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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 m^2 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

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