

Biodiversity change in heathland and its relationships with shifting local fire regimes and native species expansion

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Abstract

Aims

Understanding the relationships among disturbance, invasion and species change is essential for effective management of many systems. We investigated relationships among fire history, invasion by a native tree species, *Allocasuarina huegeliana*, and diversity change to understand the potential drivers of plant community alteration in a complex and biodiverse system.

Methods

We used plant species surveys from 1983 and 2011 to quantify species loss/gain and thence compositional changes. Additionally, we surveyed population densities of the invasive species and collated long-term fire history data for each site. General linear models and non-parametric models were used to assess the strength of relationships between the three variables of interest.

Important Findings

Within the last 30 years, ~11% of the plant species richness was lost from the reserve. At an individual site level, we found only a 4% average decrease in overall plant species richness, but large

species losses and gains that imply considerable compositional shifts. Though such shifts might be expected over 30 years, many of the gained species were common, potentially opportunistic species, while those lost were often locally rare woody perennials. In addition, gained species tended to be expanding their recorded range westward suggesting that they may be responding to the regional drying climate. The relationship between invasion density and species loss was strong over all spatial scales. We identified a potential state change to dominance by the native invasive particularly as high densities prevented species gain at the site scale. In these extreme cases of high invasive density and high biodiversity loss, we argue that there may be a need to directly address the expanding native population.

Keywords: kwongan, sandplain heath, *Allocasuarina huegeliana*, native invasion, woody encroachment

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INTRODUCTION

As global conditions shift, ecosystem compositions are changing dramatically. In many cases, species are expanding rapidly to become novel dominants, either through their introduction to entirely new regions (exotic invasion; e.g. gorse (*Ulex*

europaeus) in New Zealand) or through environmental shifts allowing rapid native species expansions (native invasion; e.g. broom snakeweed (*Gutierrezia sarothrae*) in Utah). Population expansions that shift ecosystems toward new competitive dominants have been shown to alter energy pools, nutrient flows, and ecosystem structure and composition (e.g. [Huxman](#)

et al. 2005; Knapp *et al.* 2008a, 2008b; Kurten *et al.* 2008). However, whether these expansions by individual species are a direct threat to biodiversity is at times unclear. Attribution of biodiversity change to invasive behavior is particularly difficult in the case of plant species expansions, which result predominantly in competitive and indirect effects such as shifts in mutualistic relationships; thus, their impact on ecosystems can be difficult to quantify. Large declines of species have been detected in heavily impacted areas; few, if any, proven examples exist of extinction caused by competitive exclusion (Eldridge *et al.* 2011; Gurevitch and Padilla 2004). Therefore, it is difficult in most plant expansions to unequivocally classify the invaders as a cause of species loss despite some cases of species clearly acting as drivers of detrimental change in an ecosystem.

An additional confounding factor is the common co-occurrence of novel population expansion with novel disturbance regimes and/or habitat degradation, which can have independent and interactive impacts on biodiversity (Didham *et al.* 2007). When invasion and disturbance are both present, observational and experimental attempts to pull apart the cause of biodiversity loss have had a range of results. In a study of biodiversity loss, invasion and habitat perturbation in dune systems, Veer and Kooijman (1997) found that in dune systems disturbed by nitrogen deposition and native grass invasion, the abundance and biomass of grass species was the predominant predictor of moss and vegetation species richness. In contrast, Chabrierie *et al.* (2008) studied disturbance history, plant loss and invasion in European forest and found that disturbance history correlated most strongly with final plant communities. Finally, Hay-scented fern (*Dennstaedtia punctilobula*) examples seem to emphasize the importance of both disturbance and population expansion. It is known to expand after overgrazing by deer and restrict tree seedling growth and development (Horsley 1993). Rooney (2001) reports that plots undergoing heavy deer browsing and plots with high fern density both show species impoverishment compared to undegraded forest plots. It is likely that hay-scented fern starts as a passenger of the overgrazing disturbance but moves on to become a driver of species loss. The variety of results found in previous studies imply that though the relationships among species expansion, degradation or disturbance shifts and diversity might have some generalizable patterns, the specifics will be largely system and species dependent. Thus, understanding the best way to conserve biodiversity often depends on trying to disentangle these interactions, with the nature of the relationship between them dependent on the exact circumstances and system under study (Didham *et al.* 2007).

Changed disturbance regimes or environmental conditions and native population invasion are commonly linked. They have an intuitively strong relationship since other causes of population expansion—enemy or pathogen release, new mutualisms—do not apply. Accordingly, much of the research on native invasion has found shifting disturbance regimes

to be the most likely cause of the expansion. For example, altered fire regimes have often been linked to cases of native expansion: juniper species (*Juniperus* spp.) have spread throughout southern American grasslands due to reduced fire frequency and altered grazing regimes (Ansley *et al.* 2006; Fuhlendorf *et al.* 1996) and broom snake-weed has spread to create monocultures in American rangelands due to fire regime shifts and overgrazing (Ralphs 2011). Woody invasion due to altered fire frequencies has been found to shift soil nutrient distribution, plant biomass, carbon and nitrogen pools in invaded ecosystems (Van Auken 2009) and has been correlated with species richness declines (Knapp *et al.* 2008a, 2008b).

This study considers all three aspects of loss, disturbance and native invasion together in an observational study in order to understand the potential drivers of species loss in an area of conservation priority. Though correlative studies do not allow direct causal identification, observational data are the most commonly available in management scenarios. A lack of relationships among variables suggests they are not causally related. Finding relationships suggests potential causation (hence potential drivers) and can guide further study to improve mechanistic understanding and help guide management action.

We focused our study on kwongan, a highly biodiverse sandplain heath system in southwestern Australia (Beard 1984; Pate and Beard 1984). These systems are historically fire prone, with much of the biodiversity composed of pyrogenic species with life-history strategies adapted to the local fire disturbance regime (Keith *et al.* 2002). Investigations of fire occurrence in the kwongan have found that the smaller, highly isolated fragments have a lower fire frequency, lower intensity and smaller size of fire events than unfragmented landscapes (Parsons and Gosper 2011). Changes in fire regimes can have large implications for fire-dependent species; in the absence of fire, some populations may experience sharp declines or local extinction (Keith *et al.* 2002; Quintana-Ascencio *et al.* 2003; Yates and Ladd 2010). Mallee-heath undergoes structural changes and senescence after ~45 years without fire (Gosper *et al.* 2011). In addition to directly impacting species richness and vegetative composition, the decrease of fire occurrence or intensity might allow fire-sensitive species to spread and thrive in areas previously unavailable due to repetitive fire events, potentially leading to native expansion.

This combination of factors makes kwongan an ideal system for investigating the effects of shifting disturbance. Additionally, local land managers believe that kwongan has been losing plant species diversity at dramatic rates in the past few decades. The perceived species loss is attributed to either a shift in the fire regime due to extensive land use change and fragmentation, expansion by the fire-sensitive native tree *Allocasuarina huegeliana* (L.A.S. Johnson) or both. In order to investigate these relationships, we first quantified the plant species loss in one kwongan heathland reserve over the last

30 years using observational data from plots surveyed in 1980–83 and repeated in 2010–11. We then examined patterns of tree expansion and time since last fire to address three major questions:

- 1) What is the relative strength of the relationships between disturbance regime (fire history), plant species loss and invasion density of *A. huegeliana*?
- 2) What is the relative strength of the relationship between disturbance regime (fire history) and *A. huegeliana* density?
- 3) What are the plant compositional changes over the last 30 years, including both species losses and gains and other environmental variables?

MATERIALS AND METHODS

Study Site

Our study area was Tutanning Nature Reserve (32°31'S, 117°23'E), a conservation reserve in the Western Australian Wheatbelt managed by the Department of Environment and Conservation (DEC) since the 1960s. Tutanning is a class 'A' reserve ~2140 ha in size. Located 150 km southeast of Perth, Western Australia, it is surrounded on all sides by agriculture, making it an island of remnant vegetation. Elevations on the reserve range from 320 to 430 m. It contains a mosaic of vegetation including *Eucalyptus* woodland, granite outcrop vegetation and kwongan heathland. The climate is Mediterranean, with an average annual rainfall of only 445 mm falling mostly in winter, which creates distinct seasonality in plant growth and flowering rhythms (Australian Government Bureau of Meteorology, 1891–2013). The reserve experiences low human traffic or impact and contains few non-native invasive species.

Due to its location in the agricultural landscape, Tutanning is characterized by strict wildfire control. Controlled burns for biodiversity management are now being implemented, but many individual heath sites have gone 60–70 years without fire. Within the reserve, all heath sites were identified and surveyed for plant species composition in the early 1980s (Brown and Hopkins 1983); these were the focus of this study. When original floristic surveys were completed in 1983, the time since last fire in a single site ranged from 7 to 41 years. Between that time and the recent survey, most sites experienced no additional fire, resulting in 8 of the 11 sites having >45 years without fire (time since last fire in a single site ranged from 13 to 73 years in 2011). Thus, the longer periods without fire at heath patches within Tutanning are of some management concern.

Allocasuarina huegeliana population survey

The native tree *A. huegeliana* was rare in heath historically (Bamford 1995; Main 1993) but commonly occurs in adjacent, almost monoculture woodland stands. In the last 30 years, it has been expanding in Tutanning heath sites (Maher et al.

2010). Other sites across Australia have similarly recorded an increase in *Allocasuarina* density and a corresponding degradation of historic species composition (Kirkpatrick 2004; Lunt 1998; Main 2001).

The level of expansion by *A. huegeliana* in individual heath sites was captured through population surveys conducted in all heath sites over the summer of 2010–11 (November–January). Three transects that spanned the heath area were established in each site. Transect length ranged from 100 to 280 m and was determined by the size of the site as delineated by a combination of aerial imagery and on-ground tree-line observation. Every 30 m, we surveyed a 10 m × 10 m quadrat using the transect point as the bottom right corner. In rare instances, we were forced to use the transect point as the bottom left corner of the quadrat; for example, in one site, exclosures from previous work in the site were directly adjacent to the left-hand side of the transect line. *Allocasuarina huegeliana* individuals were counted, and diameter at 0.4 m above ground level was recorded for adults (defined as any tree >1 m tall) and 0.1 m above ground level for seedlings <1 m tall. When investigating potential environmental correlations with *A. huegeliana* populations, we used population density measures (tree ha⁻¹). As a possible explanatory environmental variable input into all other analyses, however, we used the area coverage (AH.Area in reported results), which we defined as the average quadrat sum of πr^2 , where r is half the measured diameter of each tree.

Floristic surveys

We followed the nested survey design laid out in Brown and Hopkins (1983). In the original survey, 13 sites were surveyed in spring (September–November) over 3 years from 1980 to 1983. Each site was surveyed an unknown number of times within that 3-year interval (maximum of three times).

The surveys included 13 collection points over 11 individual sites, two of which—Sites 5 and 6—were surveyed at two points each. Site 5 was bisected by a woodland stand of *Banksia attenuata* and so subdivided, and Site 6 contained two areas with different fire ages. In 2010–11, we reassessed whether to keep Sites 5 and 6 as two collection points. In the original survey, there was no significant compositional difference between 6 and 6a and no physical separation between the sites. Therefore, we did not survey 6a separately. Sites 5 and 5a, however, were still split by a woodland stand and had some notable compositional differences; thus, we sampled them individually. Additionally, Site 8 was burned in 2010 and could not be surveyed at all due to the sensitive topsoil structure of recently burned sites. Sites 1, 5 and 5a were burned in 2011 and so were surveyed in 2010 only. In our surveys, therefore, we had 10 sites and 11 collection points (Fig. 1), three of which had a lower sampling effort than the other eight.

In each of the surveyed sites, the bottom left corner of a 10 m × 10 m quadrat was staked with a permanent marker in 1983. In 2010, the quadrats were relocated and re-surveyed for presence

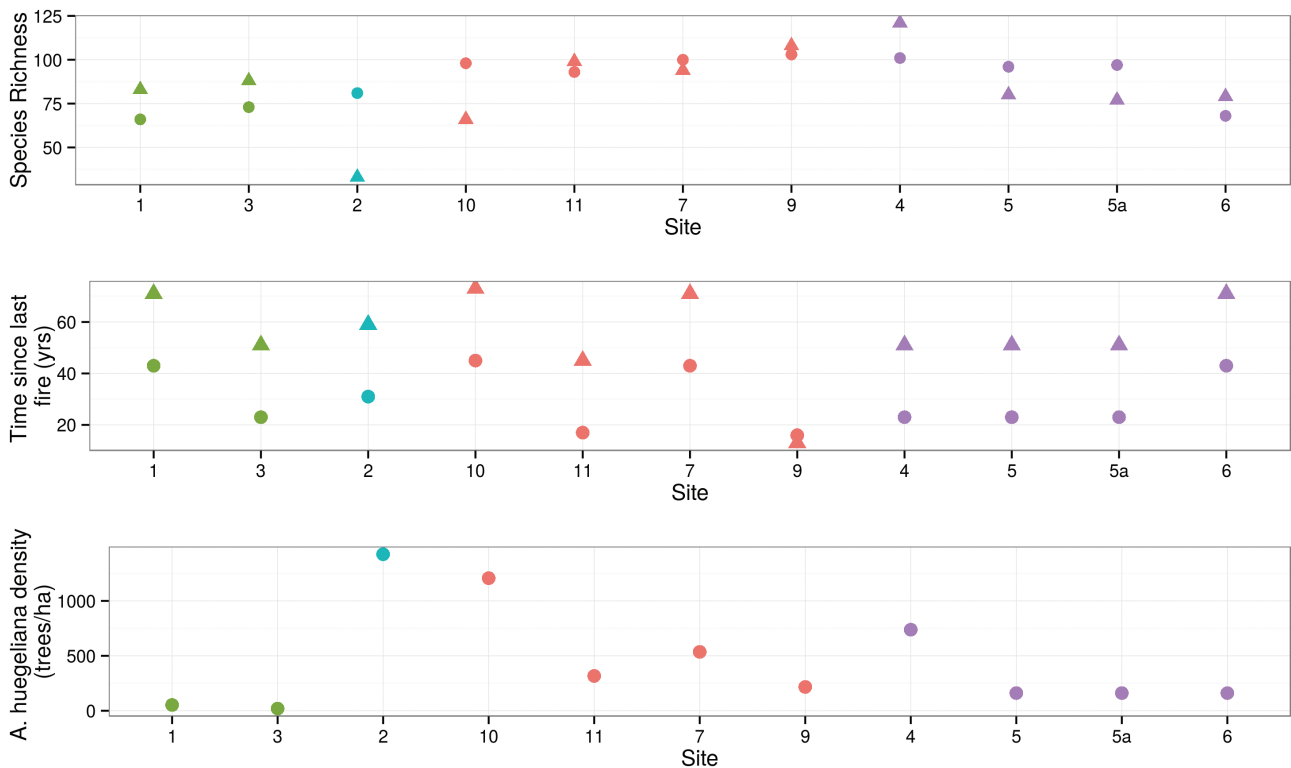


Figure 1: each site surveyed in 2011 including the site number with variables of interest on the y-axis: species richness (top), time since fire (middle) and *Allocasuarina huegeliana* density (bottom) in 2010 (see Floristic surveys section for further explanation). Species richness and time since fire show values for both 1983 (triangles) and 2011 (circles). The sites are grouped by soil type: laterite (sites 1 and 3), sandy-laterite (site 2), duplex (sites 10, 11, 7, and 9), and sand (sites 4, 5, 5a, and 6). All data were collected at the site scale.

data on all species. As in the 1983 surveys, the marker was then used as the bottom left corner of an expanded quadrat measuring 10 m × 50 m and then expanded again to 20 m × 50 m. In both survey periods, the rest of the heath site was then blanket surveyed for any missed species. In 2010, we referenced the 1983 species list for this expanded search to help prevent small vegetation shifts from resulting in skewed absence recordings. The surveys were conducted in the spring of 2010 and 2011 to match the previous surveys. Rainfall over the 2010–11 period showed extreme behavior. In 2010, there was a severe summer drought and rainfall well below average in winter, while in 2011, there was consistently high rainfall in all seasons. The data captured species loss, species gains and both considered together as changes in total raw species richness. We combined all unique records for 1980–83 together to make a single list (in the remainder of this article, we refer to this as the 1983 data) and did the same for 2010–11 (referred to as 2011 data). Species loss is defined here as any species recorded in the original surveys but not recorded in the recent surveys, while species richness is the total number of species found in each site in the 1983 data or similarly in the 2011 data.

Environmental variables

Average slope, elevation and aspect were determined for each heath site from a georeferenced digital elevation map (DEM)

available from the U.S. Geological Survey, while distance from the edge of the site (Dist in reported results) to the edge of the reserve was estimated using 2007 aerial imagery. Aspect data from the DEM (*A*) were transformed for use in the generalized linear models (GLMs) using the equation:

$$a = \cos\left(\frac{A \times \pi}{180}\right)$$

The resulting data ranged from -1 (south) to 1 (north) with 0 representing directly east or west. Site size (Size) and species richness in 1983 were taken directly from [Brown and Hopkins \(1983\)](#).

Soil information and time since last fire were obtained from DEC records. Over the 11 sites, there were six soil types: laterite, sandy-laterite, yellow sand, gray sand, duplex and sandy clay. We combined yellow sand with gray sand and duplex with sandy clay according to similarities in soil description, location and vegetation composition, thus leaving four soil classifications (laterite, sandy-laterite, sand and duplex).

Surveys in 1983 and 2011 were conducted by different surveyors and there were possible inconsistencies in the distance and detail each surveyor used in collecting species outside the quadrats. Because of this possible inconsistency, and because compositional changes could potentially differ across spatial scales, we performed three analyses of species loss and gains:

whole reserve (all sites combined), site (all species recorded in a site, both within and outside the quadrats; henceforth, referred to as ‘site scale’) and quadrat (only those species found within the nested quadrats; henceforth, referred to as the ‘quadrat scale’). We separately analyzed individual scales and focused on specific species or groups that were lost within each scale. However, for analyses of richness and floristic composition within a given year, we utilized all collected floristic data.

Statistical analysis

We analyzed invasive species population data for correlation with the floristic results. We also explored correlations of the floristic patterns and invasive species population results with environmental variables to test the hypothesis that shifted fire regimes have a strong correlative—and thus potentially causal—relationship with the species loss and/or *A. huegeliana* density. Species gains, *A. huegeliana* density and species richness were all modeled using Poisson GLMs. We checked for overdispersion and found the Poisson model to be a good representation of the data. We used a binomial GLM to model species loss because species loss is a binary lost-or-retained distribution. All continuous explanatory variables were scaled to have means of zero and standard deviations of one for ease of relative effect size interpretation. We did not include interaction terms in our modeling due to our low total degrees of freedom (10).

There is a growing recognition that *P* values may have limited potential to model the explanatory ‘significance’ of a result (Nuzzo 2014). Model selection based on Akaike information criterion (AIC) values presents a sound alternative to determine significance of explanatory variables, while the use of confidence intervals and effects sizes can more clearly communicate the biological importance of result. Thus, model selection was carried out using a combination of model minimization and AIC selection criteria (Crawley 2007). Starting with the maximal model, we used stepwise deletion of non-significant continuous terms (Crawley 2007), based on chi-square tests (Zuur et al. 2009). Once all continuous variables had been reduced as much as possible, we then grouped non-significantly different soil categories together, one pairing at a time.

Permutational analysis of variance (PERMANOVA) was used to identify environmental variables that contributed significantly to explaining differences in composition among sites (Anderson 2001). We used Bray–Curtis distance as our measure of compositional dissimilarity. The best models were found by first fitting the full model and then stepping backward by dropping non-significant ($P > 0.05$) variables until only significant variables remained, or the tested drop caused a loss of explanatory power of the model. In all analyses, only first-order interactions were considered due to the limited number of data points. For comparing composition between the 2 years, we performed non-metric multidimensional scaling (MDS) for exploratory analysis (Faith et al. 1987). All

statistical models were run in R (R Development Core Team 2009) using either the base program or the vegan library modeling functions for non-parametric and permutational analyses (Oksanen et al. 2011).

It is important to note that this is not a mechanistic or manipulative study. Conclusions are by necessity only hypotheses supported by the data. As Mumby et al. (2004) point out, causation may be inferred through the testing and discounting of other plausible explanations. This is achieved through statistical modeling that tests the likelihood of relationships and discounts those hypotheses with little or no evidence supporting them. Our study focuses on these methods of inference in order to understand biodiversity dynamics over large temporal and spatial scales in the Tutanning kwongan.

RESULTS

Allocasuarina huegeliana density

Surveys of *A. huegeliana* density showed large variation in density among heath sites (Fig. 1), ranging from 20 (SE = 8) trees/ha in Site 3 to 1425 (SE = 3) trees/ha in Site 2. When compared to the findings of Maher (2007), we found an increase in *A. huegeliana* density from 2007 to 2010 in all but one of the 11 sites. In some sites, the increase was small (an additional ~6 trees/ha) and could be a stochastic result of the sampling. However, other sites experienced a large increase of up to ~150 trees/ha with a high density of seedlings, implying a significant and real intensification in the invasion. The maximal model of *A. huegeliana* density was not able to be reduced without significant loss of model explanatory power (deviance explained = 99.9%; degrees of freedom = 1), i.e. all variables were significant in explaining *A. huegeliana* density, with slope and soil having the two largest effect sizes (3.75 and 11.35, respectively) and time since fire having one of the two smallest (0.25).

Species losses and gains

When excluding species outside the quadrats (quadrat-scale analysis), we found that an average of 39% of those species recorded in 1983 was lost by 2011 (Fig. 1). The strongest predictor of loss was soil type (Table 1), with the sandy-laterite and duplex soils showing significantly more loss than the laterite soils and sand. Species gains were fairly high within the quadrats, with 27% of 2011 species found to be new recruits not recorded in the 1983 surveys. At the quadrat scale, richness therefore decreased by 14%. Increasing time since last fire, higher elevation, gentler slopes and laterite soils all correlated with increasing species gains. All other soils showed similar gains.

We found that including the species outside the 20 m × 50 m quadrats (site-scale analysis) made some differences in the analysis results of species losses and gains. Species richness changes were distinct at the two different scales, with an average of 27% species lost from the 1983 surveys balanced by 22% new species gains in the 2011 surveys leading to only

Table 1: final results for the GLMs including the proportion of null deviance explained (Dev), the remaining degrees of freedom (df) of the final model, the model intercept and all of the estimated parameter values with 95% confidence intervals

Response	Dev	df	Intercept	AH.Area	TSF
Loss (in quadrats)	0.96	3	-2.29 ± 1.10	0.22 ± 0.18	NS
Loss (all)	0.96	6	-1.16 ± 0.16	0.24 ± 0.16	NS
Gains (in quadrats)	0.91	6	2.8 ± 0.16	NS	0.38 ± 0.26
Gains (all)	0.94	3	4.56 ± 0.18	-0.50 ± 0.28	1.32 ± 0.60
Richness loss (in quadrats)	~1	3	0.94 ± 0.07	0.03 ± 0.01	0.06 ± 0.03
Richness loss (all)	~1	2	0.01 ± 0.01	0.14 ± 0.01	-0.24 ± 0.04
Richness 1983	0.89	5	5.28 ± 0.62	NS	NS
Richness 2011	0.96	5	5.44 ± 0.5	NS	NS
Response	Size	Dist	Elevation	Aspect	Slope
Loss (in quadrats)	0.47 ± 0.22	-0.64 ± 0.23	2.17 ± 0.94	0.26 ± 0.25	NS
Loss (all)	0.18 ± 0.20	-0.40 ± 0.19	NS	NS	NS
Gains (in quadrats)	NS	NS	0.71 ± 0.36	NS	-1.25 ± 0.54
Gains (all)	NS	NS	2.93 ± 1.60	NS	-2.64 ± 0.98
Richness loss (in quadrats)	0.21 ± 0.03	-0.10 ± 0.03	0.54 ± 0.06	NS	NS
Richness loss (all)	0.09 ± 0.02	-0.16 ± 0.02	-0.31 ± 0.04	NS	0.4 ± 0.08
Richness 1983	0.11 ± 0.09	NS	0.55 ± 0.52	NS	NS
Richness 2011	NS	NS	0.78 ± 0.21	0.16 ± 0.08	NS
Response	Soil (laterite)	Soil (laterite 2)	Soil (sand)		
Loss (in quadrats)	NS	NS	-4.66 ± 1.86		
Loss (all)	NS	1.19 ± 0.56	NS		
Gains (in quadrats)	-0.95 ± 0.78	NS	NS		
Gains (all)	-6.60 ± 3.55	4.53 ± 2.66	-2.71 ± 2.43		
Richness loss (in quadrats)	-1.9 ± 0.15	NS	-1.3 ± 0.12		
Richness loss (all)	0.48 ± 0.11	-0.67 ± 0.20	NS		
Richness 1983	-1.72 ± 1.24	-0.57 ± 0.4	-1.22 ± 1.02		
Richness 2011	-1.91 ± 1.0	-1.3 ± 0.43	-1.62 ± 0.82		

Because model selection was a combination of model minimization and AIC selection criteria, non-significant variables were dropped from each model. This is captured in the table by cells labeled 'NS' (non-significant). We do not present *P* values as all remaining variables are considered significant in explaining the response variable. The table details models for species losses, losses excluding species outside the quadrats, species gains, gains excluding species outside the quadrats, diversity loss (or gain), diversity loss excluding species outside the quadrats and species richness for 1983 and 2011. Parameters include *Allocasuarina huegeliana* area coverage (AH.Area), distance to the edge of the reserve (Dist), site size (Size), soil type, elevation, aspect and time since last fire (TSF).

4% richness decline, smaller results than when analyzing the quadrats only. Similar variables were found to be significantly related to losses and gains at the two scales. However, losses at the larger site scale showed weaker responses to those variables than losses at the quadrat scale. Gains at each scale showed the reverse—with stronger relationships found at the larger scale than those found at the smaller, quadrat scale. Notably, at the site scale, *A. huegeliana* area coverage had a significant, negative correlation with species gains.

Composition of losses and gains was relatively consistent regardless of the inclusion of species outside quadrats. New gains (Table 2) tended to be common species, many of which (57%) were herbaceous (e.g. *Ericksonella saccharata*, *Hydrocotyle pilifera* and *Trachymene pilosa*). Some were found to be either specialized for drought tolerance such as *Calandrinia corrigioloides* (Harrison *et al.* 2008) or relatively prolific seeders such as *Lepidobolus chaetocephalus* (Meney and

Dixon 1988). Lost species were both herbaceous and woody; however, there was a predominant loss of shrub species (e.g. *Acacia* sp., *Jacksonia* sp., *Leucopogon* sp. and *Persoonia* sp.) and little corresponding gains of woody species. Both herbaceous and woody species that were lost often showed characteristics opposite of those that were gained: some such as *Crassula* sp. have shown sensitivity to heat and drought (Facelli *et al.* 2005), while others such as *Persoonia* sp. have been found to have extremely low recruitment rates with likely dormancy mechanisms (Abbott 1984).

Average net richness change per site similarly varied depending on the inclusion of species recorded outside the quadrats. When only analyzing the quadrat richness, there was an average loss of 14% richness per site. However, when including all species recorded in each site, diversity loss per site of heath decreased to only a 4% loss. Models of diversity loss on both scales showed significant, but

small, relationships with all environmental variables (with one exception: slope was dropped from the quadrat-scale model). The largest relationships at both scales were with soils (Table 1). On a broader scale, species richness over all sites combined decreased by 11%. The losses were slightly

weighted toward woody shrub species (Table 3), and most species that were lost were originally recorded in only one or two sites total and thus were locally rare in 1983. There was one exception to this pattern—*Stylidium affine* was recorded in eight sites in 1983 and not recorded once in 2011—but this is likely a taxonomic misidentification between surveyors.

Table 2: species gained in at least three sites between 1983 and 2011 including their growth structure (tree, shrub, perennial herb or annual herb), the number of sites in which they were gained in 2011 and the total number of sites in which they were found in 2011

Species	Life/growth form	Sites gained	Total sites
<i>Eucalyptus accedens</i>	Tree	4	5
<i>Baekkea floribunda</i>	Shrub	7	8
<i>Boronia ramosa</i>	Shrub	3	5
<i>Daviesia incrassata</i>	Shrub	5	7
<i>Jacksonia racemosa</i>	Shrub	6	6
<i>Lysinema ciliatum</i>	Shrub	3	4
<i>Verticordia chrysantha</i>	Shrub	3	3
<i>Rytidosperma setaceum</i>	Perennial	3	4
<i>Caustis dioica</i>	Perennial	7	7
<i>Ericksonella saccharata</i>	Perennial	6	7
<i>Lepidobolus chaetocephalus</i>	Perennial	5	6
<i>Lepidosperma pubisquamum</i>	Perennial	3	5
<i>Logania tortuosa</i>	Perennial	4	4
<i>Thysanotus thysoides</i>	Perennial	3	3
<i>Tricoryne elatior</i>	Perennial	3	4
<i>Calandrinia corrigioloides</i>	Annual	5	5
<i>Hydrocotyle pilifera</i>	Annual	4	4

Composition and richness

We found relatively consistent correlations between certain environmental variables and both composition and richness, though there were slight differences found between years and between the two compositional measures (Tables 1 and 4). Elevation and soil type were significant in both years' compositional PERMANOVAs. For richness in 1983, size of the site was also consistent in all models, while aspect was found to be significant for richness in 2011. In compositional analysis, only elevation and soil type were found to be significant in the final model for 1983. Analysis of 2011 composition found the addition of slope retained in the final model.

The MDS plot of composition in 1983 and 2011 (non-metric $r^2 = 0.989$) showed close similarities between years in the same sites (Fig. 2). Only Site 2 was found to have dramatic differences between 1983 and 2011 floristic surveys (Bray–Curtis dissimilarity distance = 0.51 versus an average Bray–Curtis dissimilarity distance of 0.19 for all other patches).

DISCUSSION

Long-term studies such as this provide important quantification of the degradation patterns seen by local managers. In

Table 3: species lost from all combined heath sites between 1983 and 2011 including their growth structure (tree, shrub, perennial herb or annual herb), the number of sites in which they were recorded in the 1983 surveys

Species	Life/growth form	Sites	Species	Life/growth form	Sites
<i>Crassula closiana</i>	Annual	1	<i>Calothamnus planifolius</i>	Shrub	1
<i>Levenhookia dubia</i>	Annual	1	<i>Cryptandra nutens</i>	Shrub	1
<i>Siloxerus multiflorus</i>	Annual	1	<i>Eutaxia parvifolia</i>	Shrub	1
<i>Asteridea nivea</i>	Perennial	1	<i>Hakea gilbertii</i>	Shrub	1
<i>Burchardia congesta</i>	Perennial	2	<i>Hakea trifurcate</i>	Shrub	2
<i>Diuris longifolia</i>	Perennial	2	<i>Hibbertia microphylla</i>	Shrub	2
<i>Erodium cygnorum</i>	Perennial	1	<i>Hybanthus floribundus</i>	Shrub	1
<i>Goodenia caerulea</i>	Perennial	1	<i>Isopogon divergens</i>	Shrub	1
<i>Hypoxis glabella</i>	Perennial	2	<i>Leucopogon polymorphus</i>	Shrub	1
<i>Leporella fimbriata</i>	Perennial	3	<i>Melaleuca lecanantha</i>	Shrub	1
<i>Paracaleana nigrita</i>	Perennial	2	<i>Monotaxis grandiflora</i>	Shrub	1
<i>Stylidium affine</i>	Perennial	8	<i>Persoonia elliptica</i>	Shrub	1
<i>Stylidium emarginatum</i>	Perennial	2	<i>Persoonia trinervis</i>	Shrub	1
<i>Wurmbea pygmaea</i>	Perennial	1	<i>Pimelea sulphurea</i>	Shrub	1
<i>Acacia alata</i>	Shrub	1	<i>Verticordia acerosa</i>	Shrub	2
<i>Banksia prionotes</i>	Shrub	1	<i>Verticordia densiflora</i>	Shrub	1
<i>Banksia squarrosa</i>	Shrub	1			

Table 4: PERMANOVA results of composition models for 1983 and 2011 presented as *P* values for the significance of environmental variables

	AH.Area	TSF	Slope	Aspect	Elevation	Dist	Size	Soil
Comp1983	—	X	X	X	<0.01	X	X	<0.01
Comp2011	X	X	<0.01	X	<0.01	X	X	<0.02

Variables with Xs were included in the full model but dropped during step-wise model selection due to lack of significance.

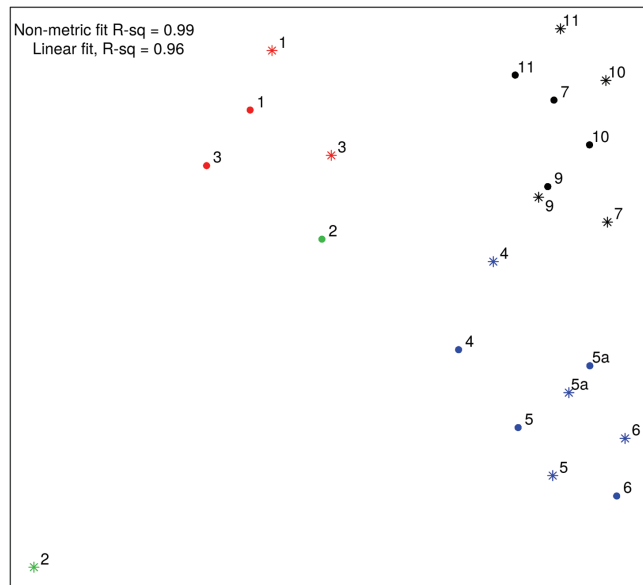


Figure 2: MDS plot indicating similarities and differences between sites in terms of floristic composition, as surveyed in both 1983 (dots in the plot) and 2011 (stars). Each pair of points is labeled with the site number. Note that the points group by soil type: laterite (sites 1 and 3), sandy-laterite (site 2), duplex (sites 10, 11, 7, and 9), and sand (sites 4, 5, 5a, and 6).

this extremely biodiverse and complex ecosystem, we were able first to describe the vegetation changes over time and second to investigate the empirical support for two hypothesized drivers of ecological degradation. This study spans 30 years, covering at least a full generation time for much of the vegetation within the ecosystem. Though we focus on only two time points, a total of 5 years of survey are included in the data. The 1983 data set recorded all species appearances for 3 years, while the 2011 data set records all species appearances for 2 years. Each of these ‘windows’ within the time points had both high and low rainfall periods. Thus, the species presence data likely present a reliable depiction of the long-term dynamics occurring at the site.

Compositional changes differed across the three spatial scales studied: whole reserve (all sites combined), site (all species recorded in a site) and quadrat (only those species found within the nested quadrats). On the reserve scale, we found

an 11% decrease in overall plant species richness. Those species that were lost were predominantly a mix of low seed-producing woody perennial species. The second large groups of species loss were herbaceous species such as *Siloxerus multiflorus* whose natural habitat is adjacent to, but not present in, heath and thus might just have been opportunistic records in the 1980–83 surveys. On the site scale, the richness loss was 4%. The large difference (11–14%) in species richness declines between the reserve and site scales imply that species unique to each site are those being lost on the reserve scale, while the difference (4–14%) in richness declines between the site and quadrat scales imply that species densities may be thinning within individual sites.

Most of the species changes we found were compositional shifts rather than simple diversity loss. We found 14% richness loss on the quadrat scale, with less gains at this scale than at the site scale. Gains at the site scale in certain sites, notably 1 and 4, reached as high as 25%. However, the types of species gained and lost were similar among all scales, showing a pattern of compositional shift throughout the reserve. While some compositional shift may be expected over 30 years, the shifts are significant in that they were directed toward gains of herbaceous species or common shrub species that are widespread in the regional landscape. Further, some caution is needed in assuming the long-term nature of the gains. Surveys in 2011 occurred after an exceptionally good year of steady rain, and some gains on the site and quadrat scales appear to be opportunistic herbaceous species. Kwongan is characterized by its predominantly woody structure (Beard 1984) as well as the prevalence of rarity and endemism in plant species and large amounts of variation among sites (Hopper and Muir 1984). Thus, conservation of locally rare woody and perennial species is the management priority for heath, and these most important species were found to be dropping out of the system at all scales.

We found strong correlations between *A. huegeliana* density and species richness declines and species loss. In our analysis, the relationship between *A. huegeliana* density and species loss on both scales was consistently significant; *A. huegeliana* density showed either no (quadrat scale) or negative (site scale) relationships with species gains. We suggest that the relationship between expansion of *A. huegeliana* and species loss is being driven by the native invasive. Given the strength of the correlation, this hypothesis is the most supported by the data. Interspecific competition (Tilman 1982) and other indirect effects such as nutrient shifts, changes in canopy structure and heavy litter fall (Lunt 1998) associated with *Allocasuarina* invasion are all potential drivers of richness and species loss (Fig. 3). In a resource-limited setting such as the wheatbelt, competitive exclusion could be a cause of diversity decrease over time and has been shown to restrict the presence of certain locally rare woody species in Western Australian shrublands (Lamont *et al.* 1989). *Allocasuarina huegeliana* is an example of a highly competitive species appearing in greater abundances in the heath that we hypothesize



Figure 3: example of advanced stage *Allocasuarina huegeliana* expansion into Tutanning Nature Reserve heath site (left) with little living but some dead heath species in the understory; example of an *A. huegeliana* expansion front into Tutanning heath site (right).

might be leading to competitive exclusion. However, correlation does not determine causation and it is also potentially the loss of species and species declines that have allowed expansion of *A. huegeliana* into each site. Though the statistical model and results suggest that larger decreases in species richness are found with higher densities of *A. huegeliana*, there are some sites that have retained, and even increased in, species richness despite high current densities of *A. huegeliana*. It remains unknown why this has occurred but may be due to soil type. Due to the long temporal scale and the lack of *a priori* interest in *A. huegeliana* impacts over that time period, information on other potentially pertinent information—such as its first appearance and relative competition with other species on particular soil types—in these sites is missing. Thus, explicitly mechanistic investigation into the impact of *A. huegeliana* on other local species and *vice versa*, as well as into its interaction with fire and abiotic variables such as soil type, is necessary.

We found that at multiple scales, *A. huegeliana* density links with the highest species declines once the invasion has progressed to a certain density level (Fig. 4). Sites 2 and 10 are almost completely converted to *A. huegeliana* woodland (>1200 trees/ha) and experienced the highest number of species lost as well as the highest loss of species richness. There is potentially a state change at a certain density threshold in which the system rapidly reconfigures from highly biodiverse heath to woodland with sparse understory richness. Invasive species have been known to act as drivers of state changes in ecological systems. For instance, woody invasion due to fire suppression in prairie barrens in southern Illinois have been shown to alter the impacts of reinstated fire regimes and prevent barren return (Anderson et al. 2000). It is unknown whether this threshold is operating in heath systems and whether it would be reversible. Abrupt change does not necessarily imply that the new state is stable or resilient to stress (Beisner et al. 2003). Though recolonization by many of the woody species would be unlikely due to low dispersal distances (Suding et al. 2004), the longevity of many of these

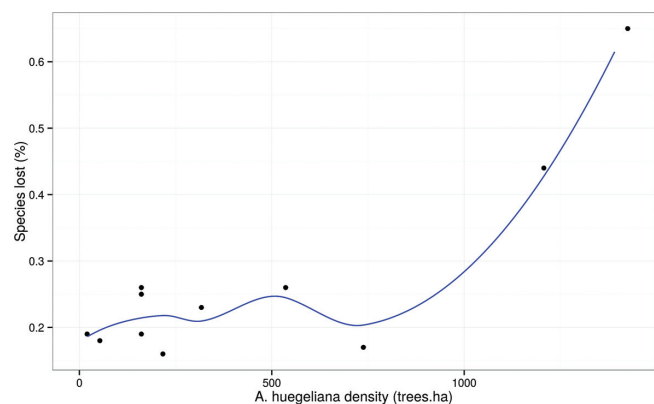


Figure 4: percent species loss by *Allocasuarina huegeliana* density. Percent species loss is the percentage of species found in the 1983 surveys lost by the end of the 2011 surveys. The fitted line is a fitted polynomial surface using local fitting (created with the loess package in R for illustration purposes).

species in the seedbank may allow them to reestablish given altered conditions.

Disturbance had more ambiguous relationships in the ecosystem dynamics. Fire-cued strategies underlay our hypothesis that there would be a correlation between species loss and fire history. However, the effect of time since last fire did not appear in our final model of species loss. Based on the results of previous findings, the lack of strong correlation between fire history and species loss was not wholly unexpected. In other similar heath systems, plant species diversity has been found to peak immediately after a fire, decrease for a short time period and then stay steady despite longer spans of fire-free periods (Gosper et al. 2011). Canopy and structural senescence, however, were found to occur after ~45 years, a finding confirmed for sandy and duplex sites at Tutanning: those exceeding 45 years since the last fire showed major structural senescence (N Shackelford, personal observation). Above-ground senescence and structural loss are more likely

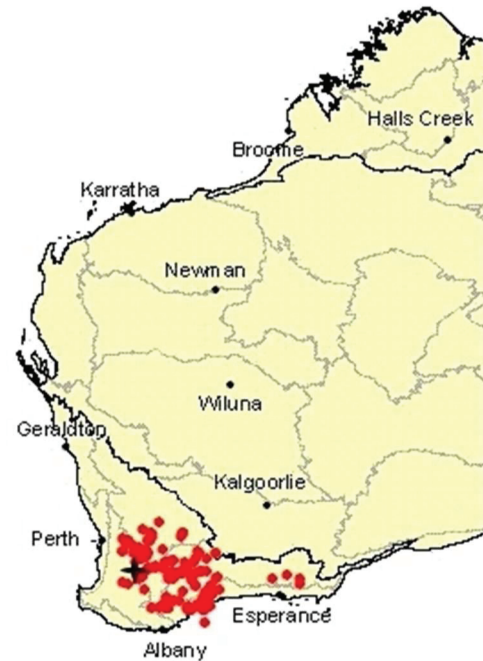
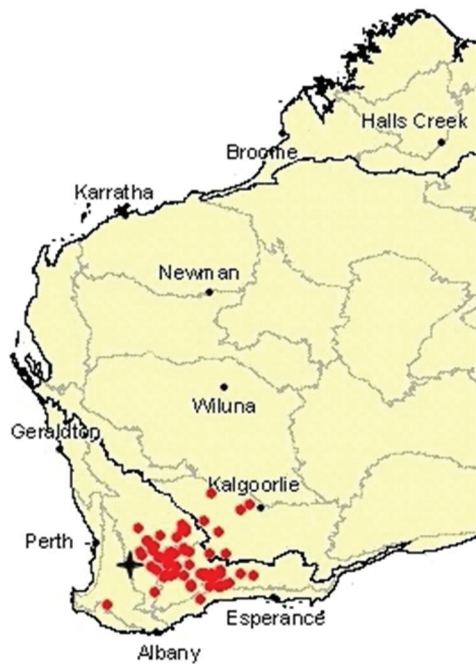
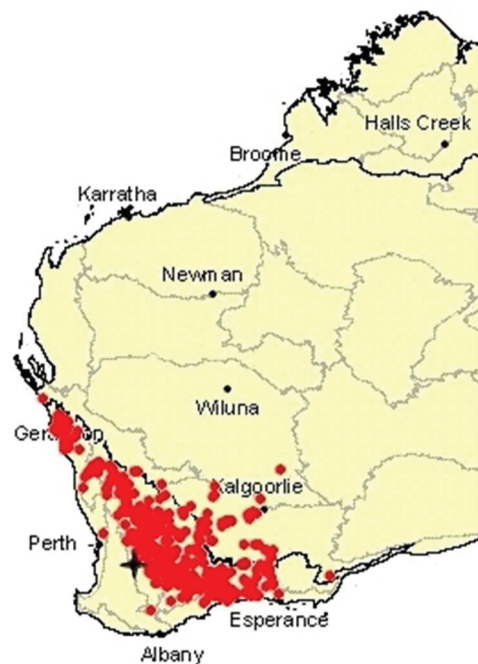
Chloanthes coccinea*Jacksonia racemosa**Logania tortuosa**Verticordia chrysantha*

Figure 5: florabase (Western Australian Herbarium 1988) distribution maps of *Chloanthes coccinea*, *Jacksonia racemosa*, *Logania tortuosa* and *Verticordia chrysantha*, all species gained in more than three sites and the latter three new species recorded in Tutanning heath. The black star on each map is the approximate location of Tutanning.

results of shifted fire regimes in this system than species loss. If species loss was based on lack of fire cues, woody and perennial losses might be only above-ground loss, with the next fire or other necessary environmental condition leading to the breaking of seedbank species dormancy. There have

been many studies finding that species in heath systems survive dormant in the soil seedbank for long periods of time (Auld *et al.* 2000; Auld and Ooi 2008). The evidence does not support this mechanism of species disappearance, however, and the almost equal loss of canopy-stored and soil-stored

species brings it into further doubt (as per expert consultation with staff at Kings Park Botanic Gardens; T. Erickson, personal communication). The implications of this for long-term recovery and renewed recruitment are potentially bleak even if the historical fire regime were to be reinstated.

If shifts in the disturbance regime were the predominant driver behind *A. huegeliana* expansion, strong correlations would be found between time since last fire and *A. huegeliana* density. Were this the case, reinstating historic regimes may be the only necessary management action needed to return the system to its previous state. However, fire history's relationship with *A. huegeliana* density was significant but small and implies that there are other causes that might be involved in the population expansion. The largest and most obvious factor in *A. huegeliana* density was the presence of laterite soil: regardless of other factors, density at the two laterite sites was <55 trees/ha. All other surveyed populations were at least three times that density. Abiotic conditions of particular sites, however, have been shown to significantly reduce invasion density. In the Chihuahuan Desert of New Mexico, shrub invasion into grassland has been found to be significantly lower in shallow sandy soils than deep sandy soils (Browning et al. 2012) due to the water retention properties of each. State-and-transition model development generally depends on climate, geomorphology and soils to define general models and ecological potential (Bestelmeyer et al. 2009). For *A. huegeliana* spread, lateritic soils may be too shallow or too high in the landscape to allow *A. huegeliana* to become well established. This creates natural resistance to invasion that might have cascading effects on species composition. Species loss was lowest on laterite sites at the site scale (18 and 19%) and lowest but one at the quadrat scale (22 and 33%) and might be due to these cascading effects or other resistance factors contributed by the soil type. Further management actions such as focused population control and targeting of vulnerable sites might be necessary in this case, particularly if the *A. huegeliana* population creates a resilient alternative state. Continued investigation is needed to confirm and quantify the nature of the potential state changes linked with *A. huegeliana* expansion.

Ecological changes in Tutaning heath sites are complex, and broad generalizations from our study rely on observational evidence alone. Other factors not explicitly considered in our study, such as climatic variables, also might play a major role. Many of the site- and quadrat-scale species gains were herbaceous species potentially responding to the unusually high rainfall in 2011. On a larger and longer scale, the climate in Western Australia has become drier and warmer over the last few decades as global climate change has progressed (Bates et al. 2008; CSIRO 2007). Species better adapted to these environments may become more dominant and shift the overall composition to reflect the novel climate. Many of the species gained on the reserve scale seem to be on their western-most range extensions, implying their likely preference for the drier, warmer conditions found further inland to the east. Of those species gained over the whole reserve, approximately one third of them appear to occupy ranges in

which Tutaning was on the western-most edge (Fig. 5), indicating a possible western movement of these species over time. Additionally, due to the limited number of site replicates, we were unable to capture interactions between *A. huegeliana* density and disturbance, a key component of the overall degradation that might change the impact of one or both of the individual factors (Didham et al. 2007). Though wide, our range of fire intervals was necessarily restricted in variation, increasing difficulties in pulling out potential relationships between fire return interval and ecological processes. Fire management has been initiated in the reserve and this may provide the opportunity to disentangle the interactions further.

Causal links among disturbance, invasion and environmental degradation are often difficult to establish in management scenarios when observational data are the primary source of information. Correlations between species loss and expansion by a novel dominant or shifts in disturbance regimes do not necessarily lead to the result that either is the underlying cause behind species loss. However, observational data such as those presented here are often the main or only source of information available to provide essential information from which more detailed studies and experimental management programs can be designed. As persistent, continual anthropogenic influences such as invasion, disturbance regimes shifts, climate change and nutrient enrichment increasingly alter ecosystems that we value, studies utilizing long-term data such as this are essential to determine and potentially mediate the repercussions of human activity.

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