Divergent small-scale spatial patterns in New Zealand's short tussock grasslands

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Abstract: Spatial studies of ecology rarely look at small-scale spatial community organisation within multiple plots on multiple sites therefore it is difficult to draw conclusions that can be generalised. We hypothesised that small-scale spatial patterns of *Festuca* tussock grasslands should be consistent within a site and between various sites because their functional ecology is likely to be similar. Tussocks were mapped in 15 plots ranging in size from 56 to 400 m^2 spread over four sites. Ripley's K, inhomogeneous Ripley's K and inhomogeneous pair correlation functions were implemented to detect patterns of aggregation, regularity and not significantly different from random at scales up to 300 cm. While Ripley's K indicated a general trend of regularity up to small scales (c. 20 cm) and aggregation up to larger scales (>40 cm), these patterns were not upheld by the inhomogeneous Ripley's K and inhomogeneous pair correlation function analyses, which did not yield consistent patterns. Our results suggest that within- and between-site variation of spatial patterns cannot be assumed to be consistent.

Keywords: *Festuca matthewsii; Festuca novae-zelandiae*; inhomogeneous pair correlation function; inhomogeneous Ripley's K; spatial ecology

Introduction

Ecology is inherently spatial, and spatial organisation is particularly important in plant communities where immobile individuals interact primarily with their direct neighbours (Silvertown et al. 1992; Tilman 1994). Consideration of spatial patterns in ecological research and modelling has become increasingly important as spatial structure is now recognised as the result of one or more of various ecological processes, and such patterns also have consequences for current and future processes (Silvertown et al. 1992; Tilman 1994; Murrell et al. 2001; Stoll & Prati 2001; Turnbull et al. 2007; Worster & Mundt 2007). While the identification of spatial patterns can be used to test hypotheses of ecological processes (Dale 1999; McIntire & Fajardo 2009), the occurrence of multiple processes resulting in similar patterns reduces the effectiveness of such tests (Pielou 1960; Lepš 1990; Law et al. 2009). The identification of spatial patterns is not a final goal in itself, but by identifying such patterns we can begin to understand which processes may be important in structuring ecosystems (Lepš 1990; Dale 1999; Fortin & Dale 2005).

Research focusing on spatial ecology in New Zealand plant communities is still relatively uncommon. In New Zealand's short tussock grasslands, Scott (1959, 1961) examined the spatial relationships between tussocks and inter-tussock herbs using nearest neighbour techniques, and found that tussocks influenced the zonation of each species differently; however, he did not examine the patterns of the tussocks themselves. Bellingham (1998) investigated the spatial relationships of short tussocks and invading shrubs in montane areas of the South Island, using Ripley's K function, and showed that while both the shrubs and short tussocks were intraspecifically aggregated, interspecific relationships were regular. Lord (1992, 1993) assessed the spatio-genetic relationships of *Festuca novae-zelandiae* using isozyme electrophoresis and found that the fragmentation of a single tussock into separate smaller tussocks may contribute to tussock regeneration, but that this is unlikely to be important to the regeneration of the grassland as a whole.

In both New Zealand and elsewhere most spatial ecology research has focused on the spatial patterns of only a few plots within a site or small region (Scott 1961; Thórhallsdottir 1990; Lord 1992, 1993; Tilman 1994). It is difficult to determine if the results from such studies can be generalised across larger areas or across a range of sites that are dominated by a variety of physical processes (e.g. alluvial terraces or moraines). Such generalisation can be important for management (e.g. determining an appropriate grazing regime or instigating weed control). In this study we quantified small-scale spatial patterns of *Festuca* tussocks over a variety of geographically distant sites to determine if these patterns are consistent both locally within a site and regionally between sites. With only limited prior knowledge of the spatial patterns of New Zealand's short tussock grasslands, we provisionally hypothesised that these tussocks will have similar spatial patterns over a variety of sites with the same vegetation type (short tussock grassland) as they are likely to be functionally similar and analogous ecological processes (e.g. below-ground resource competition, and vegetative reproduction) should be occurring across all sites at these small scales. While physical processes influence spatial patterns, this hypothesis assumes that at small scales (up to 3 m in this study) the influence of variation in biophysical processes would be small.

Methods

Study sites

The study was conducted at four sites all dominated by short tussocks. All four sites have low levels of grazing by either

domestic stock and/or wild hares and rabbits, have little or no slope, are generally well drained, have a low fertility status but no chemical limitations to plant growth, and have no history of fertiliser application. However, these sites do differ in terms of broad climatic parameters, especially rainfall (Table 1).

All of the sites used in this study are short tussock grasslands dominated by *Festuca novae-zealandiae* (Lake Lyndon, Cass Valley and Mt John) or *F. matthewsii* (South Branch of Hurunui River) with similar cover of a suite of common native species[1] (*Wahlenbergia albomarginata, Leucopogon fraseri, Brachyglottis bellidioides, Geranium sessiliflorum, Luzula rufa*) and the exotic invasive species *Pilosella piloselloides* subsp. *praelta* (formerly *Hieracium praealtum*). However, there are some compositional differences between sites (Table 1). In particular, the Mt John site and two of the Cass Valley plots (5 and 6) all have a high abundance of *Pilosella officinarum* (formerly *Hieracium pilosella*), with moderate levels of mat-forming *Coprosma* species and *Anthoxanthum odoratum*. *Agrostis capillaris* is also present at both Mt John and Cass Valley. The Lake Lyndon site and three of the Cass Valley plots (7, 8 and 9) all have a high abundance of *Agrostis capillaris* and *Anthoxanthum odoratum*, with low to moderate *Pilosella officinarum*. The South Branch of the Hurunui is dissimilar to all the other sites, having low exotic invasive cover.

Although *Festuca novae-zelandiae* and *F. matthewsii* are different species, both are perennial herbaceous hemicryptophytes with rolled leaves and a maximum mean height of approximately 1 m (Edgar & Connor 2000; Landcare Research 2010). Both are wind-pollinated, are capable of vegetative reproduction and may be the dominant species in short tussock grasslands (Edgar & Connor 2000; Landcare Research 2010). In addition, genetic evidence and hybridisation experiments indicate that they are likely to be closely related (Connor 1968; Lloyd et al. 2007). These similarities suggest that these two species may share similar functional ecology and therefore small-scale spatial patterns.

Data collection

Fifteen square plots ranging from 56 to 400 m² were established at the four sites; five at Cass Valley (plot sizes: 56–100 m²), four each at Mt John (all 400 m²) and South Branch Hurunui River (all 100 m²), and two at Lake Lyndon (both 400 m²). The range in plot size reflected differences in tussock density, with the aim being to sample at least 100 tussocks in each plot (total number sampled 111–1050 per plot). The plots were situated on flat terrain at the plot scale in an attempt to minimise any environmental gradients across the plot, and were at least 30 m apart. The position of each *Festuca* tussock within the plot was mapped using a coordinate system to the nearest centimetre (Fig. 1), and two perpendicular basal diameter measurements were recorded for each tussock. Because *Festuca* tussocks are known to reproduce vegetatively by rhizomes (Lord 1992), for the purposes of this study a single tussock was regarded as physically separate from others at ground level if the gap was >1 cm.

In addition, the cover abundance of all vascular species was visually estimated within each plot using five cover classes (<1%, 1–10%, 11–33%, 34–66%, >66%).

Data analysis

The spatial patterns of *Festuca* tussocks in each plot were analysed for scales up to 300 cm, with a 10-cm grain size, using Ripley's K-function (*K(t)*) (Ripley 1981, 1988; Cressie 1993; Dale 1999; Diggle 2003; Fortin & Dale 2005), inhomogeneous Ripley's K-function (*inhom K(t)*) and inhomogeneous pair correlation function (*inhom PCF*) (Baddeley et al. 2000). These functions were calculated in R (R Development Core Team 2010) with the spatstat package (Baddeley & Turner 2005) using an isotropic edge correction (Ripley 1988; Hasse 1995; Goreaud & Pélissier 1999) and Monte Carlo analysis with 79 simulations to produce upper and lower significance envelopes (α = 0.05) (Griffith 1988). The inhomogeneous Ripley's K-function and inhomogeneous pair correlation

Table 1. *Festuca* study site environmental attributes.

Study Site	South Branch of Hurunui River	Lake Lyndon	Cass Valley	Mt John
Location (NZGD1949)	42°45'50"S 171°59'12"E	43°20'19"S 171°40'35"E	43°40'34"S 170°22'49"E	42°45'50"S 171°59'12"E
Altitude (a.s.l.)	840 m	835 m	1080 m	760 m
Landform	Alluvial flats	Flat moraine terraces	Alluvial flats	Gently rolling moraine
Mean annual rainfall [1]	2400 mm	1200 mm	3000 mm	600 mm
Annual water deficit [2]	0	0	0	273 mm
Mean annual temperature [2]	7.9°C	8.2°C	7.0°C	8.5°C
Dominant short tussock species	*F. matthewsii*	*F. novae-zelandiae*	*F. novae-zelandiae*	*F. novae-zelandiae*
Vascular species richness [3]	18 ± 2.2	14.5 ± 0.7	22.6 ± 2.6	18 ± 2.2
Total native cover (%) [3]	94.3 ± 34.7	16.0 ± 12.02	71.1 ± 23.8	33.8 ± 21.1
Total exotic cover (%) [3]	7.5 ± 0.4	101.0 ± 24.0	73.4 ± 31.4	82.6 ± 19.1
Pilosella officinarum cover (%) [3]	0.38 ± 0.3	3.0 ± 3.5	26.3 ± 22.2	66.3 ± 19.3

[1] Interpolated from New Zealand Meteorological Service unpublished 1970 rainfall maps.
[2] Derived from underlying data of LENZ (Anon. 2003).
[3] Mean ± one standard error.

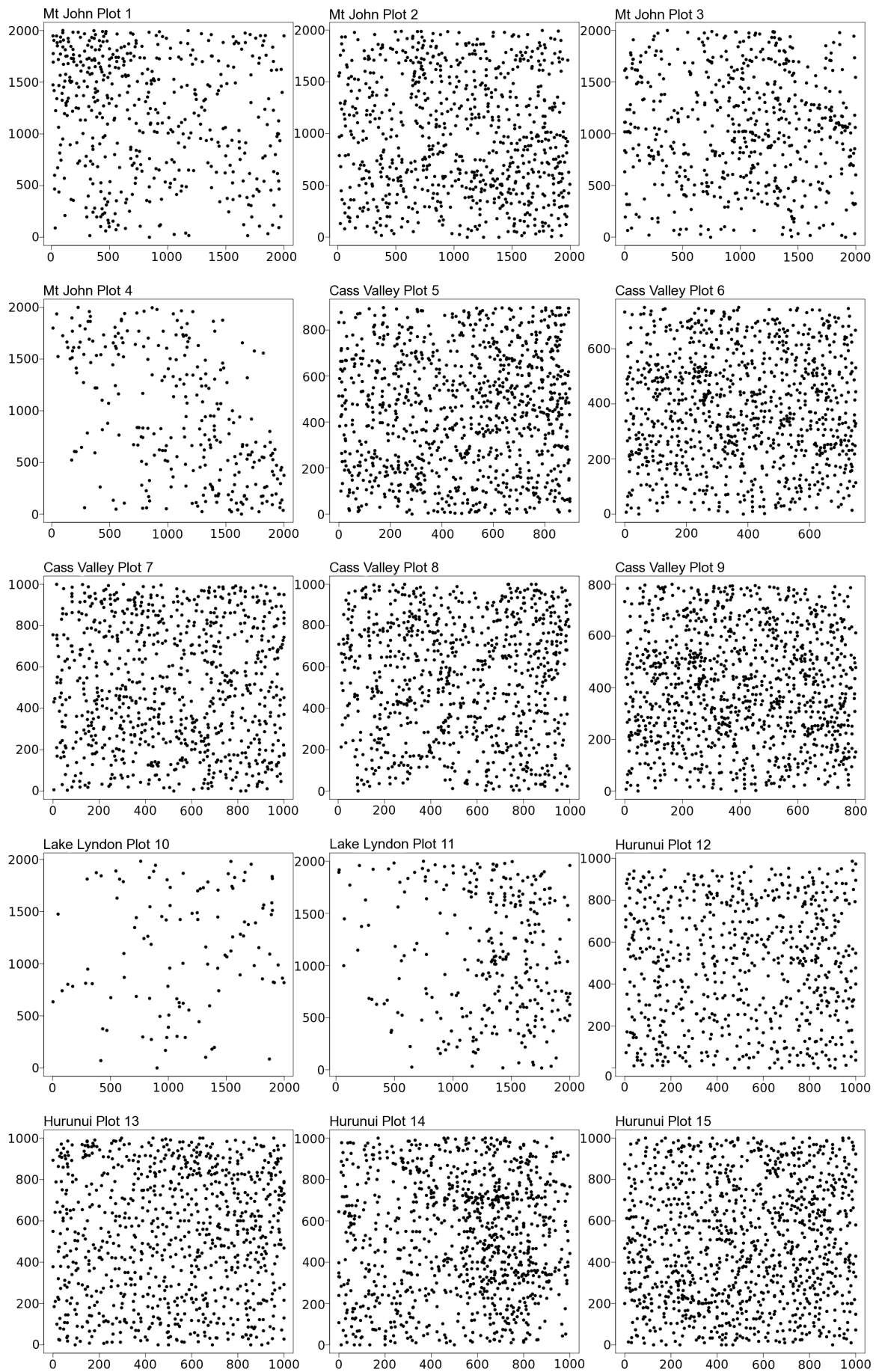[1] Plant names follow the New Zealand Plant Names Database (Allan Herbarium 2002–2010).

Figure 1. Map of each plot showing the location of tussocks. Axes units in centimetres.

functions were implemented using the default 'leave-one-out' kernel smoother to estimate the intensity surface in spatstat (Baddeley & Turner 2005).

All three spatial data analyses utilised in this study investigate different facets of a spatial pattern (Perry et al. 2006). First-order patterns are those produced by variation in the point process intensity across the plot, while second-order effects reflect the point patterns nested within this variation of intensity (Perry et al. 2006). In ecology, first-order patterns may be produced by environmental or resource gradients. Ripley's K analysis assumes stationarity, and therefore homogeneity of the point process intensity (λ) across the plot (first-order patterns). In contrast, inhomogeneous Ripley's K is a modified form that does not assume stationarity, by using a local estimate of the point process intensity to control for inhomogeneity. Therefore differences between Ripley's K and inhomogeneous Ripley's K may indicate the relative importance of first- and second-order effects, with the former reflecting the combination of both first- and second-order effects and the latter reflecting second-order effects while controlling for first-order effects (Perry et al. 2006). While patterns identified by inhomogeneous spatial statistics may be described as indistinguishable from random, the underlying intensity surface may be variable in the density of tussocks across the area. In addition, Ripley's K is cumulative, detecting patterns *up to* a given scale. This contrasts with the inhomogeneous pair correlation function, which uses annuli and is not cumulative, and detects patterns *at* a given scale.

For each plot, a trait of either (1) regularity, (2) aggregation, or (3) not significantly different from spatially random, for each 10-cm scale between 0 and 300 cm, was determined. Hierarchical clustering utilising the average linkage method with Hamming's coefficient of similarity of these traits was then used to group the plots into similar spatial patterns in R (R Development Core Team 2010). In addition, non-metric multidimensional scaling (NMDS) was used with Gower's distance to ordinate the patterns on two axes using the Vegan package (Oksanen et al. 2010) in R (R Development Core Team 2010).

Results

The Ripley's K analysis shows largely consistent patterns across all of the plots and sites (Fig. 2). Generally the plots demonstrate regularity or indistinguishable-from-random patterns up to small scales (c. 20 cm), with indistinguishable-from-random or aggregated patterns up to larger scales (c. 50 cm). Hierarchical clustering of these patterns indicates that the majority of the plots across all sites have similar spatial
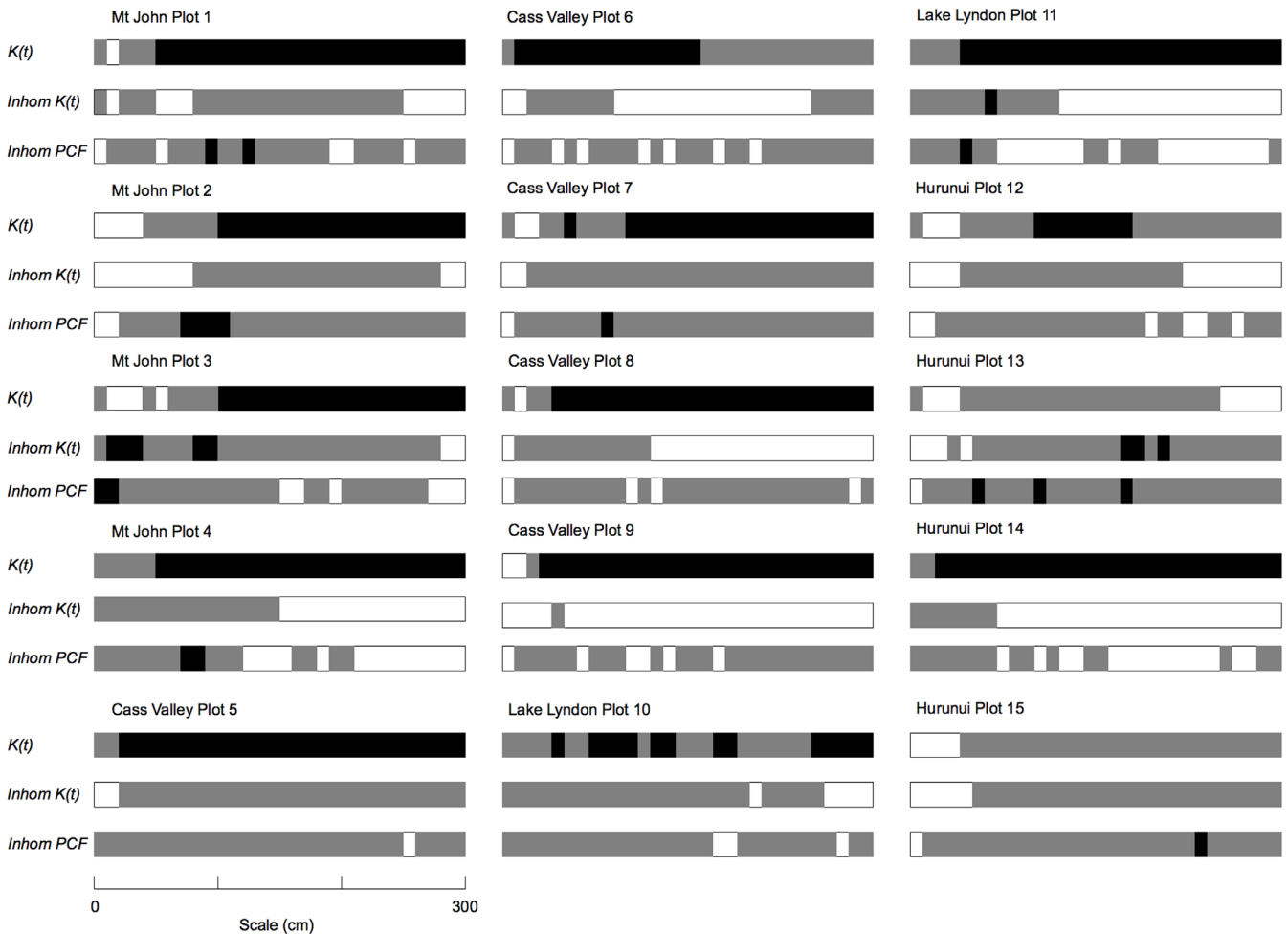

Figure 2. Summary of the spatial patterns detected by Ripley's K (*K(t)*), inhomogeneous Ripley's K (*inhom K(t)*), and inhomogeneous pair correlation function (*inhom PCF*). Each bar represents scales up to 300 cm. Grey areas indicate that the spatial pattern at that scale does not significantly differ from spatially random ($\alpha = 0.05$); white, that it is regular; and, black, that it is aggregated.

patterns (Fig. 3). In contrast, Plots 13 and 15 are notably different with no aggregation; furthermore, Plot 13 indicates regularity up to large scales (c. 250 cm). Plots 12 and 6 show intermediate patterns, with characteristics similar to both branches of the dendrogram.

In contrast, the inhomogeneous Ripley's K analysis shows a range of patterns (Figs 2 & 4); however, these differ greatly from the initial Ripley's K analysis. Patterns indistinguishable from random dominated most of the plots up to all scales. Only three of the plots exhibited aggregation up to any scale (Plots 1, 3 and 13). Eleven of the plots indicated regularity up to scales above 200 cm. Ten of the plots indicated regularity at small scales (<40 cm). The hierarchical clustering of these patterns suggests that there are two dominant types of patterns, one dominated by regularity and the other indistinguishable from random up to many scales (Fig. 4). The variety of patterns presented does not indicate consistency either within or between sites.

The inhomogeneous pair correlation function shows a range of patterns (Figs 2 & 5), with little consistency. Eight of the plots show aggregation at some scale, including all plots at the Mt John site. Nine of the plots demonstrate regularity at small scales (<20 cm), with one plot demonstrating aggregation (Plot 3), and the remainder not significantly different from random. Seven of the plots indicate regularity at one or more large scales. Similar to the inhomogeneous Ripley's K analysis, the variety of patterns presented does not indicate consistency either within or between sites (Fig. 5).

These results (consistency of Ripley's K, and inconsistency of inhomogeneous Ripley's K and pair correlation function) occurred irrespective of the dominant tussock species (*Festruca matthewsii* or *F. novae-zelandiae*), and the level of exotic species including the invasive exotic *Pilosella officinarum*.
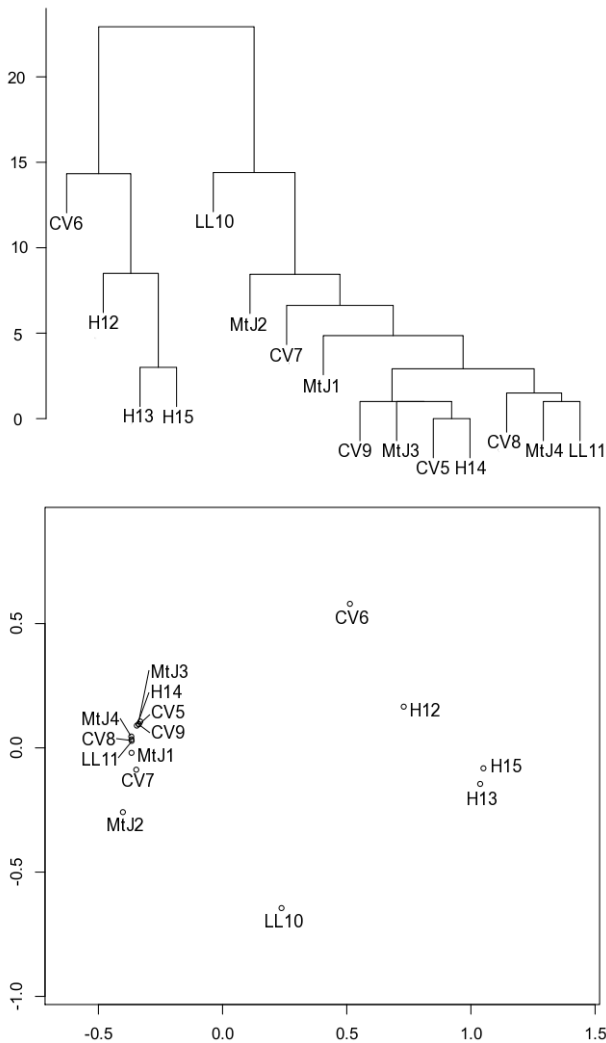
Figure 3. Dendrogram and NMDS ordination showing similarity of small-scale spatial patterns of *Festuca* tussocks in each plot as analysed by Ripley's K. Plots are labelled MtJ for Mt John, CV for Cass Valley, LL for Lake Lyndon and H for Hurunui; followed by the plot number (1–15). The axis on the left of the dendrogram indicates the number of traits or scales that differ (regularity, indistinguishable from random, or aggregated). The NMDS ordination has a final stress of 4.77, and an RMSE of 3.13×10^{-05}.
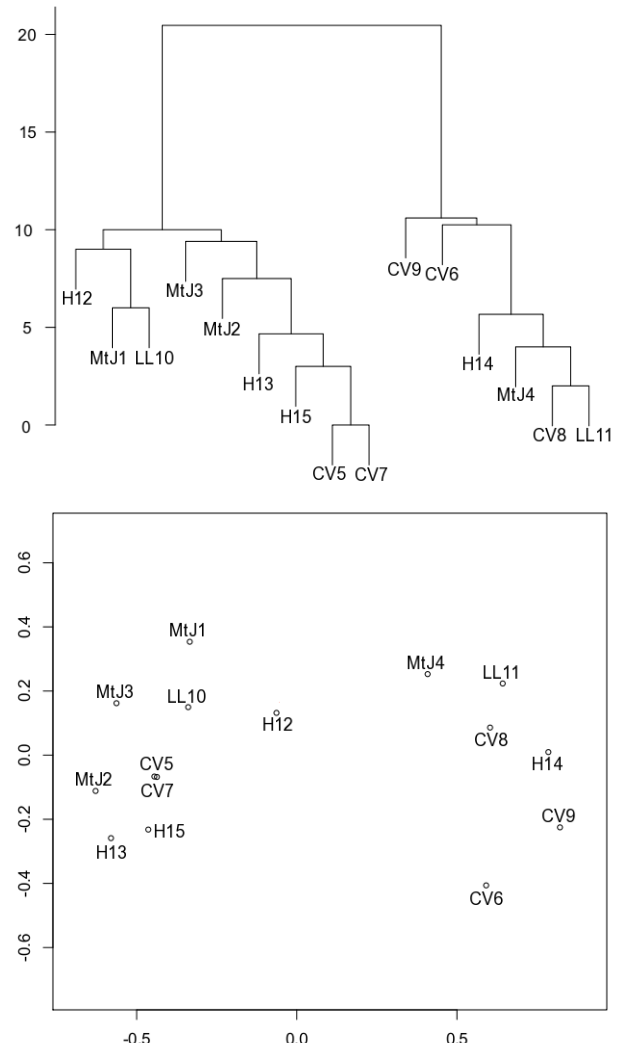
Figure 4. Dendrogram and NMDS ordination showing similarity of small-scale spatial patterns of *Festuca* tussocks in each plot as analysed by inhomogeneous Ripley's K. Plots are labelled MtJ for Mt John, CV for Cass Valley, LL for Lake Lyndon and H for Hurunui; followed by the plot number (1–15). The axis on the left of the dendrogram indicates the number of traits or scales that differ (regularity, indistinguishable from random, or aggregated). The NMDS ordination has a final stress of 3.42, and an RMSE of 1.41×10^{-05}.
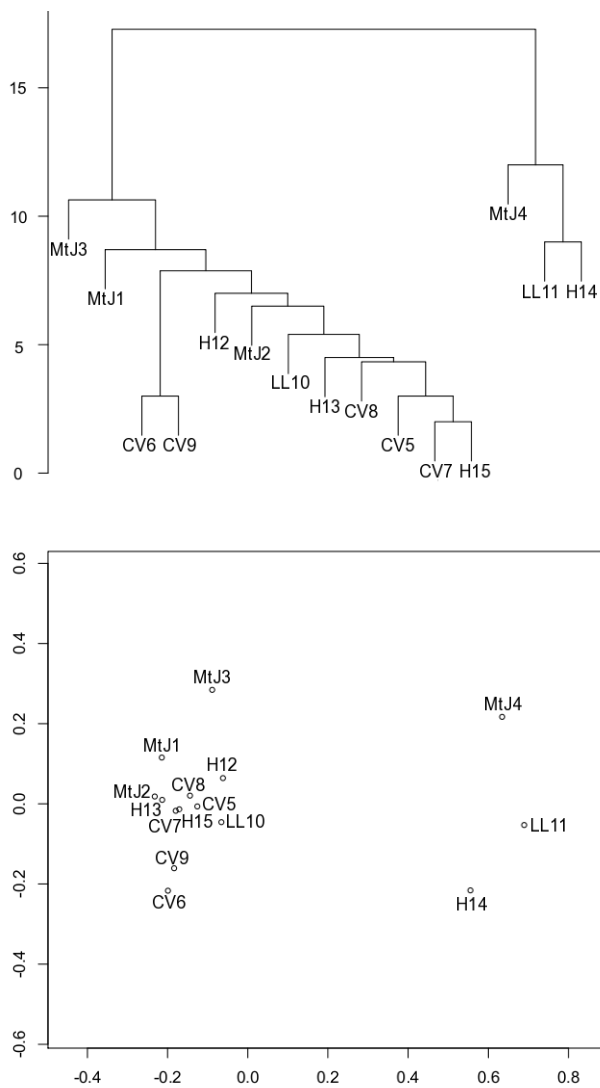
Figure 5. Dendrogram and NDMS ordination showing similarity of small-scale spatial patterns of *Festuca* tussocks in each plot as analysed by inhomogeneous pair correlation function. Plots are labelled MtJ for Mt John, CV for Cass Valley, LL for Lake Lyndon and H for Hurunui; followed by the plot number (1–15). The axis on the left of the dendrogram indicates the number of traits or scales that differ (regularity, indistinguishable from random, or aggregated). The NMDS ordination has a final stress of 7.00, and an RMSE of 1.82×10^{-05}.

Discussion

Spatial patterns of tussock grasslands, as indicated by Ripley's K, are generally consistent across most plots and sites, with regularity or indistinguishable-from-random patterns at small scales; and aggregated or indistinguishable-from-random patterns at large scales. Similar spatial patterns were detected by Bellingham (1998). By controlling for first-order patterns inhomogeneous Ripley's K can identify second-order patterns and the differences between the Ripley's K and the inhomogeneous Ripley's K analyses suggest that there is variation in the point process intensity within the plots. This may indicate that there are small-scale environmental or resource gradients within the plots producing the apparent aggregation of tussocks detected by Ripley's K.

Festuca tussocks reproduce vegetatively (Lord 1993), and it is interesting to note that the inhomogeneous Ripley's K and inhomogeneous pair correlation functions did not detect strong patterns of aggregation at small scales in all plots. This suggests that while vegetative reproduction may still be an important process in shaping small-scale spatial patterns, other ecological processes such as competition or resource availability greatly modify this pattern.

The variety of spatial patterns identified by the inhomogeneous Ripley's K and inhomogeneous pair correlation function indicates that spatial patterns can vary both within sites and between sites with apparently similar vegetation communities. While there have been many studies of the spatial patterns of a variety of ecosystems, in a variety of biomes (Murrell et al. 2001; Turnbull et al. 2007; Worster & Mundt 2007), these have typically focused on one or a few plots usually in one community and/or site. There has been little research that has looked at spatial patterns in many plots of a similar community both within and between sites. Our data show that variation in second-order small-scale spatial patterns within sites and between sites can be substantial. While studies of spatial organisation, which utilise only one plot or site, are of interest and may answer specific questions, they should not be relied upon to provide a complete picture of spatial patterns more generally for a community type, as these patterns can vary over even small distances. This has important implications for management of these communities, as it suggests that it may not be possible to generalise results from management actions implemented at one site to other sites where spatial patterning is not consistent. We recommend that studies of spatial patterns should examine multiple plots within a site, and also preferably multiple sites, so that the variation of spatial patterns can be properly assessed. The long-term stability of small-scale spatial patterns in vegetation is also generally unknown, and we recommend evaluating this using repeatedly mapped permanent plots rather than space-for-time substitution. Such information is likely to be important for the sustainable management of vegetation.

Acknowledgements

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