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# Plant invasions as a biogeographical assay: Vegetation biomes constrain the distribution of invasive alien species assemblages

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ABSTRACT

Plant assemblages define vegetation patterns at different scales, from plant communities at the scale of small plots to broad biomes. Species assemblages are traditionally investigated with a focus on native species, and the spatial patterns and dynamics of alien species assemblages have received much less attention. Here, we explore the biogeography of a subset of invasive alien plants (IAPs) in South Africa and derive several "alien biomes" based on the alien plant assemblages and associated environmental drivers. We propose six hypotheses (the Weed-Shaped Hole; the Biome Decides; Goldilocks; a New World Order; Something In The Way You Move; and Random Tessellation) based on different drivers (disturbance, competition, climate, global change, introduction dynamics, and null respectively) that might explain distribution patterns. In particular, we explore whether invasive plant assemblages are controlled by the same fundamental factors that define native plant assemblages and biomes. A cluster analysis of the spatial distribution of 69 invasive alien plant species revealed five clearly delineated geographic clusters, three of them significantly aligned with the distribution of vegetation biomes (fynbos, grassland and savanna). The major determinants of the distribution of IAP clusters were identified based on a classification tree analysis. We found that broad environmental variables, especially vegetation biomes, explained the distribution of IAP clusters (60% classification accuracy). We could not find a strong relationship with anthropogenic factors, such as land cover or anthromes, even at a finer scale. Our results indicate that vegetation biomes are characterised by hard environmental barriers which also constrain the distribution of IAPs in South Africa. This supports the development of biome-level strategies for the control of alien plant species in South Africa.



## 1. Introduction

Humans have intentionally or accidentally moved organisms around the world for many centuries (Elton, 1958). This has resulted in many species establishing self-sustaining populations outside their native ranges, i.e. in regions separated from the native ranges by substantial biogeographic barriers. The human-mediated reshuffling of the world's biota has intrigued researchers for many decades, especially the last few decades (Thuiller et al., 2006; Van Kleunen et al., 2010a; Richardson, 2011). Many introduced species have become invasive and can have detrimental effects in recipient ecosystems (e.g. Gaertner et al., 2009; Vilà et al., 2011). Understanding the patterns and drivers of alien species distributions, especially invasive species, is critical to inform management strategies.

Many aspects of the biogeography and ecology of biological invasions have been well studied (Pyšek and Richardson, 2006; Van Kleunen et al., 2010b; Richardson, 2011). However, the spatial patterns and dynamics of alien species assemblages (i.e. how alien species assemble and co-occur across landscapes) have received much less attention (but see Pyšek et al., 2005; Hui et al., 2013). Species assemblages are traditionally investigated with a focus on native species. Indeed, alien species are often considered "background noise" in such studies and are therefore ignored.

Plant assemblages define vegetation pattern at different scales—from plant communities at the scale of small plots to biomes at a regional level. Understanding vegetation pattern, through classification or ordination, has helped to unpack the drivers of vegetation change and predict the impacts of human activities on vegetation

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patterns (Chytrý et al., 2011). Several approaches have been proposed to classify vegetation based on one or several factors which include physiognomy, structure, species composition, soil or climatic conditions. Although there is no universally accepted classification scheme, vegetation types provide a useful tool for basic and applied research (Kent, 2011; De Cáceres and Wiser, 2012). Biomes are typically defined on the basis of broad vegetation types and the biophysical features that exercise fundamental control on the distribution of plants (O'Neill, 1986; Cox and Moore, 2000). Assemblages of native plants are mediated by direct and indirect biotic interactions over evolutionary time scales. However, invasive alien plants (IAPs) now dominate vegetation in many parts of the world, and so it is important to know whether the same rules apply to *assemblages* of invasive plants—do they cluster in predictable ways?

IAPs are recent arrivals, and their distribution and abundance can usually be explained by assessing life-history traits and their interactions with elements of the introduction history, notably aspects of introduction and dissemination pathways such as propagule pressure, the level of exposure to potentially invasible ecosystems and residence time (Wilson et al., 2007; Richardson et al., 2011, 2014). Such determinants have typically exercised influence over relatively short time scales—decades to centuries. In addition, the widespread alteration of ecosystems by humans caused by agriculture, urbanisation and other land uses has led to the formation of globally-significant ecological patterns. Anthropogenic biomes ('anthromes') have been defined to reflect this new ecological order (Ellis and Ramankutty, 2008). As such, the distribution of invasive species might be expected to follow the distribution of anthromes.

One of the fundamental reasons underlying the success of some invasive species is the lack of a shared evolutionary history with the components of recipient ecosystems (Cox, 2004). Many invasive species have dramatically altered many features of invaded vegetation (South African examples include: Yelenik et al., 2007; Iponga et al., 2008; Van Wilgen et al., 2008; Gibson et al., 2012). There is, however, little understanding of how assemblages of alien plants are collectively affected by biotic and abiotic features. Biological invasions can be used as a natural experiment for exploring the determinants of vegetation boundaries—as a bioassay. However, a complicating factor is that few, if any, invasive species have sampled all potentially invasible habitats in their introduced ranges—it is for this reason that the roles of traits and introduction histories typically override those of the fundamental biological processes in shaping the distributions of invasive alien plants (Thuiller et al., 2006 and Wilson et al., 2007).

Many taxa in South Africa's introduced plant flora were introduced to the region more than two centuries ago and have been widely disseminated within the region. Although many of these species have yet to occupy all environmentally suitable areas (Rouget et al., 2004), such species arguably provide an intriguing opportunity to test whether invasive plant assemblages are controlled by the same fundamental factors that define native plant assemblages and biomes. As far as we know, invasive species have yet to be used as a "bioassay" in this way, and South Africa provides a good opportunity for testing the utility of this approach. We explore the biogeography of a subset of invasive alien plants in South Africa and derive several "alien biomes" based on the current alien plant assemblages and associated environmental drivers. This work builds on previous studies by Richardson et al. (2004) and Hugo et al. (2012) who investigated aspects of alien plant species assemblages in South Africa. We provide a more detailed analysis and test several hypotheses to explain the observed biogeographic patterns. In particular we explore the role of vegetation biomes and spatial scale in shaping the spatial patterns of alien plants in South Africa. To this end we propose six hypotheses to explain the current distribution of invasive plant species in relation to vegetation biomes (Table 1). We suggest ways of testing each hypothesis based on the spatial pattern of alien plant species and highlight implications for understanding and management (Table 1).

## 2. Materials and methods

### 2.1. Data source

Distribution records of invasive plant species (IAPs) were obtained from the Southern Africa Plant Invader Atlas (SAPIA; Henderson, 1998 and see also Richardson et al., 2005 for further details). SAPIA is the most comprehensive source of data on the distribution of IAPs in South Africa. IAPs invading natural areas have the greatest ecological impacts (Richardson and Van Wilgen, 2004). In this study, we focused on the drivers of the distribution of terrestrial alien species invading natural habitats. We therefore removed records occurring in "transformed habitats" from the database (e.g. gardens, cultivated areas); and only used records from natural and semi-natural terrestrial habitats. Species with <50 records were ignored. This resulted in a total of 69 species. Most of the species included in this analysis have a large residence time (at least 50 years, with a median value of 150 years) which provided ample opportunities for the species to establish and spread throughout their suitable habitat.

To test the effect of spatial scale, two datasets of varying spatial resolution were compiled: one at a 15-minute resolution (9432 presence/absence records in 1281 grid cells, up to 34 species per cell, with a median value of 5 species) and the other at a 5-minute resolution (13,602 presence/absence records in 2915 grid cells, up to 26 species per cell, with a median value of 4). All duplicate records of the same species in the same grid cell were removed, hence there were fewer records in the 15-minute resolution dataset than in the 5 minute one. We hypothesised that the drivers of invasions might differ depending on the spatial scale of investigation. From our proposed hypotheses (Table 1), we assumed that broad-scale environmental drivers (such as those that have shaped biomes) would be more important at a broad-scale (i.e. 15 min) whereas anthropogenic drivers and possibly competition would explain better the distribution of IAPs at finer scales (i.e. 5 min; see Rouget and Richardson, 2003 for discussion).

To test our hypothesis of random tessellation, a null model of alien species distribution was generated. The null model retained the number of records and their spatial autocorrelation for each species. Specifically, we first calculated the occupancy and spatial correlation of each species (Hui et al., 2006) and then estimated the colonisation rate of each species under a constant local extinction rate (= 0.05) using the pair approximation of the patch occupancy metapopulation model (Hui and Li, 2004; Hui, 2011). Finally, we ran a cellular automaton for each species based on estimated colonisation rate and randomly assigned introduction location (e.g. Roura-Pascual et al., 2009; Caplat et al., 2014; Donaldson et al., 2014). We ran the model at the 15-minute resolution to mitigate the influence of linear sampling scheme for data capture (along roads).

To test the hypothesis that IAP clusters correlate with vegetation biomes, we used the vegetation biomes dataset from Mucina and Rutherford (2006). This dataset represents the original distribution of 10 large ecological zones defined on the basis of vegetation structure and climate. These are (in descending order of extent): Savanna (covering 32% of South Africa), Grassland (26%), Nama Karoo (20%), Fynbos (7%), Succulent Karoo (7%), Azonal vegetation (2%), Albany Thicket (2%), Indian Ocean Coastal Belt (1%), Desert (<1%) and Forest (<1%).

To test the hypothesis that IAP clusters correlate with anthropogenic factors, we used the anthromes dataset for Africa (Ellis and Ramankutty, 2008) and the 2009 national land cover (SANBI, 2009). The anthrome dataset represents 19 anthromes in South Africa that are defined on the basis of major anthropogenic activities that affect vegetation. The national land cover represents seven broad land-use classes for each 1-minute pixel.

We also used elevation and eight climatic factors from the South African Agro-Climatic Atlas (described in Schulze et al., 1997) that are known to be associated with plant species distribution (Rouget et al., 2004). These include mean annual temperature, mean annual