

Communication

Plant Invasions: Symptoms and Contributors Rather Than Causes of Environmental Degradation

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Abstract: Native or exotic woody plants can proliferate in dry and moist eucalypt ecosystems shading out many other native species, contributing to chronic decline of eucalypts and reinforcing unnatural fire regimes and nutrient cycling processes. Whether native or exotic, they proliferate as a consequence of disturbances which impact directly on these ecosystems. The most extensive ongoing disturbance since European occupation of Australia has been the disruption of frequent mild burning by humans. This burning maintained dynamically stable nutrient cycling processes and a competitive balance in dry and moist eucalypt systems and prevented plant “invasions”.

Keywords: eucalypt; invasive plants; fire; nutrient cycling; competitive balance; man; disturbance

1. Introduction

In the invitation to this special issue, Professor Jose proposed that invasion by alien plants can alter fire regimes, nutrient cycling, hydrology and energy budgets, affecting the abundance and persistence of native species. However, Australia’s ecological history suggests the reverse. Alterations to the natural (pre-European) fire regime have affected nutrient cycling, hydrology and energy budgets allowing a few native or exotic plants to proliferate and suppress many smaller native plants [1]. A recent review of invasions around the world found that many ideas at the foundation of invasion ecology have been accepted without testing or despite equivocal evidence [2]. Many lines of research looking at traits of successful invaders or susceptible ecosystems yielded contradictory results. The

review concluded that disturbance was a weak predictor of exotic plant invasions and that change to disturbance regime was a better predictor [2].

Evidence from eucalypt ecosystems in Australia suggests that disturbance needs to be better defined. Droughts and floods have been regarded as natural disturbances whilst burning by humans has been seen as anthropogenic disturbance. However eucalypt ecosystems were shaped by droughts and/or floods as well as human burning over many thousands of years and these factors maintain a dynamic stability by controlling plants that are not adapted to them whilst favoring plants that are adapted and dependent on them [3]. Disturbance should be seen as an unnatural factor outside the “range of experience” of the ecosystem in question. This requires historical and physical evidence of the environmental history of the ecosystem [3]. In this context, it can be seen that disturbance upsets a natural competitive balance favoring a few native or exotic plants at the expense of many other natives [1]. Successful “invaders” are plants that respond positively to disturbance and the traits of successful invaders vary according to the type of disturbance. This concept is examined by reference to some “invasive” native and exotic plants responding to disturbance in native eucalypt forests.

2. Discussion

2.1. *Invasions in Eucalypt Systems*

Chronic eucalypt decline originally occurred as a result of disruption of Aboriginal burning by European settlers, and increased dramatically in Australian forests during the late twentieth century as a result of reduced burning and/or grazing [4]. Declining stands often develop dense understoreys of a few native or exotic shrubs and decline has sometimes been attributed to reduced water and nutrient status as a result of competition from these “invasive” understoreys [5,6]. However several studies have shown that soil water and nitrogen status is increased in declining stands, and trials of understorey removal have failed to ameliorate declines [7]. In the absence of burning, changes in soil physics and chemistry including reduced aeration and drainage, increasing acidity and availability of toxins such as aluminium, and reduced relative availability of nutrients such as phosphorus, adversely affect eucalypts while favoring some pests, parasites and competitors [8].

Nitrogen accumulation is the main driver of changes in soils and consequent changes in species composition across a wide range of ecosystems around the globe [9]. Chronic eucalypt decline in the absence of fire is one facet of this global phenomenon that is more commonly associated with industrial emissions or agricultural fertilizers in other regions [4,9,10]. Lantana is an invasive exotic that is involved in eucalypt decline in some areas of subtropical eastern Australia, and is thought to contribute to the problem by increasing the nitrogen content of the soil [6]. However, lack of burning directly increases nitrogen in comparison to the natural system because nitrogen in litter and humus is not removed by volatilization [8]. (After low intensity fires, mineral nitrogen released by heating soil organic matter is quickly taken up into standing biomass [8]). Decline is consistently associated with high levels of nitrogen and low carbon:nitrogen ratios in soils but it is not related to the floristic composition of the understorey (for example, [11]). In temperate areas where the climate is not suitable for lantana, native shrubs are mostly involved in the process [4]. Some of these can contribute to the

problem by fixing nitrogen [8], but there are other cases where the invasive shrubs are not nitrogen fixers or where there are no invasive shrubs involved in the process [4].

Where invasive understoreys are involved, the onset of decline may precede shrub invasion, and understorey development may accelerate as the declining canopy permits more light to reach the forest floor [4]. However, if potentially aggressive understorey species are already present in low densities, decline and understorey development can proceed simultaneously as lack of burning directly impacts on soil conditions and trees whilst permitting mass establishment of fire-sensitive shrub seedlings [1,8].

Grazing by domestic stock (exotic animals) in eucalypt forests is widely regarded as a disturbance with adverse ecological consequences [12]. However, Australia's ecological history shows that grazing has frequently served as an analogous ecological process to frequent burning [3,4]. Grazing removes some nitrogen in livestock biomass and by volatilization from faeces and urine and also prevents establishment of woody seedlings. Grazed woodlands in Sydney have no greater exotic species richness or cover than ungrazed woodlands, whereas areas obtaining nutrients from urban runoff have higher exotic richness and cover [13].

River regulation as well as fire exclusion has disturbed ecosystems on the floodplains of the Murray Darling Basin by reducing the frequency and extent of flooding [3]. Forests of river red gum (*Eucalyptus camaldulensis*) have invaded former treeless wetlands and woody understoreys have invaded naturally grassy woodlands. Dwarf cherry (*Exocarpos strictus*) and mistletoe (*Ameyma miqueli*) are two native parasites that have proliferated in river red gum forests as a consequence of the combined disturbances. These disturbances have altered fire regimes, nutrient cycling, hydrology and energy budgets and the native parasites have consequently flourished and reinforced the alterations [3].

2.2. Traits of Successful "Invaders" and Properties of Susceptible Ecosystems

Potentially aggressive species in eucalypt systems are species that are shade tolerant—they can establish under a eucalypt canopy—and shade providing, but are sensitive to mild fires in the seedling stage. In the natural (pre-European) system these species were either confined to moist and often fertile fire refugia, for example pittosporum (*Pittosporum undulatum*) [14] and ti tree (*Leptospermum scoparium*) [15], or scattered in low densities across more exposed sites, like sheoak (*Allocasuarina littoralis*) [16] and cherry (*Exocarpos strictus*) [17].

Pittosporum has a fleshy fruit that is attractive to frugivorous birds. It slowly invades from the edges of dry bushlands around Sydney where exotic trees and shrubs with similar fruits occur on the urban fringe and attract such birds [14]. Nutrient enrichment of these bushlands by urban runoff and rubbish dumping improves the habitat for pittosporum (though it may not be recognized as an invasive species where it is within its natural range) (for example, [18]). Lantana (*Lantana camara*) and two privets (*Ligustrum*) are exotics that have similar traits to pittosporum and can invade dry bushlands around settlements or rainforests (which contain many species with fleshy fruits) in a similar fashion [14]. Like pittosporum, long distance dispersal of lantana and privet are limited by a scarcity of frugivorous birds in dry eucalypt forests (pers. obs.). Nutrient enrichment is also a critical prerequisite

for invasion of Sydney's dry bushlands by exotic plants [18]. Exclusion of fire leads to nitrogen accumulation [8] whilst urban runoff and rubbish dumping contribute to nutrient enrichment [14].

Pittosporum, lantana and privet are not invaders of extensive dry eucalypt forests where fleshy fruits and frugivorous birds are naturally scarce and nitrogen accumulates slowly in the absence of fire [8]. Sheoak occurs naturally in some of these forests as scattered small trees and is "invasive" or aggressive in the absence of frequent fire. Sheoak is shade tolerant and fixes nitrogen. It has fire-sensitive seedlings whose establishment is naturally limited by frequent fires. With disturbance by fire suppression, dense stands expand outwards from mature trees, shading out many groundcover species and exacerbating chronic decline of eucalypts [1]. A similar process occurs when ti tree spreads from damp microsites within dry eucalypt systems in the absence of fire [15].

Release from natural predators is not a cause of plant invasions in Sydney's bushlands, however invasiveness of exotics is consistently associated with high specific leaf area (SLA) [18], a trait associated with shade tolerance. Pittosporum is a shade-tolerant species [14] and is the dominant species in 49% of forests in the Azores where it is exotic [19]. In contrast, a review of the ecological implications of shade tolerance suggested that invasive plants are not frequent in dark forest understoreys because they are usually shade intolerant, performing well in high-light and highly disturbed environments [20].

This highlights the need to focus on disturbance and avoid generalizations, because traits of successful invaders and properties of susceptible ecosystems will vary with the nature of the disturbance. Shade intolerant species can be invasive where disturbance increases light whereas shade tolerant species can be invasive when disturbance reduces light. Exclusion of frequent mild fires is a disturbance that favours fire-sensitive, shade-tolerant, nutrient-loving "invaders" over intolerant, fire-demanding eucalypts adapted to infertile soils [4]. Susceptible eucalypt ecosystems are associated with sheltered sites on infertile, poorly buffered and poorly drained soils where shade and adverse soil conditions develop quickly in the absence of fire [5,8].

Tall wet eucalypt forests on sheltered sites with fertile, well-structured and well-buffered soils are a different proposition [21]. Invasive natives or exotics are generally absent. These forests have a dense subcanopy of native shade-tolerant species. Naturally infrequent high intensity fires temporarily destroy the canopy and subcanopy, allowing the highly intolerant, fast-growing, light-demanding eucalypts to regenerate from seed and quickly establish a new canopy under which the shade-tolerant native subcanopy species can develop. These fires are not a disturbance, and no single species—whether tolerant or intolerant—gain an unnatural competitive advantage. For example, lantana can invade naturally grassy moist eucalypt forests in the absence of fire, but it does not invade the tall wet eucalypt forests with a subcanopy of rainforest species [21].

2.3. Disturbance and Plant Invasions

Frequent mild burning in dry and moist eucalypt systems and infrequent high intensity lightning fires in wet eucalypt systems are not disturbances and they do not facilitate plant invasions, rather they maintain natural competitive interactions—a "balance of nature". Most modern ecologists consider that a balance of nature does not exist [22] or that if it does exist it is exceedingly difficult to demonstrate [23]. However the concept of disturbance in ecology implies that some sort of balance or

stability has been disrupted [23]. Current opinion is that “secondary succession” after “disturbance” does not conform to generalizations, so concepts of persistence within stochastic bounds [23] or over a range of states [24] have developed.

Australia’s ecological history of plant invasions and chronic eucalypt decline does not support these new concepts. A study of long-term vegetation changes involving two “invasive” native species has not yet found any equilibrium developing after two centuries of disturbance by fire exclusion [16]. Sheoak has invaded the site over the past seven decades and continues to increase in density whilst most other species continue to decline [16]. In contrast, frequent burning in dry eucalypt ecosystems maintains diversity, resilience and fire safety [1].

From the fifteenth century, the Azores were disturbed by human activity and many exotic plants were introduced. Pittosporum invasion has been ongoing since the nineteenth century and no equilibrium has developed [19]. Harvesting pittosporum for bioenergy has been proposed as a stabilizing process [19]. This would be similar to commercial thinning of unnaturally dense stands of the native species river red gum (*Eucalyptus camaldulensis*) and white cypress (*Callitris glaucophylla*) for timber in Australia [3].

Australia was disturbed by human occupation about 40 Ka before present. Biomass burning increased markedly as evident from increased charcoal in sediment cores (Figure 2 in [25]). Mesic vegetation yielded to sclerophylls, herbs and grasses, and megafaunal extinctions occurred [1]. Fire regimes and vegetation stabilized (subject to long-term climatic variation) within a few millennia [1,25]. European occupation two centuries ago disrupted the equilibrium established by Aboriginal burning and facilitated “invasions” by native and exotic plants [1]. Equilibrium can be reestablished and these invasions can be controlled by appropriate fire regimes or analagous management such as thinning, grazing or slashing [3,4]. For example, lantana can be controlled by frequent burning in eucalypt forests (Figure 5 in [26]).

3. Conclusions

Disturbance is an extrinsic factor that upsets the dynamic equilibrium of an ecosystem and interferes with natural competitive interactions allowing a few species to proliferate at the expense of many others. Plant “invasions” are a consequence of disturbance. Nitrogen accumulation is a major global disturbance causing proliferation of native and exotic “invasive” plants.

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Conflict of Interest

The author declares no conflict of interest.

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