

# A plant strategy approach to understand multidecadal change in community assembly processes in Australian grassy woodlands

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## Summary

**1.** The mechanisms of community assembly underpinning plant invasion are contested; limiting similarity predicts divergence in the traits of native and alien species whilst habitat filtering predicts trait convergence. Using site-based floristic data collected three decades apart, we ask whether the competitor–stress tolerator–ruderal (CSR) strategies of herbaceous alien and native plant species in Australian woodlands show evidence of divergence (indicating limiting similarity) or convergence (indicating habitat filtering). We also ask whether increasing dereliction between the two sampling periods, as a result of declining fire frequency, has influenced habitat filtering processes.

**2.** Null models were used to assess the similarity in CSR strategies of native and alien species in order to identify the community assembly processes driving woodland invasions. The observed frequencies of CSR types were also compared to randomly assembled communities from null models for species experiencing increases, decreases or static abundance changes between the two surveys to assess the impacts of dereliction on habitat filters.

**3.** The spectrum of CSR strategies of the most common aliens ( $n = 25$ ) was highly convergent with the strategies of the most common natives ( $n = 51$ ). Competitive–ruderal species dominated the flora (> 30% of all species), and strict competitors were absent. No aliens exhibited a stress-tolerant strategy, and ruderals were more common in the alien flora (i.e. 36% vs. 18% of native species). Null models revealed differences in the CSR strategies of increaser and decreaser species at three of the ten sites examined, although none of these trends were consistent across the sites, indicating that increasing dereliction has not dramatically altered the habitat filters determining species admission.

**4. Synthesis.** The similarity of CSR types between alien and native species indicates that habitat filtering is the principal community assembly process operating in the study region. We discuss our findings with respect to suggestions that limiting similarity and environmental filtering may be occurring simultaneously to structure plant communities. Species abundance changes due to dereliction were not evident as a coordinated shift in the functional composition of woodland dominants suggesting that time lags between altered management regimes (dereliction) and the functional response of species to habitat filters may still be playing out.

**Key-words:** Australia, community assembly, CSR plant strategy scheme, habitat filtering, limiting similarity, plant invasion, woodland

## Introduction

A growing number of studies have compared the functional traits of coexisting species in an attempt to determine whether habitat filtering or limiting similarity is the primary determi-

nant of plant community assembly (see recent reviews by Götzenberger *et al.* 2012 and Price & Pärtel 2013). The limiting similarity hypothesis proposes that niche-based processes mediate coexistence where contrasts in the functional traits and consequent differences in niche occupation promote the long-term coexistence of neighbouring species (MacArthur & Levins 1967; Abrams 1983). Limiting similarity therefore predicts that divergence in the functional traits of native and alien species is an essential component of successful

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invasions because invaders must occupy a niche that is unoccupied by resident species. Conversely, the habitat filtering hypothesis predicts convergence in the functional traits of alien and native species as both groups possess traits that pre-adapt them to the local abiotic environment (Weiher & Keddy 1999; Cornwell, Schilck & Ackerly 2006; Ordonez, Wright & Olf 2010; Weiher *et al.* 2011). This theory suggests that plant communities are a result of environmental filters (e.g. climate, soil) that successively constrain which functional types from the regional species pool can persist in a given habitat (Keddy 1992; Diaz *et al.* 1999; Lavorel & Garnier 2002). Community assembly studies have revealed mixed and often contradictory evidence for limiting similarity and habitat filtering in experimental and natural plant communities (e.g. Fargione, Brown & Tilman 2003; Hooper & Dukes 2010; Bernard-Verdier *et al.* 2012; Wilson & Stubbs 2012; Gross *et al.* 2013; Tecco *et al.* 2013). The variability of these outcomes has led to considerable debate regarding the expected conditions under which limiting similarity and habitat filtering are thought to operate (e.g. Grime 2006; Wilson 2007), indeed if they operate at all (Hubbell 2001).

Grime's (1974, 1977, 1979, 2001) competitor, stress-tolerator, ruderal (CSR) scheme categorizes plants into three primary strategy types based on adaptive trade-offs between resource acquisition in productive habitats (C), persistence in unproductive habitats (S) and disturbance tolerance (R). Competitive plants (C types) are characterized by allocation to resources in the vegetative growth phase. The traits associated with increased competitive ability include fast relative growth rate (RGR), high specific leaf area (SLA), high root:shoot values and high biomass (Grime *et al.* 1997). Stress-tolerant strategy types (S types) are slow growing, long-lived and have the ability to store resources allowing them to 'persist and resist' the resource-poor conditions of their habitat (Grime *et al.* 1997; Grime & Pierce 2012). Conversely, ruderal species (R types) demonstrate 'fast fecundity and fatality' allowing for rapid completion of the life cycle in habitats where disturbance frequently destroys biomass (Grime *et al.* 1997; Grime & Pierce 2012). Associated traits include high SLA, high RGR and greater investment in the reproductive phase of the life cycle relative to the vegetative phase resulting in high seed production and rapid reproduction (Grime *et al.* 1997). In addition to the three primary strategy types, intermediate strategies (e.g. CR, CSR, SC, etc.) are recognized (Grime 2001). As they encompass the major axes of variation between plants, differences in CSR strategies are indicative of the resource acquisition and disturbance niches occupied by plant species (Grime *et al.* 1997; Radford 2013). The scheme is regarded as one of the best developed plant ecological strategy schemes and has been used to investigate the mechanisms underpinning invasion by comparing the functional similarity of alien and native plants in a range of floras (e.g. Thompson, Hodgson & Rich 1995; Lambdon, Lloret & Hulme 2008; Pyšek *et al.* 2009; Jansen, Ewald & Zerbe 2011; Dainese & Bragazza 2012; Radford 2013).

Trait-based approaches have also been used to examine changes in the functional composition of vegetation communities

following altered land use (Lloret & Vilá 2003; Moog, Kahmen & Poschold 2005; Mayfield *et al.* 2010; Vallet *et al.* 2010). By modifying the habitat filters mediating species admission, altered disturbance regimes can change the functional composition of plant communities as species with traits maladapted to novel habitat conditions decline and better-adapted species increase (Moles, Gruber & Bonser 2008; Mouillot *et al.* 2013).

Decreases in disturbance frequency following relaxed land management is commonly referred to as dereliction. Long-term monitoring of derelict communities, in conjunction with community assembly studies, provides much needed insight into how disturbance regimes and assembly processes interact to shape vegetation composition. By measuring the functional traits and determining the CSR strategies of herbaceous native and alien species, and determining which of these species experienced positive, static or negative changes in abundance over 31 years, we addressed the following questions: (i) Does the functional composition of native and alien species in woodlands lend support to the habitat filtering or limiting similarity hypothesis? (ii) Has dereliction due to relaxed management regimes between the two sampling periods resulted in changes to the dominant CSR types present in grassy woodland communities?

## Materials and methods

### STUDY AREA AND PLANT SURVEYS

This study was conducted in remnant grassy woodlands on the Dundas Tablelands and Brim Brim Plateau in south-western Victoria, Australia. Mean maximum and minimum temperatures for Casterton (approximately 15 km from sites) are 27.3°C in February and 4.9°C in July, respectively, and mean annual rainfall is 656 mm (1956–2014). Soils in the area are predominately shallow, acidic clays and sandy loams (Gibbons & Downes 1964). Prior to European settlement, grassland and grassy woodland vegetation dominated a large proportion of south-eastern Australia (Lunt & Bennett 2000). Pre-settlement woodlands are thought to have been dominated by eucalypt species with a mostly herbaceous understorey dominated by tussock grasses, a large forb component and rarely tall shrubs (Blackburn & Gibbons 1956; Gibbons & Downes 1964; Willis 1964). Following settlement in the 1850s, many former woodland areas were cleared for agriculture and approximately 5% of the original distribution remains in a highly fragmented state (Sutton & Morgan 2009). Most of these remnants now occur along roadsides and were burnt frequently from the 1960s to 1990s. Remnant woodland patches are no longer actively managed and most had not been burnt for over a decade prior to this study (see Sutton & Morgan 2009 and references therein). Declines in the active management of remaining woodland remnants, particularly reduced fire frequencies, have been implicated in native species extirpation (Williams *et al.* 2006) and invasion by alien species in the region (Sutton & Morgan 2009).

Twelve sites varying in size from 2 to 39 ha were surveyed in 1975 and re-sampled in 2006 (see Sutton & Morgan (2009) for a full description of the sampling methodology). In both sampling periods, the abundance of all species observed was ranked on an approximately log-scale: 1 = 'very rare' (less than two dozen individuals

seen across the site), 2 = 'rare' (dozens of individuals), 3 = 'common' (hundreds of individuals), 4 = 'very common' (thousands of individuals). A total of 426 species were observed across both sampling periods (Sutton & Morgan 2009). Floristic data from 10 of the 12 sites were used in the current study.

#### SPECIES INCLUDED IN THE CURRENT STUDY

The abundance of herbaceous species, including graminoids, between the years 1975 and 2006 was examined for sites re-visited by Sutton & Morgan (2009). Only herbaceous species were included because at the time, a simple and valid method for allocating CSR strategies to woody species was unavailable (Hodgson *et al.* 1999; Pierce *et al.* 2013). As woody species typically exhibit slow growth rates, long time periods are expected before these species show any response to dereliction whereas these changes are likely to be more rapid within the herbaceous component. Consequently, the omission of the woody component is not expected to have significant bearing on the conclusions made here.

Native species that had (i) increased in abundance by at least two abundance rank classes (approximately two orders of magnitude, e.g. 'very rare' to 'common'), (ii) decreased in abundance by at least two abundance rank classes (e.g. 'very common' to 'rare') or (iii) remained at the same abundance or changed by one abundance class between the sampling periods (hereafter 'static') were selected for study. Alien species were selected on the basis of their 2006 abundance; an invader must have been dominant (i.e. given a 3 or 4 abundance rating) in at least 3 of the 10 sites sampled in 2006 for inclusion, hence emphasizing alien species that are widespread and potentially dominant in the native habitat. A total of 76 species were assessed for their plant strategies, comprising 51 native and 25 alien species. The species selected for analysis provided a good representation of the dominant native and alien species in the flora as well as representative species from each of the three groups (increase, decrease, static).

#### TRAIT MEASUREMENTS AND CSR STRATEGY ALLOCATION

The CSR strategy of a species can be determined using easily measured traits that correlate with the major axes of variation between plants (Grime *et al.* 1997; Hodgson *et al.* 1999). The seven traits used to characterize CSR types using this method were canopy height (six-point classification), SLA ( $\text{mg mm}^{-2}$ ), leaf dry weight (mg) and leaf dry matter content (%), lateral spread of roots (six-point classification), flowering period (months), and flowering start time (Hodgson *et al.* 1999). Because the method of Hodgson *et al.* (1999) was developed in the northern hemisphere, the six-point flowering start time classification was reversed to suit the southern hemisphere. Trait values were measured either *in situ* or following specimen collection using the trait-measurement protocols outlined in Cornelissen *et al.* (2003). Trait values were then used to assign each CSR values using the methods described in Hodgson *et al.* (1999) and Hunt *et al.* (2004). To ensure useful sample sizes in each CSR strategy, we allocated species to one of the seven fundamental strategies originally proposed by Grime (1979) (CSR, CR, R, S, C, SR or CS) rather than the 19 he proposed later on (Grime 2001). To graphically represent CSR strategies of plant groups, ternary diagrams showing the relative contribution of C, S and R elements to the overall CSR strategy of native and alien species were plotted.

#### ANALYSES

A range of analysis techniques have been used to investigate trait-based differences between species and community assembly mechanisms. The null model approach is one such approach (e.g. Bernard-Verdier *et al.* 2012; Ordonez & Olff 2013). By the randomization of observed data matrices, null distributions and associated confidence intervals are produced to assess the degree to which observed ecological patterns diverge from those derived from models built on random expectations (Miklós & Podani 2004; Ulrich & Gotelli 2007). Null distributions were derived using row and column totals from the observed data set, with random re-assignment of the test feature (alien or native and increase, decrease or static) (Wilson & Stubbs 2012).

#### NULL MODEL-BASED ON NATIVE AND ALIEN CSR-TYPE COMPARISONS

Similarities in species composition across the 10 sites permitted a single analysis on the differences in CSR types between the native and alien groups. The alien/native comparisons were undertaken on the basis of their abundance in the 2006 surveys. A matrix of CSR type X species origin (i.e. native or alien) was used to construct null models. There were no C-type species present at any of the sites, so this type was omitted from analyses. Row and column totals were preserved throughout 10 000 permutations where status as either native or alien was re-randomized to CSR type. The observed number of native or alien species in each CSR group was then compared against the expected number of species in that group, derived from the lower 2.5th and 97.5th percentiles (i.e. the 95% confidence intervals) of the 10 000 permutations. Differences between alien and native species were deemed to be significant when the observed number of individuals in each CSR group and origin class (i.e. native or alien) was above or below the upper and lower 95% confidence intervals produced by null models. This procedure allowed us to determine whether or not alien or native species were more or less likely than random expectations to exhibit a particular CSR strategy type. Significant differences in observed and modelled distributions of the CSR types of native and alien species were interpreted as evidence of limiting similarity whilst no significant differences between observed and expected value was interpreted as evidence for habitat filtering.

#### NULL MODEL-BASED ON INCREASER, DECREASER AND STATIC CSR-TYPE COMPARISONS

Species were rarely consistent in the way their abundance changed from one site to another between the two survey periods, so these analyses were made on a site-by-site basis (Table in Appendix S1 in Supporting Information). A permutation procedure similar to that used in native/alien comparisons was performed to determine the degree of similarity in the frequency of CSR strategies amongst species experiencing increases, decreases or no changes in abundance between the 1975 and 2006 surveys. With row and column totals preserved, trend class (increaser, decreaser or static) was re-randomized to CSR type in 10 000 permutations to generate corresponding expected distributions of the number of species in each CSR functional group at each site. Similar to native and alien species comparisons, any differences between increaser, static and decreaser groups were deemed to be significant when the observed number of individuals from each trend and CSR group was above or below the upper and lower 95% confidence intervals produced by null models. Significant differences in observed and expected distributions of the CSR types of increaser and decreaser

species were interpreted as shifts in composition of CSR types over the 33 years between plant surveys, as a consequence of dereliction.

## Results

### NATIVE VS. ALIEN CSR STRATEGY COMPARISONS

Native and alien plant species occupied similar regions of CSR space (Fig. 1a; see Table in Appendix S1 for individual species trait scores and CSR strategy determination). Six of the seven CSR strategies were represented, with competitors (C) being absent from both native and alien components of the flora (Fig. 2b). Species with competitive–ruderal (CR) strategies were dominant in the native flora (31%) and equally dominant (36%) with ruderal (R) species in the alien flora; 18% of native species were R strategists (Fig. 1b). Stress tolerators–competitors (SC) were least represented, contributing 4% of the sampled aliens and 6% of sampled natives (Fig. 1b). Approximately equal proportions of alien (12%) and native (14%) species exhibited a stress-tolerant–ruderal (SR) strategy. Stress-tolerant species (S) were absent in the alien flora, but represented approximately 10% of the native flora. Natives showed a greater tendency towards a generalist strategy with 21% of natives demonstrating a CSR strategy compared to 12% of sampled aliens (Fig. 1b). None of the observed frequencies for the CSR types for either the native or alien components of the flora departed significantly from expected values generated by null models (Fig. 1b).

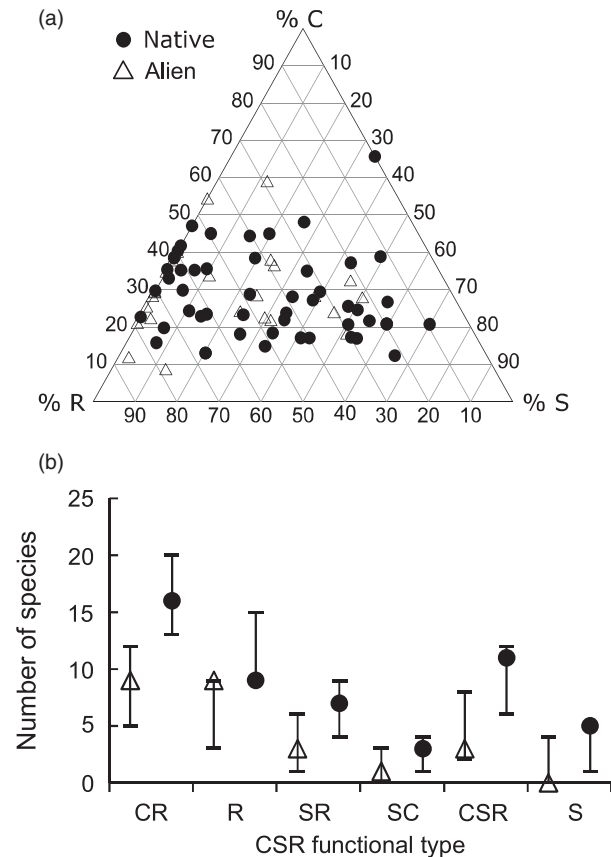
### INCREASER–DECREASER CSR STRATEGY COMPARISONS

The number of increaser, decreaser or species that showed no change in abundance in each of the CSR types rarely departed from null model expectations. Significant departures were evident at only three of the ten sites (Fig. 2), and only in one functional group at each site. These changes were unique to each site; the frequency of CSR decrease was higher than expected at Site 3 (Fig. 2e), the frequency of CR increase was higher than expected at Site 5 (Fig. 2g) and the frequency of SR decrease was lower than expected at Site 8 (Fig. 2i).

## Discussion

### CSR STRATEGIES OF HERBACEOUS WOODLAND SPECIES

Competitive–ruderals (CR) and ruderals (R) were the dominant CSR types in the study flora. In productive habitats, species with a high ruderality component are likely to persist under regimes of frequent disturbance due to their resprouting ability. As the study region experiences moderate rainfall, has relatively fertile soils (Gibbons & Downes 1964), has historically experienced regular burning (Sutton & Morgan 2009), and remnants typically have high edge to area ratios, the dominance of CR and R functional types is consistent with the predictions of CSR theory. The low proportion of

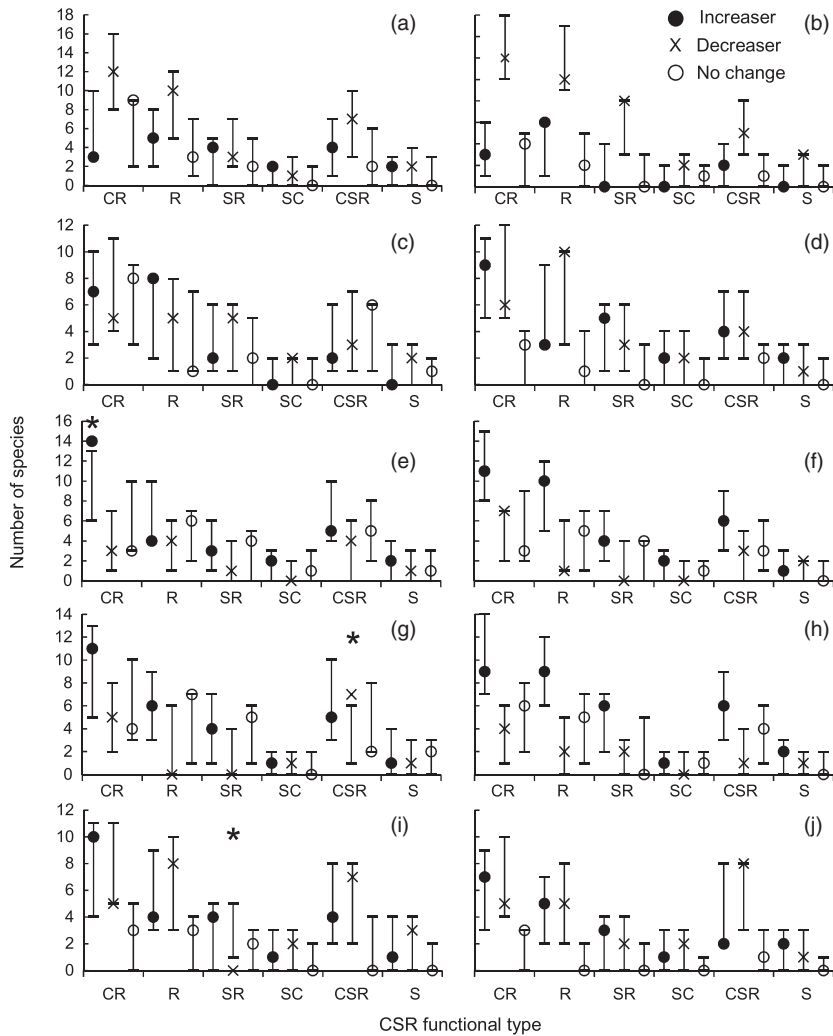


**Fig. 1.** (a) Ternary plot of functional competitor–stress tolerator–ruderal (CSR)-type differences between native and alien species in south-east Australian grassy woodlands. Each axis represents the relative contribution of C, S and R components to the overall CSR score of each species. (b) Number of alien (Δ) and native species (●) belonging to six CSR functional groups represented in south-east Australian grassy woodlands. Bars show the upper and lower 95% confidence intervals of expected proportions of each group obtained from null models with 10 000 iterations where alien or native status was randomized to CSR group.

stress-tolerating (S) and stress-tolerating ruderal (SR) species is also in line with the predictions of CSR theory. These functional types are typically found in habitats where extreme conditions (e.g. low temperatures, extreme nutrient or water deficiencies) hamper growth (Grime 1977, 1979, 2001), conditions which seldom occur in the study region. Although our study did not aim to explicitly test the utility of CSR on the Australian flora, historic management regimes (regular disturbance) and the abiotic conditions (moderate nutrient availability and rainfall) of the habitat have promoted the persistence of CSR types adapted to such conditions. The agreement between the dominant CSR types and site characteristics indicates that the CSR scheme is indeed transferrable to regions outside Britain (see also Cerabolini *et al.* 2010).

### COMMUNITY ASSEMBLY MECHANISMS IN THE WOODLANDS

The theory of habitat filtering predicts that local habitat conditions determine the composition of plant communities by



**Fig. 2.** Number of species belonging to different functional (competitor–stress tolerator–ruderal (CSR)) groups of species experiencing increases (●), decreases (X) or static (○) changes in abundance between 1975 and 2006 at 10 sites (Sites 1–10, a–j) in southeast Australian grassy woodlands. Symbols show the observed number of species, black lines indicate the upper and lower 95% confidence intervals of the expected number of species in each group generated from null model randomizations. \* indicates observed distribution of functional group outside of confidence intervals from simulated null model distribution.

constraining the functional traits that can persist there (Keddy 1992; Gross *et al.* 2013). According to this theory, invasion success is contingent on trait convergence between native and alien plant species, as successful invaders must exhibit traits suited to conditions of the invaded habitat. The opposing theory of plant community assembly, limiting similarity, predicts that alien and native species should display divergent suites of strategies due to niche differentiation. Recent work has suggested that limiting similarity and environmental filtering are not two contrasting processes but instead may operate on different traits or at different spatial scales (Mason *et al.* 2011; Bernard-Verdier *et al.* 2012; Dainese & Bragazza 2012; Grime & Pierce 2012; Maire *et al.* 2012; Gross *et al.* 2013). These sentiments have been formalized in the ‘twin-filter model’ of Grime & Pierce (2012) and the ‘two-step framework’ of Bernard-Verdier *et al.* (2012), both of which have clear links to Poff’s (1997) ‘hierarchical filters’ concept. Both models suggest that plant community composition is the product of a two-staged process leading to patterns of trait convergence and divergence amongst species. According to these models, habitat filtering leads to the exclusion of species with maladapted traits from the larger regional species pool in the

first stage of community assembly which results in trait convergence (Bernard-Verdier *et al.* 2012; Grime & Pierce 2012). CSR strategies are representative of the key differences in niche occupation by plants, and the convergence in the CSR strategies types found here indeed suggests that habitat filtering is the principal determinant of species admission; species with CSR strategies maladapted to the productivity and disturbance regimes of the habitat have been excluded via filtering processes acting on the regional species pool whilst species with CSR strategies adapted to site conditions have been admitted to the community from this species pool.

In the second stage of community assembly, the twin-filter and two-step framework suggests that patterns of trait divergence may be evident in traits influencing performance within the local community (Bernard-Verdier *et al.* 2012; Grime & Pierce 2012). Under the twin-filter model, patterns of trait divergence are expected in traits not entrained within the CSR framework (e.g. pollination mechanisms, seed dispersal, pathogen resistance) whilst the two-step model does not specify which traits are more or less likely to show divergence or convergence due to differences in trait dispersion patterns along productivity gradients (Bernard-Verdier *et al.* 2012;

Grime & Pierce 2012). It was beyond the scope of the current study to examine community assembly mechanisms beyond those exerting major control on species admission. However, we acknowledge that the actions of alternate assembly mechanisms may be operating at finer scales than were investigated here or on different traits and encourage further investigations to explore these concepts (e.g. Lai *et al.* 2015).

#### HAS DERELICTION RESULTED IN CHANGES TO THE FUNCTIONAL COMPOSITION OF THE WOODLAND COMMUNITIES?

Shifts in plant functional composition have been revealed following alterations to disturbance regimes and land-use change (Lavorel 1999; Lloret & Vilá 2003; Moog, Kahmen & Poschold 2005; Garnier *et al.* 2007). Detailed land management histories of each site examined here are unavailable, but valuable insights into past and present site management have been provided by local residents who reported a decline in the frequency of prescribed burning from almost biennial burning to no burning more recently across the region (see Sutton & Morgan 2009 for further details). Such dereliction should lead to substantial changes in the strategies of species that re-assemble in the changing environment as disturbance can alter the habitat filters determining which CSR types can and cannot enter the local species pool. We expected to see divergence in the CSR strategies of species experiencing increases and decreases as a result of dereliction-induced changes to habitat filters; however, this was not evident.

A shift in dominance from species exhibiting ruderal (R types) strategies to species with more competitive strategies (e.g. CR types) should occur during the middle stages of succession, whilst dominance by species with competitive (C types) and stress-tolerant (SR types) strategies is achieved at successional climax (Grime 2001; Grime & Pierce 2012; Roman & Gafta 2013). Consequently, we expected 'increasing' species to be significantly more competitive and 'decreasing' species to occur in strategy groups adapted to frequent disturbance (i.e. ruderals). However, such changes in CSR strategies were extremely rare in the study region (three of ten sites only, and one functional type of six at these sites), and can easily be accounted for by type I error (3 significant cases/180 independent tests (10 sites  $\times$  6 strategy types  $\times$  3 trends/site)). The lack of deviation from null expectations for a coordinated shift in strategy across all sites suggests that the primary habitat filters ('CSD-filters' *sensu* Grime & Pierce 2012) determining the admission of CSR types into the woodland communities have remained unchanged between the initial (1975) and recent (2006) sampling periods despite increasing dereliction. However, the lack of consistency across the 10 sites with regard to whether a species increased, decreased or was static in abundance between the two sampling periods suggests that although the principal habitat filters have not changed, habitat-specific processes (perhaps differences due to the action of non-CSR-related traits) play an important role in determining longer term plant success in the woodlands. Our results are consistent with those found in

other fragmented Australian woodlands where the long-term success of understorey plant species was highly site-specific and dependent on both historic and contemporary management regimes (Prober, Thiele & Speijers 2013) and similar processes appear to be at play in human-dominated landscapes elsewhere (e.g. Vandewalle *et al.* 2013).

#### Conclusion

The convergence in the CSR strategies of native and alien species found here indicates that niche differentiation is not an important precursor of invasion success as is predicted by limiting similarity. Our study did not aim to unravel the fine-scaled community assembly processes such as the simultaneous operation of habitat filtering and limiting similarity, but our data lend support to the assertion that habitat filtering is the principal community assembly mechanism governing plant community composition and adds another important piece to the community assembly puzzle.

Convergence in the CSR strategies of species experiencing increases and decreases in abundance over 31 years across the 10 sites examined indicates that the primary habitat filters controlling the admission of species in these communities has not been substantially altered by dereliction. Time lags between the functional response of species and changed primary filters are likely to be occurring and, as a result, more time may be required before a change in the functional composition of the sites becomes evident.

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#### Data accessibility

Species list and CSR Strategy type designations uploaded as online supporting information.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Species list and CSR types of herbaceous native and alien species in Australian grassy woodlands.