hypothesized to be directly affected by management actions: the height of tall-tussocks (measured as the average height of the tallest tussock in each 1 m^2 section of the transect) and density of short-tussocks, aspects of soil fertility related to fertilizer application (which is primarily the addition of S and P), and the abundance of exotic grasses. Tall-tussock height was included instead of density because height better reflected the openness thought to be critical for affecting *H. pilosella* establishment. Again, we included interaction terms to test whether the effect of these variables on *H. pilosella* abundance differed between short- and tall-tussock grassland. We also included soil moisture availability and potential solar radiation as additional covariates, and paddocks nested within properties as random effects.

Hieracium pilosella was absent from many transects, leading to highly skewed abundance data that were not amenable to transformation. To overcome this problem of zero-inflation we modelled the occurrence of *H. pilosella* as a two-step process (Fletcher, MacKenzie & Villouta 2005; Martin *et al.* 2005): we modelled separately the probability of *H. pilosella* presence on a transect, and its abundance on those transects where present. This also allowed us to ask whether different factors might underlie establishment (probability of presence) vs. local spread (abundance on a transect). Presence was modelled as a Bernoulli process with a logit link function. Abundance-when-present (henceforth simply abundance) was logit-transformed because the point-intercept method yielded a proportion cover instead of true abundance. This transformed abundance measure was modelled as a Gaussian process with an identity link function.

All models were fit in a Bayesian framework using non-informative, normal prior probability distributions for each of the coefficients, and broad uniform distributions for standard deviations, following Gelman (2006). Models were fit using Markov chain Monte Carlo (MCMC) methods using OpenBUGs (Thomas *et al.* 2006) called through the BRugs package of R version 2.7.1 (R Development Core Team 2008). Model convergence was assessed visually for three simultaneously running Markov chains of 20 000 iterations, following a 5000-iteration burn-in. Significance of variables was calculated as the cumulative probability that a posterior probability distribution was above or below zero.

In addition to determining *whether* past management and environmental factors had affected *H. pilosella* distribution and abundance on these six properties, we wanted to predict how *H. pilosella* was likely to respond to management across the landscape more generally. While we may be able to identify factors associated with variation in *H. pilosella* abundance across the properties we studied, predicting the likely response to management on different properties in the same environment introduces an additional level of uncertainty. To make these predictions, we used the MCMC routines to make predictions of the probability of occurrence and abundance of *H. pilosella* under different combinations of management and environmental conditions, on a hypothetical 'new' transect in a new paddock and property, conditional on all the estimated relationships and uncertainties in the model (Gelman & Hill 2007). We used the median value from the resulting predictive envelope as our best estimate of the response of *H. pilosella* to a particular combination of management actions, and used the 95% quantiles to characterize all of the uncertainty, including paddock and property-level variability. Further detail on models and model code can be found in Appendices S1 and S2.

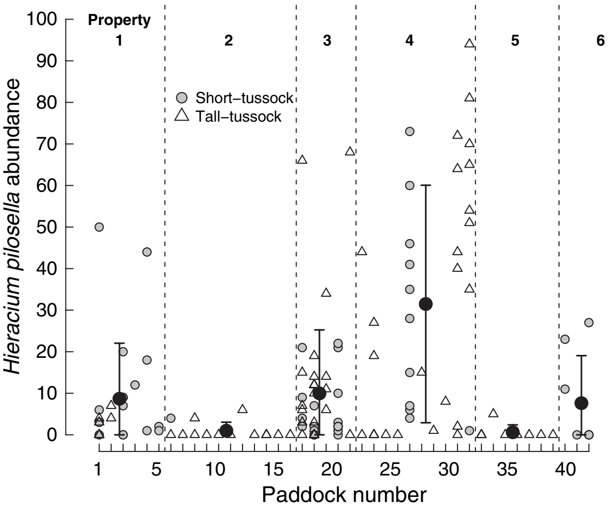

Fig. 2. *Hieracium pilosella* abundance on 129 transects, which were nested within 42 paddocks (shown along the *x*-axis) and six properties (delimited by the dashed lines and numbered). Solid black dots show the mean *H. pilosella* abundance and the standard deviation within each property. Abundance is in units of number of points (out of 100) at which *H. pilosella* was found along a 10 m transect.

Results

Hieracium pilosella abundance was highly variable across transects, paddocks and properties (Fig. 2). *Hieracium pilosella* was more widely distributed in tall-tussock grassland (present on 78% of transects compared with 55% in short-tussock). However, when present in short-tussock grassland, it tended to have higher cover (average cover of 27·3%, SD = 26·8, compared with 15·6%, SD = 17·7 in tall-tussock).

The first axis from the principal components analysis was interpreted as the dominant natural fertility gradient across the study area (Table 1; correlated with Ca, Mg, pH, K and P). This gradient is related to elevation and the shift from higher fertility short-tussock to lower fertility tall-tussock grassland. The second axis was interpreted as a response to fertilizer addition because phosphorous and sulphur are the primary nutrients added with fertilizer application (Table 1; correlated with C, P, S and K). Fertilized transects had significantly higher scores on this axis than those in unfertilized transects (ANOVA, $F = 20{\cdot}77$, 127 d.f., $R^2 = 0{\cdot}13$, $P < 0{\cdot}001$).

Table 1. Factor loadings for the first two principal components or 'fertility axes'

Variable	Axis 1	Axis 2
Ca	0·52	0·001
Mg	0·513	−0·005
pH	0·486	−0·251
K	0·371	0·368
P	0·23	0·523
S	−0·162	0·413
Organic C	−0·114	0·587
Na	−0·012	−0·115
Cumulative variance explained	0·41	0·62

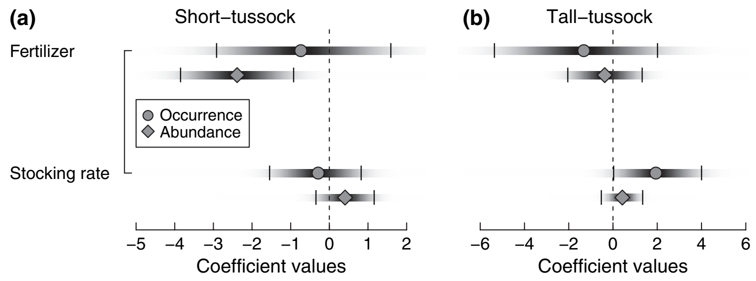

Fig. 3. Estimated effects of management on *Hieracium pilosella* occurrence and abundance on the two different grassland types. Points represent the mean estimates for *H. pilosella* presence (circles) and abundance (diamonds), bars are shaded in proportion to the posterior probability density [using denstrip package in R (Jackson 2008)], and vertical lines mark the 95% credible intervals.

PADDOCK-LEVEL MODELS

There were significant management by grassland-type interactions in the paddock-level models for both occurrence and abundance (Fig. 3). When it was present in short-tussock grassland, *H. pilosella* was found at significantly lower abundance in fertilized paddocks, but abundance did not differ significantly between fertilized and unfertilized paddocks in tall-tussock grassland. In tall-tussock grassland, the probability of *H. pilosella* occurrence increased with higher stocking rates, but this was not the case in short-tussock grassland. The remaining management by grassland-type effects had credible intervals that heavily overlapped zero.

TRANSECT-LEVEL MODELS

There were significant interactions between the transect-level variables and grassland-type. In short-tussock grassland, the presence of *H. pilosella* was less likely on transects with high exotic grass cover and high fertility axis 2 scores, and more likely on transects with a greater density of short-tussocks and high solar radiation (Fig. 4). In contrast, presence of *H. pilosella* in tall-tussock grassland was less likely on transects with higher tussock height. Presence in tall-tussock communities was also more likely on transects with higher natural fertility (fertility axis 1). The abundance of *H. pilosella* in short-tussock grasslands was lower with increased exotic grass density and higher solar radiation, and slightly reduced in sites with high short tussock density. In tall-tussock grassland, on the other hand, abundance was positively associated with greater fertility axis 2 scores and higher solar radiation.

PREDICTIONS

Predictions of the likely presence and abundance of *H. pilosella* under different management actions on a transect located on a new property follow the trends described above, but with wide confidence intervals (Fig. 5). For example, the predicted *H. pilosella* density in both fertilized and unfertilized tall-tussock sites increased with stocking rate, but were substantially lower than unfertilized short-tussock sites (Fig 5). These wide confidence intervals reflect the variability in *H. pilosella* abundance at all scales in this study: among transects within paddocks, among paddocks within properties, and among

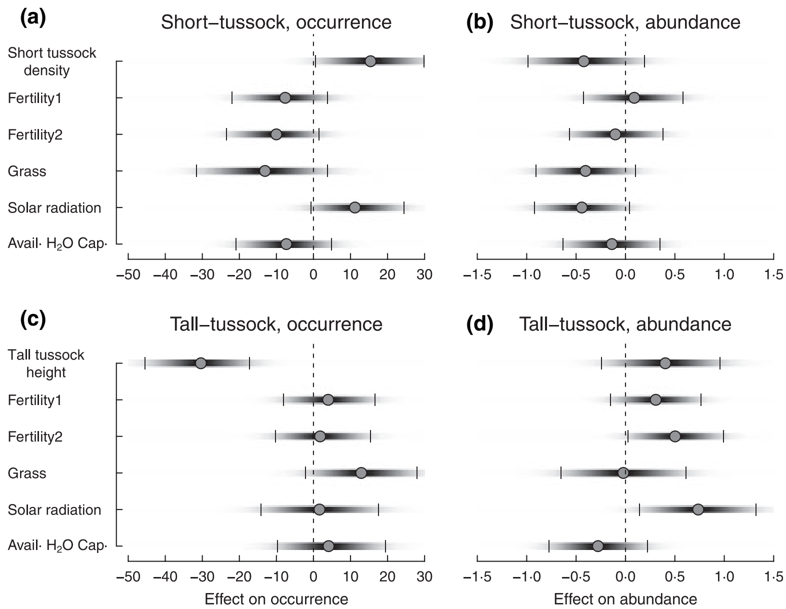

Fig. 4. Estimated effects of transect-level abiotic and biotic variability on *Hieracium pilosella* occurrence and abundance in short-tussock (a, b) and tall-tussock (c, d) grasslands. Points represent the mean estimates, bars are shaded in proportion to the posterior probability density [using denstrip package in R (Jackson 2008)], and vertical lines mark the 95% credible intervals. The same covariates were evaluated for each grassland except for short-tussock density and tall-tussock height.

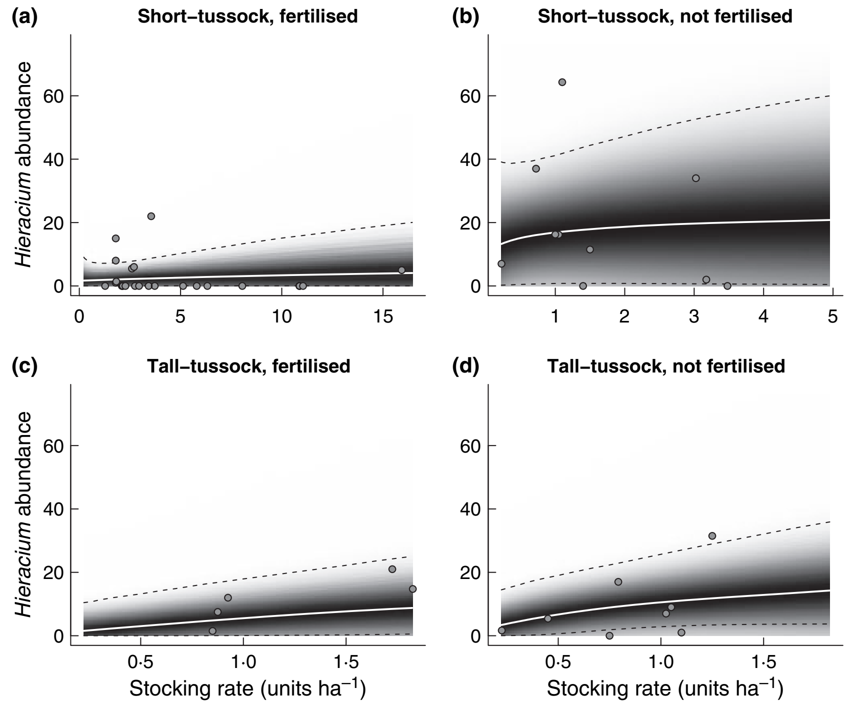

Fig. 5. Predicted abundance of *Hieracium pilosella* per 10 m^2 transect given different management decisions in different grassland communities, calculated as the product of the probability of occurrence and abundance-when-present. White lines show the mean predicted values, dashed lines the 95% credible intervals, and the shading is in proportion to the posterior densities. Points represent paddock level averages. Predictions and data for short-tussock sites are plotted on the top row, and tall-tussock sites are on the bottom. Predictions are made for both fertilized sites (on the left) and not fertilized (on the right), and are only made over the range of stocking rates (*x*-axes) used in practice by property managers in the different grassland types. Uncertainty of predictions reflects variability among transects as well as paddocks.

properties (Fig. 2). Further uncertainty probably resulted from within-transect variability in soil conditions not captured by the bulked soil samples.

Discussion

Species invasions unfold across complex landscapes, characterized by mixed land management and multiple layers of environmental variability. Although it may be intuitive that the outcome of specific management actions will depend on environmental variables, these interactions have not been well-quantified. One reason that these interactions can be difficult to incorporate into predictions of invasive species distributions is that processes often operate at different scales (Collingham *et al.* 2000; Brown, Spector & Wu 2008). In this study, we used a hierarchical study design and analysis to address this challenge for understanding the invasion of *Hieracium pilosella* in New Zealand tussock grasslands.

This system provided a useful case study because previous studies have reached conflicting conclusions regarding the role that management plays in facilitating the establishment and spread of *H. pilosella* (Treskonova 1991; Rose *et al.* 1998). Our results help reconcile differences among previous studies by demonstrating that the distribution of *H. pilosella* is linked to management actions, but that the outcome of management actions depends on the environmental context. In short-tussock grassland, the level of livestock grazing had no clear effect on the presence or abundance of *H. pilosella*, but fertilizer application was associated with reduced abundance. In tall-tussock grassland, higher levels of livestock grazing were associated with a higher probability of *H. pilosella* presence, but fertilizer application had no clear effect on presence or abundance.

Although under-explored for invasive species, the importance of this type of management–environment interaction has recently been highlighted for native species and ecosystems (Whittingham *et al.* 2007; Marini *et al.* 2008; McAlpine *et al.* 2008; Chapman *et al.* 2009). For example, McAlpine *et al.* (2008) also used hierarchical models to ask whether koalas, *Phascolarctos cinereus*, respond differently to fragmentation across regions. They showed that the koala's relationship to some key land management decisions, such as forest patch size, differed across regions because of variation in edaphic and land-use factors. On the other hand, responses to landscape-level habitat context and local occurrence of preferred host trees remained similar across different regions. Thus, species' responses to some variables may be context-dependent, whereas responses to others may remain more transferable.

INTERACTIONS AND SCALE

For many invasive species, interactions between land management and environmental variability may be challenging to understand because of the complicating effect of scale:

management decisions are often applied at scales that differ from the underlying environmental variability. Therefore, the results of management actions may commonly be constrained by larger geographical gradients (for example climate, soils, vegetation, etc.), and be non-uniform within management units because of local environmental and biotic heterogeneity (Shea *et al*. 2005; Pauchard & Shea 2006). These complex interactions across scales may help to explain some of the 'context-dependence' that can occur in applying management actions (Liancourt, Viard-Cretat & Michalet 2009).

The hierarchical analysis in this study helped to clarify these interactions. By first considering responses of *H. pilosella* to paddock-level management variables, and then relationships with transect-level variables hypothesized to be affected by paddock-level management, we could explore the mechanisms by which management affects local site conditions, and in turn affects *H. pilosella* abundance.

Our findings were consistent with previous hypotheses regarding factors thought to limit the establishment and spread of *H. pilosella*. In short-tussock grassland, adding fertilizer increases soil concentrations of P and S (Scott 1993), increases the cover of exotic grasses and quantities of soil C (McIntosh *et al*. 1999), and reduces the density of short-tussocks because these become more palatable to livestock. At the transect level, all of these variables were associated with lower abundance of *H. pilosella*, and our results are consistent with the hypothesis that in short-tussock grassland fertilizer input can lead to local dominance by exotic grasses and competitive exclusion of *H. pilosella* (Scott *et al*. 1990). In contrast, *H. pilosella* abundance was not significantly related to fertilizer application or exotic grass cover in tall-tussock grassland. On these less-fertile soils at higher elevation exotic grasses do not respond vigorously to fertilizer addition because of lower base fertility levels and cooler temperatures. Consequently, fertilizer addition does not result in a dense enough sward of exotic grasses to competitively exclude *H. pilosella*. Instead, higher abundance of *H. pilosella* was associated with higher fertility, implying that fertilizer application in tall-tussock grassland may facilitate invasion (Fan & Harris 1996).

The mechanisms behind contrasting effects of grazing were also clarified by these models. In tall-tussock grassland, *H. pilosella* abundance was positively associated with high stocking rates and low tussock height, consistent with the hypothesis that the establishment and spread of *H. pilosella* is facilitated by the opening up of dense stands of tall-tussock that otherwise have some resistance to invasion. Unfertilized short-tussock grasslands, in contrast, have a more open structure without a closed tussock canopy even in the absence of grazing. This open structure may make short-tussock grasslands inherently susceptible to invasion by *H. pilosella* (Rose & Frampton 1999, 2007) regardless of the level of livestock grazing.

IMPLICATIONS FOR MANAGING INVASIVE SPECIES

Several broad implications for the management of invasive species emerge from this study. First, the success of different management strategies may depend on the environmental context. In this system, widespread reductions in stocking rates are unlikely to limit invasion by *H. pilosella* in short-tussock grassland. Indeed, a replicated 10-year livestock exclusion study showed no difference in *H. pilosella* abundance between ungrazed and grazed short-tussock grassland sites (Meurk *et al*. 2002). It appears possible to reduce the abundance of *H. pilosella* by applying fertilizer, but only in situations where fertilizer application will induce a vigorous response from exotic grasses. In practice, 'pasture improvement' in short-tussock grasslands tends to involve both fertilizer application and over-sowing of exotic grasses. In short-tussock grassland, we found that *H. pilosella* abundance was greater on drier sites, which are likely to be those where grass cover is reduced due to drought stress, and where fertilizer application may be less effective. In tall-tussock grassland that still has a dense tussock cover, maintaining that cover by limiting or removing livestock grazing should restrict invasion by *H. pilosella*. This may be ineffective, however, where the tussock canopy has previously been opened up by past grazing or burning. Such context-dependence in management effects is likely to be common across systems, mirroring the types of context-dependence found in biological control (Shea *et al*. 2005). Successful application of management tools therefore depends on understanding these complexities.

A second general implication to emerge from this study is that predicted effects of different land management strategies may have considerable uncertainty. Even with a clear relationship between management and *H. pilosella*, in this study, and an understanding of the environmental interactions, predictions of the likely outcomes of management on new sites remained highly uncertain. In part this reflects the fact that our predictions are targeted at a fine scale (individual transects), and there is considerable variability within and among transects even within the same paddock. In addition, management applications are not random across the landscape, making it more difficult to disentangle paddock and property effects from environmental variation. Nevertheless, this highlights the challenge of making predictions about management actions applied at a broad scale (here paddocks, but often larger areas) given underlying variability in the environment and plant population dynamics (Freckleton *et al*. 2008). Accurately communicating such uncertainties is nevertheless critical for assessing management options.

A final challenge for understanding management effects on invasion is that different factors may be important at different stages in the invasion process (Sol, Vila & Kuhn 2008). We used data on occurrence and local abundance to explore different effects on establishment and local spread respectively. For example, we found that in short-tussock grassland fertilizing had a negative effect on *H. pilosella* abundance (local spread) but not the probability of occurrence (establishment), implying that fertilizing short-tussock grassland may not limit establishment but does reduce subsequent ability to spread locally. Similarly, higher stocking rate increased the probability of *H. pilosella* presence in tall-tussock grasslands but not local abundance, implying that opening up the tussock canopy may be critical in allowing the initial establishment of *H. pilosella*, but may have less effect on subsequent local abundance. Ultimately, the effects of management on the early stages of invasion may become swamped by propagule supply (Duncan, Colhoun & Foran 1997).

While these challenges may seem intuitive – that management effects can interact with the environment across different scales, and vary across stages of invasion – these problems are under-explored. A better understanding of the interactions will help managers apply strategies across different regions or recognize when they are not transferable (McAlpine *et al.* 2008). Likewise, the idea that processes controlling invasive species are likely to be stage-dependent is well-recognized (Theoharides & Dukes 2007; Gravuer *et al.* 2008) but better integration into management scenarios may help identify windows of opportunity for control. We suggest that combining hierarchical study designs and data analysis will help efforts to forecast the establishment and spread of invasive species across complex landscapes under different management scenarios.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Paddock level model description and code.

Appendix S2. Transect level model description and code.

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