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Big and aerial invaders: dominance of exotic spiders in burned New Zealand tussock grasslands

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Abstract As post-disturbance community response depends on the characteristics of the ecosystem and the species composition, so does the invasion of exotic species rely on their suitability to the new environment. Here, we test two hypotheses: exotic spider species dominate the community after burning; and two traits are prevalent for their colonisation ability: ballooning and body size, the latter being correlated with their dispersal ability. We established spring burn, summer burn and unburned experimental plots in a New Zealand tussock grassland area and collected annual samples 3 and 4 years before and after the burning, respectively. Exotic spider abundance increased in the two burn treatments, driven by an increase in Linyphiidae. Indicator analysis showed that exotic and native species characterised burned and unburned plots, respectively. Generalised linear mixed-effects models indicated that ballooning had a positive effect on the post-burning establishment (density) of spiders in summer burn plots but not in spring plots. Body size had a positive effect on colonisation and establishment. The ability to balloon may partly explain the dominance of exotic Linyphiidae species. Larger spiders are better at moving into and colonising burned sites probably because of their ability to travel longer distances over land. Native

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species showed a low resilience to burning, and although confirmation requires longer-term data, our findings suggest that frequent fires could cause long lasting damage to the native spider fauna of tussock grasslands, and we propose limiting the use of fire to essential situations.

Introduction

Exotic species dominance in a community is often driven by environmental changes or disturbances that alter habitat and resource availability (MacDougall and Turkington 2005). When this occurs, resident species may be lost or disadvantaged, reducing competition and making space and resources available to outsiders (Davis et al. 2000; Hobbs and Huenneke 1992; Shea and Chesson 2002). Therefore, it is not surprising that invasive exotic species are often seen as opportunists that take advantage of the new conditions and recruitment limitation of native species, and not drivers of the changes in the community, hence the term 'passenger model' (Corbin and D'Antonio 2004; MacDougall and Turkington 2005; Seabloom et al. 2003). Indeed, disturbances such as fire can facilitate the presence and establishment of exotic species (Colautti et al. 2006; Fornwalt et al. 2010; Hobbs and Huenneke 1992; Mazía et al. 2010) and can be the agent for certain opportunist organisms (Baker 1974), consequently changing community structure (Mazía et al. 2010). However, the specific response of a community to a disturbance and the corresponding succession process will depend on the physical characteristics of the area or ecosystem and the traits of species present before the disturbance.

Many successful invaders share key traits such as wide environmental tolerance and habitat requirements, great dispersion ability and propagule production and fast development (Baker 1974; Perrins et al. 1992; Rejmánek and Richardson 1996; Yurkonis et al. 2005). The adaptations and requirements of these species, and their interactions (e.g. prey/predator, parasitism, resource competition) with the native species and their host environment are determinant as the success of an invasive species depends on how the new environment matches its habitat requirements

(Blackburn and Duncan 2001) such that certain habitat modifications may favour some invaders over others (Light and Marchetti 2007). Therefore, understanding the links between the dominance and characteristics of invasive exotic species and the changes that they cause in community functionality and composition requires their study at the community level.

Spiders are recognised for their importance in ecosystem functioning and their potential as indicators of ecological changes (Churchill 1997; Malumbres-Olarte et al. 2013b) and land management (Downie et al. 1999). Spiders are an ideal model taxon for studying the effects of environmental change and post-disturbance community succession because of their ubiquity, diversity and abundance (Coddington et al. 1996). Dispersal ability is a key trait of successful invaders, and certain spider species are indeed excellent dispersers. Many spiders can move by air via ballooning using strings of silk as parachutes (Bell et al. 2005a). Small size facilitates ballooning, so species with small body size and juveniles of certain larger species may be more likely to balloon. Also, the distance that a spider can run may be correlated with its size; large spiders may cover greater distances on the ground because of their longer legs (Foellmer et al. 2011). However, to our knowledge, no studies have attempted to identify these or other traits as characteristic of spider species that are more successful at invading communities.

Our study focuses on the spider communities of native tussock grasslands of New Zealand, an ecosystem of unique conservation and economic values (Jensen et al. 1997; Mark et al. 2009; Mark 1969). Although grasslands and mixtures of grass and shrubs are the most widespread ecosystems in New Zealand (Wardle 1991), the great majority of them have been modified for use as livestock pasture, often through burning (Barratt et al. 2005). It is only recently that ecologists and land managers have begun to study the effects of these burns on ecological processes, invasion of exotic plant species and the resilience of these ecosystems (Calder et al. 1992; Mark 1994; Payton and Pearce 2009).

The study that we present is part of a long-term experimental project that is evaluating the effects of burning on the physical and biological components of New Zealand native tussock grasslands (Barratt et al. 2012, 2006; Bell et al. 2005b; Espie and Barratt 2006; Payton and Pearce 2009; Malumbres-Olarte et al.

2013a). It is providing continuous data over a long period of time, and therefore, a unique opportunity to test a number of hypotheses related to colonisation and long term effects of burning. Our aim here is threefold: first, to test the hypothesis of a post-burn dominance of exotic spider species; second, to evaluate the importance of two characteristics or traits (ballooning ability and body size) in the post-burning dominance of spider species; and third, to assess the effects of exotic species on the community and the implications for conservation of native tussock grassland spiders.

Methods

The experiment was set up in the area of Deep Stream, in East Otago, South Island (45°44′S, 169°51′E). The study site is dominated by mid-altitude (700 m a.s.l.) native New Zealand tussock grassland plant communities. This area has never been cultivated and it had not been burned for at least 30 years before the study began (Barratt et al. 2006). The site has been previously described for land tenure (ownership) and soil type (Barratt et al. 2006); altitude, slope and aspect (Barratt et al. 2009); annual rainfall and temperature (Payton and Pearce 2009) and vegetation (Espie and Barratt 2006).

Experimental design and data collection

There were two burning treatments (spring and summer burns) and unburned control plots. These treatments were intended to replicate controlled (spring) and accidental (summer) fires. Sampling occurred every year in January between 1999 and 2005, totalling seven sampling times, with experimental burns on 7 March 2001 (summer burn) and 2 October 2001 (spring burn). We applied each of the three fire regimes to three sampling plots; we established nine 1 ha square plots, each of which was assigned a regime randomly. Distances between plots ranged between 40 and 500 meters. Then, we divided each plot into 25 20 × 20 m subplots, of which we left the outer 16 out of the sampling to reduce edge-effects. At each annual sampling, we selected a subplot randomly from the remaining nine subplots, avoiding previously sampled locations.

A preliminary survey of the study area showed that 70 % was inter-tussock spaces. Therefore, we designed our sampling so that the sum of the samples would represent the plant cover similarly; in each plot and year we collected 20 inter-tussock samples (turf samples between tussocks) from four rows of five samples, and nine turf samples with tussocks (*Chionochloa rigida* (Raoul) Zotov) randomly, totalling 29 samples per plot, and 180 inter-tussock and 81 tussock samples in all nine plots per year. Each sample was a 0.1 m² turf square (0.317 × 0.317 m) approximately 0.05 m deep, dug using a metal quadrat as a reference. After collection, we transported the samples in individual paper bags to Invermay, Dunedin. We stored the samples at 4 °C until we processed them within the following 3 weeks.

For the invertebrate extraction from individual samples, we used modified Tullgren extraction funnels (Tullgren 1918), where we placed the samples inverted, 0.4 m beneath a 150 W light bulb for 7 days. We kept all the extracted invertebrates in a mixture of 70 % ethanol and 10 % glycerol at 4 °C until we separated the spiders using a low-power 6.3-40× binocular microscope.

Spider identification and classification

We identified adult specimens to species or morpho-species based on available taxonomic literature (Forster 1979; Forster et al. 1988; Forster and Wilton 1973; Paquin et al. 2010; Vink 2002) and following nomenclature by Platnick (2012). We recognised specimens belonging to undescribed species morphologically by using conspecific specimens that we had previously classified using molecular methods (Malumbres-Olarte et al. 2013a, b). We classified species into ballooners or non-ballooners and native or exotic based on bibliographic information and our own previous collection data (see Table S1 for species list and classification). Species size data came from the literature and our own measurements in the case of undescribed species. We used mean carapace length as a surrogate for size. After identification, we stored all specimens in 95 % ethanol at −20 °C.

Statistical analyses

First we calculated the densities of spider adult individuals per m² and per species, plot, year and treatment to use them as data for the analyses. As some species represented by few individuals could be

considered species with no permanent populations in the study area, we only used data on species with more than four individuals.

We built generalised linear mixed-effects models on the data from post-burning years to investigate the changes in native and exotic spider species, and the relevance of ballooning and body size in these processes. The response variables were presence/absence and density, when present, of specimens of each species, and we used binomial distribution and negative binomial distribution (because of the over-dispersion in the response variable), respectively, in the models. These response variables represented colonisation and establishment of species, respectively. The random effect variable was species, as this would account for the similarities in presence and density among the individuals of each species across plots, years and treatments. The full model included five fixed effect variables (origin, ballooning, size, treatment, year), the interaction between size and treatment and the two and three way interactions between treatment and year with origin and ballooning [(origin + ballooning) × treatment × year]. Using this full model, we selected the most parsimonious models among the ones with all possible combinations of explanatory variables under an information criterion approach, using the corrected Akaike Information Criterion (AICc) (Burnham and Anderson 2002) to account for the small sample size. Then, we averaged the models with ΔAICc < 2 with respect to the best model and calculated model weights and variable importances. If the goodness of fit and residual plots of model averages were not adequate, we discarded them and favoured adequate top models. Once we had an adequate model, we computed estimates for our variables. We repeated model fitting and selection using only data for the species of the family Linyphiidae (native and exotic). The purpose of this was to test if the patterns found in the data with all species were repeated within the family with the most exotic species.

To assess the affinity of exotic and native species to the different burning treatments and years, we used indicator species analysis (IndVal) (Dufrêne and Legendre 1997) using data from pre- and post-burning years. IndVal uses the relative abundance and frequency of species in specific groups to estimate the fidelity and specificity of species to a group. Species values range between 0 and 100, obtaining the maximum value when the species is present in all the samples of a single group. The groups used in this analysis were the clusters obtained from a Ward's clustering analysis on the Steinhaus (S_{17}) dissimilarity coefficient (Legendre and Legendre 1998). Coefficient values were calculated from data on the abundance of each species per plot, year and treatment that were previously transformed ($\sqrt{(x + 0.5)}$). For each species, we ran a significance test using a Monte Carlo randomisation procedure (1,000 permutations). For a species to be characteristic of a group, it had to be significant ($p < 0.05$) for fidelity and specificity and produce an IndVal value over 25 % (Paquin 2008). We conducted all data manipulation and analyses with R 2.14.0 (R Development Core Team 2012).

Results

We collected 4,556 adult spider specimens that belonged to 66 species/morphospecies, from 22 families. Ten species were exotic: *Eriophora pustulosa* (Walckenaer, 1841) (Araneidae), *Supunna picta* (L. Koch, 1873) (Corinnidae), *Badumna longinqua* (L. Koch, 1867) (Desidae), *Cryptachaea blattea* (Urquhart, 1886) (Theridiidae), *Steatoda grossa* (C. L. Koch, 1838) (Theridiidae), *Cryptachaea* sp. (Theridiidae), *Araeoncus humilis* (Blackwall, 1841) (Linyphiidae), *Diplocephalus cristatus* (Blackwall, 1833) (Linyphiidae), *Erigone wiltoni* Locket, 1973 (Linyphiidae) and *Tenuiphantes tenuis* (Blackwall, 1852) (Linyphiidae) but only the last five were represented by more than four individuals.

The clustering analysis based on abundance data identified two main groups; control and pre-burn plots on one side and burned plots on the other (Fig. 1). The burned plots were further separated chronologically into three clusters. One cluster included plots that were sampled in the last years of the study (post-burn stage three) and another that included two more clusters of plots sampled shortly after the burning (post-burn stage one) and in the following years (post-burn stage two).

Exotic species were only associated with burned plots (Fig. 1), for which they showed the greatest IndVal values. The species *D. cristatus* (exotic), *E. wiltoni* (exotic), *Steatoda lepida* (O. Pickard-Cambridge, 1879) (native) and *A.humilis* (exotic) were the species most associated with burned plots. The same
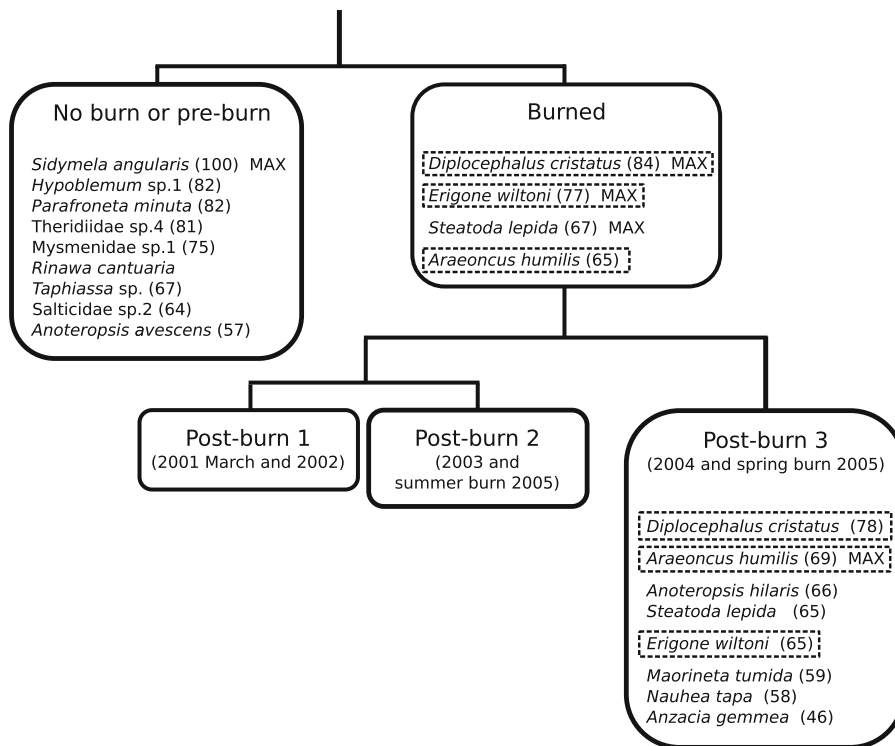
Fig. 1 Characteristic species of succession stages according to the indicator value analysis (IndVal). Stages represent clusters of species assemblages using species abundance dissimilarity (S_{17}). Indicator values are within parentheses and represent the maximum value of the species when marked with 'MAX'

three exotic species were also among the species associated with post-burn stage three, where they were the species with the first, second and fifth strongest associations. Only native species were associated with unburned plots, which included control and pre-burn plots.

Percentages of exotic spiders stayed below 20 % before the burning in all plots (Fig. 2a) but they increased after burning, peaking at values above 60 % in spring plots and at around 50 % in summer plots, three and 2 years after the burning, respectively. A similar trend occurred in Linyphiidae, with a post-burning increase in exotic species density in burned areas (Fig. 2d) and the native species showing similar values in all treatments and throughout the seven study years (Fig. 2c). Although most exotic species increased in density, *D. cristatus* was the species that showed the greatest increase (Fig. 2b).

For the post-burn species presence/absence data we obtained a model average that included the following explanatory variables: origin, ballooning, size, treatment, year, and the two-way interactions between

origin and treatment, ballooning and treatment, ballooning and year, treatment and year, and size and treatment (Table 1). In both burned treatments exotic species were more likely to be present than native species (Fig. 3a). The effect of ballooning varied depending on the treatment, with ballooners being more likely to be present in summer burn plots but less in spring burn plots than non-ballooners (Fig. 4). The estimated effects of size were 0.44, 0.48 and 0.57 for the control, spring burn and summer burn treatments, respectively (Table 1).

The top model for the density data had origin, ballooning, size, treatment, year, and the two-way interactions between origin and treatment, origin and year, and size and treatment as fixed explanatory variables (Table 1). As with the presence models, the density model estimated greater values for exotic than native species in burned plots (Fig. 3b). Size had different effects on control (0.72), spring burn (1.40) and summer burn (1.32) treatments plots.

There were 15 Linyphiidae species in the sampled plots, of which eight native and four exotic species

Fig. 2 Observed mean density of individuals m^{-2} (±SEM.) of **a** exotic spider species, **b** the exotic species *D. cristatus*, **c** native Linyphiidae species and **d** exotic Linyphiidae species. *Lines* represent control plots (*solid*), spring burn plots (*dashed*) and summer burn plots (*dotted*). Arrows indicate spring or summer burns, in March 2001 or October 2001, respectively
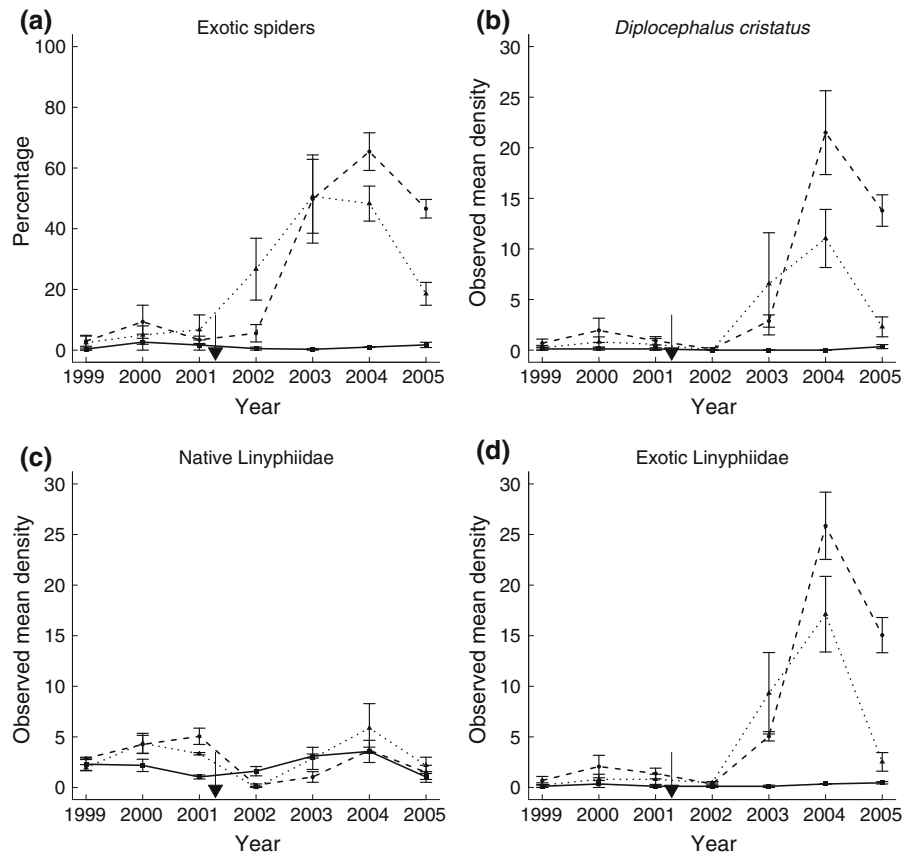
were represented by more than four specimens, and were included in the models for the analyses of this family. The explanatory variables of the model average for the presence data were size, treatment, year, origin and the interaction between treatment and origin (Table 2). The model estimated a greater presence of exotic than native species in burned plots: in control plots the estimated mean values were 0.189 (bottom value subtracting SEM. was 0.086, top value adding SEM. was 0.367) for native species and 0.041 (0.012, 0.129) for exotic species; estimates of spring burn plots were 0.001 (0.001, 0.003) for native and 0.34 (0.226, 0.477) for exotic species and in summer plots 0.001 (0.001, 0.003) and 0.34 (0.226, 0.477), for native and exotic species, respectively. Size had a positive effect (0.17) with a relative importance of 0.45. In the top model selected for the density of Linyphiidae species, the explanatory variables were treatment, year, origin and the interaction between treatment and origin (Table 2). This model estimated lower densities of exotic species in the control plots

[0.146 (0.064, 0.333)] than in spring [1.083 (0.578, 2.029)] and summer burn [(0.784 (0.415, 1.479)] treatments. Conversely, the estimated density of native species was greater in control plots [0.303 (0.136, 0.678)] than in spring [0.014 (0.007, 0.03)] and summer burn plots [0.037 (0.018, 0.078)].

Discussion

Post-burn dominance of exotic spiders

To our knowledge, this is the first study that shows an increase in the abundance of exotic spider species over time after burning. We show that although not all exotic species showed this affinity for burned areas, the strongest associations were with exotic species. Most exotic species found in the study area belong to the Linyphiidae, a dominant family in the burned plots (Malumbres-Olarte et al. 2013a). Linyphiidae species have been recorded as invaders in New Zealand and

Table 1 Model data for the presence/absence and density of spider species (n = 38) across years and treatments

Variables in averaged models	df	AICc	ΔAICc	AICc weight
Presence/absence model				
(Ballooning + size + year) × treatment, ballooning × year	22	1464.9	0	0.336
Size, (Ballooning + year) × treatment, ballooning × year	23	1465.9	0.98	0.206
Size, (size + year) × treatment, ballooning × year	23	1466.4	1.54	0.155
(Ballooning + year) × treatment	19	1466.5	1.55	0.155
Size, (ballooning + size + year) × treatment, ballooning × year	25	1466.6	1.65	0.147

Average model variables	Estimate/levels			Relative importance
Origin	Native, exotic			1
Ballooning	Yes, no			1
Size	–			0.51
Treatment	Control, spring burn, summer burn			1
Year	2002, 2003, 2004, 2005			1
Origin × treatment	6			1
Ballooning × treatment	6			0.85
Ballooning × year	8			0.85
Treatment × year	12			1
Size × treatment	3			0.30
Control	0.44			–
Spring burn	0.48			–
Summer burn	0.57			–

Variables in averaged models	df	AICc	ΔAICc	AICc weight
Density model				
Size, size × treatment, origin × year	17	1517.4	0	0.70
Size, origin × year	15	1519.1	1.66	0.30

Average model variables	Estimate (SEM.)/levels			Relative importance
Origin	Native, exotic			1
Ballooning	Yes, no			1
Size	–			1
Treatment	Control, spring burn, summer burn			1
Year	2002, 2003, 2004, 2005			1
Origin × treatment	6			1
Origin × year	8			1
Size × treatment	3			0.70
Control	0.72			–
Spring burn	1.40			–
Summer burn	1.32			–

Best models were selected based on ΔAICc and model fit, and averaged. Estimates are back-transformed. All selected models included ballooning, origin, treatment, year and the interaction between origin and treatment as explanatory variables, besides the variables listed in the table. Estimates of variable levels have been excluded from the table for simplicity

elsewhere (Eichenberger et al. 2009; Jennings 2002; Vink et al. 2004) and they are known to exploit human-created environments, such as agroecosystems or disturbed ecosystems. Part of their success at colonisation and establishment may be caused by adaptations that allow them to occupy available
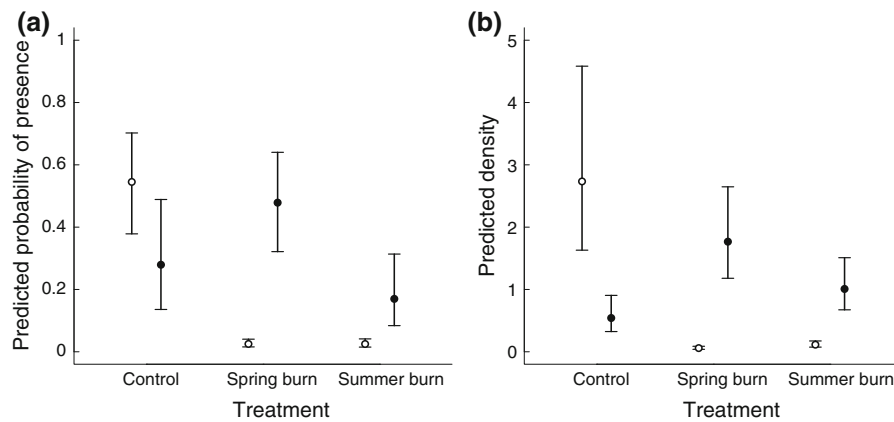
Fig. 3 Estimated effects (mean m^{-2} ±SEM.) of origin of species on the presence probability (**a**) and density (**b**) of spiders across treatments. Values are back-transformed estimations of the variable representing the interaction between species origin and treatment

habitats faster and are more willing to compete for the occupied ones (Bonte et al. 2011). Indeed, their ability to balloon makes them excellent colonisers (see below for further discussion).

Another characteristic that confers an advantage to linyphiids in their establishment is their aerial webs. In the burned grasslands we studied here, vegetation and litter were reduced and habitat availability for terrestrial prey and predators, in this case, spiders, was limited. Nevertheless, many tussock and speargrass (*Aciphylla* sp.) plants survived and retained some architecture. Flying invertebrates suitable for prey were present, and having attachment points for their webs allowed aerial web builders to thrive where other spider taxa could not, making the species of this guild successful colonisers of the burned plots (Malumbres-Olarte et al. 2013a). Although these advantages allowed quick population recoveries in most Liny-phiidae, exotic species were more successful at both colonisation and establishment, which may indicate a more efficient use of resources in the new conditions (Hill et al. 1993) and may be related to species-specific traits. For example, certain species may be more capable of adjusting their web size and shape to the three-dimensional structure of the remaining vegetation. This new hypothesis is certainly worth investigating but it will require species-specific information on web structure.

Also, native-exotic interactions, such as competitive exclusions, may prevent the establishment of native species (Bednarski et al. 2009), and the combination of other biological and ecosystem
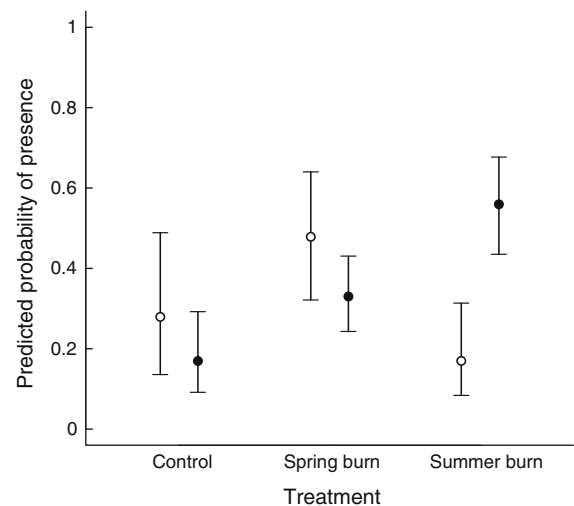

Fig. 4 Estimated effects (mean m^{-2} ±SEM.) of ballooning ability of species on the presence probability of spiders across treatments. Values are back-transformed estimations of the variable representing the interaction between ballooning ability and treatment

specific physical factors, like microclimatic conditions, could determine the success of exotic species (Lamarque et al. 2011). These traits may be instrumental in the success of *D. cristatus*, a species that has been in New Zealand almost certainly since the arrival or Europeans 150 years ago (Forster et al. 1988). *Diplocephalus cristatus* appears to have reached a wide distribution around the country, particularly in agroecosystems and human-modified areas (Topping and Lövei 1997), which it also favours in Europe.

Table 2 Model data for the presence/absence and density of Linyphiidae species (n = 12) across years and treatments

Variables in averaged models	df	AICc	ΔAICc	AICc weight
Presence/absence model				
Treatment, year, origin, treatment × origin	10	434.1	0	0.416
Size, treatment, year, origin, treatment × origin	11	434.6	0.44	0.334
Average model variables	**Estimate/levels**			**Relative importance**
Size	0.17			0.45
Treatment	Control, spring burn, summer burn			1
Year	2002, 2003, 2004, 2005			1
Origin	native, exotic			1
Treatment × origin	6			1
Variables in top model	df	AICc	$\Delta AICc_2$	AICc weight
Density model				
Treatment, year, origin, treatment × origin	10	498.1	1.43	0.435

For the presence/absence model, best models were selected based on ΔAICc and model fit, and averaged. For the density model only top models is shown. Estimates are back-transformed. $\Delta AICc_2$ represents differences in AICc between best and second best models. Estimates of variable levels have been excluded from the table for simplicity

Species traits

Although the ability of spiders to balloon did have a positive effect on the success of species in burned areas, it varied depending on the season of the burning. Contrary to our expectations, ballooners were not more likely to appear in the spring burn plots than non-ballooners. As ballooning confers the ability to move more rapidly across longer distances, we expected that ballooners would dominate, as they did in the summer burn plots. This is particularly surprising given that most exotic species were ballooners and the high winds typical of middle-altitude tussock grasslands should facilitate dispersal via ballooning. A few factors may be behind this unexpected result: all the plots were surrounded by unburned areas that could act as a source for both ballooning and non-ballooning colonisers, masking any possible differences in dispersal abilities; the effects of spring and summer burns on the spider community may differ due to differences in the life cycle or time of maturity—which determines dispersal ability—of the species present in the plots and the surrounding areas at the time of the burn; and the failure of our models to estimate their response accurately, caused by an insufficient number of replicates.

Size had a positive effect on the colonisation and establishment ability of spider species in general, and in the burned areas in particular. This is similar to the trend found across different families at a continental level in Europe, where invasive spiders were larger than native ones (Kobelt and Nentwig 2008). Larger species can cover greater distances, facilitating colonisation. They may also be more competitive, giving them advantage against smaller species that exploit similar resources (Eichenberger et al. 2009), especially if direct confrontation exists. Body size may also be correlated with reproduction and, therefore, contribute to colonisation and establishment; larger species may produce more offspring (Simpson 1995) and exert a greater propagule pressure. Indeed, propagule pressure can contribute to the invasiveness of a species (Green 1997; Kolar and Lodge 2001). Unfortunately, we lack information on viable egg production and long-range dispersal ability—whether as adults or juveniles—for most spider species, making it difficult to test these traits as potential invasion characters.

Conservation management

The post-burn domination of exotic spider species in the tussock grasslands studied here is cause of concern. Abundance does not necessarily equate to impact (Parker et al. 1999) and sometimes exotic species only take advantage of the new post-

disturbance conditions without causing a decrease in native species (Didham et al. 2005). However, in our study area a number of native species were still absent 4 years after the burning. Although only long-term data, which are still being collected, are likely to confirm it, many of the spider species present in our study area appeared to need longer post-burn recovery periods, suggesting a lack of resilience to this kind of disturbance. Exotic Linyphiidae were more successful colonisers and burning may have provided exotic spiders an initial advantage in resource competition that may eventually lead to the local extinction of certain native species. This scenario is plausible if burning is used regularly for management of tussock grasslands.

Our findings about changes in exotic spider community illustrate a potential issue in conservation—the balance between managing for the diversity of different local species. In New Zealand, burning of native tussock grasslands is partly supported for preserving native vegetation by keeping exotic shrubs and herbs in check (Calder et al. 1992). Thus, managers are tasked with taking into account several ecological interests simultaneously. Few exotic invertebrate species are known to have invaded natural ecosystems in New Zealand, including Coleoptera in tussock grasslands (Barratt et al. 2012), but this may be caused by a lack of research on the issue (Brockerhoff et al. 2010; Hann 1990). One of the aims of managers of natural ecosystems is to preserve invertebrate biodiversity, as well as the ecosystem services they provide. Only long-term monitoring data obtained through a combination of sources and sampling methods, such as turf extraction and pitfall trapping, will allow us to understand the specific interactions between native and exotic species and the physical and biological factors that determine them, which can then be used to select and apply the appropriate measures or management strategies.

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