Are transformer weeds ecological rule breakers?

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Summary Transformer weeds are increasingly recognised for the high impact that they have on native communities through transforming ecosystem processes and function. Various types of transformer weeds have been described, but the manner through which they dominate native communities has not been explored ecologically. Here we consider transformer weed invasion in the context of ecological community assembly theory. In each case we ask whether and how transformer species break these ecological rules and flaunt ecological theory. Are transformer weeds ecologically different from other plant invaders and if so how can this inform management?

Keywords Invasion mechanisms, plant community theory, WoNS.

INTRODUCTION

The Convention on Biological Diversity, amongst other relevant international policy frameworks, considers invasive alien species in terms of their economic, environmental and social impacts. Amongst invasion biologists, however, an invasive species is considered 'with reference to the "biogeographic/demographic" status of a species without any connotation of impact' (Richardson *et al.* 2000). This ecological definition captures all exotic species that manage to enter and spread in ecosystems outside their native range to become a substantive member of the new community. However, invasive plants that capture the political attention are those that have clear and significant impacts. The worst of these have attracted the term 'transformer species' (Wells *et al.* 1986, Richardson *et al.* 2000) and to quote Richardson *et al.* (2000) these are 'a subset of invasive plants (perhaps only 10%) which change the character, condition, form or nature of a natural ecosystem over a substantial area'. They often form monocultures and 'have profound effects on biodiversity and… clearly demand a major allocation of resources for containment, control or eradication'. The long-term changes to ecosystem function

and processes that they cause are often impossible or extremely difficult to reverse. Beyond smothering the existing flora, transformer weeds can also alter many abiotic conditions. Richardson *et al.* (2000) identified eight categories of transformer: (1) excessive users of resources; (2) donors of limiting resources, (3) fire promoters/suppressors, (4) sand stabilisers, (5) erosion promoters, (6) colonisers of intertidal mudflats/sediment stabilisers, (7) litter accumulators and (8) salt accumulators/redistributors. Thirteen of Australia's 20 Weeds of National Significance (WoNS, Thorp and Lynch 2000) are transformer weeds. Some examples are listed in Table 1.

Plant community ecology attempts to understand the processes underlying community assembly, i.e. that allow species to co-exist. Various ecological theories help explain this and it is now widely accepted that a range of ecological processes determines community diversity and structure. The monospecific stands formed by transformer species suggest that they do not play by the same set of ecological assembly rules as native species.

Table 1. Key transforming action and example Australian transformer weeds that through their novel phenotypes have irreparably changed the invaded communities.

Transformation	Weed
Water users	Parkinsonia, prickly acacia
Light users	Rubbervine, miconia
Oxygen users	Salvinia, cabomba
Fire changers	Gamba grass, mimosa
Sand/sediment stabilisers	Bitou bush/boneseed
Erosion promoters	Miconia
Litter/nutrient accumulators	Olive hymenachne, gorse, broom, bridal creeper
Salt accumulators	Athel pine

This paper will consider how transformer species might flout community assembly theories that form the basis of native plant community structure, at least over short time scales, to achieve domination and transformational status. First we consider mechanisms of invasion and then discuss the dominant ecological theories of community assembly in the context of transformers. Clearly a better community ecological understanding of how transformer species achieve high impact will assist efforts to manage ecosystem resilience against them.

INVASION HYPOTHESES AND MECHANISMS
There are five main non-exclusive processes that, following establishment through reproduction and/or dispersal advantages, can lead to rapid plant invasion (cf. DeWalt 2005, see Figure 1). These include:

1. Natural enemy release – (enemy-release hypothesis – ERH, Keane and Crawley 2002) where the invader is introduced into the new environment without its native natural enemies (herbivores, fungi and microbes) and there are few enemies that can suppress it.

2. Novel genotype and/or empty niche – where the new arrival is a genotype that is pre-adapted to the new environment by having a highly competitive or novel ecological functional type or physiology (e.g. nitrogen fixer, C3, C4 or CAM photosynthetic pathway) or allelochemistry, or phenotypic plasticity (around growth, flowering and/or germination) to achieve individual fitness homeostasis and is thus able to find and exploit a vacant ecological niche in the new environment.

3. Genetic adaptation – where single or multiple introductions of the invader that on their own, or through hybridisation or admixture (without parental back crossing), evolve rapidly to distinct founder population gene pools well adapted to the local conditions.

4. Resource availability – where the disturbance (light, water, nutrients, fire) regimes (anthropogenic or natural) in the new environment can be exploited by the pre-adapted invader or where available mutualisms (symbionts, pollinators or dispersers) provide the invader with resources through mutualisms in the new environment

5. Anthropogenic propagule pressure from commercial plants of exotic species.

Synergies between these processes can further assist the invasion process. For example, release from natural enemies could lead to

adaptation to other selection pressures (e.g. Blossey and Nötzold 1995), while better conditions for growth and reproduction can lead to evolutionary changes in invader life history strategies (Müller-Schärer *et al.* 2004, Metcalf *et al.* 2008). An additional mechanism for transformers is the alteration of the abiotic or ecological conditions in the community, e.g. disturbance regimes or nutrient levels, to enhance their competitive advantage.

HOW DO TRANSFORMER WEEDS BREAK
THE ECOLOGICAL RULES?
The capacity for transformer weeds to form monocultures and dominate ecosystems may be driven by an overriding advantage of recruitment success leading to the exclusion of competitors. In contrast, community assembly theory has sought to explain the lack of natural monocultures, i.e. why species recruitment is often more successful away from the parent.

In this context it is useful to re-consider the main theories available to explain plant community assembly (DeWalt 2005) and to consider how transformer species appear to be able to adapt or ignore them. These are (a) the unified neutral theory (Hubbell 2001), (b) the intermediate disturbance hypothesis (Connell 1979, Huston 1979), (c) the empty niche hypothesis (Elton 1958, Tilman 1997) and (d) the Janzen-Connell hypothesis (Janzen 1970, Connell 1971).

Under the unified neutral theory, species occupy sites as they become available based on seed availability, dispersal and chance (Hubbell 2001).
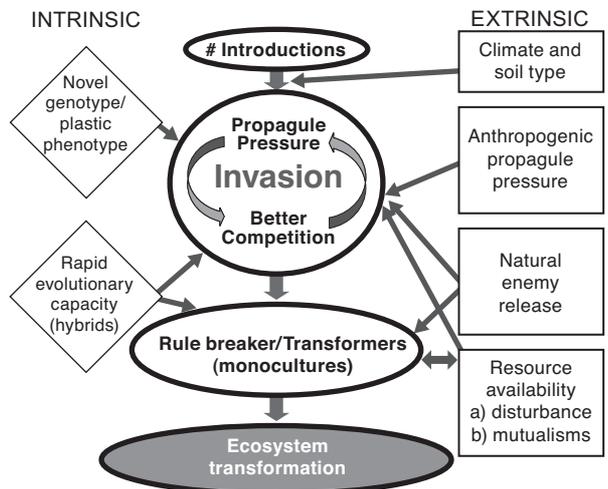
Figure 1. Schematic diagram of the common intrinsic and extrinsic factors and processes that allow some invasive plants to transform ecosystems.

Species diversity is set by probabilities of species extinction, speciation and immigration in proportion to the number of species available in the regional pool, which is also set by the size of the region of similar habitat. An underlying premise of this theory is that when a plant individual dies in the community each plant species has equivalent probability of capturing the free space. The theory was developed for tropical forests and helps explain why all patterns in diversity are not explained by underlying environmental variation. Under this theory any additional species (exotic or native), given adequate propagule pressure (number and frequency of arriving propagules) can establish in the community, but the theory still predicts they should not form monocultures (cf. Zhou and Zhang 2008). Transformer weeds break these rules by being able to circumvent the stochastic processes that result in the dispersed recruitment of native species.

The intermediate disturbance hypothesis (IDH) argues that species diversity is driven by variability in species responses to disturbance (= resource availability). The more variable the resource availability the more species the community can support. A transformer species may invade irrespective of the initial disturbance regime, but then promote (e.g. fire enhancer) or inhibit (e.g. climber) disturbance in their favour. By this means they can attain a much greater fitness advantage over resident species, and may also be assisted by enemy release and/or attraction of generalist mutualisms. According to IDH, dominance by one or a few species is more likely to occur at the high or low ends of the disturbance continuum and transformer species drive this by moving the community to either extreme of the disturbance gradient by either increasing or decreasing disturbance regimes and flattening the species richness curve as it develops a monoculture. Transformers cause a positive feedback so the disturbance responds to the community and the community to the disturbance.

The vacant or empty niche hypothesis has a scaling component similar to the unified neutral theory and is based on the idea that as spatial scale increases there will be more ecological niches available (Tilman 1997), even though novel life forms can invade at any scale (e.g. trees invading fynbos). At the small scale the number of niches is constrained and for each new, 'better' adapted invader a 'poor performer' drops out. At large scales, the number of niches available is more likely to be greater than the total species pool. Arriving exotics can establish and spread with little relative harm. This leads to an increased species pool. The vacant niche hypothesis helps explain how exotic species assisted by propagule pressure naturalise and spread at a large spatial scale, but does not provide a mechanism for the existence of monocultures at a local scale. To do this the invader must have a large competitive advantage via a capacity to modify the niche surface in its favour, possibly assisted by enemy escape or opportunistic mutualisms (cf. MacDougall *et al.* 2009).

Finally the Janzen-Connell hypothesis (Connell 1979, Janzen 1970) is based around the impacts of specialist natural enemies. Although more seeds are dispersed and more seedlings germinate near parent plants their density of successful recruitment is proportionally less due to the clustering of specialist natural enemies around the parent (Figure 2). There is an optimal distance from the parent where probability of establishment is increased. When species have a greater recruitment success away from the parent this provides a basis for explaining high local species diversity. This hypothesis is built on natural enemies as the causal mechanism for species dispersion patterns in communities and would suggest transformers may form monocultures simply because of an absence of such enemies. If a combination of this and ERH is why some transformers have been so successful it may also help explain the occasional high success of biological control programs against transformer weeds.
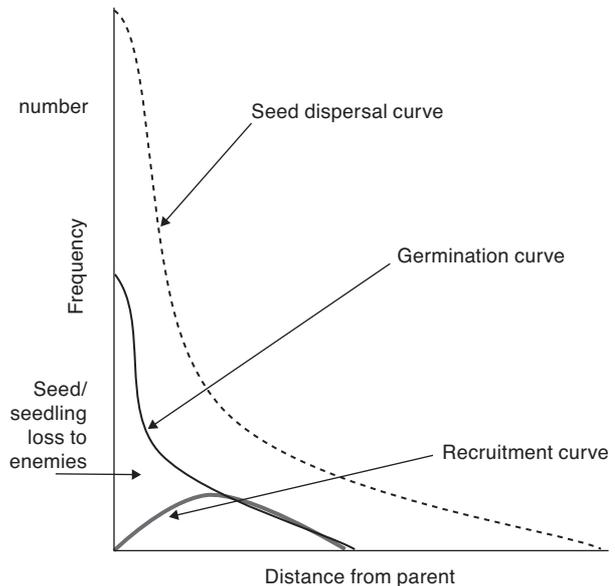
Figure 2.   Jansen-Connell hypothesis predicts higher natural enemy densities closer to the parent lead to greater seed and seedling survival with distance away from parent.

What makes a species a better competitor and therefore transformer in some situations depends on the level of critical resources. In some environments transformers (at least temporarily) will be species that can use resources quickly. In other environments transformer species have the lowest reproductive rate and are the best competitors (MacDougall *et al*. 2009).

CONCLUSIONS

Weed management investment will optimally focus on identifying, preventing and managing those species that can transform the communities they invade to the significant detriment of the resident community. These are the invasive plants that disrupt community composition and function. We have explored some of the underlying biological mechanisms that can explain the existence of transformer weeds. We have also considered widely-accepted plant community assembly theories and how transformer weeds are capable of exploiting or flouting these theories to form dense monocultures and alter ecosystem function and service provision. Indeed transformer dominance and ecosystem modification may act spatially as a positive feedback process. From these considerations of ecological theories it appears that some species transform communities and ecosystems through a combination of novel genotype competitive advantage, enemy release and/or opportunistic mutualisms and a capacity to modify the disturbance and resource availability experienced by the resident species. The relative importance of each mechanism will vary, but evaluating these may assist in managing the current high impact of weeds and identifying future transformers before they wake up.

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