Habitat specificity, dispersal and burning season: Recovery indicators in New Zealand native grassland communities

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ABSTRACT

Restoration programs for human-disturbed ecosystems rely on a good understanding of how recovery occurs. This requires elucidating the underlying succession process, which depends on species adaptations, their interactions, and the spatiotemporal characteristics of the disturbance. Using spiders, we aim to identify the drivers of succession after burning, commonly used in New Zealand native tussock grasslands, test the hypothesis of post-burning dominance of generalists over specialists, and test the presumption that managed summer burns are more detrimental than spring burns. We established a 7-year experiment, with spring and summer burn treatments and unburned control plots, and sampled annually before and after the burning. We identified changes in spider assemblages and their drivers using clustering and indicator value analyses, and we analysed the response of spider diversity and taxa through linear mixed-effect models. In both spring and summer burns, functional groups and diversity decreased and the density of individuals of generalist species increased. However, spring and summer burn treatments showed no differences in spider diversity and composition. We found evidence that adaptations, such as habitat specificity and dispersal ability, determine the recovery of spider communities, and we suggest a set of indicators for monitoring programs. Time of burning may interact with factors like flammability and fire intensity, reducing differences in the effects of burning between seasons. We recommend planning burns for wet seasons as they are easier to control. To facilitate recolonisation by rare species of spiders of tussock grasslands, we suggest maintaining unburned areas that represent different vegetation types.

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1. Introduction

As habitat and ecosystem restoration becomes a common tool for returning to pre-human or pre-transformation conditions, there is an increasing need to understand the succession processes that underpin the recovery (Aide et al., 2000; Mullah et al., 2012). Immediately after the initial ecosystem destruction, total species diversity decreases, due to direct mortality and general habitat loss. In the early post-destruction succession stages, the species that can cope with the new environment flourish as the species that depend on particular habitats struggle to re-establish. However, the latter will regain competitiveness as the lost habitats become available again. As niche evolution theory predicts, these competitive interactions will lead to the development of differing strategies; specialist species will evolve in stable habitat conditions and generalists when habitat alterations prevail (Futuyma and Moreno, 1988).

A inverse trend in the abundance of specialist species in relation to habitat alterations and homogenisation has been found in large scale studies (Warren et al., 2001; Swihart et al., 2006; Devictor and Robert, 2009). However, experimental studies are still required in order to understand the competitive interactions that occur at the community level and explain larger scale processes. This knowledge could possibly allow the development of appropriate actions for biodiversity conservation.

In the case of certain disturbances like fire, the physical and temporal context of the destruction event may critically influence the changes in the community. Indeed, severity and frequency of

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fire, and the weather conditions can determine the diversity and structure of the ecosystem (Whelan, 2006). Given the correlation between time of burning and meteorological conditions, the season in which fire occurs is a factor to consider. Time of burning influence the effects of fire on grassland vegetation (McMurphy and Anderson, 1965), vertebrates (Hailey, 2000) and arthropods (Freire and Motta, 2011). Fires occurring during different seasons may have varying effects on the plant species dominance in grasslands (Copeland et al., 2002), and summer fire can have a greater modifying effect on plant community than spring fire (Lloyd, 1968). However, in other cases, spring and summer fires have been found to have similar effects on presence and abundance of mammals (Litt and Steidl, 2011) and invertebrates (Barratt et al., 2009).

New Zealand native tussock grasslands are of much conservation, ecological and economic and ecosystem function value because of their high levels of species endemism and specialisation, and their use for agriculture and as source of aquifer water (Jensen et al., 1997; Brockerhoff et al., 2008; Mark et al., 2009). However, the response of tussock grassland invertebrate diversity to human modification is not well understood, which hinders the development of conservation strategies. These grasslands have been eliminated or transformed into improved pasture using controlled burning since the 19th century (Barratt et al., 2005). A common practice is the use of spring burns (September–November), when temperatures are lower and vegetation moisture higher than in summer (December–February) (Barratt et al., 2006), so that fires can be more easily controlled. In tussock grasslands, fire affects plant physiology by reducing growth (Mark, 1965), changes tissue nutrient concentrations (Payton et al., 1986), and reduces micro-arthropod abundance (Yeates and Lee, 1997; Barratt et al., 2006). While it is known that fire alters the structure of native biota, facilitates the establishment of exotic plant species, and increases soil erosion (Payton and Pearce, 2009), little is known about post-fire successional processes in invertebrates.

The ability of spiders to respond to environmental changes makes them ideal indicators of disturbance in biological systems. Spiders are globally abundant and diverse (Churchill, 1997), and they play a crucial role as generalist predators in most terrestrial food webs (Marc et al., 1999). Spiders have been used as indicators of anthropogenic disturbance, such as habitat fragmentation (Maelfait and Hendrickx, 1998), land management (Gibson et al., 1992) and effects of fire (Moretti et al., 2002). However, there has been little research on spiders in New Zealand grasslands despite the common use of fire for management and the knowledge that spiders are one of the most important groups of invertebrates in tussock ecosystems (Barratt et al., 2005) and can be used to assess changes in habitat structure (Malumbres-Olarte et al., in press).

This study is part of an ongoing experimental project that aims to understand species composition and abundance in relation to human-management of New Zealand native tussock grasslands from a multidisciplinary view (Bell et al., 2005b; Barratt et al., 2006, 2011; Espie and Barratt, 2006; Di Menna et al., 2007). To our knowledge, this is the first study that uses replicated experimental grasslands burning to obtain pre- and post- fire data for the analysis of succession in spider communities, and probably one of the few on invertebrates. We have three objectives: (1) identify the drivers or indicators of post-fire succession in an endemic tussock grassland; (2) test the hypothesis of a post-disturbance dominance of generalist species; and (3) test the hypothesis that summer fires are more detrimental than spring fires for species diversity.

2. Methods

We conducted this study at Deep Stream, on the East Otago Plateau, an example of mid-altitude (700 m a.s.l.) native New Zealand tussock grassland. The area has never been cultivated, and no fire had occurred there for at least 30 years previous to the study (Barratt et al., 2006). Apart from some low density grazing, the area has remained relatively unmodified for the last 25 years due to its use as a water reserve for the nearby city of Dunedin. Descriptions of the site have previously been given for tenure and soil type (Barratt et al., 2006); altitude, slope and aspect (Barratt et al., 2009); vegetation (Espie and Barratt, 2006); and annual rainfall and temperature (Payton and Pearce, 2009).

2.1. Experimental design and data collection

We carried out experimental burns on 7 March 2001 (summer fire) and 2 October 2001 (spring fire) in conditions typical of controlled spring fires and accidental summer fires. Surface temperatures during the fire were 500–1010 °C in spring and 300–500 °C in summer (Barratt et al., 2006). Invertebrate sampling occurred annually in January between the years 1999–2005. We took an additional sample set in March 2001, immediately after the summer fire treatment, although we did not sample spring-burned plots at this time as the purpose of these samples was to compare a recently burned area and an unburned area. We set up nine 1 ha square plots and we assigned each of the three fire regimes – spring and summer burn treatments and the unburned control – randomly to three plots, so that each regime had three replicates. We divided each plot into 25 20 m × 20 m subplots and excluded the 16 outer subplots from the sampling to minimise edge-effects. From the remaining nine subplots in the centre of the plot, we selected one subplot randomly at each sampling event. Within the selected subplot, we collected 20 turf samples between tussocks (inter-tussock samples) from four rows of five samples each. We collected nine turf samples that included tussocks (Chionochloa rigida (Raoul) Zotov) randomly in order to have an approximate representation of the grassland plant cover in the study area, as a preliminary survey indicated that inter-tussock areas occupied 70% of the study area. Therefore, we collected a total of 180 inter-tussock and 81 tussock samples every year. We avoided previous sample locations in subsequent collections.

Samples consisted of 0.1 m² turf squares (0.317 × 0.317 m) dug to a depth of approximately 0.05 m using a metal quadrat as a guide. We transported the samples to the facilities at Invermay, Dunedin, in individual paper bags, and stored them at 4 °C for a maximum of three weeks until we processed them. In the laboratory, we extracted the invertebrates from individual samples by placing them inverted in modified Tullgren extraction funnels, 0.4 m beneath a 150 W light bulb for seven days. We stored all the extracted material in 70% ethanol with 10% glycerol at 4 °C until sorting. We separated all spiders from the other invertebrates using a low-power 6.3–40× binocular microscope.

2.2. Spider identification and classification

We identified only adult spiders to species or morphospecies, because of the difficulties and uncertainty of juvenile identification. We identified species and genera based on available taxonomic literature (Forster and Wilton, 1973; Forster, 1979; Forster et al., 1988; Vink, 2002; Paquin et al., 2010) and followed nomenclature by Platnick (2012). We recognised a number of specimens of undescribed species morphologically as conspecific to those classified previously using molecular methods (Malumbres-Olarte et al., in press) and we named them accordingly. After identification, we stored all specimens in 95% ethanol.

We classified species into ecological guilds (defined as groups of species that share resources) following Uetz et al. (1999) and taxonomic literature. Based on available bibliographical information, we also categorised species according to habitat or ecosystem specialisation; we considered a species a specialist or generalist when

it had been recorded in a single or multiple habitat types, respectively (Table A3). We assumed that morphospecies (undescribed) were specialists as they had not been recorded yet and tussock grassland species tend to be specialists. Although we admit that current species data have their limitations, we believe that the information we used is reliable and our assumptions well grounded. Finally, we considered 11 of the species found indicators of tussock abundance (Mysmenidae sp.1, *Laetesia trispathulata* (Urquhart, 1886)), wetland or shrubby vegetation (*Anoteropsis hilaris* (L. Koch, 1877), *Hypoblemum* sp., *Laetesia minor* Millidge, 1988, Micropholcommatidae sp.2, Orsolobidae sp.1) and plant diversity (*Nauhea tapa* Forster, 1979, *Rinawa cantuaria* Forster, 1970) (Malumbres-Olarte et al., in press). *Anoteropsis flavescens* L. Koch, 1878 and *Diploplecta duplex* Millidge, 1988 were considered indicators of both plant diversity and tussock and shrub abundance, respectively.

2.3. Statistical analyses

Prior to analyses, we standardised the number of spider individuals (total and per guild, family and species), and the number of species and families per 1 m^2, for each combination of plot and year.

We first assessed differences in spider assemblages between different treatments and years using two dissimilarity measures: Steinhaus (S_{17}) and Sørensen (S_8) coefficients based on previously transformed data ($\sqrt{(x + 0.5)}$). Sørensen coefficient accounts for presence/absence of species whereas Steinhaus coefficient also considers abundance (Legendre and Legendre, 1998). We used species dissimilarity matrices for ordination analyses of spider diversity in different years and treatments. We used non-metric multidimensional scaling (NMDS) as it reproduces the distances that represent similarity between samples or points in a multidimensional space. In comparison to other types of ordination, NMDS allows the use of biologically meaningful data, such as matrices based on dissimilarity coefficients of species diversity, preservation of dissimilarity rank order in the distance rank order and identification of a wider range of spatial arrangements among the collected samples (McCune and Grace, 2002). We applied Ward's minimum variance method to dissimilarity matrices based on abundance and presence/absence to identify similarity in spider diversity and composition between years or treatments (Ward, 1963). This clustering analysis aims to minimise the total sum of squares with new partitions and is a step-wise hierarchical agglomeration method.

In order to understand the general trends in spider assemblages over time and treatments, we analysed five diversity measures: total density of spider individuals, number of species, number of families, Shannon's *H'* species diversity index and species richness estimator ACE (Chao and Lee, 1992). Number of individuals represented the total number of spiders, both adults and juveniles, whereas number of species and families were based on adult specimens. To identify the specific drivers of succession, we then analysed changes in the percentage of individuals per guild, the number of individuals belonging to potential indicator species and families (Malumbres-Olarte et al., in press) and the percentage of generalists and specialists. We excluded samples from March 2001 and we only included data from January samples in the models so that the time between sample collections was the same.

In addition, we tested the ability of models to detect trends and the effect of treatment through linear mixed-effects models. As the time between samples was the same, we applied an auto-regressive correlation structure to the models. In each model, we set the diversity or community structure measure as the response variable, with burn treatment, year and their interaction as the potential fixed effects and the identity of the plot as the random effect,

since samples from the same plot were spatially correlated. We discarded inadequate models by checking the goodness of fit and inspecting the residual plots. Most of these models were on taxa for which there was insufficient data. Then, models with different combinations of the three explanatory variables were compared using corrected Akaike Information Criterion (AICc) (Burnham and Anderson, 2002) to account for the small sample size. This allowed the selection of the best model and established the explanatory ability of treatment. When data on a diversity measure or indicator taxon was sufficient for modelling, we used the most parsimonious model to estimate the means and standard errors of each combination of year and treatment using REML estimation.

We detected characteristic species of each treatment with the indicator species analysis (IndVal) (Dufrêne and Legendre, 1997). IndVal takes into account the relative abundance and frequency of each species in zones or groups determined by the user to estimate two measures of the affinity of a species to a group of samples: the presence of a species in all the samples of a cluster (fidelity), and the level of exclusiveness of the species to the cluster (specificity). We favoured this method over other indicator species analyses such as TWINSPAN because of its greater identification sensitivity (Dufrêne and Legendre, 1997). We applied IndVal analysis to the species assemblage clusterings or typologies created by Ward's method on abundance and presence/absence dissimilarity coefficients. Indicator values range between 0 and 100, reaching this maximum when a species is present in all the samples of a single treatment or zone. We performed a significance test by a Monte Carlo randomisation procedure (1000 permutations) for each species and we only considered a species characteristic of a cluster when it was significant ($p < 0.05$) for both fidelity and specificity with an IndVal value greater than 25% (Paquin, 2008). We conducted all data manipulation and analyses using the software R 2.14.0 (R Development Core Team, 2012).

3. Results

A total of 31,965 spiders, of which 4556 were adults, were collected. Sixty-six species and morphospecies of spiders belonging to 22 families were identified and classified into the guilds of runners, aerial web builders, sheet web builders, stalkers and ambushers.

3.1. General succession trends

NMDS ordinations based on dissimilarity (abundance and presence/absence) showed differences in spider assemblages between plots with no previous event of fire — either control plots or preburn spring and summer plots — and burned plots after burning. The NMDS based on the abundance dissimilarity coefficient (stress = 6.11 and R^2 = 0.99) separated control and unburned plots from burned plots along the first axis (Fig. 1a). Burned plots could be further separated according to the time since burning; plots could be aligned diagonally over both axes and grouped into clusters that represented different succession stages (Fig. 1a). Therefore, we placed plots into four categories: no (or before) burn, post-burn 1, post-burn 2 and post-burn 3. The presence/absence based ordination (stress = 11.62 and R^2 = 0.99) showed similar patterns in assemblages, with plots clustered according to whether they had been burned and the sampling time (Fig. 1b).

The Ward's clustering analyses separated unburned and preburn plots from plots after burning (Fig. 2). The abundance dissimilarity clustered plots first according to presence or absence of burning, next into a group of plots with samples collected in the last years of the study, and then into a cluster of plots from the years immediately after the burning and another from the following years (Fig. 2). Clusters created using presence/absence also
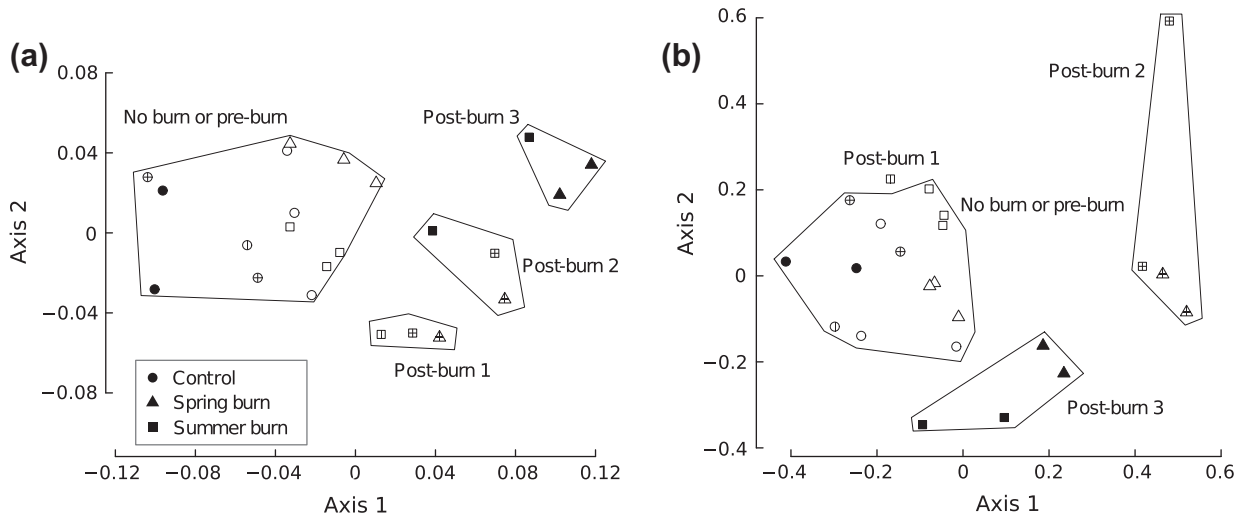
Fig. 1. Non-metric multidimentional scaling ordinations of spider assemblages from different years and treatments based on the (a) presence/absence (S_8) and (b) abundance (S_{17}) dissimilarity coefficients. Plots are represented chronologically, depending on whether they were sampled before 2002 (white), in March 2001 (filled with vertical line), in 2002–2003 (filled with cross) or in 2004–2005 (black). Polygons represent chronological succession stages.
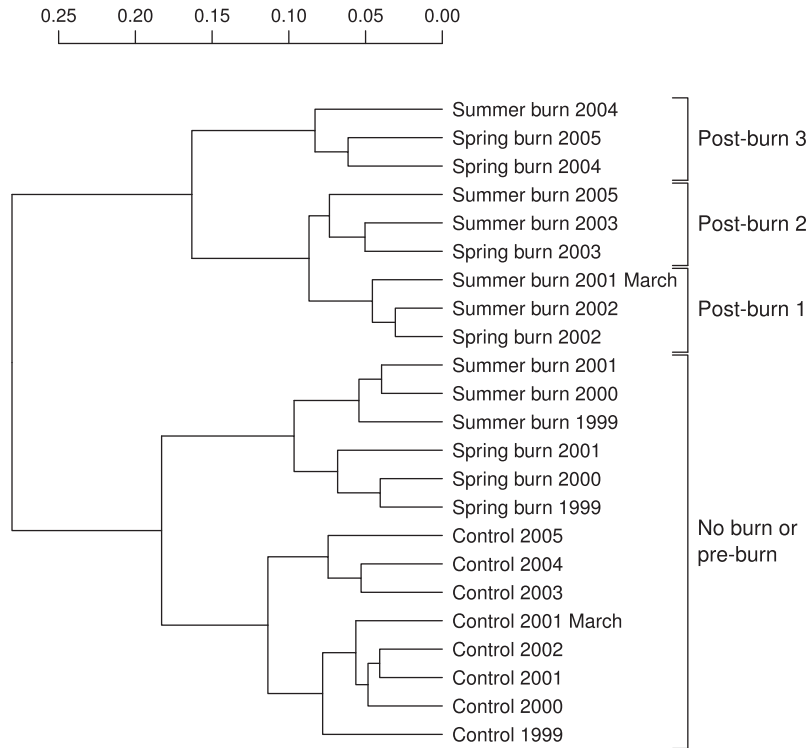

Fig. 2. Clustering analyses of spider assemblages using Ward's minimum variance on abundance data. Each terminal branch represents the species assemblage of the plots under the treatment and from the year indicated in the name. Clusters are named according to the chronological succession stages that they are thought to represent.

separated plots that had experienced burning recently and those in the later years of the study from others with no history of burning (Fig. A1). However, the spider assemblage from March 2001 summer-burn plots (immediately after a summer burn) was closer to unburned than post-burn stage 2, and the control plots from 1999 (2 years before burning) were grouped with the samples collected in burned plots in 2004 and 2005 (3 and 4 years after the burning, respectively).

The observed density of spider individuals fluctuated in all three treatments throughout the 7 years of the study (Fig. 3a), with differences between control plots and the two burn treatments before (2001) and after the burning, when burn treatments had fewer

(2002 and 2003) and more (2004) individuals. Observed species density was greater in control plots than in burn treated plots in the 2 years following the burning (Fig. 3c). There were more species in the spring burn plots than in the control and summer burn plots in the year 2001. Number of families and ACE and Shannon's *H*′ values showed patterns very similar to those of species (Fig. 3e).

The best models for all community measures included the interaction between treatment and sampling year as an explanatory variable (Table 1). Although the second best model varied across measures, the variable treatment always improved the models. Models of diversity measures provided estimations that differed from observed values (Fig. 3b and d). The model of the number of individuals
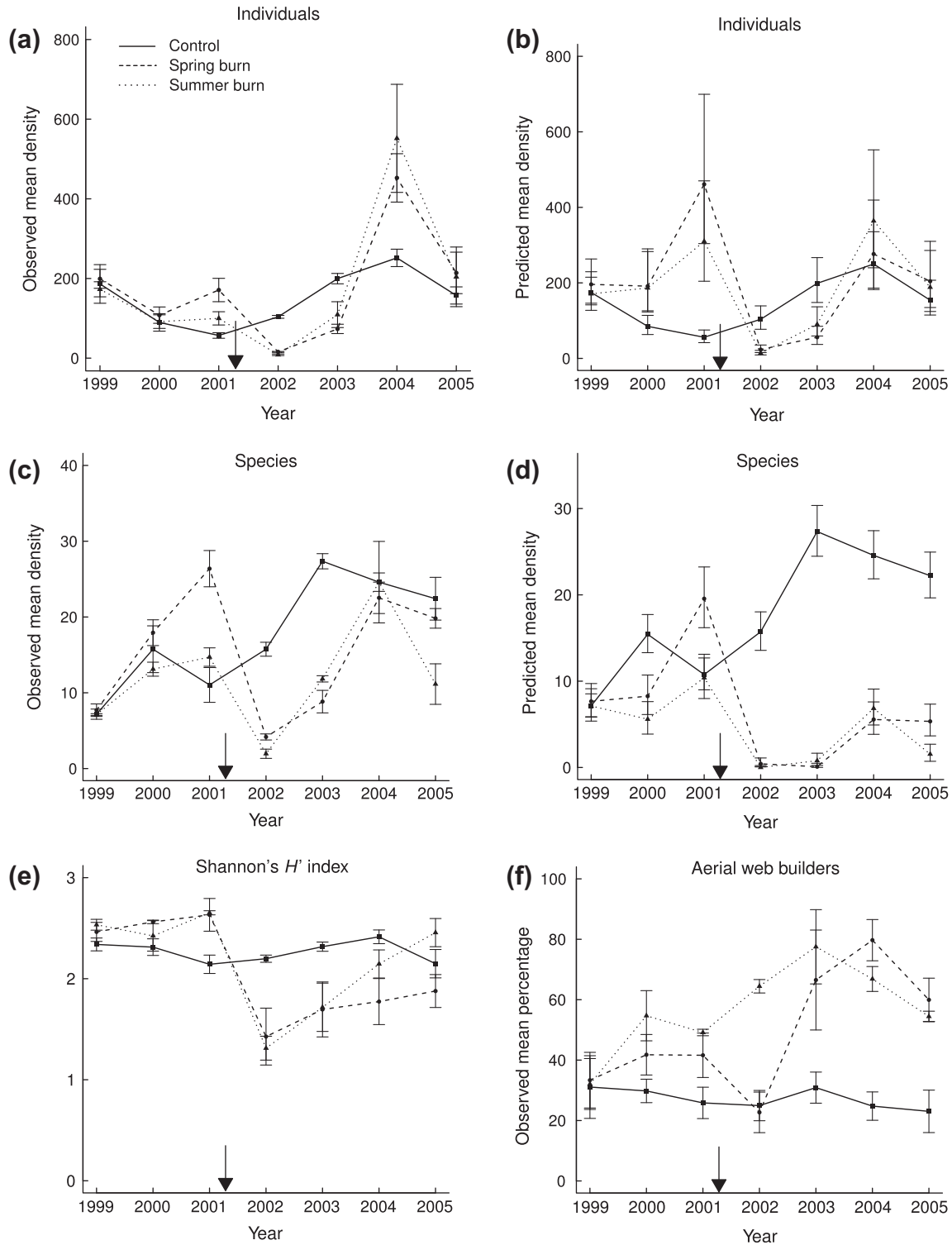
Fig. 3. Mean density m^{-2} (±SE) of observed (a, c, e, f) and modelled (b and d) measures of spider diversity and aerial web builders in control plots (solid lines), spring-burn plots (dashed lines) and summer-burn plots (dotted lines) over the sampling years. The arrow indicates when spring and summer fires occurred (both between January 2001 and January 2002).

overestimated values in the 2 years before burning and underestimated them for the year 2004 (Fig. 3b). Densities of species, families, and ACE and Shannon's *H'* values in burn treatments were underestimated after the burning, increasing the difference between them and the control plots (e.g. Fig. 3d). The variable estimation capacity of models may be due to the limited number of replicates in this study, which could be improved with additional plots.

3.2. Drivers of succession and habitat specificity

Among the guilds and taxa analysed for the identification of the drivers of succession, only a few showed evident trends over time. Although control plots always contained lower proportions of aerial web builders than summer-burn plots, the differences increased considerably in post-burn treatments (Fig. 3f). Model estimations

Table 1
AICc values for the selection of fixed effects models with measures of spider diversity and community structure as response variables ($n = 63$). For all response variables, the explanatory variables in the best model ($k = 23$) were year, treatment and the interaction between them. Columns show explanatory variables and number of parameters (k_2) in second best models, AICc values of best models (AICc$_1$), differences in AICc between best and second best models (ΔAICc$_2$) and AICc weights of best models.

Response variable (transformation)	Explanatory variables 2nd model	k_2	AICc$_1$	ΔAICc$_2$	AICc Weight
Diversity measures					
Number of individuals (log$_{10}$)	Year	9	−5.76	29.93	1
Number of species (square root)	Year + Treatment	11	106.09	50.70	1
Number of families (square root)	Year + Treatment	11	87.01	56.37	1
ACE (square root)	Year	9	97.62	12.81	1
Shannon's *H*'	Year	9	47.63	3.92	0.88
Guilds					
Aerial web builders (%, arcsine)	Year + Treatment	11	−33.82	5.46	0.93
Families					
Linyphiidae (log$_{10}$)	Year + Treatment	11	6.77	34.16	1
Specialisation					
Generalists (%, arcsine)	Year + Treatment	11	−38.62	16.76	1

for aerial web builders were similar to observed values. The family Linyphiidae was slightly more abundant in burn treated plots than in control plots before burning but after a drop in 2002, there was an increase that peaked in 2004 (Fig. 4a). Models overestimated Linyphiidae density in 2001 and underestimated it in 2004. None of the 11 species considered indicators could be modelled adequately because of the small number of collected individuals and only two showed burn-related trends. *Diploplecta duplex* (Fig. 4b) and *A. hilaris* (Fig. 4c) increased in density after the burning, especially in 2004. It is worth mentioning that *Sidymella angularis* (Urquhart, 1885), originally not considered an indicator species, disappeared in the burned plots after the burning (Fig. 4d).

IndVal identified species characteristic of the plots grouped into the four stages that were recognised in the NMDS and Ward's clustering analyses: control or pre-burn, post-burn 1, post-burn 2 and post-burn 3 (Figs. 5 and A2). No species was dominant in the entire study area, represented by samples collected in all plots and years. According to the analysis on abundance dissimilarity, plots with no history of burning were characterised by an ambusher, two stalkers, five web builders and a ground active species (*S. angularis, Hypoblemum* sp., Salticidae sp.2, *Parafroneta minuta* Blest, 1979, Theridiidae sp.4, Mysmenidae sp.1, *Rinawa cantuaria,* Anapidae sp.2 and *A. flavescens,* respecively), all of them with indicator values over 60 (Fig. 5). In contrast, four aerial web builders were significantly associated with plots where burning occurred (*Diplocephalus cristatus* (Blackwall, 1833) (Linyphiidae), *Erigone wiltoni* Locket, 1973 (Linyphiidae), *Steatoda lepida* (O. Pickard-Cambridge, 1879) (Theridiidae) and *Araeoncus humilis* (Blackwall, 1841) (Linyphiidae)), with the first three having the highest indicator values for this assemblage. Within the cluster of plots affected by burning, the analyses on abundance identified only species characteristic of the later stage in the post-burn succession: *Diplocephalus cristatus, Araeoncus humilis, A. hilaris* (ground active), *Steatoda lepida, Erigone wiltoni, Maorineta tumida* Millidge, 1988 (aerial web builder), *N. tapa* (ground active) and *Anzacia gemmea* (Dalmas, 1917) (ground active). Presence/absence-based analysis identified *Clubiona clima* Forster, 1979 (ground active) and *Tenuiphantes tenuis* (Blackwall, 1852) (aerial web builder) as characteristic of March 2001 summer-burn plots (Fig. A2).

As for the habitat specificity, the observed percentage of generalists was similar in control and burn treatments before the burning, despite annual fluctuations. After the burning, a pronounced increase occurred in 2002 in summer burned plots and in 2003 in spring plots. Generalist density reached its maximum values in 2004, in both burn treatments (Fig. 4e). Estimations for generalist density were similar to observed values (Fig. 4f).

3.3. Spring vs. summer burn

Different analyses gave contrasting results for the comparison of the two burn treatments. The NMDS and Ward's analysis on the abundance coefficient grouped summer and spring plots together before the burning but separately after (Figs. 1 and 2). In contrast, observed changes in spider diversity and density of different taxa were, in general, similar in spring and summer burned plots (Figs. 3 and 4). There were small differences between the two treatments in the density of individuals in 2001 (Fig. 3a), species in 2001 and 2005 (Fig. 3c), and the Shannon's index (Fig. 3e) and Linyphiidae (Fig. 4a) before and after the burning. The greatest differences between burn treatments were in the density of aerial web builders (Fig. 3f), *D. duplex* (Fig. 4b) and generalists (Fig. 4e) in 2003, with the highest values in summer plots.

4. Discussion

Despite the initial post-burn decrease in all diversity measures, spiders were present in all sampled plots immediately after the burning and they returned to pre-burn densities and diversity in the ensuing years. As colonisation of disturbed sites depends on their patchiness and distance from undisturbed areas (Thomas et al., 1990), the unburned areas surrounding the plots likely acted as the source of re-colonisation. In addition, as the vegetation recovers, the physical complexity may increase (Calder et al., 1992), affecting, in turn, spider composition (De Souza Teixeira and Parentoni Martins, 2005) by providing greater three-dimensional space for webs and number of different habitats (Malumbres-Olarte et al., in press). Given some pre-burn differences in spider communities between control and burn plots, it could be argued that stochastic variation in population dynamics may be a confounding factor when measuring post-burn differences between treatments. However, we found a range of successional changes caused by burning that go beyond a decrease and a subsequent increase in diversity.

4.1. Drivers and indicators of succession

Post-burn changes in spider species composition and relative abundance reflect changes in vegetation, microclimatic conditions and habitat availability that alter species interactions (Dennis et al., 2001; Moretti et al., 2002; Malumbres-Olarte et al., in press). Therefore species diversity and assemblages along the successional gradient should represent the ability of organisms to colonise or adjust to the new conditions (Langlands et al., 2011). This is
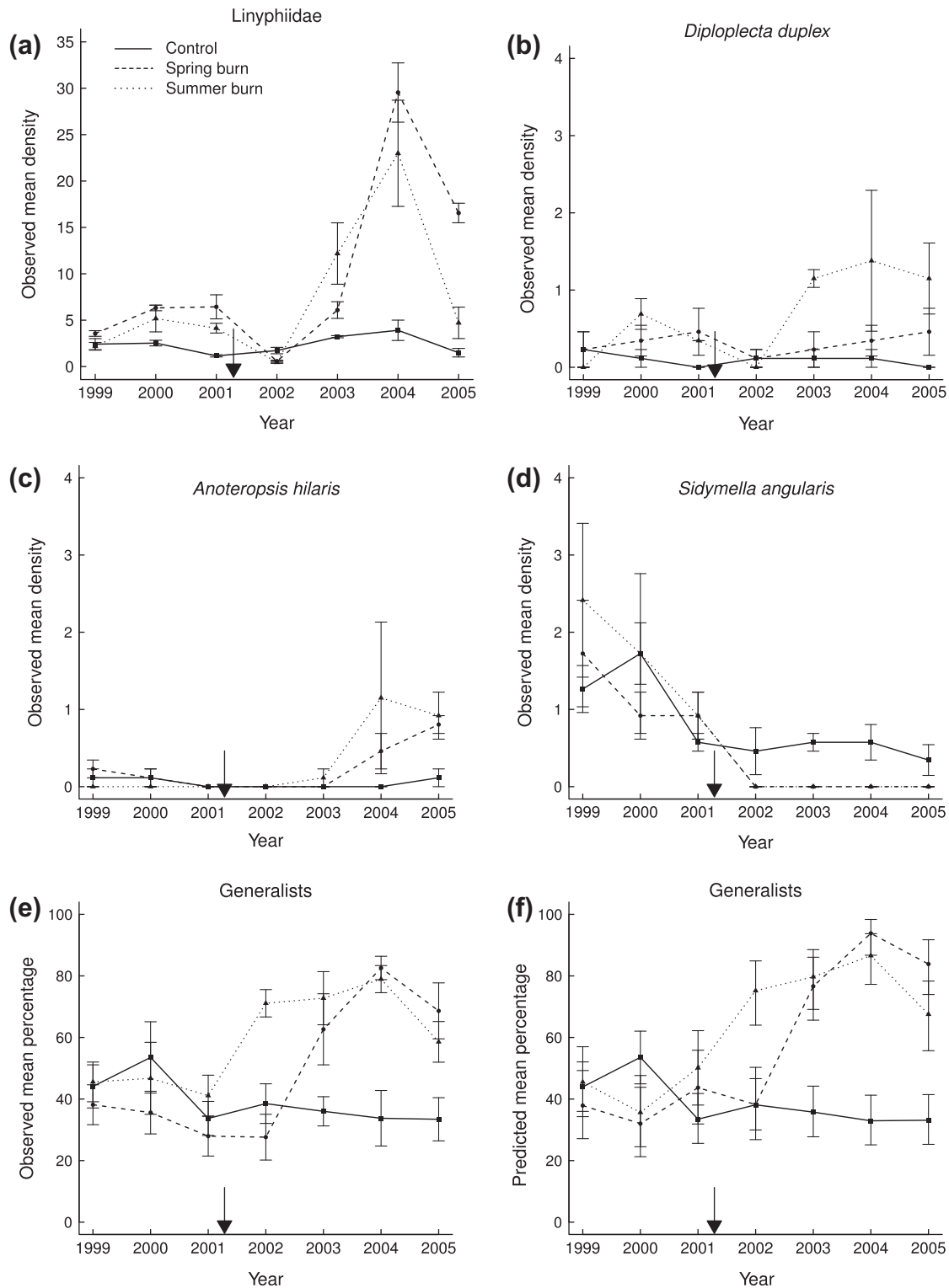
Fig. 4. Mean density m^{-2} (±SE) of observed (a–e) and modelled (f) indicator taxa and generalists in control plots (solid lines), spring-burn plots (dashed lines) and summer-burn plots (dotted lines) over the sampling years. The arrow indicates when spring and summer fires occurred (both between January 2001 and January 2002).

reflected by the post-burn dominance of ground active and aerial web building (mainly from the family Linyphiidae) species shown by the IndVal analysis and the increase in their density. Newly created open spaces are likely to favour the dispersal of ground active and web building species, which take advantage of the absence of obstacles that impede their movement on the ground or in the air via ballooning (Bell et al., 2005a). *Anoteropsis hilaris* (Lycosidae), for

example, will recolonize open spaces in tussock grasslands (Malumbres-Olarte et al., in press), as do other Lycosidae elsewhere (Brennan et al., 2006). The presence of *T. tenuis* and *C. clima* immediately after the summer burn may be due to their seasonal activity, which peaks in autumn, as well as their preference for disturbed conditions or open habitats left by burning (Moretti et al., 2002). Our observations suggest that *C. clima* is an efficient
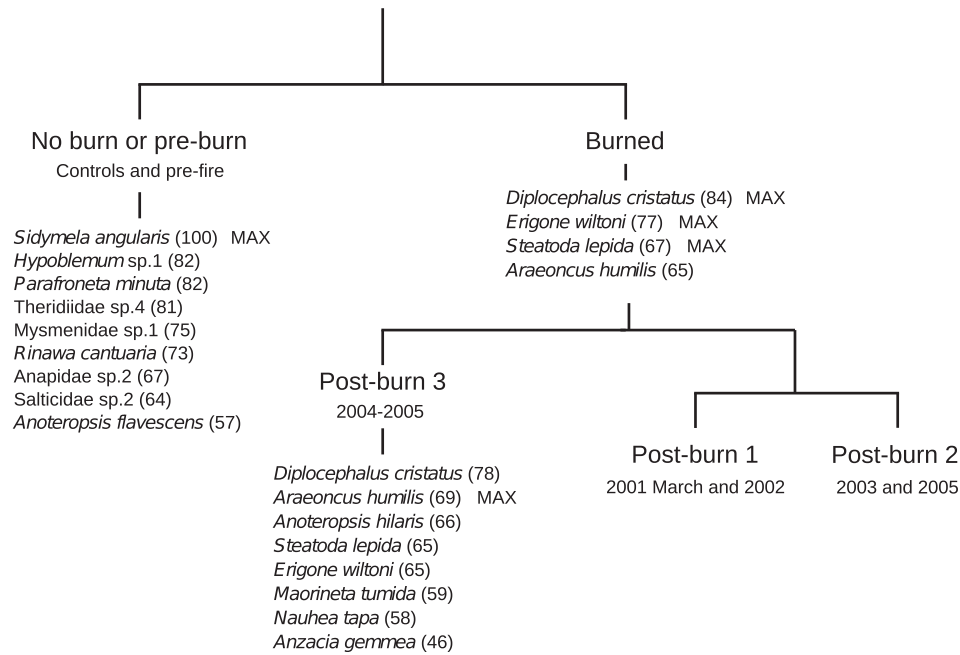
Fig. 5. Species characteristic of the succession stages. Each succession stage represents a set of plots grouped by Ward's clustering analysis on species abundance dissimilarity – see Fig. 2. Only species significantly associated ($p < 0.05$) with each cluster are shown. Indicator values of each species are shown within parentheses, with 'MAX' indicating the cluster where a given species had its maximum value.

disperser and therefore well-adapted for rapid colonisation of disturbed areas. This is probably due to its ability to balloon, as several *Clubiona* species have been recorded ballooning (Bell et al., 2005a) and the limited phylogenetic diversity in many New Zealand *Clubiona* species points to good dispersal ability in the genus (Malumbres-Olarte and Vink, 2012). Similarly, the exotic species *T. tenuis* is one of the most abundant colonisers of experimental grass swards and recently disturbed areas as a result of active ballooning (Haughton et al., 2001), and can survive in regularly disturbed areas and stay active all year (Topping and Sunderland, 1994).

In contrast, ambushers, stalkers and sheet web builders were only associated with unburned plots. *Sidymella angularis* (Thomisidae), an ambusher species that appears to favour undisturbed native ecosystems (Phil Sirvid, pers. comm.), was present in all unburned plots but absent in burned plots. This absence can be attributed to a reduction in humidity, leaf litter and number of plant species, such as ferns, that this species inhabits (Forster and Forster, 1999). Although widely distributed and a priori a good disperser, this species did not recolonise the burned plots. Therefore, it is possible that, under frequent burning regimes, species with poor dispersal abilities or/and restricted habitat requirements become locally extinct, unless unburned areas are preserved. Unfortunately, the identification of endangered tussock grassland spiders – and other invertebrates – is hindered by the lack of information about the distribution and habitat requirements, as is the case for most New Zealand spiders.

4.2. Habitat specificity: specialists vs. generalists

To our knowledge, this study is the first showing in detail the post-disturbance chronological changes in grassland spider communities in relation to habitat specialisation. Our results validate the hypothesis of a post-burn dominance of generalist species at the community level with qualitative and quantitative evidence. First, six specialist species were associated with unburned or pre-burn plots: a foliage specialist (*S. angularis*); litter specialists (*P. minuta*, *R. cantuaria* and probably the undescribed species Anapidae sp.2); and tussock specialists (*A. flavescens* and the species Mysmenidae sp.1). The undescribed species Theridiidae sp.4 and Salticidae sp.2, also appear to be specialists, given their habitat preferences, although this is yet to be confirmed. Generalist species like *D. cristatus*, *E. wiltoni*, *A. humilis*, *M. tumida*, *S. lepida*, *A. gemmea*, *N. tapa*, *A. hilaris* abounded in burned areas. Second, generalist density increased remarkably a year and 2 years after the burning in summer and spring burned plots, respectively. The density of *A. hilaris*, for instance, increased in burned plots. We suggest that unburned areas, with greater plant diversity and complexity, greater range of environmental conditions and more abundant prey, provide spiders with more resources to exploit, and allow for a more diverse spider community containing many specialist species. In contrast, post-burn conditions may constrain the access of specialists to certain resources that are eliminated or reduced by the burning. Such circumstances would allow generalist species that are capable of using alternative resources to outcompete specialists and dominate, especially when the former have greater dispersal abilities. One of our concerns is the fact that four out of the eleven dominant species in burned areas are exotic. This leaves the question of whether their dispersal ability and generalist character is not only allowing them to successfully invade altered native ecosystems but, perhaps, to also compete with native species, causing longer lasting changes in the community composition.

4.3. Spring vs. summer burn

There were no overall differences in spider diversity between spring and summer-burn treatments. Previous work in the same location also found no differences in the effects of burning on beetles and overall number of invertebrates between spring and summer burns (Barratt et al., 2009). As spiders depend directly on plant biomass (Malumbres-Olarte et al., in press), they may not show differences because biomass loss after each burning was similar (75.4% in spring and 74.4% in summer) (Payton and Pearce, 2009). In theory, spring burn plots could be less diverse because: (1) the recorded ground surface temperatures were twice as high

in the spring burning than the summer burning and (2) there was less time for recovery in spring plots — sampled three months after the burning — than in summer plots — sampled after ten months. The latter may explain the greater initial increase in the density of aerial web builders and generalists in 2002, and Linyphiidae, in 2003 in summer plots. In general though, the effects of these two factors may have been compensated by a greater detrimental effect of summer burnings. The soil and the vegetation in the study area were drier, and fire intensity greater during summer than during spring (Payton and Pearce, 2009). The number of reproductively active adults increases in tussock grasslands as summer progresses (J. Malumbres-Olarte, unpublished data) and a disturbance at this critical life stage could have a severe effect on future populations.

Our experimental design provides pre- and post-burn invertebrate data vital for the understanding of the recovery and for the management of endemic tussock grasslands, including the identification of indicator species. Mark (1994) pointed out the need for indicators of the condition and trend of the vegetation in rangelands – including modified tussock grasslands – for the application of the legislation (Resource Management Act 1991) and the continuing use of their resources. Indicators based on plant characteristics have been suggested (Gitay et al., 1992) but a comprehensive assessment of the state of the ecosystem requires knowing the condition of the other key components of the trophic web, such as invertebrate herbivores and predators. The indicators of the community structure and recovery that we identify here are based on our findings that adaptations, such as habitat specificity and dispersal ability, influence local extinction and recolonisation of spider communities. For example, *D. cristatus*, A. *humilis*, *E. wiltoni* and *A. hilaris* could be used to delimit the early stages of recovery and *S. angularis*, *Hypoblemum* sp.1, *P. minuta*, *Mysmenidae* sp.1 and *A. flavescens* to detect signs of recovery in the community. Furthermore, some of them, like *A. hilaris* and *A. flavescens* have already been identified as indicators of plant diversity and composition in tussock grasslands (Malumbres-Olarte et al., in press). These indicators can also be seen as warning signs of the simplification of spider community, and perhaps the local extinction of specialist species, driven by the dominance of generalists, which is likely to have happened in other taxa that are considered highly specialist. This process may be occurring at a larger scale, both in magnitude and space, given the high levels of endemicity in other taxa from New Zealand tussock grasslands, and the elimination or modification of large areas around the country. We hope that future programs for monitoring tussock grassland recovery will consider using the spider taxa that we suggest as ecological indicators.

4.4. Repercussions for conservation

Time of burning may interact with other factors, including flammability and fire intensity, reducing differences in the effects of human-induced fire in different seasons, and we suggest a precautionary approach when choosing the time for burning, whether it is for conservation or agricultural purposes. Burning has been proposed as a tool for maintaining water yield and for the conservation of tussock vegetation by preventing invasion of shrubs and exotic plants (Calder et al., 1992). At this stage, we do not believe that this approach is applicable everywhere as our findings indicate a detrimental effect of burning on the native invertebrate species. Also, it is likely that there were short-term negative effects on vertebrates, such as skinks and birds, whose diet is based on invertebrates. Long term studies on multiple taxa may confirm these conclusions and provide data for species prioritisation and the selection of the adequate burning regime in each case. When used for agricultural production, we recommend favouring spring over summer burns, provided that they are wetter, to facilitate control, prevent overburning and to create or preserve patches of native vegetation that are necessary to foster recolonisation, especially by poor disperser or specialist species. Farmers will continue to utilise planned burns, so it is necessary from a conservational perspective to use these experimental studies to find evidence for ecological benefit from small changes in land management, such as the creation of small refugia.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.bio-con.2013.01.004. These data include Google maps of the most important areas described in this article.

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