We examined floristic change across remnant native grasslands over a two-decade period. We found evidence in support of the biotic homogenisation hypothesis in grasslands that underwent a period of rapid urbanisation and declines in natural disturbance regimes, but not in frequently burnt rural grasslands. Biotic homogenisation was largely driven by an increase in commonly shared non-native plants across urban grasslands.

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Biotic homogenisation in an increasingly urbanised temperate grassland ecosystem

Ben J. Zeeman, Mark J. McDonnell, Dave Kendal & John W. Morgan

Zeeman, B.J. (Corresponding author, BZeeman@ltu.edu.au)¹

McDonnell, M.J. (markmc@unimelb.edu.au)²

Kendal, D. (dkendal@unimelb.edu.au)^{2, 3}

Morgan, J.W. (J.Morgan@latrobe.edu.au)¹

¹ Department of Ecology, Environment and Evolution, La Trobe University, Bundoora, Victoria, 3086, Australia;

² School of BioSciences, The University of Melbourne, Victoria, 3010, Australia;

³ School of Ecosystem and Forest Sciences, The University of Melbourne, Burnley, Victoria, 3121, Australia

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Abstract

Question: How does urbanisation and associated declines in fire frequency alter the floristic composition of native temperate grasslands? Does it lead to: 1) biotic homogenisation, i.e. compositional similarity between remnants increases; 2) biotic differentiation, whereby similarity between remnants declines, or; 3) clustered differentiation, where similarity between remnants remains unchanged, but composition shifts from the historical state?

Location: Victoria, Australia

Methods: Using site-level surveys, we examined changes in the floristic similarity of 29 urban grasslands from 1992 to 2013 and compared these changes to those of 63 rural grasslands from 1989 to 2014. Community-level changes in the representation of key functional traits were also examined in urban grasslands, with traits advantaged following disturbance regime change and urban fragmentation predicted to increase in frequency.

Results: Our results supported the biotic homogenisation hypothesis in urban grasslands. Compositional similarity between grasslands increased principally because of an increase in commonly shared non-native species, with change in native composition comparatively minor. However, no evidence of biotic homogenisation was found in rural grasslands, with no significant change in overall composition identified. The most urbanised sites had the highest number of non-native species in both the current and historical datasets, yet non-native composition over the past two decades changed the most in sites on the urban fringe, becoming more similar to sites closer to the urban core. As expected, following declines in fire frequency and increased urbanisation, the overall composition of urban grasslands shifted to taller plant species, while native species capable of vegetative reproduction and exotic species with an annual life-span increased in frequency.

Conclusion: Urbanisation was an important driver of biodiversity change in the investigated system, with increasing competition intensity in response to disturbance regime change a likely cause of biotic homogenisation. Our results demonstrate that non-native species are a key driver of biotic homogenisation, emphasising the importance of managing non-native immigration and maintaining historical disturbance processes once native ecosystems become urbanised.

Key-words

Biotic differentiation; disturbance; alien species; extinction; habitat fragmentation; immigration; invasion; plant functional traits, vegetation dynamics

Introduction

Human activities are transforming native ecosystems across the globe (Vitousek et al. 1997; Steffen et al. 2007). Urbanisation is a particularly threatening process, reducing the area of native vegetation and isolating remnant patches through fragmentation (McDonald et al. 2008; Secretariat of the Convention on Biological Diversity 2012). Once bound within the urban matrix, resource supply between communities is disrupted and species dispersal is constrained (Ricketts 2001; Williams et al. 2006; Ibanez et al. 2014). Additionally, historic disturbance regimes are altered (Harrison & Bruna 1999), and environmental conditions are modified (Grimm et al. 2008), shifting the nature of species interactions, and creating novel ecosystems through the extinction of native populations and the immigration of non-native species (Kowarik 2011).

Urbanisation has been hypothesised to cause the composition of fragmented communities to become increasingly similar to each other over time, a process termed biotic homogenisation (Kuhn & Klotz 2006; Schwartz et al. 2006; Fig. 1a). Homogenisation is determined by the relative rates of immigration and extinction. For example, immigration of regionally widespread non-native species will increase similarity between fragments (Olden 2006), as will the extinction of rare native species (Rooney et al. 2004; Schwartz et al. 2006). When both mechanisms co-occur, ecological specialists are replaced with generalists, reducing functional diversity, and simplifying ecosystem composition and processes (McKinney & Lockwood 1999; Olden et al. 2004). This may increase the susceptibility of ecosystems to further non-native immigration, and increases their vulnerability to environmental change (McGrady-Steed et al. 1997; Smith & Knapp 2001). However, despite these expectations, evidence of biotic homogenisation in response to urbanisation is often lacking (Aronson et al. 2014; Hahs & McDonnell 2016; Lososova et al. 2016)

Long-term ecological change following fragmentation can result in vegetation patterns other than homogenisation. Olden and Poff (2003) proposed that “biotic differentiation” can occur when fragments become increasingly dissimilar over time (Fig. 1b). This can occur when immigration is idiosyncratic, i.e. each site receives a different suite of non-native species which consequently become rare across the landscape, or, alternatively, when widespread native species become locally extinct. Several empirical studies have found support for biotic differentiation driven by both idiosyncratic immigration (Kuhn & Klotz 2006), and the local extinction of widespread native species (Smart et al. 2006).

Here we add a third hypothesis, that fragments will remain unchanged in their similarity to each other over time, but their composition will shift significantly from their historical state (Fig. 1c). We term this process “clustered differentiation”. This could occur when patterns of immigration and extinction are counterbalanced. For example, the establishment of regionally rare non-native species occurs at the same rate as the extinction of rare native species or, alternatively, widespread non-native species establish at the same rate as widespread native species become extinct. Unlike biotic homogenisation and biotic differentiation, clustered differentiation occurs when extinction and immigration of widespread or rare species are in equilibrium, as skewness in either direction will cause either an increase or decline in the similarity between fragments (Fig. 2).

In this study, we compared the recent and historic floristic composition of fragmented and disturbance-dependent urban grasslands against models predicting biotic homogenisation, biotic differentiation, and clustered differentiation, as well as a fourth model of no change where neither composition nor similarity significantly changed over time (Fig. 1d). Given that the frequency of historical fire events has declined with urbanisation in the investigated system (Williams et al. 2005b), we predicted that the local extinction of rare native species and the immigration of widespread non-native species will have caused grasslands to have homogenised. We also predicted that species possessing functional traits that provide a competitive or opportunistic advantage in the absence of fire disturbance would be favoured, and that these traits will have increased in frequency across the urban landscape. We then tested these models in rural grasslands within the same region where disturbance regimes have been maintained (Dickson-Hoyle 2013), predicting these grasslands to display no evidence of biotic homogenisation.

Methods

Study area

This study focused on remnant native temperate grasslands near Melbourne, Australia (37°48' S; 144°56' E; Appendix S1), and to the west of Melbourne in rural Victoria (Appendix S2). These grasslands are protected under federal legislation as critically endangered 'Natural Temperate Grassland of the Victorian Volcanic Plain' ecological community, and once covered 2.3 million ha across south-western Victoria (www.environment.gov.au, accessed 2016). In 2007, it was estimated that 8% of this ecosystem remained (www.environment.gov.au, accessed 2016).

Melbourne sits on the south-eastern boundary of this ecosystem, and has a population of 4.25 million people, making it the most populated city in the state of Victoria, and second most populated city in Australia, covering an area of approximately 1 million ha (www.abs.gov.au, accessed 2015). Mean annual rainfall throughout the region varies from 520 mm to 720 mm, while average monthly maximum temperatures range from 14 °C to 26 °C (www.bom.gov.au, accessed 2015). The underlying geology of the region is characterised by tholeiitic to alkaline basalt soils formed approximately 2 million years ago (www.depi.vic.gov.au, accessed 2015). Grasslands near Melbourne contributing to a conservation reserve system totalling 1,877 ha, distributed across 87 sites. Grassland area varies substantially, however, sites examined in this study were generally small (Appendix S3). In rural Victoria, native grasslands on public land are restricted to roadsides and railway verges.

Plant coexistence in Victorian grasslands is dependent on frequent disturbance to constrain competitive exclusion (Lunt et al. 2012). Over the last two decades, the remaining areas of native grassland near Melbourne have experienced a period of rapid urbanisation, leading to increased isolation and a reduction in the frequency of disturbance by fire (Williams et al. 2005b). As a consequence, it is likely that grasslands have re-assembled through competitive and opportunistic processes, with a shift towards taller plants able to resist competitive exclusion and short-lived plants able to survive and disperse in the urban matrix (McKinney & Lockwood 1999; Kraszewski & Waller 2008; Fischer et al. 2013). In contrast, in rural grasslands, for the past 40-70 years, fire has been used at 1-2 year intervals to prevent fuel load accumulation and protect human assets (Dickson-Hoyle 2013). The occurrence of frequent fire in rural grasslands has played a key role in maintaining species coexistence (Lunt et al. 2012).

Field survey of urban grasslands

Between October 2013 and January 2014, we sampled 29 urban grasslands. Site-level species lists of all vascular plants were produced. Each grassland was walked in a grid pattern while recording species presence, ensuring that the entire site was sampled within the time allocated. Time

allocated to each grassland was dependent on reserve size: < 2 ha = 30 mins; 2-10 ha = 60 mins; 11 – 20 ha = 90 mins; 21-50 ha = 120 mins; 51-100 ha = 180 mins; > 100 ha = 240 mins. Once this allocated time had elapsed, an additional five minutes was allocated for the potential discovery of new species. The additional five-minute search time was re-set with the discovery of each new species until no new species were discovered, at which point the search was concluded.

Urban grassland historical data

Historical site-level species lists were generated from data collected between 1986 and 1993 for each of the 29 urban sites, consistent with the approach of previous studies of biotic homogenisation (e.g. Rahel 2000; Taylor 2004; Marchetti et al. 2006). These data were obtained from management plans, peer-reviewed research (McDougall 1987; Williams et al. 2005b) and local and state government databases. All species lists were compiled by qualified botanists. In instances where multiple management plans were commissioned for a given site within the 7 year period, species lists were combined, although differences between datasets were minimal. Government data was sourced from the Victorian Biodiversity Atlas (VBA; <https://vba.dse.vic.gov.au>, accessed 2014).

To control for false absences when making temporal comparisons, species of the same genera that are difficult to identify to species level were pooled in both the historical and recent datasets (i.e. **Aira*, *Amphibromus*, *Asperula*, *Austrostipa*, **Avena*, **Brassica*, *Cheilanthes*, *Crassula*, *Cuscuta*, *Eleocharis*, **Fumaria*, **Gladiolus*, **Hordeum*, *Hydrocotyle*, *Isolepis*, *Juncus*, *Lachnagrostis*, **Lolium*, *Maireana*, *Microstis*, *Mitrascome*, *Ranunculus*, *Rytidosperma*, *Stellaria*, *Thelymitra*, *Viola*; Asterisks denote exotic species). Unlike previous grassland studies of native plant extinctions in Victoria (Williams et al. 2005b), annual species were included in this study. These were present in the standing flora for much of the year, and often for longer periods than many native geophytic forbs. False absences were therefore considered unlikely given the timing of surveys.

Field survey of rural grasslands

Rural grassland sites were used as controls to examine long-term change in the absence of urbanisation and in the maintenance of long-term (frequent) fire regimes. Between 1989 and 1990, an extensive survey of vascular plants was undertaken across some of the highest quality native grassland remnants in rural Victoria. A total of 97 grasslands sites were sampled using a single 4 x 5 m quadrat in each and data archived at La Trobe University. Between October and December 2014, 63 of these sites were re-surveyed. Each quadrat was relocated using both GPS coordinates and

original site descriptions. As the precise location of the original quadrat was often unable to be determined with certainty, species were also recorded as present if they fell within a 1.5 m buffer of the quadrat.

In addition, for each grassland site, a site-level search was conducted for species on the original list that were not relocated in the quadrat and their presence was recorded. This ensured a conservative approach to prevent the overstating of extinction (false absences) and immigration (false presences). Site-level searches were undertaken by walking in a grid pattern and were concluded once 5 minutes passed without the discovery of a new species.

Plant functional trait data

A plant trait approach was used to explain temporal vegetation change in urban grasslands. As a consequence of declines in the frequency of disturbance across urban grasslands (Williams et al. 2006), traits that provided either a competitive advantage (i.e. height and dormant bud position), or enabled plants to exploit limited opportunities (i.e. annual life-span and vegetative reproduction; Appendix S4) were predicted to increase.

Plant height information was sourced from field guides (e.g. Australian Plant Society Maroondah 2001; Richardson et al. 2011). Life-span, vegetative reproduction and dormant bud position was sourced from a plant trait database held in the Department of Ecology, Environment and Evolution, La Trobe University and from expert knowledge. Life-span was defined as annual/biannual or perennial, vegetative reproduction was measured as present or absent, and bud position was based on the Raunkiaer system (Raunkiaer 1934).

Data analysis for urban and rural grasslands

We used the historical and contemporary species site occupancy data to examine temporal vegetation change. Changes in species composition were assessed by creating a Jaccard distance dissimilarity matrix, and ordinating the historical and recent composition of grasslands in two dimensions using non-metric multidimensional scaling (NMDS) in PRIMER-E (Version 6, PRIMER-E., IvyBridge, UK). The ANOSIM module of PRIMER-E was used to assess whether temporal differences between sites were significant. Changes in the similarity between grasslands over time were examined by comparing the historical and current Jaccard similarity index between sites. The Jaccard similarity index is the most commonly used similarity index in homogenisation studies (Olden & Rooney 2006).

Given that our urban grassland data was based on site-level surveys, and our rural grassland data was based on plot-level surveys, we were unable to make direct comparisons between urban and rural sites. Rather, we limited our statistical comparisons to within regions over time.

In order to test our model predictions on how changes in the frequency of widespread and rare species affects grassland similarity (Fig. 2), species that qualified for one of four categories were examined: widespread native species, rare native species, widespread non-native species and rare non-native species. Widespread and rare species were defined according to the Gaston's quartile criterion (Gaston 1994). To do this, species were ranked from most to least common in both the historical and recent datasets, with native and non-native species ranked separately. The top ranked 25% native and non-native species in each dataset were then considered widespread, and the lowest 25% considered rare. We then calculated the percent of total occurrence records in each dataset accounted for by widespread native species, rare native species, widespread non-native species and rare non-native species. For each species category, the historical percent of occurrences were compared to the recent percent of occurrences.

Additional spatial analysis of urban grasslands

We examined whether non-native species immigration in urban grasslands was dependent on the degree of landscape modification surrounding each grassland. Following previous urban grassland studies in Melbourne (Williams et al. 2006), we used surrounding road density as our measure of landscape modification. Road density was calculated as the total length of roads per km² within a 5 km radius of each grassland. Road density was measured and calculated from geo-referenced aerial photographs using the software package ArcMap (Version 10.2, ESRI, Redlands, California, US).

The portion of non-native species at each site in both the historical and recent datasets were then analysed against surrounding road density using linear regression. In addition, site-level changes in exotic composition over time were assessed by examining the Jaccard distance between the historical and recent exotic composition of individual grasslands. Jaccard distance is a measure of dissimilarity between sample sites, or in this case, the same site at different points in time, and is obtained by subtracting the Jaccard similarity coefficient from 1. Jaccard distance values between individual sites over time were then analysed against surrounding road density. Analyses were undertaken using linear regression in statistical package SPSS (Version 21, IBM Corp., Armonk, NY, US) and Jaccard distance values were calculated in PRIMER-E (Version 6, PRIMER-E., IvyBridge, UK).

Additional functional trait analysis of urban grasslands

The trait-weighted mean for plant height was calculated for each time period. A modified Mason Diversity Index (FD_{var} index) was also calculated to assess change in the spread of plant height values at each site, by examining the overall variation in the trait values between species (Leps & de Bello, 2008). This was used to determine homogenisation or differentiation in plant height (i.e. an increased FD_{var} index indicates homogenisation in plant height; declining FD_{var} index indicates differentiation). Macro software developed by Leps and de Bello (2008) for Microsoft Excel (2013, Microsoft, Redmond, Washington, US) was used to calculate the trait-weighted mean and FD_{var} index for plant height at each site, at each time period. Temporal differences were analysed using paired t -tests based on the total species pool, as well as native and non-native species independently.

For categorical and binary traits, differences were determined by changes in trait state frequencies (Rodríguez et al. 2009). Changes in dormant bud position were assessed for forbs only due the large representation of graminoids within the hemicryptophyte group (consistent with Rodríguez et al. 2009). Temporal differences were calculated as the difference in mean frequency values for all species, for native species alone, and non-native species alone, using paired t -tests. Analyses were undertaken in statistical package SPSS (Version 21, IBM Corp., Armonk, NY, US).

Results

Change in grassland composition and similarity

The composition of the total species pool changed significantly across urban grasslands over time ($R = 0.32$, $p = 0.01$; Fig. 3a), both for non-native species ($R = 0.41$, $p = 0.01$; Fig. 3c), and, to a lesser extent, native species ($R = 0.17$, $p = 0.01$; Fig. 3b). As predicted, biotic homogenisation was evident, with an increase in the compositional similarity between grasslands over time (Table 1). This was largely driven by an increase in non-native composition similarity across urban remnants, with a smaller increase in similarity based on native species.

In contrast, no significant differences were found between the composition of rural grassland between 1989/1990 and 2014 ($R = 0.098$, $p = 0.1$; Appendix S5), nor was there any evidence of biotic homogenisation, with the Jaccard similarity index between sites remaining unchanged over time (Table 1).

Change in the occurrence frequency of widespread and rare species

Prior to 1994, widespread non-native species accounted for 5% of species occurrence records in urban grasslands. This increased to 20% of total occurrence records in 2013/2014 (Fig. 4). Common native species remained static across the two decades (13% of occurrence records; Fig. 4). Conversely, both rare native species and rare non-native species accounted for fewer occurrence records in 2013/2014 than prior to 1994 (rare native species: pre-1994 = 20%, 2013/2014 = 13%; rare non-native species: pre-1994 = 15%, 2013/2014 = 12%; Fig. 4).

Rural grasslands remained far more stable, with less than 1% change in the frequency of both common and rare native species (Appendix S6). Changes amongst non-native species were larger, with a 31% increase in common non-natives and 27% increase in rare non-natives. However, these changes were not sufficient to alter the overall ranking of commonality groups (Appendix S6).

Urbanisation and non-native species immigration

Surrounding road density was positively associated with a high proportion of non-native species in both the current and historical urban datasets (Pre-1994: $F_{1, 27} = 12.3$, $R^2 = 0.15$, $\beta = 0.38$, $p = 0.04$; 2013/2014: $F_{1, 27} = 6.55$, $R^2 = 0.2$, $\beta = 0.44$, $p = 0.02$; Appendix S7). However, site-level differences between the historical and recent non-native species composition of urban grasslands was highest in areas of low road density ($F_{1, 27} = 9.88$, $R^2 = 0.27$, $\beta = -0.52$, $p = 0.004$; Appendix S7).

Plant functional trait changes in urban grasslands

At the same time as taxonomic homogenisation was occurring in urban grasslands, trait differentiation was also occurring; the FD_{var} for plant height increased significantly over time ($t = 3.31$, $df = 28$, $p = 0.002$; Appendix S8). However, temporal differences in FD_{var} were non-significant when native and non-native species were analysed independently (Appendix S8).

As predicted, the trait-weighted mean for plant height increased significantly over time ($t = 4.69$, $df = 28$, $p = <0.001$; Appendix S8), for both native and non-native species (native: $t = 4.84$, $df = 28$, $p = <0.001$; exotic: $t = 2.85$, $df = 28$, $p = 0.006$; Appendix S8). Changes in the frequencies of plant functional trait states were identified for life-span and vegetative reproduction. However, no significant changes were identified for the frequency of forbs in the four dormant bud classes (Appendix S9).

The frequency of annual plants increased significantly ($t = 2.83$, $df = 28$, $p = <0.006$; Appendix S9); however, native and non-native species differed in their response over time. While the frequency of native annuals significantly declined ($t = 4.43$, $df = 28$, $p = <0.001$), the frequency of

non-native annuals significantly increased ($t = 3.86$, $df = 28$, $p = <0.001$; Appendix S8). The frequency of native plants capable of vegetative reproduction increased significantly between 1993 and 2013/2014 ($t = 5.16$, $df = 28$, $p = <0.001$; Appendix S8), while the frequency of non-native plants capable of vegetative spread did not change significantly ($t = 1.67$, $df = 28$, $p = 0.1$; Appendix S8).

Discussion

We explored changes in the composition of native temperate grasslands in urbanising and rural landscapes in Victoria, Australia over two decades. Over this period, biotic homogenisation appears to have occurred in urban, but not rural grasslands. In urban grasslands, a suite of non-native plants has become increasingly widespread, increasing similarity between sites and driving a significant change in species composition. However, in rural grassland neither similarity nor composition significantly changed between the two sampling periods, lending weight to the prediction that biotic homogenisation has been an urban phenomenon in Victoria's native grasslands.

Across the globe, urbanisation has been coupled with changes to disturbance regimes (Alberti 2005). This has had major consequences for grasslands in south-eastern Australia, where frequent disturbance by fire is vital to constrain native grass dominance, and prevent the competitive exclusion of the subordinate native species that contribute most to species diversity (Lunt et al. 2012). Plant height is a trait positively correlated with competitive vigour (Kraszewski & Waller 2008; Fischer et al. 2013), and as the frequency of disturbance has declined in Melbourne's urban grasslands (Williams et al. 2006), we predicted that competition would become a strong filter on community assembly, favouring tall plants capable of accessing light amongst dense grass sward. Our results supported this prediction, with a significant shift in the composition of urban grasslands towards taller plants for both native and non-native species. Urban environments also tend to provide plant communities with enhanced access to nutrients (Brazel et al. 2000), particularly through nitrogen deposition (Pickett et al. 2001; Grimm et al. 2008), which may reinforce the dominance of tall plants by ensuring that nutrient limitation does not limit growth potential (Brooks 2003; Daehler 2003).

However, as the distribution of traits differs between the resident and immigrant flora, native and non-native species have benefited from alternative strategies. While the ability to reproduce vegetatively has proved advantageous to natives, non-native species have benefited from an annual life-span. These traits have consequently provided alternative pathways for persisting in a competitive and fragmented ecosystem.

Vegetative reproduction affords plants reliable short-distance dispersal and the ability to spread horizontally, accessing resources that have a patchy distribution or space not currently occupied by competing plants (Cornelissen et al. 2003). Alternatively, annual plants are able to persist in unfavourable environments by completing their life-cycle in an optimal temporal niche, avoiding unfavourable temperatures and drought stress often associated with urban landscapes (Diaz & Cabido 1997; Knapp et al. 2008). In addition, by minimising their investment in space, annual plants are highly tolerant of intense and irregular disturbance inherent within the urban matrix (Whitney 1985; Kowarik 1995).

Annual life-spans provide non-native species with a trait that increases the likelihood of persistence (McKinney 2002). Through a minimal investment in space and time, potential habitat is maximised. Consequently, annual plants are able to build populations around fragmented patches, and spread across patch boundaries when opportunities arise. In contrast, vegetative reproduction involves a high investment in space. Consequently, under current conditions, native species that persist into the future will likely do so by defending the space they occupy, while non-native species have the ability to re-immigrate in the event of local extinction.

Grassland homogenisation around the globe

Grasslands are considered amongst the most threatened of the earth's terrestrial ecosystems (Hoekstra et al. 2005), with a number of studies recently reporting biotic homogenisation (Ross et al. 2012; Puhl et al. 2014; Uchida & Ushimaru 2015). However, the pathways and drivers of homogenisation have been varied (Appendix S12). Similar to our results, in India, the United States, and Chile, grassland homogenisation has been driven by the spread of widespread non-native species in response to habitat fragmentation and human settlement (MacDougall et al. 2014; Dar & Reshi 2015; Martin & Wilsey 2015; Fisher et al. 2016). In Switzerland, however, the implementation of recent grassland conservation initiatives has led to homogenisation through the spread of widespread native species (Buhler & Roth 2011), while both widespread native and non-native species have increased simultaneously in Hungarian and Argentinean grasslands as agricultural land use has intensified (Totok & Szitar 2010; Puhl et al. 2014).

Biotic homogenisation in response to rare native species decline has been less commonly reported, potentially reflecting unpaid extinction debts (Hylander & Ehrlén 2013). However, Ross et al. (2012) reported the replacement of rare native species with widespread native species in Scottish grasslands, citing increased nutrient availability and extended growing seasons in response to climate warming as the drivers.

Other studies of grasslands in urban environments have reported similar patterns to our study without making the explicit link to biotic homogenisation, suggesting that the process may be under reported. For example, urban grasslands studies in Finland, Germany, Kazakhstan, and South Africa have all reported increases in non-native species and declines in native species, with thermal radiation, increased resource availability and changes to natural disturbance regimes implicated as possible drivers (Manninen et al. 2010; Albrecht & Haider 2013; Vakhlamova et al. 2014; van der Walt et al. 2015).

Biotic homogenisation in urban environments can also theoretically result from changes in species richness. However, Lososova et al. (2016) provided evidence from European cities that homogenisation results mainly from species turnover, with differences in native species richness running parallel to differences in non-native richness. This result suggested that patterns of native and non-native richness in cities are shaped by the same environmental filters (Lososova et al. 2016).

Biotic homogenisation response trends

It is likely that biotic homogenisation occurs in response to both primary and secondary drivers of change. While primary drivers have an initial effect, secondary drivers arise subsequently in response to primary drivers, having either an additive or synergistic effect. For example, biotic homogenisation in Melbourne may have been initiated in response to human settlement, but has intensified in response to associated changes to natural disturbance regimes and continuing fragmentation.

The homogenisation response may be linear in the initial stages. However, as secondary drivers are triggered, non-linear responses become more plausible (Fig. 5). For example, Alstad et al. (2016) identified that the pace of community change in remnant prairies has accelerated with time as anthropogenic drivers have intensified. Alternatively, a punctuated response may occur when an ecosystem is initially resistant to homogenisation until a threshold is breached with continued intensification among drivers. The resulting spill over may result in a short period of intense homogenisation (Fig. 5).

Interpreting trends based on paired repeated observations therefore presents a challenge to researchers and managers, as non-linear and punctuated responses often appear linear. Predicting future levels of homogenisation based on these types of studies may therefore lead to an underestimation of true trends. This limitation could be addressed through ongoing, long-term monitoring, yet such activities are currently lacking (Lindenmayer et al. 2012). An understanding of

how drivers interact would be valuable to managers charged with alleviating the negative effects of biotic homogenisation.

Conclusion and management implications

Biotic homogenisation is occurring in grasslands across the globe (Buhler & Roth 2011; Ross et al. 2012; Puhl et al. 2014). In Melbourne, biotic homogenisation has occurred following a reduction in fire frequency and an increase in urbanisation, leading to environmental change and most likely, an increase in non-native propagule pressure. Consequently, widespread non-native species have increased the compositional similarity between sites. Grasslands located within areas of intense landscape modification, as determined by surrounding road density, have the highest representation of non-native plants. However, site-level changes in non-native composition have been highest in the least modified areas of Melbourne, indicating that the cities non-native flora are spreading towards the urban boundary.

In contrast to urban grasslands, homogenisation has not been observed in grasslands across rural Victoria where historical fire regimes have been maintained. This suggests that despite intense fragmentation and agricultural land-use, the composition of native temperate grasslands can be retained provided that historic disturbance regimes are also maintained.

Declines in fire frequency have been previously linked to population extinctions in Melbourne's urban grassland (Williams et al. 2005b, 2006). However, changes in native composition identified in this current study have been relatively minor compared to changes in non-native composition. Re-introducing fire regimes at an historical frequency may therefore prevent a significant number of future extinctions.

Prescribed burning is generally considered the optimal method of biomass control in Victorian grasslands, as other methods can have unintended negative effects. For example, grazing can threaten rare species that are selectively grazed, while mowing relies on the removal of slash (Verrier & Kirkpatrick 2005). While burning for conservation purposes can also be problematic in urban settings due to societal concerns over public safety (van Wilgen et al. 2012), anecdotally, land managers have begun to re-introduce fire regimes in grasslands across Melbourne. While further research on the ecological and societal effects of this management action is needed, the long-term viability of these native grasslands is likely to be assisted by the capacity of managers to burn within expanding human settlements.

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Data accessibility

Melbourne's VVP Grasslands: site and botanical Dataverse:
<https://dataverse.harvard.edu/dataverse/MelbourneGrasslands>

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Table 1. Average similarity of native grassland at each point in time based on the Jaccard similarity index.

	Jaccard similarity index		% change
	1987-1994	2013/2014	
<i>Urban Grasslands</i>			
All species	0.26	0.34	+ 31%
Native species	0.28	0.31	+ 11%
Non-native species	0.18	0.36	+ 100%
<i>Rural Grasslands</i>	1989/1990	2014	
All species	0.26	0.26	0%
Native species	0.25	0.25	0%
Non-native species	0.3	0.29	- 3%

Fig. 1. Alternative hypothesized directions of vegetation change over time as illustrated through non-metric multidimensional scaling (NMDS) of community composition. (a) Biotic homogenisation

occurs when species composition between sites increases in similarity, (b) biotic differentiation occurs when species composition between sites declines in similarity, (c) clustered differentiation occurs when the similarity between sites remains unchanged, but the composition shifts from the historical state, and (d) model of no change where the community remains relatively stable as neither similarity nor composition significantly change. Triangles indicate historical community; circles indicate current community.

Fig. 2. Conceptual models illustrating how changes in the occurrence frequency of widespread and rare species affects similarity between sites of remnant vegetation in an urban landscape. Biotic homogenisation occurs when common species increase in frequency and/or when rare species decline in frequency. In contrast, biotic differentiation occurs when rare species increase in frequency and/or common species decline in frequency. Clustered differentiation occurs when immigration occurs at the same rate as extinction.

(a) All species

(b) Native species

(c) Non-native species

△ 1987-1994 ▲ 2013/2014 ◇ 1987-1994 ◆ 2013/2014

Fig. 3. NMDS ordination of urban native grasslands based on Jaccard distance dissimilarity. (a) All species stress = 0.15 (b) native species only stress = 0.17 (c) non-native species only stress = 0.12.

Fig. 4. Temporal change in the percent of total species occurrence records that widespread native species, rare native species, widespread non-native species and rare non-native species account for in urban grasslands. Figure includes data for widespread and rare species only (as determined by Gaston's quartile criterion).

Fig. 5. Figure demonstrates the how biotic homogenisation may transpire depending on the nature of the response. The process of biotic homogenisation can appear linear when studies rely on paired observations. However, biotic homogenization can be intensified when primary drivers of change interact with secondary drivers, leading to non-linear or punctuated response.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Location of urban grasslands reserves in Melbourne and the surrounding road network.

Appendix S2. Map identifying the locations of all study sites in urban and rural Victoria.

Appendix S3. Distribution of urban grassland reserve area by size.

Appendix S4. Table of plant functional traits examined for change in urban grasslands.

Appendix S5. NMDS ordination plots of temporal differences in rural grasslands.

Appendix S6. Plot of temporal differences in the frequency of widespread native species, rare native species, widespread non-native species and rare non-native species in rural grasslands.

Appendix S7. Plots demonstrating the correlations between species composition and road density in urban grasslands.

Appendix S8. Plots demonstrating temporal change in the frequency of plant functional traits in urban grasslands.

Appendix S9. Plots demonstrating temporal change in the frequency of plant life forms in urban grasslands.

Appendix S10. Map identifying the locations of biotic homogenisation studies in grasslands across the globe.

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Author/s:

Zeeman, BJ;McDonnell, MJ;Kendal, D;Morgan, JW

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