Role of plant functional traits in determining vegetation composition of abandoned grazing land in north-eastern Victoria, Australia

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Abstract

Question: In the Northern Hemisphere, species with dispersal limitations are typically absent from secondary forests. In Australia, little is known about dispersal mechanisms and other traits that drive species composition within post-agricultural, secondary forest. We asked whether mode of seed dispersal, nutrient uptake strategy, fire response, and life form in extant vegetation differ according to land-use history. We also asked whether functional traits of Australian species that confer tolerance to grazing and re-colonisation potential differ from those in the Northern Hemisphere.

Location: Delatite Peninsula, NE Victoria, Australia.

Methods: The vegetation of primary and secondary forests was surveyed using a paired-plot design. Eight traits were measured for all species recorded. ANOSIM tests and Non-metric Multi-dimensional Scaling were used to test differences in the abundance of plant attributes between land-use types.

Results: Land-use history had a significant effect on vegetation composition. Specific leaf area (SLA) proved to be the best predictor of response to land-use change. Primary forest species were typically myrmecochorous phanerophytes with low SLA. In the secondary forest, species were typically therophytes with epizoochorous dispersal and high SLA.

Conclusions: The attributes of species in secondary forests provide tolerance to grazing suggesting that disturbance caused by past grazing activity determined the composition of these forests. Myrmecochores were rare in secondary forests, suggesting that species had failed to re-colonise due to dispersal limitations. Functional traits that resulted in species loss through disturbance and prevented re-colonisation were different to those in the Northern Hemisphere and were attributable to the sclerophyllous nature of the primary forest.

Keywords: Dispersal; Land-use change; Life form; Specific leaf area.

Nomenclature: Ross & Walsh (2003).

Abbreviations: AM = Arbuscular mycorrhizal; ANOSIM = Analysis of Similarity; ECM = Ectomycorrhizal; NMDS = Non-metric Multi-dimensional Scaling; SLA = Specific Leaf Area.

Introduction

In Europe and North America, past land use generally has a long-term impact on the composition of vegetation of post-agricultural, secondary forest due to the time it takes species with dispersal limitations to re-colonise (Matlack 1994; Brunet & von Oheimb 1998; Bossuyt et al. 1999; Graae & Sunde 2000; Bellemare et al. 2002). These species are typically herbaceous perennials with myrmecochorous or barochorous dispersal and large seeds (Bossuyt et al. 1999; Hermy et al. 1999; Verheyen et al. 2003). In Australia, while the vegetation composition of secondary forests is known to differ from that of primary forests (Yates & Hobbs 1997; Standish et al. 2006), the role of dispersal mechanisms or other plant traits in determining vegetation composition remains largely unknown.

Australia is an arid continent with old, highly weathered soils which are poor in nutrients (Adams et al. 2004) and the Australian flora has evolved many adaptations to suit this environment. For example, sclerophylly is an adaptation to both low nutrient and water availability and sclerophyllous leaves have low specific leaf area (SLA) (Wright et al. 2001, 2004). Myrmecochory may also provide an adaptation to nutrient-poor soils since it requires relatively little nutrient investment (Westoby et al. 1991), and many Australian phanerophytes are myrmecochores (Berg 1975). In contrast, most myrmecochores in the Northern Hemisphere are hemicryptophytes (Beattie & Culver 1981; Handel et al. 1981) that occur on soils with relatively greater nutrient availability (Adams et al. 2004).

Land-use history is also an important determinant of species composition in secondary forests. For example, where an area has been grazed, traits that enable species to survive grazing may determine vegetation composition (McIntyre et al. 1995). In Australia, life form and plant height are good predictors of grazing response (McIntyre et al. 1995; McIntyre & Lavorel 2001; Dorrough et al.

2004). Annuals and species with a flat rosette growth form generally increase in abundance with grazing (Tremont 1994; McIntyre et al. 1995; Pettit et al. 1995; Dorrough et al. 2004), while species with erect or partial rosettes are sensitive to heavy grazing and decline in abundance (McIntyre et al. 1995). A high SLA may also provide an advantage under heavy grazing because species with this trait turn over leaves rapidly and therefore regrow quickly after grazing (Westoby 1999).

This study aimed to identify the role of plant functional traits in determining the response of vegetation to land-use change in south-eastern Australia involving land clearing for grazing followed by farmland abandonment. We asked the following questions:

• Does frequency of seed size and mode of dispersal differ according to land-use history?
• Does frequency of plant height and life form in extant vegetation relate to land-use history?
• For the Australian flora, do functional traits that confer re-colonisation potential and tolerance to grazing differ from those for the Northern Hemisphere? Specifically:

While we expect limited dispersal by myrmecochores, the life form of myrmecochores will be dominated by sclerophyllous phanerophytes and not hemicryptophytes.

Given that SLA is related to sclerophylly and tolerance to grazing, we hypothesize that species with a low SLA will be more frequent in primary forest, and conversely, that species with a high SLA will be more frequent in secondary forest.

Two approaches were applied; (1) the analysis of individual traits; and (2) analysis of associations between attributes and land use using a multivariate approach (following Diaz et al. 1999). We selected seven traits known to be influenced by disturbance. Seed mass, potential plant height and SLA have been proposed as predictors of response to land-use change (Westoby 1998). Life form is a robust predictor of response to grazing (McIntyre et al. 1995), while dispersal mode determines the ability of a species to re-colonise (Matlack 1994; Brunet & von Oheimb 1998). Other traits associated with response to disturbance included fire response and nutrient uptake strategy (Cornelissen et al. 2003).

Methods

Study site

The Delatite Peninsula is located on the northern slopes of the Great Dividing Range in north-eastern Victoria (145º58' E, 37º 8' S). The Peninsula was formed in 1956 by the construction of the Eildon Reservoir, which flooded the adjoining valleys. The topography is steeply dissected, with elevation ranging from 300-500 m above sea level. Soils are silty loams or light clays developed on Late Silurian to Early Devonian sandstones, siltstones and shales (Thomas 1947). Annual rainfall is approximately 850 mm falling mainly in winter and spring (Bureau of Meteorology climate averages for Eildon, 1887-2003). Mean monthly maximum temperatures range from 12.0 °C in July to 29.0 °C in January, with corresponding mean monthly minimum temperatures of 3.5 °C to 12.5 °C. The original vegetation was open-forest (Specht 1981) dominated by *Eucalyptus dives*, *E. goniocalyx*, *E. macrorhyncha* and *E. polyanthemos* (*Myrtaceae*) with a sparse understorey of *Acacia* species (*Mimosaceae*), shrubby native peas (*Fabaceae*), heaths (*Ericaceae*), grasses and herbs.

In the 1850s, land was cleared and then grazed by cattle (D'Arcy 1998) until 1952 when work on the Eildon Reservoir commenced. In the 1960s, *Pinus radiata* plantations were established on much of the farmland to the south of the Delatite Valley. However, some farmland areas remained, primarily on steep slopes unsuitable for cultivation. Grazing by sheep occurred until the late 1970s (J. Walker, pers. comm. 2005, Plantation Manager), making the secondary forests approximately 25 years old at time of survey. Historical aerial photographs show that these farmlands had a scattered cover of eucalypts at the time of abandonment, which was still present at the time of the survey. Disturbance of primary forest sites was minimal and limited to light grazing by sheep from the 1950s to late 1970s. Four of the six primary forest sites were fragmented by land clearing and only one had been burnt since 1950.

Site selection and survey

Areas of adjacent primary and secondary forest were selected in a paired-plot design. Paired sites incorporated a distinct land-use boundary that could be verified by historical photographs and old fence-lines. Sites were located 100 m from the land-use boundary to reduce the possible effect of short-distance dispersal events on vegetation composition (dispersal over a distance greater than 100 m is considered long-distance dispersal; Cain et al. 2000). A total of six paired sites were established. Each site consisted of a 56 m × 56 m plot from which

eight 7 m × 7 m quadrats were randomly positioned and vegetation cover scored according to the Domin Scale (Kershaw & Looney 1985).

Analysis of vegetation response to land-use change

Bray-Curtis similarity (Bray & Curtis 1957) in vegetation composition between primary and secondary forest was tested by one-way analysis of similarity (ANOSIM) (Clarke 1993) using PRIMER (Anon. 1994) after data was square root transformed. A paired t-test was used to determine the effect of land use on total species richness, the richness of native species and the richness of introduced species at the site level.

Trait measurements

Traits were measured for all species recorded. Seed was collected from a minimum of five plants of each species and when not available from the field, it was obtained from local suppliers. A comparison of seeds for species obtained from both sources revealed no significant effect of seed source on seed size (T. Meers, unpubl. data). Mean seed size was determined for ten air-dried seeds of each species weighed on a Mettler Toledo

AX205 Delta Range® balance with 0.01 mg precision. For seeds smaller than 0.04 mg, ten lots of ten seeds were weighed. For each species, two fully expanded healthy leaves were collected from each of five plants and leaf area (including petioles) measured using a LICOR LI3000A portable leaf area meter. Leaves were dried for 72 hours at 65 °C and SLA determined as the ratio of dry leaf mass to area. Potential plant height was determined from flora descriptions. For grasses, geophytes and flat or erect rosette species, height to the top of the rosette was used rather than height to the top of flowering stems (Westoby 1998; Cornelissen et al. 2003).

Life-form classification followed Raunkiaer (1934) with classification of growth form of hemicryptophytes following McIntyre et al. (1995) (Table 1). Classification of attributes for dispersal mechanism was based on diaspore morphology (Cornelissen et al. 2003) (Table 1). There were few ballistically-dispersed species and most were also myrmecochores. Therefore, ballistochores were classified as either myrmecochores or barochores, following Leishman et al. (1995). A seed mass of 0.1 mg was used to separate self-dispersed (termed 'mobile' *sensu* McIntyre et al. (1995)) species from barochores with heavier seed.

Table 1. Plant traits and their measurement or defining attributes.

Trait and attributes	Measurement or defining attributes
Potential plant height	Mean potential height (m) obtained from flora descriptions
Specific leaf area	Mean leaf area (mm^2) of ten leaves divided by oven dried mass (mg)
Seed mass	Mean mass (mg) of ten air dried seeds
Dispersal mechanism	
Endozoochory	Fleshy fruit
Epizoochory	Barbs, hooks, burrs or awns enabling adhesion to animal fur
Anemochory	Pappus, coma, samara or similar attachment
Myrmecochory	Eliosome attached to seed to attract ants
Barochory	No apparent seed dispersal mechanism
Mobile	Barochores with seed mass < 0.1 mg
Life form	
Phanerophytes	Trees and shrubs taller than 0.5 m
Chamaephytes	Plants whose branch system remains below 0.5 m, or plants that die back to below that height (i.e. dwarf shrubs)
Therophytes	Annuals that complete their life-cycle in one season, or biennials that complete their life-cycle within two years
Geophytes	Plants with seasonal reduction to a below ground storage organ
Hemicryptophytes	Plants with seasonal reduction to a remnant shoot system where dormant buds are close to ground level
Growth form within hemicryptophytes	
Flat or versatile rosette	All leaves radical, leaves flat or erect depending on conditions
Erect rosette	All leaves radical, leaves always erect
Partial-rosette	Radical and cauline leaves present, largest leaves on lower stem
Proto-hemicryptophyte	All leaves cauline, largest leaves towards the middle of stem
Nutrient uptake strategy	
Nitrogen fixation	Presence of root nodules
Arbuscular mycorrhiza	Presence of hyphae, vesicles or arbuscules within stained roots
Ectomycorrhiza	Presence of ECM short roots
Ericoid mycorrhiza	Epidermal cells of hair roots with hyphae
Other	Other strategies such as carnivory or root hemi-parasitism
None detected	None of the above features observed
Fire response	
Re-sprouter	Ability to re-sprout after fire
Seeder	Species killed by 100% canopy scorch

Attributes for nutrient uptake strategy were determined from roots of species grown in soil from the Delatite Peninsula. Root segments were cleared in a 3% hydrogen peroxide solution for 24 hours, and stained for 24 hours in a 0.05% trypan blue in 2:1:1 lactic acid: water: glycerol solution (Giovanetti & Mosse 1980). Nutrient uptake strategy was based on the presence or absence of mycorrhizal hyphae or root nodules after examining roots under an Olympus stereo microscope (Olympus Corporation, Japan) (Table 1).

Species response to fire was classified as either fire-killed (by 100% canopy scorch) or re-sprouter (Table 1) according to the Victoria Department of Sustainability and Environment vital attribute database (2001 unpubl.). Species killed by fire rely solely on regeneration by seed and were termed 'seeders'.

Analysis of trait responses to land-use change

To determine if the frequency of species with a particular seed mass, SLA or potential plant height range differed according to land use, these traits were converted into categorical attributes. Seed mass was split into half logarithmic categories. For potential plant heights <1 m, height was split into 20 cm categories following previous studies in secondary forests (Graae & Sunde 2000; Pykala 2004), into 2 m categories for heights 1-5 m, and then into categories of 5-10 m (large shrubs) and > 10 m (trees). Specific leaf area was split into seven categories (Table 3).

For traits on nominal scales (including the categories of traits on continuous scales), the mean frequency of attributes for each quadrat was calculated for each site. Bray-Curtis similarity between the frequency distribution of attributes in primary and secondary forests was tested by one-way ANOSIM after data were square-root transformed. Where differences were significant, a SIMPER test (Clarke 1993) was used (PRIMER, Anon. 1994) to determine the attributes that contributed most to dissimilarity in the frequency distribution of attributes between land-use types. Data analysis was not performed when an attribute was absent from one or more sites and species were excluded where trait information was missing. A paired t-test was performed to determine the effect of land use on fire response.

Multivariate analysis of attribute associations with land-use types

A matrix of species attributes was created for all species, except for those found in fewer than three quadrats and for species with incomplete trait information. Traits on continuous scales were converted into categorical attributes using the same categories described above. The 96 quadrats by 98 species matrix was multiplied by the species by attribute matrix following the methods of Diaz et al. (1999). Non-metric Multi-dimensional Scaling (NMDS) was used to examine relationships between quadrats and species attributes. Bray-Curtis similarity (Bray & Curtis 1957) was used to represent the similarity between all quadrats (according to the similarity of attributes). Ordinations were performed on the similarity matrix by NMDS for the first six dimensions with 30 random starting configurations for each dimensionality, using PC-ORD (McCune & Mefford 1999). A two-dimensional solution yielding a minimum Kruskal's stress of 0.095 (significantly lower than by chance; $P = 0.032$; Monte Carlo test of 30 permutations) was selected as stress values less than 0.1 have no real risk of drawing false inferences (Clarke 1993).

Results

Vegetation response to land-use change

Secondary forest sites were dominated by the introduced annual grasses *Aira caryophyllea*, *Briza minor*, *Vulpia bromoides* and *Bromus* spec. and other introduced annuals including *Trifolium* (*Fabaceae*) species. Introduced perennial species including *Hypericum perforatum*, *Hypochoeris radicata* (both *Asteraceae*), *Prunus cerasifera* and *Rosa rubiginosa* (both *Rosaceae*) were also present. Native trees were restricted to scattered individuals of *Eucalyptus melliodora* and *E. polyanthemos* (*Myrtaceae*) and occasional *Acacia implexa* and *A. dealbata* (*Mimosaceae*). Other native species were mostly herbaceous perennials.

In primary forest sites, the overstorey was dominated by *E. goniocalyx* with occasional individuals of *E. melliodora* or *E. macrorhyncha* and *E. polyanthemos*.

Table 2. Significance of differences in the mean number of introduced, native, and all species in sites from primary and secondary forest at the Delatite Peninsula, south-eastern Australia, as determined by paired t-tests (significant P values (< 0.05) are in bold).

Species type	Species richness		t value	P value
	Primary forest	Secondary forest		
Introduced	8.2	14.9	–4.86	**0.005**
Native	20.8	12.5	4.32	**0.008**
All species	29.0	27.4	0.52	0.623

Shrubs included *Acacia rubida* (*Mimosaceae*), *Daviesia leptophylla*, *Dillwynia sericea*, *Platylobium formosum* (all *Fabaceae*) and the heaths *Brachyloma daphnoides*, *Epacris impressa* and *Melichrus urceolatus* (all *Ericaceae*). A diverse range of native perennial herbs were present including *Aceana* species (*Rosaceae*), *Geranium potentilloides* (*Geraniaceae*), *Hydrocotyle laxiflora* (*Apiaceae*), *Wahlenbergia multicaulis* and *W. stricta* ssp. *stricta* (*Campanulaceae*). Except for *Poa sieberiana*, most of the grasses in native forests were introduced species and included *Aira caryophyllea*, *Briza maxima*, *B. minor* and *Vulpia bromoides*.

Total species richness was not significantly different between land-use types (Table 2). However, the richness of native species in primary forest was significantly greater than in secondary forest (Table 2). In turn, the richness of introduced species in secondary forest was significantly greater than in primary forest (Table 2). Vegetation composition was significantly different between land-use types (ANOSIM; Global $R = 0.509$, $P = 0.009$).

Trait responses to land-use change

The frequencies of species in SLA categories were significantly different between land-use types (Table 3). There was a greater number of species with low SLA (< 10.00 mm^2.mg^{-1}) in primary forest while those with higher SLA ($30.01 - 40.00$ mm^2.mg^{-1}) were more abundant in secondary forest, and species with SLA in these ranges contributed most to dissimilarity between land-use types (Table 3). There were no significant differences in the frequency of species in potential plant height (Global $R = 0.091$, $P = 0.195$) or seed mass categories (Global $R = 0.230$, $P = 0.050$).

The frequency of species with different life forms and dispersal mechanisms varied significantly (Table 3) according to land use, while the frequency of species with different nutrient uptake strategies was not significantly different (Global $R = 0.037$, $P = 0.299$). Therophytes were more abundant in secondary forest, while phanerophytes and proto-hemicryptophytes were more abundant in primary forest, with species with these life forms

Table 3. Mean number of species with each attribute in primary and secondary forest sites at the Delatite Peninsula, south-eastern Australia, and the mean contribution to dissimilarity between land-use types as determined by SIMPER tests (Global R and *P* values shown). Traits are only shown when differences were significant as determined by an ANOSIM test. For fire response the results of a paired *t*-test are shown (significant *P* values < 0.05 in bold). One standard deviation is shown in brackets.

Trait and attribute	Primary forest		Secondary forest		Dissimilarity (%)	
SLA categories (mm²·mg⁻¹)	(Global $R = 0.294$, $P = 0.028$)					
0-5.00	2.8	(0.4)	1.4	(1.0)	2.8	(1.9)
5.01-10.00	4.1	(1.4)	1.9	(1.3)	4.3	(1.6)
10.01-20.00	4.8	(1.6)	4.7	(0.6)	2.4	(1.6)
20.01-30.00	4.6	(1.0)	4.8	(1.9)	2.9	(1.3)
30.01-40.00	8.6	(1.8)	10.0	(1.1)	3.5	(1.4)
40.01-50.00	1.6	(0.4)	1.5	(0.5)	0.9	(1.2)
> 50.00	2.2	(0.9)	3.3	(0.0)	2.4	(1.7)
Life-form	(Global $R = 0.319$, $P = 0.013$)					
Phanerophyte	5.1	(1.4)	2.4	(1.5)	5.0	(1.6)
Chamaephyte	2.9	(0.3)	2.8	(0.6)	1.0	(1.6)
Geophyte	1.4	(0.4)	0.6	(0.4)	1.4	(1.7)
Therophyte	8.9	(3.2)	13.7	(3.9)	9.7	(1.6)
Erect rosette	5.3	(0.9)	4.7	(1.1)	2.0	(1.2)
Flat rosette	2.8	(0.9)	2.4	(0.7)	1.7	(1.4)
Partial rosette	0.6	(0.6)	0.4	(0.3)	0.9	(1.3)
Proto-hemicryptophyte	1.9	(0.8	0.6	(0.4)	2.2	(1.5)
Dispersal mode	(Global $R = 0.446$, $P = 0.002$)					
Anemochore	6.6	(1.7)	7.7	(1.5)	3.4	(1.4)
Barochore	6.8	(1.6)	6.2	(1.3)	3.7	(1.5)
Epizoochore	2.8	(0.7)	5.4	(1.8)	4.4	(1.5)
Endozoochore	0.1	(0.1)	0.1	(0.1)	0.2	(1.1)
Mobile	7.5	(1.2)	6.7	(0.7)	2.2	(1.3)
Myrmecochore	4.2	(0.9)	1.7	(1.1)	4.5	(1.8)
					t value	*P* value
Fire response						
Seeder	11.0	(4.4)	15.2	(4.2)	−4.53	**0.006**
Re-sprouter	17.4	(2.4)	11.8	(2.9)	3.94	**0.011**

contributing most to dissimilarity between land-use types (Table 3). Myrmecochorous species were more abundant in primary forest and epizoochorous species were more abundant in secondary forest with these dispersal mechanisms contributing most to dissimilarity between land-use types (Table 3).

Primary forest contained a significantly greater number of species that re-sprouted after fire than did secondary forest. In contrast, seeder species were significantly more abundant in secondary forest than in primary forest (Table 3).

Multivariate analysis of attribute associations with land-use types

The NMDS of the quadrat × attribute matrix showed a separation of most secondary forest quadrats from primary forest quadrats according to distribution of attributes (Fig. 1a). Land use was associated with the distribution of quadrats in ordination space on Axis 2 (r^2 = 0.492). The corresponding plot of attributes on a land-use gradient showed a shift in species attributes from clonal species that re-sprout after fire, with myrmecochory and low SLA in primary forest, to annuals, species with epizoochory, anemochory or mobile seeds and high SLA in secondary forests (Fig. 1b). This plot also identified a shift in nutrient uptake strategies from the predominance of ericoid and ectomycorrhizal species (ECM) in primary forest to the predominance of arbuscular mycorrhizal (AM) and nitrogen fixing species in secondary forest (Fig. 1b).

Discussion

Dispersal mode and seed mass

There were few native species in the secondary forest even though grazing ceased over 25 years ago. Consistent with studies in Europe, myrmecochores were rare in secondary forest (Brunet & von Oheimb 1998; Bossuyt et al. 1999; Hermy et al. 1999; Graae & Sunde 2000). Given that ants only carry seeds of myrmecochores an average distance of 2 m (Anderson & Morrison 1998), any plant re-colonisation by this means would be slow. Despite differences in the dominant life form of myrmecochores in Australia and Europe, the similarity in response of myrmecochores to land-use change suggests that dispersal limitation is an important determinant of species distributions in secondary forests.

Grazing reduces ant diversity in Australia and can potentially limit seed dispersal, however, ant communities can recover rapidly once grazing is removed (Woinarski et al. 2002). For severely degraded Australian tropical woodland, limited dispersal of seed by ants was due to a low diversity of ant species (Anderson & Morrison 1998). In contrast, for secondary forests in the USA, low abundance of myrmecochores was due to dispersal limitations and not a reduced diversity or abundance of ant species (Mitchell et al. 2002). For the Delatite Peninsula, any potential influence of reduced ant diversity on plant species re-colonisation is unknown.

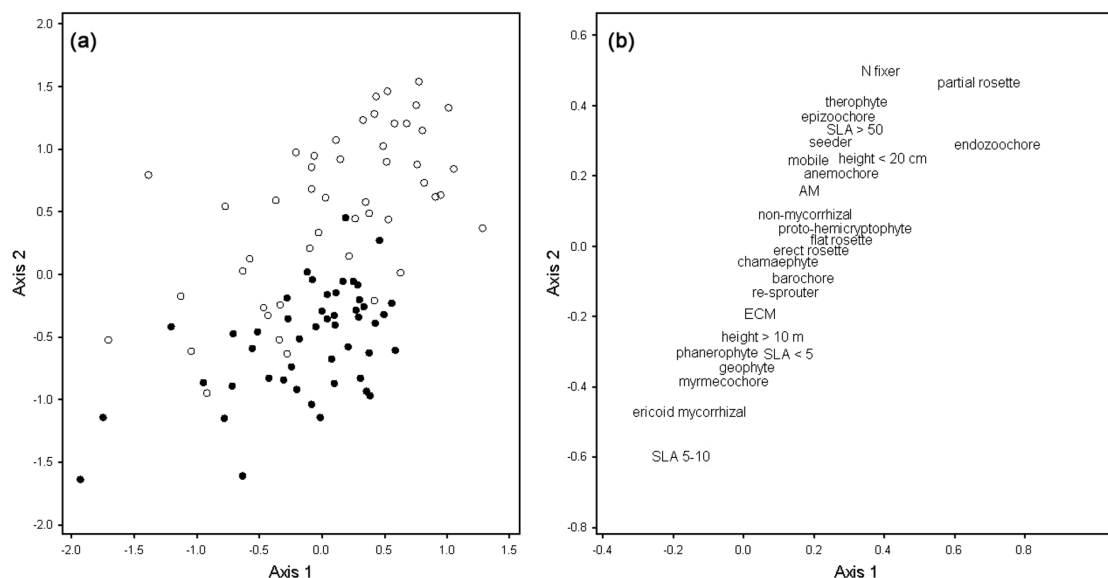Seed mass was a poor predictor of response to land-

Fig.1. Non-metric Multi-dimensional Scaling (NMDS) of quadrats (● primary forest; ○ secondary forest) at the Delatite Peninsula, south-eastern Australia, based on the similarity of the distribution of attributes. (**a**) NMDS of quadrats and (**b**) corresponding NMDS of attributes. Stress 0.095. Past land use is correlated with Axis 2 of the NMDS (r^2 = 0.492). For clarity, only categories for traits on continuous scales that show associations with particular land-use types are shown.

use change at the Delatite Peninsula. Since seed mass is only weakly correlated with dispersal mode (Hughes et al. 1994; Westoby 1998), it has limited use as a predictor of colonisation potential. Myrmecochorous shrubs that were most abundant in primary forest had relatively large seeds (2 to 35 mg). However, any reduction in the abundance of native species with large seeds in secondary forest was counteracted by the presence of introduced vertebrate-dispersed species with heavy seeds (e.g. *R. rubiginosa*, seed mass 18 mg) that were unique to secondary forest.

Plant height and life form in relation to grazing

Despite relationships found elsewhere (McIntyre et al. 1995; Diaz et al. 2001; Dorrough et al. 2004), potential plant height was not a good predictor of grazing response at the Delatite Peninsula, even though phanerophytes were less abundant in the secondary forest. In Finland, removal of grazing from pasture allowed taller species to re-establish within 10 years (Pykala 2004). A similar scenario may apply to secondary forest on the Delatite Peninsula given that 25 years have passed since grazing was removed giving taller plants ample time to recover.

Species with life forms known to be sensitive to grazing were rare in secondary forest compared to primary forest. One such group of species were the proto-hemicryptophytes that are vulnerable to grazing due to an upright growth form (McIntyre et al. 1995). Mortality through grazing and the failure to re-colonise once grazing was removed would explain the rarity of proto-hemicryptophytes in secondary forests in this study.

Specific leaf area and nutrient uptake strategy

The relative value of specific leaf area (SLA) as a predictor in this study compared to other studies of grazed land can be explained by differences in vegetation type. In Argentina and Israel where SLA was not a strong predictor of response to grazing, the vegetation was comprised solely of herbaceous species (Diaz et al. 2001). Similarly, in arid and semi-arid shrublands in Australia, SLA was also a poor predictor as shrubs were unaffected by grazing (Vesk et al. 2004). Within the Delatite Peninsula, primary forest contained sclerophyllous phanerophytes with low SLA, while the annual species dominant in secondary forest typically had high SLA. To this end, differences in SLA between primary and secondary forests on the Delatite Peninsula is best explained as the loss of phanerophytes through land clearing and their failure to re-colonise, rather than a response to grazing *per se*.

The NMDS showed that in addition to having low SLA, primary forest species typically had ericoid or ECM strategies. Nutrient uptake strategy (Cornelissen et al. 2001) and SLA (Westoby 1998; Weiher et al. 1999) are innately associated with growth rate and nutrient availability, so a shift in dominance from species with low SLA to those with high SLA, and from ericoid and ECM species to AM species, indicates a shift from slow to relatively fast growing (ruderal type, *sensu* Grime 1979) species in secondary forest. Land clearing and grazing can increase soil nitrate availability (Bukata & Kyser 2005; Schmidt et al. 1998) which removes the advantage held by ericoid and ECM species with putative access to organic nitrogen sources (Read 1996). Ericoid and ECM species therefore face competition from AM species which have the potential to access mineral nitrogen sources more effectively (Michelsen et al. 1998).

Annual grasses are an example of ruderal type species that can arrest the process of succession through competition with forest species (Davis et al. 2005). Despite the removal of degrading processes, degraded *Eucalyptus* woodlands in New South Wales (Prober et al. 2002) and secondary forests in Western Australia (Standish et al. 2006) continued to be dominated by introduced annual grasses due to high soil nitrate concentrations. A similar process may operate at the Delatite Peninsula, where annual grasses continue to dominate secondary forests that have greater soil nitrogen concentrations than primary forests (S. Kasel unpubl. data). Apart from increases in nitrate availability through land clearing and grazing, an increased abundance of atmospheric nitrogen fixers (*Trifolium* species in particular) in secondary forests may have further increased nitrogen availability (Sanford et al. 1995).

Increased light availability in combination with increased soil nitrogen availability also favours ruderal type species (Granger et al. 1994). For the Delatite Peninsula however, we expect any impact from differences in light availability between land-use types to be limited due to the shallow light gradients typical of eucalypt woodlands (Wright et al. 2006).

We cannot discount the possibility that some of the native shrub species in the secondary forest here survived grazing as suppressed rootstocks (e.g. Matlack 1994) and therefore regenerated vegetatively rather than through seed dispersal. However, this is unlikely given that native species are often eliminated during conversion to agriculture through burning of slash, competition with pasture species, and grazing and trampling (Bellemere et al. 2002). For secondary forest in this study, there was a significant decrease in the abundance of dispersal-limited species and species that re-sprout after fire. This trend is contrary to that expected if there was a significant degree of plant regeneration from rootstock.

Introduced species

The presence of introduced species in primary forests indicates that they have not entirely escaped disturbance through grazing or land fragmentation. Box woodlands (*Eucalyptus albens*) in New South Wales were prone to weed invasion under slight disturbance through grazing, even though they had not been cleared (Prober & Thiele 1995). Fragmentation also increases the likelihood of the movement of nutrients, fauna and plant propagules into remnant vegetation (Saunders et al. 1991), increasing the potential for invasion by introduced species (Hobbs & Huenneke 1992).

Similar to other studies (e.g. Graae & Sunde 2000; Dorrough et al. 2004), introduced species were more abundant in secondary forest. Many of the introduced annuals were grasses which are commonly dispersed by epizoochory (Dorrough et al. 2004), an attribute that was associated with secondary forest. Grazers may be directly responsible for this by importing propagules, both by epizoochory (Couvreur et al. 2004) and in faeces (Cosyns et al. 2005), or indirectly by disturbing the soil and creating gaps, providing introduced species with establishment opportunities (Hobbs & Huenneke 1992; Dorrough et al. 2004).

Conclusions

Our starting premise was that certain traits would be predictors of species' response to clearing, grazing and abandonment. This was true to a certain extent for dispersal mode, life form, fire response and nutrient up-take strategy, but did not hold for seed mass or potential plant height. Traits typifying species restricted to primary forest (myrmecochorous phanerophytes with low SLA) were those that provided adaptation to nutrient poor soils. In contrast, species with traits providing adaptations to frequent disturbance (therophytes with high SLA) were more abundant in secondary forest. For many sclerophyllous shrubs in Australia, natural re-colonisation of abandoned farmlands is slow and should not be relied upon as a means of returning such species to regenerating forests, even where nearby native forest fragments provide a potential source of propagules.

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