The role of habitat complexity on spider communities in native alpine grasslands of New Zealand

JAGOBA MALUMBRES-OLARTE,[1] COR J. VINK,[2,3] JAMES G. ROSS,[1] ROBERT H. CRUICKSHANK[1] and ADRIAN M. PATERSON[1] [1]Department of Ecology, Faculty of Agriculture and Life Sciences, Lincoln University, Christchurch, New Zealand, [2]Biosecurity Group, AgResearch, Lincoln Science Centre, Christchurch, New Zealand and [3]Entomology Research Museum, Lincoln University, Christchurch, New Zealand

Abstract. 1. Physical structure and species composition of vegetation determine spider diversity through habitat availability. Here, we assess, for the first time, the role of plant structure on spider communities in New Zealand native alpine tussock grasslands. We investigate the specific associations between spider assemblages and plant communities and test the hypothesis that spider diversity increases with plant diversity and tussock cover.

2. Spiders were sampled using density- and abundance-activity-dependent methods. Data on physical characteristics and species composition of plants revealed gradients in vegetation, driven by distinct intra-ecosystem plant communities. Effects of vegetation on spider diversity and composition were assessed through linear mixed-effects models. Redundancy analysis was used to determine and visualise the spider species–level response to gradients in plant compositions.

3. There was a positive relationship between plant diversity and spider diversity, while the effects of tussock cover varied with spider taxa. Overall, physical structure and species composition of vegetation had effects on the abundance of a similar number of spider species and families.

4. Gradients in vegetation were matched to gradients in spider communities, whose diversity and composition varied according to their habitat preference. The family Orsolobidae was associated with wetland vegetation, and Linyphiidae with shrubs. The abundance of certain spider families and species, such as Lycosidae and *Anoteropsis hilaris*, was consistently affected by vegetation.

5. Environmental factors, such as soil moisture, may affect plant species composition and physical structure in tussock grasslands, which in turn determine spider assemblages. Lycosidae were identified as potential indicators of structural changes in tussock grassland plants and could be valuable for ecological monitoring in conservation management.

Key words. Gradients, habitat, management, New Zealand, physical structure, plant diversity, spiders.

Introduction

As a major element of global biodiversity (Wilson, 1987; Chapman, 2009), arthropods provide fundamental functions in natural and modified ecosystems (Beare *et al.*, 1992; Bradford *et al.*, 2002), and they are increasingly being used in nature conservation management (Schmidt *et al.*, 2008). For this purpose, however, it is necessary to understand the interactions between arthropods and their physical and biotic environment (Murray *et al.*, 2006). Such interactions have been the topic of much research (Pimentel, 1961; Price *et al.*, 1980; Stein *et al.*, 2010), with some of it focused on taxa, such as spiders, with key ecological functions (Birkhofer *et al.*, 2008; Diekötter *et al.*, 2010).

Correspondence: Jagoba Malumbres-Olarte, Department of Ecology, Faculty of Agriculture and Life Sciences, Lincoln University, PO Box 94, Lincoln 7647, New Zealand. E-mail: jagoba. malumbres.olarte@gmail.com

As generalist predators, spiders (Araneae) play a major role in terrestrial ecosystems (Wise, 1993; Romero & Harwood, 2010). Spiders have a significant effect on invertebrate herbivore pests (Sunderland, 1999); their wide range of predatory behaviours allow them to occupy a variety of niches (Wise, 1993), and species distribution and assemblages are influenced by environmental conditions (Ziesche & Roth, 2008) and natural or human disturbances (Doran *et al.*, 1999; Buddle *et al.*, 2000; Noel & Finch, 2010). These characteristics of spiders, along with their ubiquity and ease of collection, make them appropriate indicators of ecological changes (Churchill, 1997), the effects of land management (Downie *et al.*, 1999), prey availability and habitat quality (see Marc *et al.*, 1999 for a review).

Plant architecture or physical complexity can determine spider species diversity and composition (see Uetz, 1991 and Langellotto & Denno, 2004 for reviews). Structurally diverse vegetation increases the number of available habitats, providing niches that correspond to different foraging techniques (Greenstone, 1984; Dennis *et al.*, 1998) and offering protection from vertebrate predators (Gunnarsson, 1990). Botanical composition of the vegetation may also determine spider assemblages by affecting the abundance of herbivore prey associated with specific plant species (plant–host associations) (Dennis *et al.*, 2001), while spider communities can enhance plant diversity by exerting control over invertebrate herbivores (Schmitz, 2003). Some studies (Dennis *et al.*, 1998; Jimenez-Valverde & Lobo, 2007) have supported the habitat heterogeneity hypothesis (Hart & Horwitz, 1991), which predicts an asymptotic increase in arthropod abundance and number of species with greater plant structural heterogeneity and species richness.

Plant–spider relationships have been investigated in grasslands (Dennis *et al.*, 2001). However, this is the first study that looks explicitly at spider diversity patterns in relation to the physical and compositional characteristics of vegetation in high-altitude native New Zealand tussock grasslands. Although New Zealand tussock grasslands have been the subject of much ecological research, this has mainly focused on conservation values, and the ecological, economic and ecosystem functions of their botanical components (e.g. Mark, 1969; Bulloch, 1973; Jensen *et al.*, 1997; Brockerhoff *et al.*, 2008; Mark *et al.*, 2009). Invertebrate biodiversity patterns in tussock grasslands and their response to human modification and disturbance are still poorly known (Barratt *et al.*, 2005, 2009). With a few exceptions (White & Sedcole, 1993; Murray *et al.*, 2006; Hay *et al.*, 2008; Kelly *et al.*, 2008), there is little information on the interactions of invertebrates with their physical environment or the botanical component. Such research could provide valuable information for conservation management as the protection of certain endangered invertebrate species may depend on preserving or enhancing particular vegetation types.

The objective of this study is threefold: (i) to test the hypothesis that spider diversity increases as plant diversity, and/or tussock cover and density increase, (ii) to evaluate the effects of the physical characteristics versus the botanical composition of the vegetation on spider communities, and (iii) to identify the spider assemblages associated with the different vegetation types or plant communities present in tussock grasslands.

Methods

Sampling was conducted within Te Papanui Conservation Park (45°40′S 169°45′E), on the Lammermoor and Lammerlaw ranges in Central Otago, South Island, New Zealand. This livestock-free park is regarded as an area of high ecological and landscape value as well as economically important because of its water catchment function for the nearby city of Dunedin (Department of Conservation, 2009).

Altitude in the park ranges between 420 and 1150 m, and the mean annual temperature and rainfall vary with altitude between approximately 4 and 8 °C, and 1000 and 2000 mm, respectively (NIWA, National Institute of Water and Atmospheric Research, 2003a,b). Most of the ranges are part of an alpine plateau and although shrubby and wetland vegetation is also present in scattered patches around alpine ponds, narrow-leaved snow tussock [*Chionochloa rigida* (Raoul) Zotov] up to 1.5 m high is the dominant vegetation. Snow tussock is characterised by a compact base formed by tightly packed leaves and an open dome-shaped top. This shape allows the collection of moisture from the leaves and its retention in the base.

Data and sample collection

Tussock grasslands are often a mosaic of areas with different types of vegetation and levels of tussock density. After an initial selection of potential study sites that included a range of vegetation covers, five sites were chosen randomly from them. Sites were located within 500 m either side of the mountain track that runs through the centre of the park in order to minimise time taken for sample collection and transport to the vehicle. Five circular plots were set up in the shape of an 'X' within each site, with one plot in each corner and one in the centre. Within each site, the distances between the centres of the corner plots and the centre plot, and between the centres of the corner plots were 50 and 70.7 m, respectively. Each plot had an area of 400 m^2 (radius of 11.3 m).

Spiders were collected by turf extraction and pitfall trapping, which had previously been found to be an effective sampling method for spiders in tussock grasslands (Malumbres-Olarte, 2011). Turf samples were collected randomly from the outer area of each plot avoiding an inner circle of 6 m radius in order to prevent disturbance effects on the capture of pitfall traps, which were placed in the centre of each plot. The turf sampling unit was 0.1 m^2, and extraction of spiders using heated Tullgren funnels was carried out as described by Barratt *et al.* (2005). One pitfall trap was set up per plot, giving five traps per site for a total of 25 traps. Each trap consisted of a metallic cylinder with a pot, 8 cm in diameter and 9 cm high, and a 15 × 15 cm metal roof to prevent plant litter and rain from falling into the trap. Monopropylene glycol was used in pitfall traps as it prevents captured specimens from drying out in the field and adequately preserves specimens for later molecular analyses (Vink *et al.*, 2005). These two sampling methods were used in combination in order to obtain a more complete picture of spider assemblages. Turf samples provided information about the density of spiders, whereas

pitfall traps targeted ground-active and nocturnal species that may not have been captured by turf sampling.

Adult spider specimens were identified morphologically using available taxonomic literature (Forster, 1970; Forster & Wilton, 1973; Forster, 1979; Forster & Platnick, 1985; Forster *et al.*, 1988; Vink, 2002; Paquin *et al.*, 2010), following the classification of Platnick (2011), and using DNA analyses as an additional tool (see Appendix S1 in Supporting Information for methods and criteria). Juvenile specimens were not identified to species or family, because of the lack of necessary taxonomic information, but were counted for the analyses of the total number of spider individuals. Specimens were stored in 95% ethanol and kept at −20 °C. At each plot, three turf samples were collected and one pitfall trap emptied seven times, once every 2 weeks, during the summer of 2007/2008 between December and March in order to cover the most active period of the year for spiders. Three additional turf sample collections were conducted in December 2008, and January and February 2009. In the field, from each turf sample, data were collected on a set of variables representing physical and botanical characteristics of the vegetation and the plots: (i) basal area, (ii) mean height, (iii) maximum height, (iv) per cent cover and (v) number of tussocks, and per cent cover of (vi) plant litter, (vii) woody plants, including shrubs and other plants with secondary growth, (viii) lichens, (ix) mosses and (x) other plants. Percentage covers of plants and litter were measured per $0.1 \ m^2$ using a 31.7×31.7 cm metal quadrat, whereas basal area and height of vegetation were measured using a diameter tape and a measurement pole, respectively. Altitude and slope of plots were also recorded. A study of the plant species composition was conducted in March 2009 to estimate the per cent cover of each species in the study plots. A total of fifteen $0.1\text{-}m^2$ quadrats ($1.5 \ m^2$) were surveyed per plot.

Statistical analyses

The area used as sample unit in all analyses of turf data was $1.5 \ m^2$. As the analyses focused on the plot level, all samples collected from the same plots throughout all sampling dates were pooled separately for turf and pitfall samples and then their mean was calculated for an area unit of $1.5 \ m^2$ (15 quadrat samples) and individual pitfall trap, respectively, prior to any analyses. Pearson correlation coefficients revealed strong correlations between a number of variables related to tussock presence or abundance, such as tussock cover, height of the vegetation and litter cover, and woody plant cover. Therefore, data were reduced by combining correlated and non-correlated variables through principal component analyses (PCA) to create new composite variables that represent trends or gradients in the variables that they explained best. The variables included in the PCA were the 10 variables recorded in turf samples, plot slope, plant species richness, and the Shannon's *H′* and Simpson's *D* diversity indices for plant species. Principal component analyses was selected because of the mostly linear relationships between these variables (Legendre & Legendre, 1998; McCune & Grace, 2002). By reducing data, information from such explanatory variables can be retained while avoiding collinearity between them, which can sometimes hinder interpre-

tation and analysis of ecological data (Graham, 2003). The new composite variables can then be used in analyses, such as linear regression models or ANOVA (Ellison *et al.*, 2004; Boyer & Fong, 2005; Beals, 2006), by using the values of the sites, or plots in the case of this study, on the principal components. Before performing the PCA on the physical and botanical characteristics of the vegetation ($PCA_{physical}$), data were standardised and pooled per plot and the mean calculated per unit area. The first component (PC1, explained variance = 52%) was strongly negatively correlated with variables related to tussock abundance, such as tussock cover (−0.91), litter cover (−0.91) and maximum vegetation height (−0.82), and positively with woody plant (0.86) and moss (0.75) cover. The second component (PC2, explained variance = 18.3%) correlated positively with plant species richness (0.84), and Shannon's *H′* (0.66) and Simpson's *D* diversity indices (0.63). Hence, PC1 was considered to represent a gradient from tussock-dominated areas to areas with shrubby vegetation (tussocks-to-shrubs gradient), and PC2 a gradient from species-rich to species-poor areas (plant diversity gradient). Another PCA was conducted on the per cent cover for each plant species in each plot, per unit area ($PCA_{botanical}$). Plant species with a total cover equal to or lower than $0.025 \ m^2$ (0.0667% of the total area) were excluded from the analysis. The values of the remaining species were subjected to square root ($x + 0.5$) transformation to reduce the weight of dominant species, and to Hellinger transformation to give low weights to rare species (Legendre, 2001). These transformations were conducted to ease the interpretation of gradients and to reduce the effects of such species on following analyses as they were not considered to indicate the environmental conditions that this study was focused on. The produced PCA provided axes based on the values of the principal components that showed gradients in plant composition. The first component (explained variance = 59.2%) of this second PCA was positively correlated with wetland plant species such as *Kelleria dieffenbachii* (Hook.) Endl. (0.98) and negatively with *C. rigida* (tussock) (−0.86). Therefore, the first component was regarded as the representation of a gradient from tussock to wetland vegetation–dominated areas (tussocks-to-wetland gradient). The second component of $PCA_{botanical}$ (explained variance = 11.3%) was considered to represent a gradient between areas with many to few shrubby plants (shrub abundance gradient) as it was positively correlated with shrub species, such as *Coprosma petriei* Cheeseman (0.80) and *Coprosma perpusilla* Colenso (0.80). The first principal component of $PCA_{physical}$ (tussocks-to-shrub) and PC1 of $PCA_{botanical}$ (tussocks-to-wetland) gradients were positively correlated (0.88) with each other. A nonlinear redundancy analysis (RDA) (Makarenkov & Legendre, 2002) was carried out to explore the effects of the physical and botanical characteristics of the study plots on spider assemblages. The final model was built through forward selection of terms from non-correlated physical variables of plots and the first two axes of $PCA_{botanical}$, which represented the tussocks-to-wetland and the shrub abundance gradients in vegetation. An ANOVA like permutation test (1000 permutations)

was conducted to test for the significance of the constraints under a reduced model followed by a partial RDA to obtain the variance explained by each term.

As the nested design did have an effect on spider assemblages, linear mixed-effects models were constructed for three groups of response variables: (i) total number of spider individuals (adults and juveniles), species richness and family richness (both based on adult specimens), (ii) number of adult spider individuals per family, and (iii) number of adult spider individuals per species. Models included the random effects of sites and three sets of explanatory variables as fixed effects: (i) the values of the first two principal components obtained in PCA$_{physical}$; (ii) the values of the first two principal components obtained in PCA$_{botanical}$; and (iii) the values per plot of the variables included in the first PCA. Using PCA components as explanatory variables in the models allows the analysis of the changes in the response variables in relation to detected gradients, giving a broader view of the patterns of spider assemblages than that provided by individual explanatory variables. Minimal adequate models were initially identified by forward selection of variables using Wald tests (Agresti, 2002). Where there were several similar models, their corrected Akaike information criterion (AICc) scores were utilised to select the most parsimonious model (Burnham & Anderson, 2002). All data analyses were carried out using the software R 2.11.1 (R Development Core Team, 2010) and Gen-Stat 12 (Payne *et al.*, 2009) for the linear mixed-effects models.

Results

A total of 14 465 spider specimens, of which 2119 were adults belonging to 29 described species and an additional 24 morphospecies from 18 families, were collected through turf extraction during the two sampling seasons. Pitfall traps captured 3634 individuals, of which 1137 were adults of 20 species and 13 morphospecies from 15 families.

Spider diversity in relation to plant diversity and tussock cover

Mixed-effects models based on turf data showed an increase in the number of spider individuals along the gradient from tussock to shrub-dominated areas (PC1 of PCA$_{physical}$) (Fig. 1 and Table S1), whereas pitfall data indicated that this increase occurs as the tussock cover becomes greater (Table 1). Spider species and family richness increased along the gradient in plant diversity (PC2 of PCA$_{physical}$) (Fig. 1) in the tussock grassland under study. Turf data models found that along the tussocks-to-wetland gradient (PC1 of PCA$_{botanical}$), family richness increased with tussock cover and the number of spider individuals was greater in areas dominated by wetland vegetation (Fig. 2 and Table S2). Pitfall trap data indicated that spider species richness and family richness were lower in areas with abundant shrubs (Fig. 2). The analyses of individual variables and turf sample data indicated an increase in the number of spider individuals, and species and families richness (Table 1) with greater plant species diversity. The same data also showed that there was a positive effect of woody plant cover on the number of spider individuals and of tussock cover on spider species and families richness (Table 1).

Physical characteristics vs. botanical composition of the vegetation

The same number of spider species showed positive and negative responses in abundance to the tussocks-to-shrubs gra-
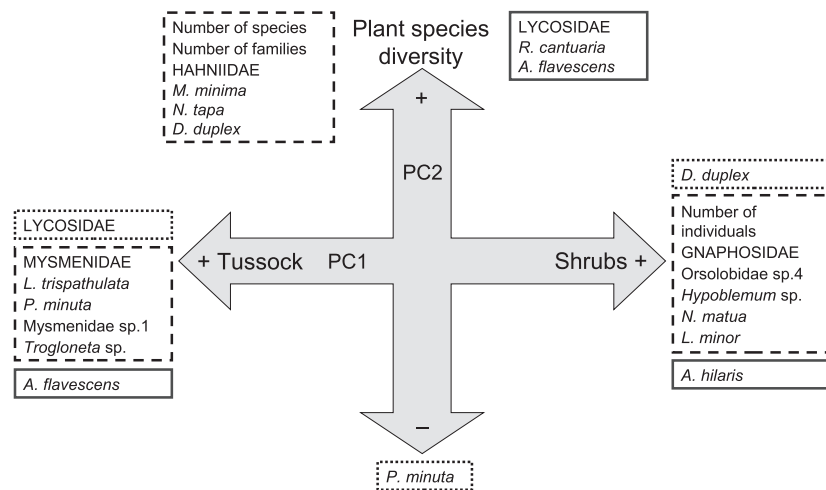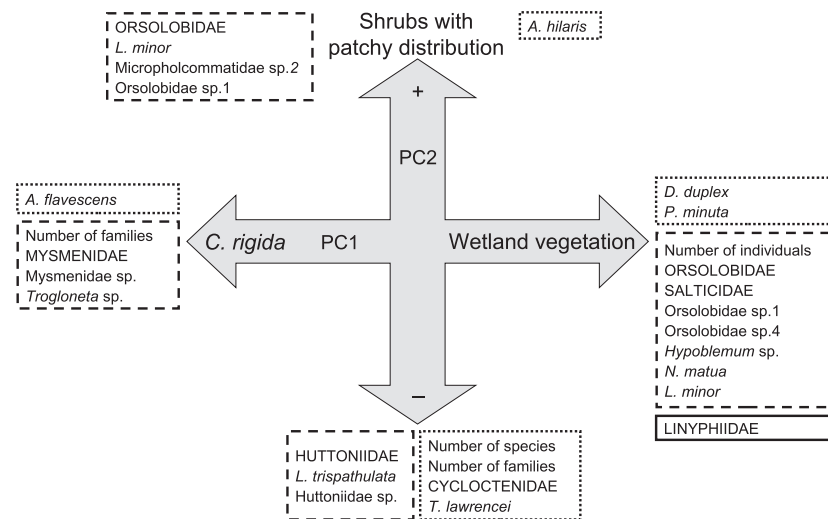

Fig. 1. Summary of the effects of the physical gradients in vegetation on spider abundance at species and family levels. Arrows represent PC1 (tussocks-to-shrubs gradient) and PC2 (plant diversity gradient) of PCA$_{physical}$. Spider richnesses and taxa presented in boxes showed a significant increase in abundance ($P < 0.05$) in response to the vegetation gradients represented by PC1 and PC2, as detected from the analyses of turf data only (dashed line), pitfall data only (dotted line) or both (solid lines). Spider families are in capital letters, and species in lower case.

Table 1. Effects of individual physical and botanical characteristics of the vegetation on the number of spider individuals, species, families, and the number of individuals of each family obtained through linear mixed-effects models.

Response variable (transformation)	Explanatory variable	Average effect	Std. error	Wald statistic	n.d.f.	F statistic	d.d.f.	F pr
Turf samples								
(a) Spider diversity								
Number of individuals (L)	Woody plant cover (%)	0.603	0.251	5.77	1	5.77	22.6	0.025
	Number of plant species	0.037	0.012	9.65	1	9.65	19.9	0.006
Number of species (LI)	Tussock cover (%)	0.9123	0.2078	19.28	1	19.28	3.3	0.018
	Simpson's D	0.58	0.206	7.91	1	7.91	21.1	0.01
Number of families (LI)	Tussock cover (%)	0.8813	0.1255	49.29	1	49.29	3.2	0.005
	Simpson's D	0.44	0.143	9.48	1	9.48	20.4	0.006
(b) Spider families								
Agelenidae (SQ)	Mean height (m)	−5.644	2.025	7.76	1	7.76	22.8	0.011
Gnaphosidae (SQ)	Simpson's D	0.794	0.194	16.74	1	16.74	22.7	< 0.001
Linyphiidae ((LI)	Woody plant cover (%)	1.208	0.374	10.43	1	10.43	21.7	0.004
Lycosidae (LI)	Tussock cover (%)	2.46	0.3871	22.64	1	22.64	4.2	0.008
	Simpson's D	1.402	0.327	18.39	1	18.39	11.7	0.001
Mysmenidae (LI)	Woody plant cover (%)	−1.674	0.2402	48.57	1	48.57	3.6	0.003
Orsolobidae (LI)	Woody plant cover (%)	2.686	0.803	11.2	1	11.2	22.2	0.003
Salticidae (SQ)	Woody plant cover (%)	1.047	0.3054	11.76	1	11.76	5.6	0.016
Pitfall traps								
(a) Spider diversity								
Number of individuals (L)	Tussock cover (%)	4.2	0.615	46.7	1	46.7	3	0.006
(b) Spider families								
Linyphiidae (SQ)	Tussock cover (%)	−1.568	0.655	5.74	1	5.74	9.9	0.038
Lycosidae (LI)	Tussock cover (%)	3.051	0.772	15.62	1	15.62	3.1	0.027

Data obtained from turf and pitfall samples. Only explanatory variables from the selected best fitting models are shown. Values of F pr indicate change in deviance when variables are dropped from the full model. Transformations: $L = \log(x)$, $LI = \log(x+l)$, $SQ = \mathrm{sqrt}(x + 0.5)$.

Fig. 2. Summary of the effects of the botanical composition of the vegetation on spider abundance at species and family levels. Arrows represent PC1 (tussocks-to-wetland gradient) and PC2 (shrub abundance gradient) of PCA$_{botanical}$. Fonts and box lines as indicated in Fig. 1.

dient, according to the selected models (Fig. 3). Models including the variable representing a gradient in plant species diversity only showed positive effects (Fig. 3) and models on the tussocks-to-wetland and shrub abundance gradients had more positive effects on spider species than negative effects. Overall, physical characteristics of the vegetation, such as tussock and
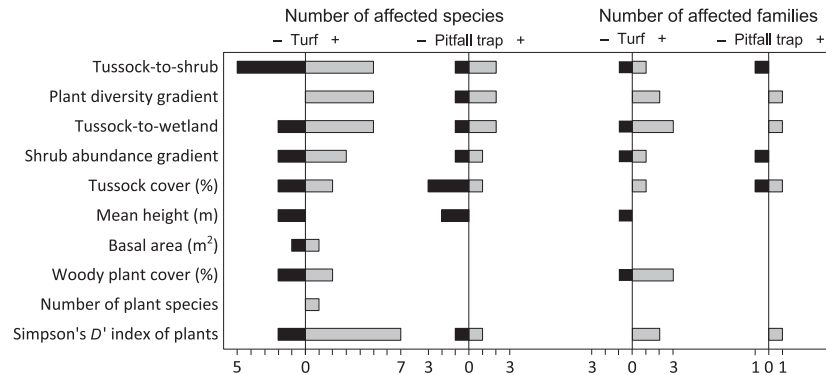
Fig. 3. Number of species and families affected by the detected gradients in vegetation and the individual physical and botanical characteristics. Only species and families used in the best-fitting models based on data from turf and pitfall samples are included. Bar lengths are equivalent to the number of either species or families affected by each explanatory variable. Black and light grey bars represent negative and positive effects, respectively.
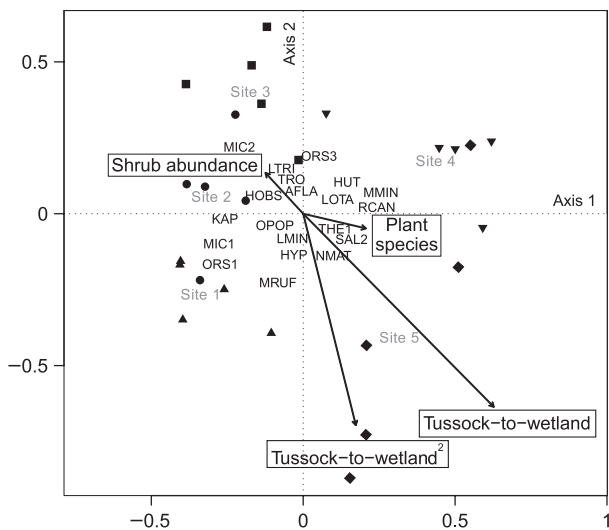

Fig. 4. Redundancy analysis ordination diagram of the effects of the vegetation on spider assemblages. The ordination shows the significant continuous variables (arrows), the factorial variable (site names in grey), plots from site 1 (triangles), site 2 (circles), site 3 (squares), site 4 (inversed triangles) and site 5 (rhombuses), and species with large abundances in the direction of either or both axes. Species are represented by abbreviations: *Anoteropsis flavescens* = AFLA, Huttoniidae sp. = HUT, *Hyperafroneta obscura* = HOBS, *Hypoblemum* sp. = HYP, *Kapanga* sp. = KAP, *Laestrygones otagoensis* = LOTA, *Laetesia minor* = LMIN, *Laetesia trispathulata* = LTRI, *Mahura rufula* = MRUF, *Metafroneta minima* = MMIN, Micropholcommatidae sp.1 = MIC1, Micropholcommatidae sp.2 = MIC2, *Neoramia matua* = NMAT, *Orepukia poppelwelli* = OPOP, Orsolobidae sp.1 = ORS1, Orsolobidae sp.3 = ORS3, *Rinawa cantuaria* = RCAN, Salticidae sp.2 = SAL2, Theridiidae sp.1 = THE1, *Trogloneta* sp.1 = TRO.

woody plant cover, and Simpson's *D* index of plant species, had effects on similar numbers of spider families and species (Fig. 3).

Associations between spiders and vegetation type

A number of response variables had strong relationships with tussocks-to-shrubs and plant species diversity gradients. Among all the physical and botanical variables included in $PCA_{physical}$, those that appeared to have the greatest effect on the response variables when selected individually were tussock cover, woody plant cover and Simpson's *D* (Table 1). On the whole, more significant relationships were detected in the analysis of turf data compared to pitfall data.

Analyses of the data from turf samples revealed a series of responses of Gnaphosidae and Mysmenidae to the characteristics of the vegetation. The number of Gnaphosidae individuals showed a positive relationship with the tussocks-to-shrubs gradient (Fig. 1) and the Simpson's *D* index of plant species diversity (Table 1). Mysmenidae were more abundant in tussock areas, according to models that included the tussocks-to-shrubs (Fig. 1) and the tussocks-to-wetland gradients as variables (Fig. 2). The numbers of Mysmenidae had a negative relationship with woody plant cover (Table 1). Linyphiidae showed a positive relationship with the tussocks-to-wetland gradient, which was confirmed by both turf and pitfall data (Fig. 2), and with woody plant cover (Table 1). Turf data identified an increase in the number of Orsolobidae as wetland vegetation and shrubby species became more abundant, according to the tussocks-to-wetland and shrub abundance gradients, respectively (Fig. 2). The number of Orsolobidae and Salticidae also increased with woody plant cover (Table 1). Pitfall trap data indicated an increase in the number or activity of Lycosidae along the gradient towards tussock areas (Fig. 1), which was supported by the models including tussock cover as a separate explanatory variable (Table 1). According to the turf data, the number of Lycosidae had a positive relationship with Simpson's *D* index of plant species diversity (Table 1).

The two gradients identified by $PCA_{botanical}$ showed different relationships with different spider species. For instance, *Anoteropsis hilaris* (L. Koch, 1877) was positively affected by the gradient in abundance of shrubs, and *Anoteropsis flaves-*

cens L. Koch, 1878 negatively affected by the tussocks-to-wetland gradient (Fig. 2), according to pitfall data. The number of *Rinawa cantuaria* Forster, 1970 was greater in botanically more diverse areas, *A. hilaris* was more abundant in shrubby areas, and *A. flavescens* increased with tussock cover. These trends were revealed by both sampling methods (Figs. 1,2). A number of spider species showed an increase in abundance with tussock cover and Simpson's *D* index (Fig. 3). The full list of the effects of the four identified gradients represented by the two-first components of $PCA_{physical}$, $PCA_{botanical}$ and individual variables on spider families and species can be seen in Tables S3–S5.

In the RDA that modelled the response of spider species assemblages to the physical and botanical characteristics of plots, constraints explained 58.2% of the variance, of which RDA1, RDA2 and RDA3 explained 33.4%, 21.1% and 17.1%, respectively (Fig. 4). The variables included in the final model of the RDA were the tussocks-to-wetland gradient ($F = 5.4426$, $P = 0.001$, explained variance = 14.2%), the quadratic term of the same gradient ($F = 4.3491$, $P = 0.001$, explained variance = 9.7%), the shrub abundance gradient ($F = 1.8168$, $P = 0.032$, explained variance = 5.2%), plant species richness ($F = 1.9957$, $P = 0.011$, explained variance = 6.7%) and site ($F = 2.1693$, $P = 0.001$, explained variance = 40.6%).

Discussion

Gradients in vegetation

The results of this study show the heterogeneity in the physical structure and botanical composition of the vegetation in tussock grasslands. Plant communities dominated by tall tussocks and large amounts of litter, shrubs or woody vegetation and plants typical of wetlands are represented in the study area. The shrub areas are dominated by *Gentiana grisebachii* Hook.f., *Lycopodium fatigiatum* R.Br., *Gaultheria depressa* Hook.f., *C. petriei* and *C. perpusilla*, all of which, except for the first, have a patchy distribution in alpine tussock grasslands (C. D. Meurk, pers. comm.). The tussocks-to-wetland gradient placed tussocks on one end and the species *Astelia linearis* var. *novae-zelandiae* Skottsb., *Carpha alpina* R.Br., *Euprasia* sp., *Gentiana bellidifolia* Hook.f., *Veronica odora* Hook.f., *Kelleria dieffebachii* (Hook.) Endl. and *Oreobolu pecinatus* Hook.f. on the other. The presence of these seven plant species, typical of moist or marshy environments, appears to reflect a gradient in the drainage or moisture conditions of the soil. Resemblance in the response variables affected by the tussocks-to-shrub and the tussocks-to-wetland gradients may be explained by the high correlation between the two components and the fact that both of them were negatively correlated with tussock (*C. rigida*) cover. These gradients confirm what was observed in the field. The study area in the Lammermoor and Lammerlaw ranges are mostly covered by tussocks with scattered patches of marshland or boggy vegetation on water logged soils, and shrubby or woody vegetation in gullies or areas where tussocks have not established.

Spider diversity in relation to plant diversity and tussock cover

The hypothesis that spider diversity is greater in areas with higher tussock cover or density and in areas with greater plant diversity is supported by the data from turf samples. The positive effect of tussock cover on spider species and family richness indicated by modelling of individual variables, and the tussocks-to-wetland gradient in the case of family richness, suggested that tussock cover determines spider diversity. Furthermore, the decrease in spider species and family richness detected by pitfall traps as the abundance of woody plant species with patchy distribution increases seems to indicate that spider diversity may be conditional upon the homogeneity of the tussock cover. A possible explanation is that a continuous and dense tussock cover may provide more habitats and protection from predators and adverse environmental conditions, for both spiders and their prey, than shrubs.

Models based on vegetation gradients provide partially differing results. Turf sample data indicated that the overall number of spiders increases as tussock cover decreases and woody plant cover increases. However, data from pitfall traps point to an increase in spider numbers with greater tussock cover. These results are in line with the idea that tussocks can act as refugia or shelter for invertebrates against unfavourable weather conditions in the same way as layers of plant litter (Schmidt *et al.*, 2008). The discrepancy between the results obtained through the two sampling methods may be explained by the different spider taxa that each method is designed to capture. The differing habitat requirements of these taxa mean that they respond differently to changes in the vegetation. Therefore, the overall number of spiders collected in certain types of vegetation will change depending on the sampling method and the spider taxa captured (see discussion on the associations between spider assemblages and vegetation types).

Spider diversity, represented by species and family richness, increases with plant diversity. Modelling of individual variables related to plant diversity confirms this trend, with number of spider individuals, and spider species and family richness increasing as plant species richness and values of plant diversity indices increase. Habitats with diverse vegetation are likely to provide a greater range of resources for herbivorous invertebrates (Harmon *et al.*, 2003; Crist *et al.*, 2006), which in turn can become more abundant and serve as prey for predators, such as spiders. The increase in spider diversity with increase in plant species diversity may be partly due to such plant–herbivore–predator interactions. If it is considered that greater tussock cover and plant diversity mean greater complexity in the ecosystem, then these results support the contention that a more complex vegetation or environment sustains a greater density and diversity of spiders (Rypstra *et al.*, 1999; Jimenez-Valverde & Lobo, 2007).

Physical characteristics vs. botanical composition of the vegetation

The evaluation of the overall effects of vegetation on spiders suggests that physical characteristics of plants are as relevant in

determining spider assemblages as plant species composition. The results of this study show that different plant covers have an effect on the abundance of approximately as many spider species and families as plant species diversity measures, which contrasts with observations of plant diversity having a smaller effect on the diversity of spiders than measures related to plant physical complexity (Dennis *et al.*, 2001; Dennis, 2003). These results also contradict observations suggesting that Simpson's *D* index may not be useful when used with plant species to predict the response of spider communities (Beals, 2006).

Associations between spiders and vegetation type

Plant architecture and density have previously been identified as factors that determine spider assemblages (Gibson *et al.*, 1992; Downie *et al.*, 1995), either directly or perhaps indirectly by affecting their prey (Dennis *et al.*, 2001). This study indicated that the presence and abundance of individuals belonging to specific families will also depend on the physical characteristics of the vegetation. A number of spider families seem to respond to changes in such characteristics, with a few families displaying particularly consistent patterns.

The increase in the number of Lycosidae as tussock cover increases could be explained by the fact that greater tussock cover equates to more leaf litter, which can create beneficial microclimates and physical shelters for ground-active spiders (Rypstra *et al.*, 1999). Two ground-active spider families respond differently to the structure of the vegetation. Orsolobidae favour areas with less tussock cover and with scattered woody species or boggy vegetation, whereas Gnaphosidae are also more abundant in areas with fewer tussocks, but with greater plant diversity. Neither of these families build webs to capture their prey (Forster & Platnick, 1985; Uetz *et al.*, 1999); therefore, it is reasonable to expect that they will prefer areas with fewer tussocks and more open spaces. More specifically, these results concur with the observation that Orsolobidae prefer moist habitats with a large moss component (Forster & Platnick, 1985).

The Linyphiidae present in the study site favour areas with greater cover of woody plants and less tussock cover. Although Linyphiidae have previously been thought to favour areas with a greater presence of tussock-forming plants (Cherrett, 1964), they have also been found to differ in their response to tussock height (Dennis, 2003), which is often correlated with tussock abundance. The general response of this family to vegetation composition may, therefore, depend on the particular Linyphiidae species present in the area under study and their specific habitat requirements. However, given that the species of this family tend to build webs that require multiple attachment points, it is reasonable to expect that these spiders will be abundant in areas covered with woody plants with complex three-dimensional structures. It is worth noting that data from turf samples reveal some patterns in Mysmenidae, a poorly known family in New Zealand (Paquin *et al.*, 2010). Their preference for areas with more tussocks and less woody plants may reflect their need for plants that provide close attachment points for their small webs.

The general patterns exhibited by certain spider families in response to the characteristics of the vegetation can be broken into spider species–specific responses. Two Lycosidae species show distinct habitat preferences: *Anoteropsis flavescens* favours areas with high tussock cover, whereas *A. hilaris* prefers areas with fewer tussocks and more woody plants. *Anoteropsis flavescens* was thought to prefer marshy areas (Vink, 2002) in tussock grasslands. The findings of this study contradict this, as *A. flavescens* was more abundant in dry areas with greater tussock cover. These results are supported by data from both sampling methods and indicate clear differences in habitat preferences between the two *Anoteropsis* species, suggesting habitat and perhaps resource partitioning between them.

Another example of differing species requirements in spiders is found in the genus *Laetesia*; *Laetesia trispathulata* (Urquhart 1886) prefers areas with greater tussock and less woody plant cover, whereas the opposite is true for *Laetesia minor* Millidge 1988. *Laetesia trispathulata* and *L. minor* may be another example of resource partitioning by two closely related species although further studies designed specifically to investigate this hypothesis are required. The discovery of specific habitat preferences highlights the need for more ecological studies focused on native spider species in New Zealand, where environmental and habitat requirements are still largely unknown. On the whole, changes in vegetation have a significant effect on spiders. Results from RDA also support the idea that plant species richness and composition drive spider assemblages, with gradients in tussock cover and the abundance of shrubs explaining a considerable amount of the variation.

Implications for conservation and management

The differing habitat requirements among congeneric spider species could allow them to be used as indicators of habitat availability. Although *A. hilaris* has previously failed as a bioindicator of insecticide contamination (Hodge & Vink, 2000), it could potentially be used to detect changes in plant structure, or perhaps invertebrate communities, in native grasslands over time, and to infer the recovery stage of a tussock grassland area after disturbance. The use of *A. hilaris* and *A. flavescens* as bioindicators will, however, require further research on their response to particular environmental variables. Nevertheless, *A. hilaris* and *A. flavescens* are captured in large numbers and their identification is relatively easy (Vink, 2002), and therefore they appear to be appropriate potential bioindicators for monitoring in restoration projects of native tussock grasslands.

The results of this study have implications for both fundamental questions about plant–arthropod interactions and applied ecology. First, this study supports previous findings about the general effects of the vegetation on spider abundance and composition, which have identified vegetation structure as a major driver of spider diversity (Greenstone, 1984; Sunderland & Samu, 2000; Dennis *et al.*, 2001). Second, this is the first study that has confirmed such relationships in New Zealand tussock grasslands. Third, the information provided in this study can assist conservation management as it highlights the characteristics of tussockland vegetation that determine spider (and probably other arthropod) diversity. Conservation managers should therefore

consider the effects of increasing tussock cover or removal of shrubby vegetation on arthropod diversity when planning programmes aimed at improving or restoring protected areas.

Acknowledgements

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/j.1752-4598.2012.00195.x:

Appendix S1. DNA analyses for specimen classification.

Table S1. Effects of the first two principal components of PCA$_{physical}$ on the number of spider individuals, species, families, and the number of individuals of each family and species obtained through linear mixed-effects models.

Table S2. Effects of the first two principal components of PCA$_{botanical}$ on the number of spider individuals, species, families, and the number of individuals of each family and species obtained through linear mixed-effects models.

Table S3. Effects of the first two principal components of PCA$_{physical}$ on the number of individuals of each species obtained through linear mixed-effects models.

Table S4. Effects of the first two principal components of PCA$_{botanical}$ on the number of individuals of each family and species obtained through linear mixed-effects models.

Table S5. Effects of individual physical and botanical characteristics of the vegetation on the number of individuals of each family and species obtained through linear mixed-effects models.

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