



Integrating the Passenger-Driver hypothesis and plant community functional traits to the restoration of lands degraded by invasive trees



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ABSTRACT

Our study examined the response of ten plant communities across Victoria, Australia to the infestation and subsequent removal of *Pittosporum undulatum*, a tree native to south Eastern Australia that is increasingly viewed as an invader within and particularly beyond its native range. At sites where *P. undulatum* removal has occurred over a 1–14 year period, species richness, canopy cover and functionality were compared against nearby invaded and remnant temperate Eucalyptus bushland, so as to gauge the direction and magnitude of community change over time. There are four main findings: (1) Low levels of native and non-native species richness and canopy cover were recorded at communities impacted by dense *P. undulatum* populations; (2) very low densities of *P. undulatum* at all cleared areas after removal; (3) removing *P. undulatum* caused an increase in species richness, particularly for native species; and (4) over time, management intervention lead to increasing similarity in community composition and function between cleared areas and remnant controls. Our case study demonstrates how the Passenger-Driver hypothesis (PDH) can be used effectively to understand the mechanisms at play between native and exotic drivers of community composition and function. Results are discussed in relation to how ecological theory can be applied to inform and improve invasive species management and restorative actions.

1. Introduction

Rapid globalisation is affecting the composition and structure of ecological communities through the reduction of barriers to biological invasions (Hulme, 2009; Pyšek et al., 2012). Invasive exotic species can result in dramatic biodiversity loss, diminished community function, reduced ecosystem services and altered disturbance regimes (Brooks et al., 2004; Liao et al., 2008; Pejchar & Mooney, 2009; Simberloff, 2011). Native species may also possess invasive characteristics, placing further stress upon ecological communities within their natural environment (Adair, 2008; Carey et al., 2012; Simberloff et al., 2012; Taylor et al., 2016). Restoration ecology is increasingly being viewed as a tool to combat the damaging effect of invasive species, and in doing so it is also being used to improve the integrity and resilience of native ecological communities (CBD, 2011; Chazdon, 2008; Suding, 2011). Significant interest and investment through the Convention for Biological Diversity and initiatives such as the Bonn Challenge which calls for the restoration of 350 million hectares of degraded forest globally by 2030, strongly support restorative practices (Aronson & Alexander, 2013; Verdone & Seidl, 2017). Despite this, a disjunction between on-

ground restoration effort and scientific theory is apparent. Several authors have called for greater integration of established ecological theory into the practice of ecological restoration (Dickens & Suding, 2013; Giardina et al., 2007; Hobbs & Norton, 1996; Matzek et al., 2014). Furthermore, the practice of follow up monitoring, although strongly advocated, has until recently been infrequent at best (Funk et al., 2008; Suding, 2011; Wortley et al., 2013). Greater understanding of the capacity for restoration programs to restore ecological integrity is needed in order to efficiently and effectively rehabilitate degraded landscapes (Suding, 2011). The challenge for researchers is to synthesise theory into a format applicable to practical on-ground management (Dickens & Suding, 2013; Matzek et al., 2014). Here, we explore both the Passenger-Driver Hypothesis (MacDougall & Turkington, 2005; Bauer, 2012) and community functionality (Pokorny et al., 2005; Funk et al., 2008; Mouillot et al., 2013) in their capacity to enhance ecological restoration projects through a wide-scale invasive species treatment and monitoring program.

The PDH categorises species according to their response to change. Species that become invasive as a direct result of environmental change are considered Passengers; invasive species that drive change

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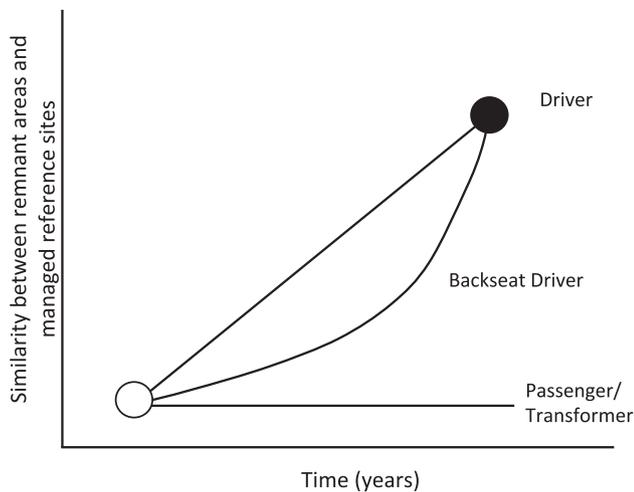


Fig. 1. Conceptual diagram depicting the response of a heavily invaded plant community (white circle) to invasive species removal. Plant community response is considered relative to a biodiverse high quality reference community (black circle). Removal of Passenger species is expected to alter the invaded community but not to a state similar that of the remnant reference community. Removal of Driver and Backseat Driver species is expected to lead to ecosystem recovery. However, if the disturbance initially enabling the establishment of a backseat driver is not addressed, the recovery of affected communities may be delayed. Removal of Transformer species will not lead directly to ecosystem recovery and for this reason the response of native plant communities to Transformer and Passenger species removal cannot be distinguish. Transformation of the ecosystem can make it difficult for native species to re-establish. Therefore altered stable states must be factored into management planning.

independently of any environmental alteration are considered Drivers; species that establish after environmental change but then proceed to drive plant community change independently from the initial disturbance are considered Backseat Drivers (Bauer, 2012; Chabrierie et al., 2008). Finally, at the most extreme end of the spectrum, Transformer species can alter community dynamics beyond local thresholds, pushing the community to a new stable state (Fig. 1) (Catford et al., 2012; Fukami & Nakajima, 2011; Richardson et al., 2000).

The PDH provides a useful perspective for placing a focal invasive species in a whole community management context (MacDougall & Turkington, 2005). This context can assist land managers to differentiate the effects of a focal invader species driving change within a community (Driver species) from other underlying ecological issues that may be the true cause behind landscape degradation. For example, Richardson et al. (2007) describe alien *Tamarix* shrub species that have established across arid Western USA. These species are considered invasive, as they are thought to degrade riparian habitats, consume large volumes of water, alter hydrological processes, salinize soil and reduce habitat values (Zavaleta et al., 2001). However, as Richardson et al. (2007) note, many of these same ecological issues may have been in place prior to and facilitated the establishment of *Tamarix* across the area.

Removal of a Passenger species is analogous to treating a symptom, with the target species and/or other invaders likely to reinvade (Fig. 1). A more successful approach will be to treat the underlying environmental change that enabled the invader to first establish. Removal of both Driver and Backseat Driver species should see a direct return of native plant communities, although in the case of the Backseat Driver this may take longer due to initial disturbances that allowed invasive species to establish (Fig. 1). Neither the removal of Transformer or Passenger species is expected to promote the reestablishment of native communities, and for this reason the PDH cannot distinguish between these two types of invaders. However, defining the role of a target invasive species as a Passenger, Driver, Backseat Driver or Transformer of a system should better enable land managers to modify conditions more favourable to native species (Lindenmayer et al., 2015;

Bauer & Reynolds, 2016). The PDH therefore enables the primary issues facing the area to be addressed.

The response of a species to abiotic and biotic constraints along with its role as a Passenger, Driver, Backseat Driver or Transformer within a community is ultimately governed by its functional traits. Traits reflect a species' resource capture, reproduction, dispersal and environmental strategies/tolerances (McGill et al., 2006; Reich et al., 2003; Westoby et al., 2002). Species trait values can therefore be used to characterise the functional diversity of a community. Emphasis on a community's functional diversity provides a perspective different to the traditional emphasis on species richness, and allows one to view community processes in a way that may promote greater invasion resistance, long-term stability and improved ecosystem functioning (Díaz & Cabido, 2001; Funk et al., 2008; Montoya et al., 2012; Pokorny et al., 2005). Trait based analysis has been advocated as a method to reveal the functional status of a recovering community (Cadotte et al., 2011; Mouillot et al., 2013). Plant height, photosynthetic performance and reproduction are three traits considered particularly informative when examining a species' life history strategy (Diaz et al., 2016; Westoby, 1998; Westoby et al., 2002). Height indicates plant competitive ability at maturity, seed mass represents the trade-off between dispersal ability and resources available to a germinating seedling, SLA (fresh leaf area divided by oven dry mass) indicates the productivity of a leaf (Cornelissen et al., 2003). Together with an understanding of the community and its environment, these traits can help to gauge restoration success and guide the strategic direction of future works (Drenovsky et al., 2012; Funk et al., 2008; Funk & McDaniel, 2010).

Here, we present the results of a study of plant communities over time following the removal of *Pittosporum undulatum* Vent (Sweet Pittosporum), a woody plant native to coastal areas of South Eastern Australia that has become invasive outside of its original range. Specifically we aim to: (1) determine the capacity for communities to re-establish and resist reinvasion following invasive woody tree removal; (2) use *P. undulatum* as a case study to test the Passenger-Driver hypothesis, examining the species role as a Passenger, Driver, Backseat Driver or Transformers within plant communities; and, (3) examine the response of functional traits in communities after invader removal. We hypothesise that if *P. undulatum* is a Passenger/Transformer, then communities will continue to display both low species and functional richness following the removal of the wood invader. However, if the target species is acting as a Driver/Backseat Driver we expect that removal of the invasive species will be sufficient to make significant improvements to community richness and function through time.

2. Methods

2.1. Species description

Pittosporum undulatum is a shade tolerant small tree or tall shrub native to coastal areas of south eastern Australia. Plant communities dominated by *P. undulatum*, both within its native range and beyond, often display low species richness and density (Gleadow & Ashton, 1981; Gleadow et al., 1983; Gleadow & Walker, 2014). These characteristics are shared by many heavily invaded indigenous communities (Webster et al., 2006; Lorenzo et al., 2012). Present across a range of habitat types, *P. undulatum* is most commonly found in wet and temperate rainforests (Gleadow & Ashton, 1981). Altered fire regimes, introduced vectors, peri-urban disturbance and horticultural propagation have all contributed to the spread of this species after European arrival (Gleadow, 1982; Gleadow & Ashton, 1981; Gleadow & Rowan, 1982; Gleadow et al., 1983). Presently, *P. undulatum* is considered invasive within many regions across Australia as well as Lord Howe Island and Norfolk Island (Eurobodalla Council, 2017; Mornington Peninsula Shire et al., 2012; Yarra Ranges, 2017). *P. undulatum* has also become a major issue globally, with invasive populations in New Zealand, Portugal, Jamaica, Hawaii, and is an emergent invader in South Africa

(Gleadow & Ashton, 1981; Goodland & Healey, 1996; Hortal et al., 2010; Lourenço et al., 2011; Mokotjomela et al., 2013). *P. undulatum* is known to establish quickly after disturbance (Bellingham et al., 2005; Rose & Fairweather, 1997), although it may also invade undisturbed locations (Gleadow & Ashton, 1981; Gleadow & Walker, 2014; Rose & Fairweather, 1997). Mature individuals growing in sheltered rainforests produce large spreading canopies and can reach heights of up to 30m, whilst those established across more exposed and coastal environments often display stunted growth (Mullett, 1999). Within dry sclerophyll eucalypt forests, individuals rarely exceed 15m. Populations are often observed to form dense, compact canopies, shading out the undergrowth and reducing structural diversity, floristic composition and the integrity of ecological systems (Gleadow & Ashton, 1981; Mullett, 2001).

2.2. Site description

We investigated the ways in which intact native plant communities responded to the infestation and subsequent removal of *P. undulatum*. Ten sites across peri-urban areas of Melbourne, in south-eastern Australia, were identified to evaluate the success of *P. undulatum* removal and its influence on community richness and function (Table 1 and Fig. 2). The Dandenong Ranges, 45km east of Melbourne, and the Mornington Peninsula 85km south-east from Melbourne, both represent a temperate, wet climate (Table 1). Sites were selected based on the following three conditions (1) presence of a high quality area of remnant vegetation that would act as a positive control – “remnant control”; (2) an area where work had been conducted to remove *P. undulatum* – “cleared treatment”; and (3) an area currently infested by *P. undulatum* to act as a negative control – “invaded control” (not included at Birdsland, Ferntree Gully and Sherbrooke Forest). Positive and negative controls enable an assessment of both the direction and magnitude of any change in the treated community (Guido & Pillar, 2017). Site selection was refined to ensure a comparison of similar vegetation within any one site. Ecological Vegetation Class (EVC) mapping (supported by on-ground observations) was utilised to ensure each sampling condition within a site supported similar vegetation (DELWP, 2017). Sampling conditions within each site ranged in size from 1 ha to 12 ha. Information on the density of *P. undulatum* at the cleared areas, invasive species management practices and disturbance regime was included in the analysis. The management area at each site was characterised as having a severe *P. undulatum* infestation prior to removal work. *P. undulatum* density at each site ranged from 30% to 70% canopy cover (Table 1). To remove the effect of different management practices, sites were chosen based upon the intensity of follow up monitoring after the treatment of the invasive species. With the exception of the Wonga Park site, which was cleared in 2016, all sites have experienced some degree of follow up maintenance within 12 months of the initial *P. undulatum* removal. Maintenance was conducted at least twice after *P. undulatum*

removal for sites aged three years and older. Approximately half of the sites have been exposed to control burns within the past 15 years. Control burns were used on remnant conditions only as a means of maintaining the natural disturbance regime and stimulating biodiversity (Penman et al., 2011). Unlike other studies (e.g. Gleadow & Narayan, 2007), fire was not used in the initial control of *P. undulatum* at the study sites. Cleared areas and invaded controls had not been burnt within the timeframe of this study (14 years).

2.3. Vegetation sampling

Sampling was conducted from late October to early December of 2016. To determine the effect of *P. undulatum* on local plant diversity, 6–10 randomly stratified quadrats were established at each sampling condition within each site. Quadrat size was determined using a species area curve performed within the remnant section at each site. Quadrat size was determined to be the point at which no additional species were encountered. Minor variation in species densities across sites meant that quadrats varied from $3 \times 3 \text{ m}^2$ to $4 \times 4 \text{ m}^2$ in size, depending on the site. Each individual plant within a quadrat was identified to species level wherever possible (VicFlora, 2017) and assigned a percentage score for canopy cover, including overhanging canopy (based upon visual estimates).

To examine the functional recovery of sites following *P. undulatum* removal, plant functional trait values were assigned to 205 of the 348 observed species for which data was available. Trait data availability therefore limited our capacity to examine all species present. The trait values recorded for each species were maximum height (Bull, 2014), seed mass (Meers et al., 2010; Royal Botanic Gardens Kew, 2017; Williams et al., 2005) and specific leaf area (SLA) (collected from sources in Appendix A – see supplementary data). These three traits are considered particularly influential to the overall plant species life strategy.

2.4. Statistical analysis

All analysis was conducted using the base package within the R statistical program (R Core Team, 2017). Multiple linear regression was utilised to examine the effect of time since clearing on the relative species richness at cleared treatments within each site. Principal components analysis (PCA) ordination techniques were used to visualise variability in species presence/absence and percentage canopy cover between conditions and across sites. The functional response of communities to *P. undulatum* infestation and its subsequent removal was also investigated through PCA, using mean site trait values, weighted by mean percentage cover scores. Differences in observed values between conditions within each site were used for inter-site comparison. All data were centred and scaled to unit variance prior to analysis. Species with canopy cover scores of < 1% were given a value of 0.5 to

Table 1

Site details including location, vegetation type, *Pittosporum undulatum* density prior to removal, year of removal and climate. Ref no refers to labelling format in Fig. 6a–c.

Site name	Ref no.	Latitude	Longitude	Ecological vegetation complex (EVC)	Initial <i>P. undulatum</i> density (%)	Year of <i>P. undulatum</i> removal	Mean annual rainfall (mm)	Elevation (m)
Wonga Park (WP)	1	–37.755709	145.283738	Grassy dry forest	50	2016	807.5	141
Greens Bush (GB)	2	–38.418634	144.958019	Damp sands herb rich woodlands	50	2015	779.4	176
Panton Hill (PH)	3	–37.642608	145.242843	Grassy dry forest	70	2014	688.5	181
Woods Reserve (WR)	4	–38.288326	145.091165	Lowland forest	50	2012	904.3	91
Birdsland Reserve (BR)	5	37.924444	145.340278	Grassy dry forest	30	2011	1113.6	170
Glenfern Valley Bushlands (GFVB)	6	–47.909783	145.314540	Valley Grassy Forest	60	2010	1056.8	187
Ferntree Gully (FTG)	7	–37.879164	145.306283	Grassy Dry Forest	50	2006	928.4	276
Red Hill (RH)	8	–38.401103	145.040113	Herb Rich Foothill Forest	60	2006	1008.9	114
Montrose (M)	9	–37.820394	145.346866	Grassy dry forest	60	2005	1031.9	409
Sherbrooke Forest (S)	10	–37.905239	145.369618	Wet Forest	50	2002	1261.5	495



Fig. 2. Map depicting the distribution of sites across peri-urban Melbourne, Australia, and the Mornington Peninsula. Black circles denote site locations in reference to Melbourne (black pentagon). White and grey sections indicate land and ocean respectively. WP – Wonga Park, GB – Greens Bush, FTG – Ferntree Gully, PH – Panton Hill, M – Montrose, BL – Birdsland Reserve, WR – Woods Reserve, RH – Red Hill, GFVB – Glenfern Valley Bushlands, S – Sherbrooke Forest.

enable statistical analysis. Euclidian distances between points were calculated on the principal components plane. Multiple linear regression was used to examine relationships between time since management action, and the relativised Euclidian distance between remnant controls and cleared treatments on the graph.

3. Results

We compared the species richness, percent cover and functional diversity of plant communities where *P. undulatum* was present, where it had been removed, and in areas historically free of this species. There were four main findings: (1) low levels of native and non-native species

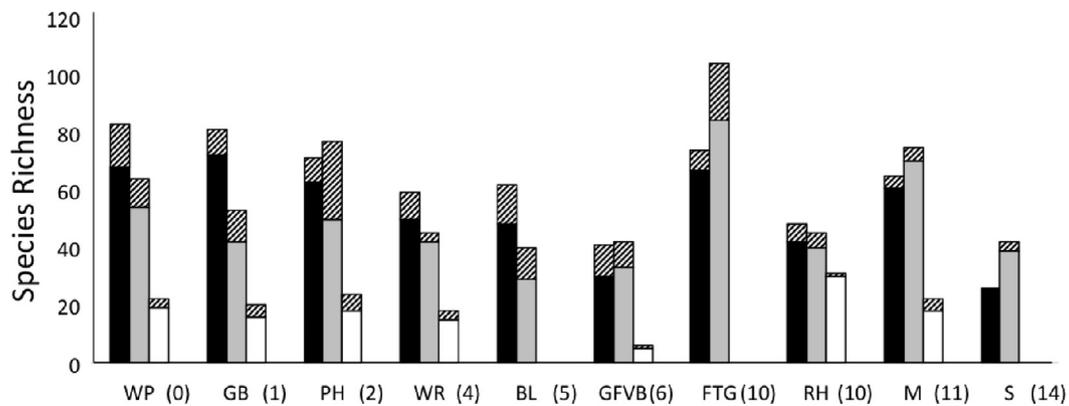


Fig. 3. Variation in species richness across sites and within sampling areas. Site labels relate to site names and years since *Pittosporum undulatum* removal found in Table 1; WP – Wonga Park, GB – Greens Bush, PH – Panton Hill, WR – Woods Reserve, BL – Birdsland Reserve, GFVB – Glenfern Valley Bushlands, FTG – Ferntree Gully, RH – Red Hill, M – Montrose, S – Sherbrooke Forest. Remnant control – remnant bush land (black), Cleared treatment – *Pittosporum undulatum* removed (grey), Invaded control – high-density *Pittosporum undulatum* (white). Hatched sections indicate the proportion of non-native species recorded within each sampling condition. For statistical analysis see Table 2.

richness and canopy cover were recorded at communities affected by dense *P. undulatum* populations, indicating the suppressive effect of *P. undulatum* on native biodiversity; (2) a very low density of *P. undulatum* was recorded at all cleared treatments after removal, regardless of years since removal (1–14 years); (3) removing *P. undulatum* resulted in an increase in species richness, particularly for native species, and; (4) increasing time since management intervention saw increasing similarity in community composition and function between cleared treatments and remnant controls.

3.1. Species richness and canopy cover

Invaded controls, where *P. undulatum* was in high density, supported low species richness, with an average of 21.1 species present across 10 sites (see supplementary data – Appendix B). Very few species were recorded growing under a *P. undulatum* canopy and these species were regularly observed at low densities (Fig. 3). The removal of *P. undulatum* resulted in an increase in species richness (Fig. 3). Species richness in quadrats at cleared treatments increased to levels comparable to remnant control communities (Fig. 3). A strong relationship was detected between relative species richness at cleared treatments and the time since *P. undulatum* treatment took place ($F = 4.575, p = .014$) (Table 2, Fig. 4). The distance between cleared treatments and remnant controls did not appear to have a significant impact on the relative species richness of restored plant communities ($p = .887$) (Table 2). The proportion of native species at cleared areas was higher than that of exotic species (Fig. 3). Cleared treatments did not see an increase in *P. undulatum* canopy density over time (Fig. 5).

Principal components analysis (PCA) detected a clustering effect across sites for invaded controls, but varied across sites for cleared and remnant areas (Fig. 6a, b). However, there was a trend in the direction of the remnant control i.e. cleared areas appeared closer to their corresponding positive remnant controls. Two exceptions were sites 3 and 7, both of which were exposed to higher levels of disturbance. When examining the effect of time since management action on the relativized Euclidian distance between remnant and cleared areas, a significant negative linear trend was detected, with the state of cleared treatments becoming more similar to remnant conditions with increasing time since management intervention (Fig. 7a, b: $F = 3.752, p = .119$ and $F = 2.735, p = .03$, Table 2).

3.2. Functional trait analysis

To examine the community response to *P. undulatum* removal from a functional perspective, species were classified according to functional traits (Fig. 6c). A clustering effect was again found for communities at

Table 2

Statistical analysis of the effect of time since clearing on the relative species richness observed at cleared treatments across sites (data presented in Fig. 3), along with the relativized Euclidian distance between remnant control and cleared areas within sites (data presented in Fig. 7a–c). * Denotes significance at 95% confidence. Species Richness: Adjusted $r^2 = 0.442$, F statistic = 4.575. Presence/Absence: Adjusted $r^2 = 0.478$, F statistic = 3.752. Canopy Cover: Adjusted $r^2 = 0.366$, F statistic = 2.735. Functional Richness: Adjusted $r^2 = 0.007$, F statistic = 1.024.

		Estimate	Std. error	T value	p value
Species richness	Intercept	0.663	0.137	4.812	0.001*
	Time since clearing	0.052	0.016	3.227	0.014*
	Distance to remnant site (m)	0.000	0.000	0.147	0.887
Presence absence	Intercept	1.421	0.515	2.754	0.033*
	Time since clearing	0.122	0.067	-1.814	0.119
	Distance to remnant site (m)	0.000	0.000	1.025	0.345
Canopy cover	Intercept	3.495	0.869	4.021	0.006*
	Time since clearing	-0.309	0.113	-2.722	0.034*
	Distance to remnant site (m)	0.001	0.000	-1.617	0.156
Functional richness	Intercept	2.923	1.244	2.349	0.057*
	Time since clearing	-0.269	0.162	-1.655	0.149
	Distance to remnant site (m)	0.000	0.001	-0.554	0.599

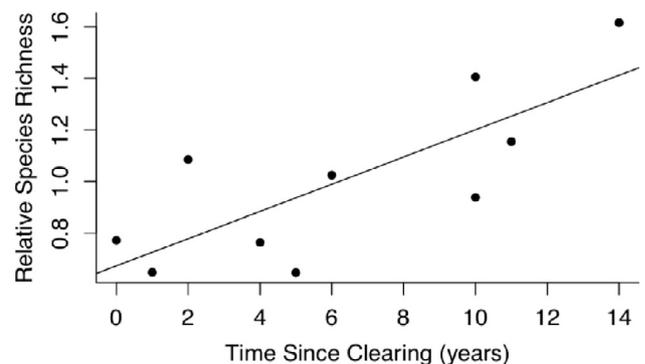


Fig. 4. Relationship between time since *Pittosporum undulatum* removal at cleared treatments and relative species richness (species richness at cleared treatment divided by species richness at remnant control). Adjusted $r^2 = 0.442, p = .014^*$. For full statistical analysis see Table 2.

invaded controls. When examining the relative Euclidian distance between remnant controls and cleared treatments a non-significant negative linear trend was detected such that cleared treatments areas

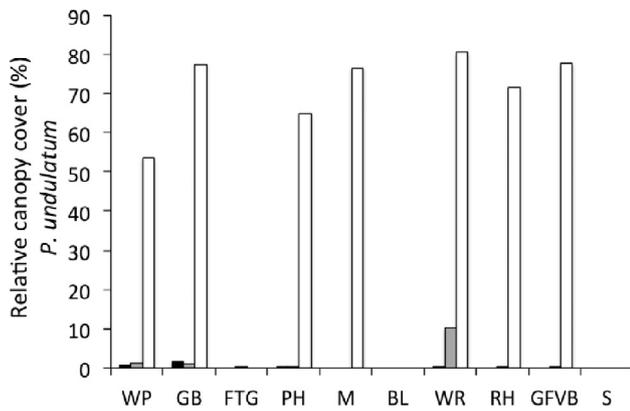


Fig. 5. Mean percentage cover of *Pittosporum undulatum* within treatments and across sites. Remnant control – remnant bushland (black), cleared treatment – *Pittosporum undulatum* removed (grey), negative control – high-density *Pittosporum undulatum* (white). A negative treatment was not included at FTG, BL and S treatments. WP – Wonga Park, GB – Greens Bush, PH – Panton Hill, WR – Woods Reserve, BL – Birdsland Reserve, GFVB – Glenfern Valley Bushlands, FTG – Ferntree Gully, RH – Red Hill, M – Montrose, S – Sherbrooke Forest. For full statistical analysis see Table 2.

became increasingly similar in function to remnant controls, with greater time since *P. undulatum* removal (Fig. 7c) ($p = .149$, $F = 1.024$).

4. Discussion

The targeted removal of invasive species such as *P. undulatum* can greatly influence the composition, structure and functionality of native plant communities. *P. undulatum* removal resulted in an increase in native flora richness and a proportionally small increase in the presence of exotic species. Once *P. undulatum* was cleared, very low rates of re-establishment were detected. Importantly, the removal of this species appears to have altered the state of cleared treatments. Control of *P. undulatum* produced a trend whereby the species richness, canopy cover and functionality of plant communities within cleared areas became increasingly similar to nearby positive reference controls over time.

4.1. How has the removal of *Pittosporum undulatum* influenced the capacity for indigenous plant communities to re-establish and resist reinvasion?

Our results highlight how the removal of a targeted woody invader can alter community composition and structure. More broadly, results demonstrate the capacity for ecological theory to strengthen practical on-ground restoration efforts. Treatment of *P. undulatum* reduces its presence within cleared treatments. A near complete absence of *P. undulatum* regrowth at all cleared treatments, even 1–14 years after control works, underlines the importance of knowing the ecology of the focal species. *P. undulatum* holds most of its seed within the canopy, thus once mature trees are removed from the system, so is the majority of its seed (Gleadow & Narayan, 2007). Removal of a dominant woody invader such as *P. undulatum* diminishes its capacity to compete with resident native species, whilst alleviating pressure for nutrients, moisture and light (Gleadow & Ashton, 1981; Gleadow et al., 1983; Levine et al., 2003). It has been suggested that *P. undulatum* may also have an allelopathic effect on its neighbors (Gleadow, 1982; Gleadow & Ashton, 1981). Thus, removal of this species from the system may reduce any suppressive effect *P. undulatum* has on competitors, in addition to increasing the availability of resources (Del Fabbro & Prati, 2015).

The viability of remaining *P. undulatum* seeds within the soil seed bank is considered poor if exposed to hot dry conditions in the absence of a shading canopy, or if buried more than 4 cm deep in the soil (Gleadow & Rowan, 1982; Gleadow & Narayan, 2007). The abiotic

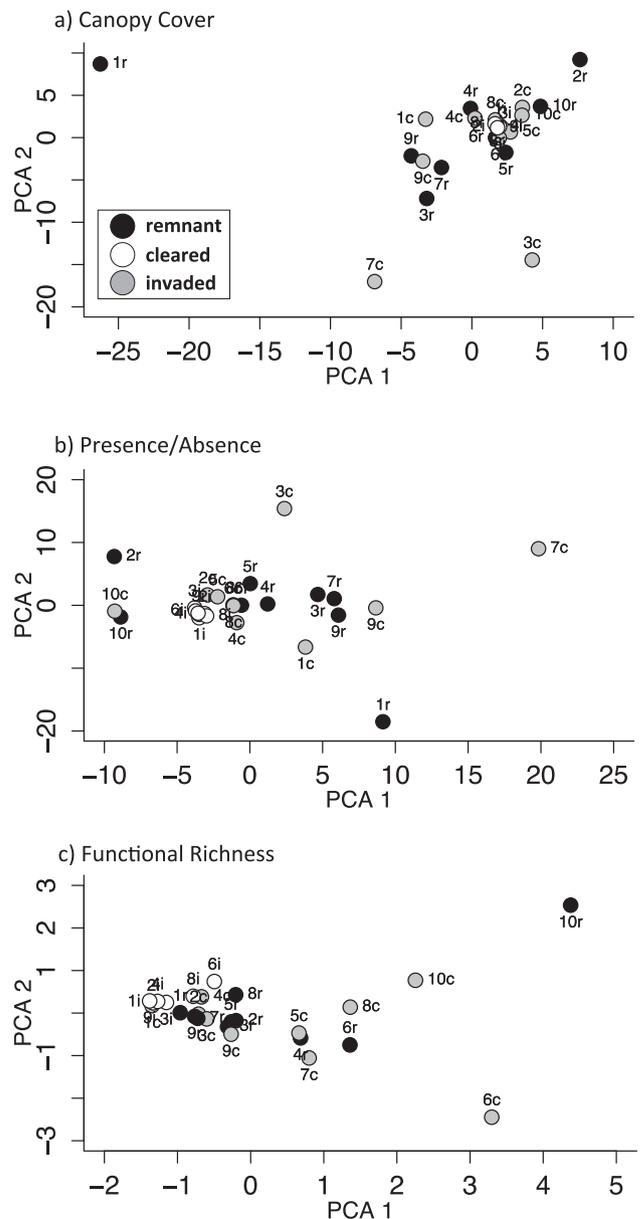


Fig. 6. Principal components analysis showing the change in community similarity in terms of (a) mean canopy cover, (b) species presence/absence and (c) the relative functional similarity of all sampling conditions within sites. Points were composed of mean weighted trait values for each sampling condition across all sites based upon the trait values of 205 species. Sampling conditions are labelled by site “ref no” found in Table 1 and treatment type. 1 – Wonga Park, 2 – Greens Bush, 3 – Panton Hill, 4 – Woods Reserve, 5 – Birdsland Reserve, 6 – Glenfern Valley Bushlands, 7 – Ferntree Gully, 8 – Red Hill, 9 – Montrose, 10 – Sherbrooke Forest. r = Remnant control – remnant bushland (black circles), c = Cleared treatments – *Pittosporum undulatum* cleared (grey circles), i = invaded control – high density *Pittosporum undulatum* (white circles). For full statistical analysis see Fig. 7a–c and Table 2.

environment was altered principally through the removal of *P. undulatum*'s dense shading canopy. Thus, removal of the canopy will influence light and moisture levels, in turn changing the local microclimate whilst also helping to suppress the re-establishment of remaining *P. undulatum* seedlings (Roundy et al., 2014). *P. undulatum* presence and its removal will also change the regulation of microbial processes, leading to altered nutrient availability (Lindsay & French, 2005; Marchante et al., 2009).

Our results suggest *P. undulatum* dispersal mechanisms are unlikely to interfere with the recovery of indigenous plant communities. Bird species such as the Silver eye (*Zosterops lateralis*), Pied Currawong

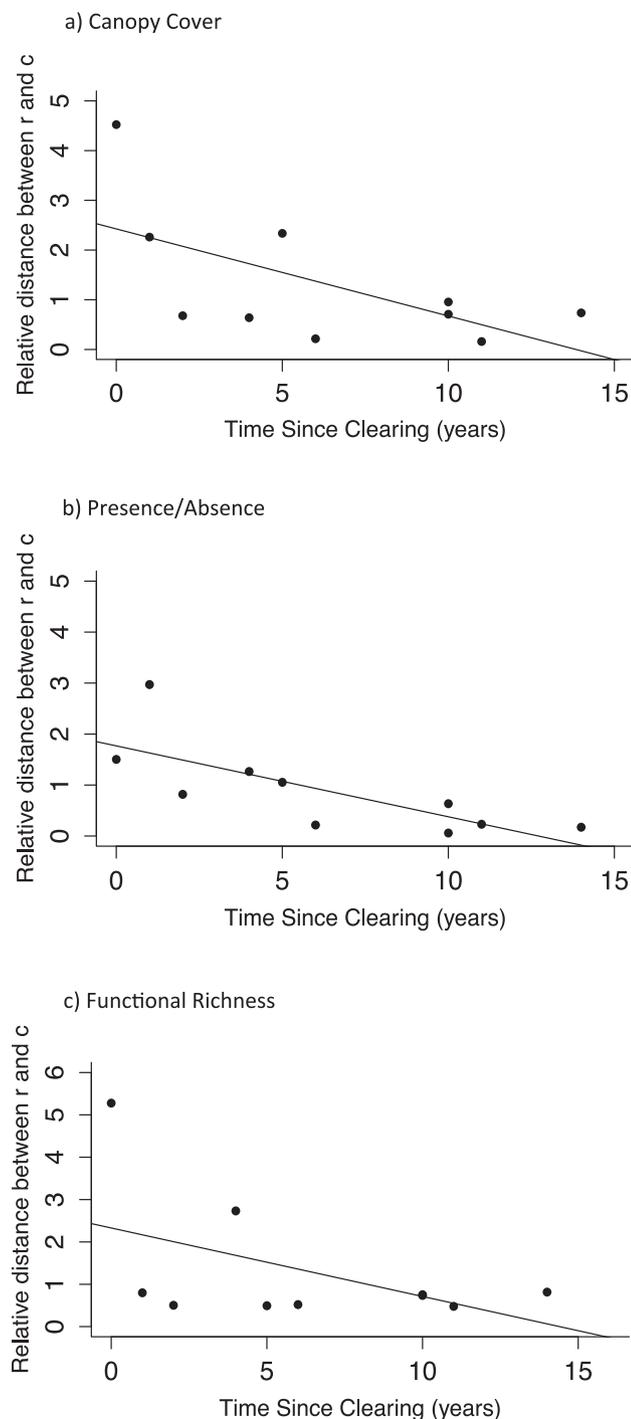


Fig. 7. The relative Euclidian distance between remnant controls (r) and cleared treatments (c) across time since management action for (a) Canopy Cover, adjusted $r^2 = 0.3664$, $p = .034^*$, (b) Presence/Absence, adjusted $r^2 = 0.478$, $p = 0.119$; and (c) functional richness $r^2 = 0.007$, $p = .149$. Distances are relative to the distance between remnant and invaded conditions within a site. For full statistical analysis see Table 2.

(*Strepera graculina*) and particularly the introduced European Blackbird (*Turdus merula*) are considered important dispersers of *P. undulatum* seed (Gleadow, 1982; Mullett, 1996). Observations of these species at all 10 sites (ALA, 2017) suggests that their role as vectors may not strongly influence the recovery of native plant communities after *P. undulatum* management.

Beneath the deep shading *P. undulatum* canopy full sunlight has been recorded at just 24% and 8% through summer and winter respectively (Gleadow, 1982; Gleadow & Narayan, 2007). Low light levels

may preclude the recruitment of other invasive species, and may help to explain the low level of exotic species observed at cleared areas. Furthermore, the deep shade may also inhibit the germination of indigenous species present within the soil seed bank. Thus, native species that are in situ are able to quickly re-establish after removal of *P. undulatum*.

4.2. Is change within floristic communities driven by the focal species, or does it act as a passenger or transformer of change?

Monitoring the ecological response of native communities after invasive species removal enables the assessment of the target species along the Passenger - Driver spectrum (Lindenmayer et al., 2015; MacDougall & Turkington, 2005).

In our study, species richness rapidly increased following removal of *P. undulatum* and the communities tended to shift back towards a state similar to that of remnant controls. A shift such as this is more typical of a Driver species (Lindenmayer et al., 2015; MacDougall & Turkington, 2005). Legacy effects such as long term soil nitrification or altered disturbance regimes are characteristic of some driver species and the absence of these effects in the current study could be interpreted to mean that *P. undulatum* is acting as a passenger or backseat driver (Bauer, 2012). However, where legacy effects are the result of the presence of the plant itself, for example through allelopathy, the effect may be short lived (Del Fabbro & Prati, 2015). If *P. undulatum*'s purported allelopathic effects (Gleadow & Ashton, 1981) are short lived, then this could account for the apparent absence of any legacy effect and indicate that *P. undulatum* is indeed a driver species. Following the PDH process helps to indicate the importance of disturbance to invader establishment (Hobbs, 2007; Lindenmayer et al., 2015). Information such as this can assist land managers to decide if invasive species treatment is likely to lead to ecosystem recovery, define expectations, form management programs and to set realistic goals (Guido & Pillar, 2017; Lindenmayer et al., 2015). Defining *P. undulatum* as a Driver of change helps to improve our understanding of this invasive woody species. Furthermore it underlines the suitability for investment and targeted removal of *P. undulatum* to restore high quality remnant bush land. If communities had responded to *P. undulatum* removal with a Passenger/Transformer response, careful amelioration of the disturbance regime and abiotic processes would have been suggested, along with the adjustment of restoration goals see (Lindenmayer et al., 2015, see Fig. 1). This process can be evaluated only after the removal of invasive species and therefore cannot inform initial management actions. However, dominant invasive species are often targeted for removal by a range of stakeholder groups, e.g., Government bodies, Parks associations and volunteer groups. Researching the results of these efforts via a basic floristic assessment together with nearby remnant and invasive controls (in a similar fashion to this study) would be highly informative to the development of further action plans. Whilst every effort was made, not all factors that may initially have facilitated the establishment of invasive *P. undulatum* populations could be incorporated into the study design. Historical disturbances, for example, may have created specific conditions suitable to *P. undulatum* (Mosher et al., 2009). In the absence of ongoing historical disturbance, the conditions that could have assisted the re-establishment of *P. undulatum* populations may no longer be present.

4.3. Do floristic communities recover after restoration work from a functional standpoint?

The analysis of community recovery from a functional traits perspective provides an additional lens to judge and evaluate the effect of restoration actions. Greater functional diversity means that available resources are utilised more efficiently across an area, improving community resilience, long term stability and invasion resistance (Cadotte et al., 2011; Díaz & Cabido, 2001; Funk et al., 2008). A negative trend

regarding differences between remnant controls and cleared areas suggests that removal of *P. undulatum* has altered the functional richness of managed plant communities (Figs. 6c, 7c). Plant communities appear to become more functionally similar to positive remnant conditions with increasing time since management action took place. Similar patterns of increases in species diversity and functionality support the idea that the rate at which plant functionality increases may be limited by the rate at which new species can return and re-establish (Aerts & Honnay, 2011). The level of disturbance, soil stored seed bank and time also constrain the natural re-establishment of highly functional native plant communities. Activities that cause high levels of disturbance such as invasive species removal can promote the establishment of colonizing species, which outcompete less vigorous growers and late successional species (Bohn et al., 2014; Palma et al., 2017). Colonizing species often share many functional attributes e.g. short lifespan, small seed size, rapid growth strategies (Bohn et al., 2014; Webster et al., 2006). Thus, whilst functional richness may increase, if functionally similar species are entering the region, overall community functionality may not rise significantly (Aerts & Honnay, 2011). The rate of increasing species richness and by extension the rate of increasing functional richness will therefore depend upon both the time it takes for seed from more distant areas to reach the site, along with the time it takes for successional processes to diversify niche space within the environment.

5. Conclusions

Comparing restoration successes and failures is made difficult by the paucity of monitoring after intervention. Despite this, some evidence exists suggesting that given sufficient time, often in the order of decades, and the necessary human will, ecosystems can recover from serious disturbance. These concepts are supported by the data presented here. Our study demonstrates how ecological theory can be used to understand native communities response to invasive species and ecosystem change, leading to more informed restoration projects in the future. As global demand for restoration solutions increases, application of theory-based approaches will become increasingly important. We therefore encourage greater monitoring and data collection integrated within each restoration project and support a whole ecosystem approach to monitoring restorative effects including fauna, ecosystem process, soil microbe and soil nutrient analysis.

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Supplementary material

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