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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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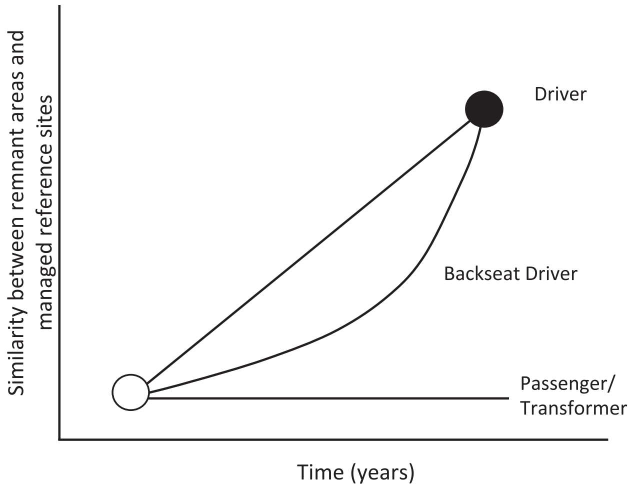

Fig. 1. Conceptual diagram depicting the response of a heavily invaded plant community (white circle) to invasive species removal. Plant community response is considered relative to a biodiverse high quality reference community (black circle). Removal of Passenger species is expected to alter the invaded 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; Chabrerie 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 Diver 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