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URBAN INVASIONS

Small urban centres as launching sites for plant invasions in natural areas: insights from South Africa

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Abstract Alien species are often first introduced to urban areas, so it is unsurprising that towns and cities are often hotspots for invasions. However, while large cities are usually the first sites of introduction, small towns are more numerous and have a greater chance of launching invasions into natural areas as they have proportionally larger interfaces with their surroundings. In this paper we develop a set of scenarios as hypotheses to explore the role of small towns in facilitating within-country dispersal of alien plants. In particular, we developed ten scenarios for how introductions to small towns, agricultural and natural areas can lead to landscape-scale invasions. We tested a part of these scenarios using a case study of a highly invaded region in South Africa (the Berg River catchment in the Western Cape). We specifically investigated the main plant invasion routes between 12 small towns and their surrounding agricultural and natural areas. This was accomplished by conducting urban-specific alien plant surveys in towns, then comparing these results to regional databases of naturalized and/or invasive plants. Many of the alien plants found in urban areas were listed as invasive or naturalized in the catchment (over 30% of the total alien species pool). Despite marked environmental gradients across the study area, we found no relationships between the alien plant species richness in towns and climatic variables or with levels of anthropogenic disturbances. All towns hosted large numbers of invasive plant species and nearly half of the alien species found in towns were naturalized or invasive in surrounding areas. The likelihood of alien plants being naturalized or invasive outside urban areas increased in proportion to their local abundance in towns and if they were tall and woody. Ornamental horticulture was the main reason for introduction of these alien species (69%). Small towns can and do harbour significant populations of plant taxa that are able to spread to surrounding natural areas to launch invasions. Comparing lists of species from urban alien

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plant surveys with those from naturalisation records for the region is a useful protocol for identifying species which may be moving along the introduction–naturalization–invasion continuum.

Keywords Alien plants · Gardens · Horticulture · Invasion pathway · Invasive species · Mode of introduction · Small towns · Urban ecosystems · Urban invasions

Introduction

Biological invasions are a major cause of the loss of global biodiversity and understanding the patterns and processes of invasions is becoming increasingly important. A positive relationship between alien species richness and human population density has been reported for many parts of the world (van Rensburg et al. 2009; Spear et al. 2013; Aronson et al. 2014a, b). Urban areas host many alien species, and act as important foci from which some alien species spread and invade surrounding natural areas (Alston and Richardson 2006; Gelbard and Belnap 2003; Dostálek et al. 2014). For example, Cilliers et al. (2008) found similar patterns of invasion of species from urban areas into surrounding fragmented grassland in both southern Africa and Australia, while Dodd et al. (2016) showed how most records of first naturalization occurred near major population centres.

Horticulture is an important pathway for the introduction and dissemination of alien plants around the world (Hodkinson and Thompson 1997; Reichard and White 2001; Richardson et al. 2003; Dehnen-Schmutz et al. 2007a, b; Foxcroft et al. 2008; Lambdon et al. 2008). This pathway explains much of the number and diversity of alien plant species in cities (Sanz-Elorza et al. 2008; Marco et al. 2010; Asmus and Rapson 2014).

Horticultural plants are largely protected from natural disturbance regimes and large herbivores while in cultivation. However, the surrounding urban areas are often disturbed, which provides opportunities for recruitment (Alston and Richardson 2006)—the so-called weed-shaped hole (Buckley et al. 2007). Moreover, edaphic factors like soil fertility, acidity and (seasonal) moisture content are often also controlled and modified in urban environments. Finally, plants are moved to many different localities by gardeners who buy from suppliers and trade, share or otherwise move propagules or whole plants, i.e. there is significant human-mediated dispersal similar to the "long-jump dispersal" observed in China by Horvitz et al. (2017).

Marco et al. (2010) demonstrated the propensity of certain plant species to begin invading natural areas surrounding urban dwellings based on their growth characteristics and their position in the garden. The closer plants were to the outer edge of gardens, the more likely they were to "jump the fence" and escape into natural and semi-natural habitats. Key traits such as the capacity to reproduce vegetatively, and tolerance of dry soils and high pH levels also facilitated invasiveness of some species. Similarly, human movements within and out of urban spaces facilitate the dispersal of propagules to the surrounding natural areas, particularly seeds which can be transported an appreciable distance by cars (Zwaenepoel et al. 2006; von der Lippe and Kowarik 2008; von der Lippe et al. 2013).

There is, however, an important distinction to be made between the size and location of urban areas and the role such areas play as launching sites for invasions. Large cities typically have much greater alien species richness than small rural towns and villages, and are often the first places in a country to which a plant is introduced (Pyšek 1998; Vitousek et al. 1997; Dodd et al. 2016). However, most large cities have a relatively small interface between urban and wildland ecosystems (though there are some notable exceptions, e.g. the City of Brasilia in Brazil, which is surrounded by a national park and three other large protected areas). In small rural towns and villages all gardens are relatively close to the urban edge. Despite this obvious risk and the fact that small towns outnumber large urban centres, most studies conducted on plant invasions in urban areas have focussed on big cities (e.g. Alston and Richardson 2006; Lambdon et al. 2008; Botham et al. 2009; Aronson et al. 2014a, b; Lenda et al. 2014).

Although the requirements for establishment, growth and reproduction for many alien species are met in urban ecosystems, the opportunities for spread (i.e. invasion) to areas outside the urban environment are often limited, especially where conditions across the interface between urban and surrounding areas differ significantly. As a result, many introduced plant species fail to survive in new environments outside active cultivation (Reichard and White 2001). This is very important in areas such as the Western Cape of South Africa, where areas outside urban centres experience regular intense fires, often have nutrient poor soils, and are subjected to high temperatures and drought in summer (Bugan et al. 2012). A large cohort of naturalising plants and/or listed "weeds" (i.e. problem plants) found primarily or only in urban areas would suggest that those plants were unable to spread from there into the surrounding natural areas. If this were the case, one might argue to ignore the contribution of urban environments to invasions in surrounding areas. Alternatively, the same species might represent a future landscape invader, i.e. are part of the invasion debt (Rouget et al. 2016). We formalise these different hypotheses as a set of scenarios.

Invasion scenarios

Alien plants can be introduced directly to one or several urban areas, agricultural fields, or natural ecosystems. From there, they can either remain in the initial habitat or naturalise and invade a different habitat type. Here we consider ten scenarios for the potential sequence of arrival and movement of alien plant species within towns and from towns into surrounding habitats (Fig. 1). Each scenario corresponds to categories of invasion status following the proposed unified framework for biological invasions (Blackburn et al. 2011).

Our aim was to gain an understanding of the type and abundance of alien plant species found within small urban centres using our study system (the Berg River Catchment, South Africa) as a case study. We also investigated regional databases of invasive plant records and records of plant naturalization, both from outside urban areas. We then analyse and interpret species' records at various intersections between these datasets, and infer directionality of spread based on literature regarding each species' introduction history. The aforementioned scenarios explain the options to plant arrival and spread and we address several of these using data from our case study area. The most important of these is Scenario 3 (those potential future invaders that have 'jumped the garden fence') since these plants will have the largest management implications.

Methods

Study area

We sought a study system with a large number of towns of varying sizes close to natural areas for which comprehensive data on alien plant occurrence were available. We selected the Berg River Catchment in South Africa's Western Cape province (Fig. 2). It is bounded by the high (over 1500 m.a.s.l.) Jonkershoek and Hottentot's Holland mountains in the south and east and the Atlantic Ocean in the northwest. The Berg River is approximately 294 km long. The predominantly winter rainfall over the catchment varies from less than 300 mm yr^{-1} at the mouth to 3200 mm yr^{-1} in the mountainous south. The soils are typically nutrient-poor, reflecting the underlying geology of quartzites and sandstone derived from the Cape Supergroup in the upper reaches and Cape Granites in the middle reaches with more recent sediment deposits near the coast (de Villiers 2007). The catchment supports dryland agriculture (mainly wheat) in the northern and western sectors, while irrigated soft fruit forms the bulk of agriculture in the wetter south and adjacent to the mountain ranges. Natural areas comprise mostly fynbos shrublands with high species diversity and levels of endemism. Many rare native plant species in this region are threatened with extinction, due to their very narrow range of environmental tolerance coupled with expanding urban areas and pressure from invasive alien plants. Riparian habitats along the Berg River are dominated by alien trees and shrubs (Tererai et al. 2013). Within this catchment 457 species of native plants are listed as threatened of which 270 are either Endangered or Critically Endangered (South African National Biodiversity Institute 2006).

Another reason for selecting this catchment as study domain was that it is a major water source for the urban and agricultural concerns in the area, most notably the city of Cape Town which lies c. 70 km to the southwest, just outside the catchment. This means there is substantial interest in environmental issues in the area, including the management of invasive species (Ruwanza et al. 2013; Fill et al. 2017). Two

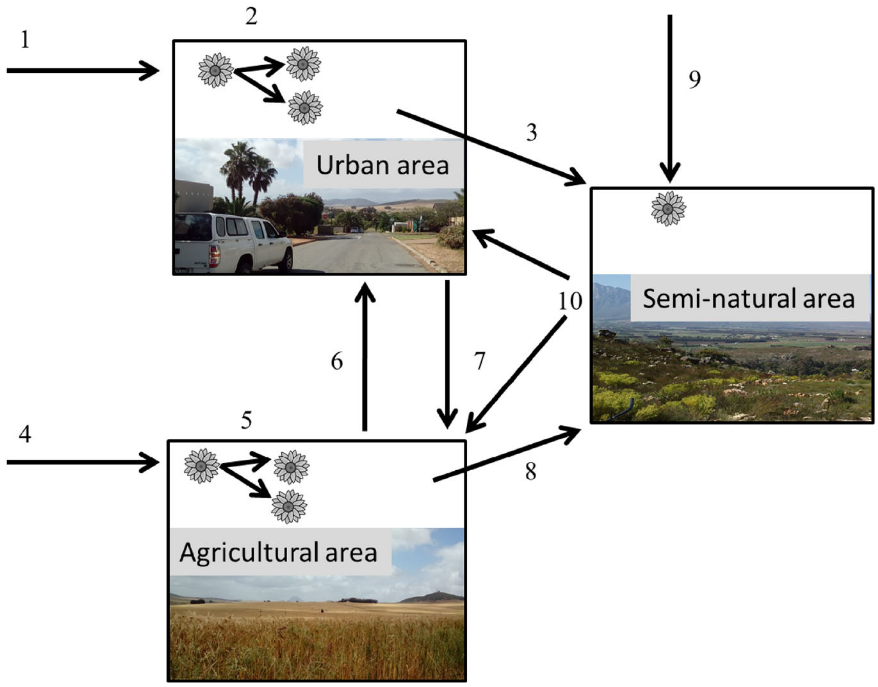

Fig. 1 Scenarios for the different routes of introduction and subsequent spread of alien plants between small towns and surrounding agricultural and natural areas. Usage of all terms and concepts relating to introduction, naturalization and invasion conforms with the definitions proposed by Richardson et al. (2000, 2011). Invasion status is defined as per the unified framework for biological invasions (Blackburn et al. 2011), except that we relax the stipulation in the unified framework that naturalised (regularly reproducing) or invasive (spreading over substantial distances) taxa (categories C–E in the unified framework) need to be in "wild" environments

Scenario	Description	Invasion status	Implications for management
1: Urban only, not naturalized	Taxa introduced directly into a town and remain confined to this space (i.e. no naturalized populations).	B2	Could contribute to the invasion debt, but if there is a mechanism known to restrict reproduction could be on a permitted list.
2: Urban only, naturalized	Taxa introduced into towns, able to naturalize within this space, but not outside of the altered conditions that the urban environment provides.	C2-E	Unless a mechanism is known to prevent naturalisation in the wild, should be considered as a future environmental invader. Regardless of invasiveness, there might be socio-economic impacts that justify management.
3: Jumped the garden fence	Taxa introduced into towns and able to naturalize and spread into surrounding natural areas.	D1-E	Environmental impacts need to be assessed, and potentially measures implemented to prevent spread from towns, or to prohibit plantings in towns.
4: Agricultural only, not naturalized	Taxa introduced into agricultural areas that remain confined to these altered environments.	B2	As for scenario 1
5: Agricultural only, naturalized	Taxa introduced into agricultural areas able to naturalize, but remain confined to the agricultural landscape.	C2-E	As for scenario 2

organizations conduct or coordinate most invasive alien plant management operations in the catchment: the Working for Water (WfW) programme of the national Department of Environmental Affairs, and CapeNature (the provincial conservation agency in the Western Cape). WfW is a government initiative that

Fig. 1 continued

Scenario	Description	Invasion status	Implications for management
6: Agro-Urban invader	Taxa originating from the agricultural space but able to naturalize and spread into nearby urban areas.	D1-E	As for scenario 2, but with greater concern for impacts.
7: Urban-Agro invader	Taxa naturalized in towns and subsequently spreading into agricultural areas.	D1-E	As for scenario 2, but with greater concern for impacts.
8: Jumped the farm fence	Taxa introduced into agricultural areas and able to naturalize and spread in natural areas.	D1-E	As for scenario 3
9: Environmental introductions	Taxa introduced directly into natural areas.	B3-E	An invasive risk analysis should have been conducted prior to release, and should be done retrospectively if not.
10: Environmental introductions spreading to agricultural and/or urban areas	Taxa introduced directly into natural areas able to naturalize and spread into agricultural and/or urban areas.	E	This scenario describes successful, established invaders. These may or may not be receiving management attention in natural areas. If so, effort should be made to remove any ingress into urban areas to prevent these areas acting as refugia for future re-invasion of surrounding natural areas.

employs mainly unskilled labour to control invasive plants while simultaneously creating jobs (van Wilgen and Wannenburgh 2016). CapeNature is the entity mandated to manage provincial protected areas, including the control of invasive species therein. Relatively good data on the distribution of invasive plants exist at the landscape scale for this catchment, mainly from the management plans and other records of the aforementioned organizations and from the Southern African Plant Invader Atlas (SAPIA; for details see Henderson and Wilson 2017).

Within this geographical area are 28 urban areas (see Supplementary Table 1) that range in population size from 330 to just over 100,000 with population densities ranging from 10 to 5000 people/km^2.

For the purposes of this study we used a population-dependant settlement hierarchy (Doxiadis 1968) and thus defined 'small towns' as those containing between 1000 and 15,000 inhabitants (as defined by census information from 2011 available from Statistics South Africa). This gave us a set of twelve towns that varied in population size, density, number of households and household size distributed throughout the catchment, from coastal (Velddrif) to mountainous areas (Pniel) (Supplementary Table 1).

Plant species data for towns

Each selected small town was surveyed to determine alien plant species richness and abundance. Based on the results of a previous systematic survey of one of the towns (that found 84% of alien plant species recorded were present in gardens and along roadsides, P. McLean, unpubl. data), we developed a sampling strategy to estimate the alien plant species richness in each town. Streets were treated as transects and the following zones were surveyed in every town: (1) the main (commercial) road of the town, (2) the main access road into/out of the town (if this was different to the above), (3) at least one road parallel to the main road, (4) at least one road perpendicular to the main road, (5) one urban edge road (where houses are found along one side of the road, while the other is open to the environment—preferably not agricultural), and (6) one road in the low income neighbourhood.

Along each transect we recorded and identified all alien plants. Spreading plants and those with multiple

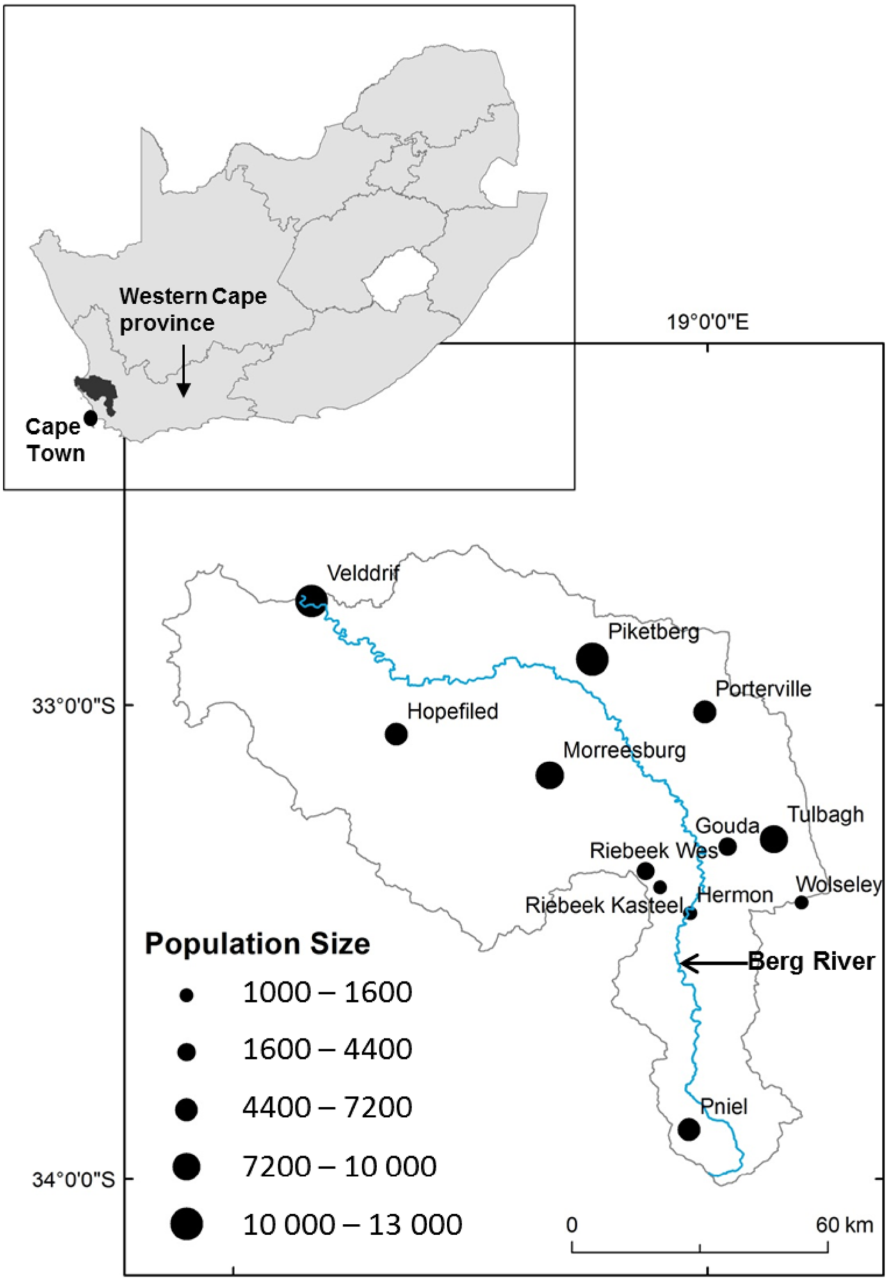

Fig. 2 Location of the Berg River catchment within South Africa's Western Cape province. Surveyed towns are indicated by dots with sizes that are proportional to human population sizes. The Berg River is indicated with the arrow. The total catchment is 7715 km^2 in extent. For further details of the towns see Supplementary Table 1

stems or creepers were measured using a square-metre cover estimate, with 1 m^2 of groundcover taken as equal to one plant in the analyses. All scientific names were checked against The Plant List (Version 1.1, 2013; accessed October 2016). Some individuals of the genera *Eucalyptus*, *Melaleuca* (including *Callistemon*) and *Pinus*, and some horticultural plants (e.g. *Bougainvillea*, *Lavandula* and *Rosa* species) could not always be identified to species level. This was because species in these genera often require one to be in very close proximity to an individual plant to observe the minute or subtle differences in morphology (flower, fruit, leaf and/or bark) that are required for a positive identification. Such close access was often not possible at the study sites as many plants are on access-controlled private property. We therefore considered these groups at the genus level only to avoid representational biases.

The reason for introduction of each species recorded was sourced from local literature on invasive and problem plants in the region (Henderson 2001; Bromilow 2010). These were: (1) Horticulture (all ornamental species); (2) Agricultural (including species used in agriculture but not as a harvestable crop, e.g. trees used as wind breaks but not agroforestry); (3) Agroforestry (in this broad category we included species originally imported for dune stabilisation); (4) Accidental (typically contaminants or hitchhikers). We also categorised species into different growth forms: (1) Tall woody (adults over 2 m in height, woody stems); (2) Short woody (adults under 2 m in height, woody stems); (3) Herbaceous (any height but lacking woody stems); (4) Succulent; (5) Creeper (scrambling or climbing, but not self-supporting); (6) Aquatic; (7) Grass; and (8) Palm.

Plant species data for natural areas in the catchment

Catchment-wide alien plant data were collated from existing databases from five independent sources: (1) Southern African Plant Invaders Atlas (SAPIA) records (accessed 9 June 2016), (2) clearing records from the Working for Water program (WfW) (accessed 13 September 2016) which include data from Provincial and National Departments of Environmental Affairs as well as regional NGOs and municipal contractors acting as implementing/clearing agents for WfW, (3) iSpot Citizen Science network (accessed 1 November 2016), (4) clearing records from SANBI's Invasive Species Programme (Wilson et al. 2013), and (5) CapeNature (for protected areas only; accessed 18 August 2016). Only records from within the boundary of the Berg River catchment were used.

We generated a conceptual Venn diagram (Fig. 3) which graphically explains the contents of each dataset and shows which intersections we anticipated to be most useful in determining the extent of the scenarios investigated in this research.

Analysis

To determine the similarity of the catchment-wide alien plant data to the data from our survey of urban areas, we used Venn diagrams with the same format as Fig. 3. We did this both for all alien plant species, and for the alien plants that were most frequently encountered in towns (i.e. those that had 100 or more records, 149 species in total). This level of high abundance across all towns indicates either frequent planting or that these species are naturalized in this habitat. Either way, species in our "most abundant" set are most likely contributing the greatest propagule pressure into the surrounding environment.

We ran generalised linear models to investigate how alien species richness per town is affected by climate and anthropogenic disturbance. Climatic variables were extracted from BioClim, an online global data resource with a spatial resolution of 1 km^2 (WorldClim version 1.4, 2016). We selected those parameters in the region which vary most across the catchment: Bio1 (mean annual temperature) and Bio12 (annual precipitation). The Human Footprint index was used as a proxy for anthropogenic disturbance. It is an indicator of the degree of human-mediated disturbances in an area ranging from 0 (*wild*) to 100 (*highly disturbed by humans*). It is derived from global records of population pressures (i.e. population density), human infrastructure (i.e. urban areas), and transport access (i.e. roads and railroads), and was obtained for the region from the SEDAC database (Sanderson et al. 2002). This index has proved useful in modelling invasive plant distribution in southern Africa (e.g. Richardson et al. 2010).

We also analysed each town in terms of the proportion of that town's total alien taxon list for which there was evidence of naturalisation elsewhere in the catchment (i.e. inclusion in SAPIA or one of the clearing agencies' databases; Intersection D from Fig. 3). The rationale for this was that such a comparison would indicate whether a particular town showed a different pattern of hosting risky taxa, thereby flagging these towns for management consideration.

Results

We noted 28,609 records of alien plants, representing 365 species and 64 genera (Supplementary Table 2). This was 14 and 9 times more than the total number of species in databases maintained by the management agencies (26 and 40 species for CapeNature and WfW respectively) and is also higher than the SAPIA

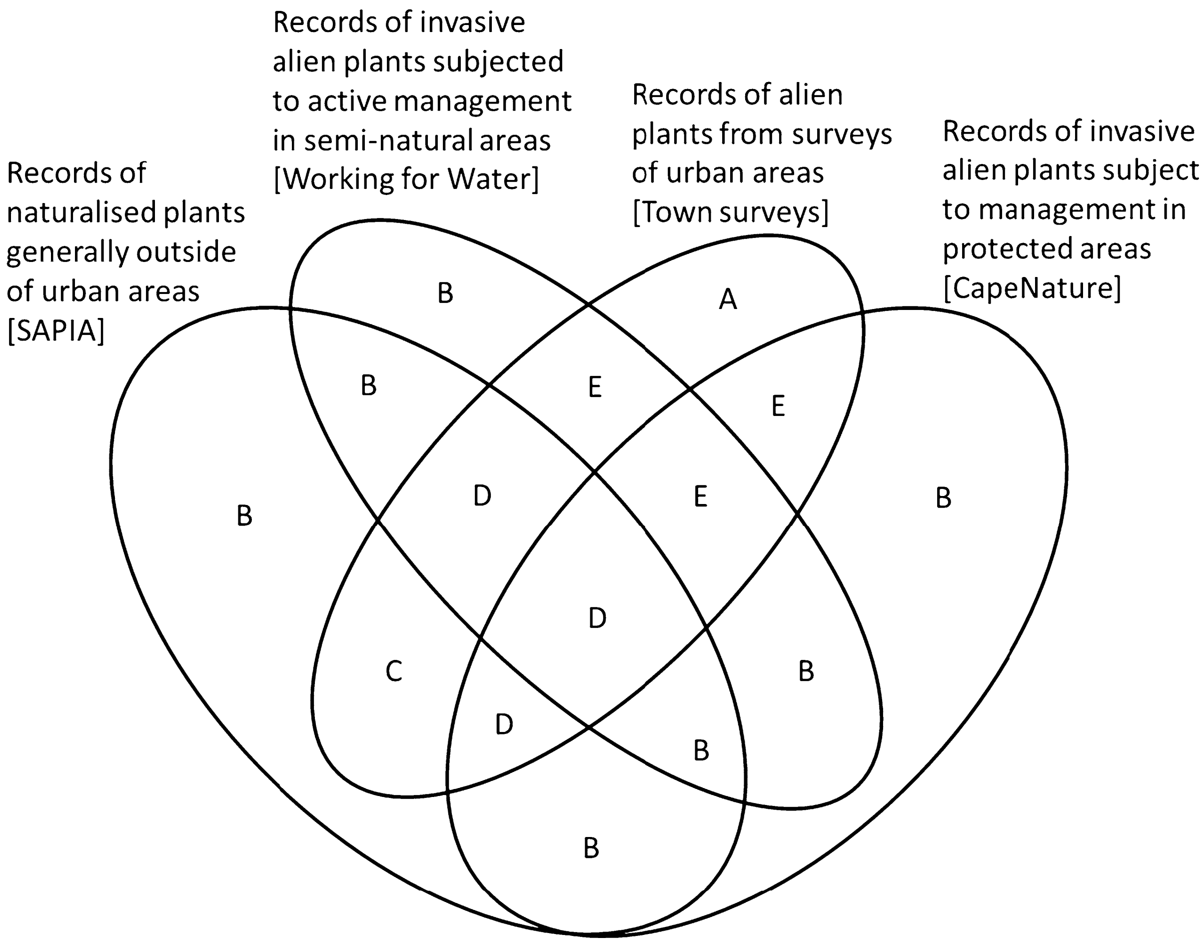

Fig. 3 Conceptual diagram indicating the composition of information within each of the datasets used in this study while explaining the key intersections between these datasets and how this relates to the set of scenarios in Fig. 1. Intersection A: Species recorded within town surveys only. These correspond with Scenario 1 plants from Fig. 1. Intersection B: Species recorded only within the dataset of naturalized species outside of urban areas. Species occurring in this category correspond with Scenario 8 and 9 from Fig. 1. Intersection C: Species recorded in both town survey data and records of naturalized species outside of towns but not recorded within either dataset of invasive plants subject to management in semi-natural areas. These species correspond with Scenario 3 in Fig. 1. Intersection D: Species recorded in town survey data, regional naturalization records as well as either (or both) datasets for invasive plants subject to management actions. These species are established invaders and correspond with Scenario 6, 8 and 10 in Fig. 1. Intersection E: Species recorded in towns and regional invasive species datasets but are not recorded in the regional naturalization dataset. These are Scenario 6 species which have either spread into towns only or are yet to be detected in natural areas

database (regional naturalization records) for the study area (216 species) (Fig. 4). We recorded between 78 and 121 alien plant taxa per town, with between a third and a half of the taxa per town having been recorded as naturalised in the catchment (see Supplementary Table 1).

In total across all datasets, 456 alien plant taxa were recorded in the catchment (Fig. 5a). Most of these species (448 species; 98%) were recorded in either the town surveys or in regional naturalization records (SAPIA). The data sets from management agencies reflect their focus on the relatively few species that cause landscape-scale impacts (i.e. 46 species threatening ecosystems services such as water supply; Fig. 5a). The 15 taxa represented in all catchment databases as well as in our town survey are well-known and well-established invading plants in the region: *Acacia baileyana*, *A. cyclops*, *A. longifolia*, *A. mearnsii*, *A. melanoxylon*, *A. pycnantha*, *A. saligna*, *Eucalyptus* spp., *Lantana camara*, *Paraserianthes*

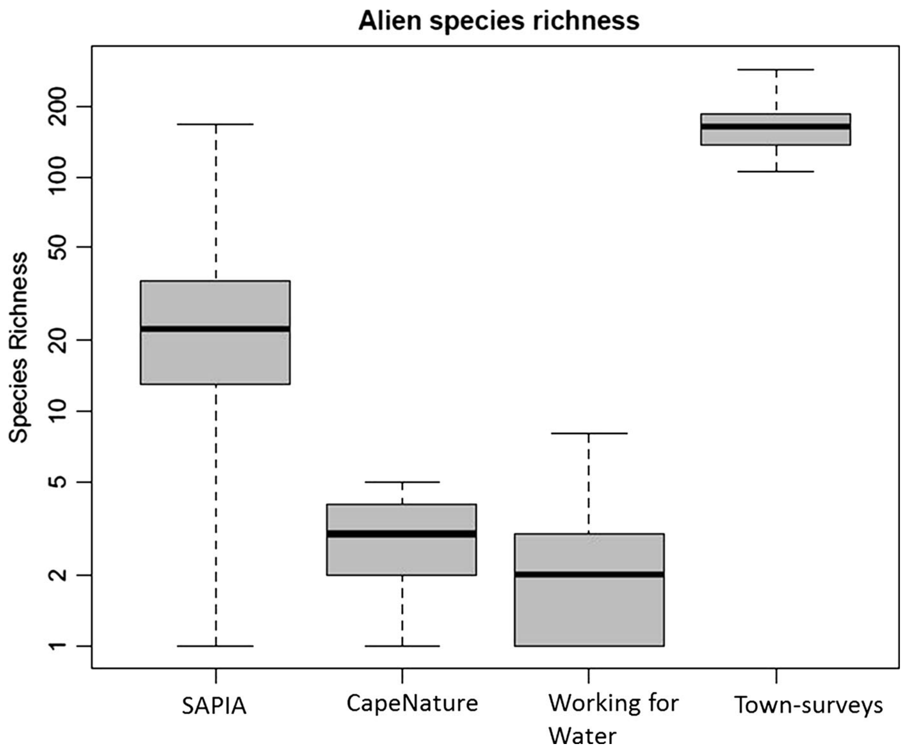

Fig. 4 Alien plant species richness per quarter-degree grid cell as recorded from three different data sets and our study survey of 12 small towns in the Berg River catchment (South Africa). SAPIA is the Southern African Plant Invader Atlas and consists of records of naturalized species predominantly outside urban areas. CapeNature is the provincial nature conservation authority and has records of invasive plants subject to management intervention within protected areas. Working for Water (WfW) is a national program for invasive plant management which operates predominantly in areas of strategic importance as water catchments. Species listed in the WfW database are subject to management intervention in semi-natural areas outside of urban development. Boxes represent the upper and lower quartiles of each dataset with the median shown by the thick central line. The whiskers extend to the maximum and minimum data points for each dataset

lophantha, *Pinus* spp., *Rubus* spp., *Sesbania punicea*, *Solanum mauritianum*, and *Xanthium strumarium* (Wilson et al. 2014). Of these invaders, only *Rubus* species have a direct link to agriculture and only *L. camara* (with the added possibility of some *Eucalyptus* and *Pinus* species in the past) have any horticultural connection. The group of species recorded in the town-survey, SAPIA and WfW datasets (but not in CapeNature) include the grass species *Arundo donax*, *Cortaderia selloana*, and *Pennisetum clandestinum*, as well as tree species in the genera *Casuarina*, *Populus* and *Quercus* which are associated with agriculture. WfW records indicate that R 52 million (approximately US$ 4.5 million) was spent on invasive plant clearing efforts on these species in this catchment between 2001 and 2016.

The surveys in the 12 towns revealed 227 alien plant species which are not found in the other datasets, and 105 species that are also listed in SAPIA as being naturalized in the catchment (Fig. 5a). The species which are present in towns and in another other data set (thus either listed as naturalising or invasive somewhere in the study area) account for 38% of the total number of taxa recorded for all towns. Similar trends are apparent if we consider only abundant plant species from towns (i.e. those with 100 or more records; Fig. 5b). Seventy (47%) of the most abundant species within towns are either naturalized or invasive in this catchment, and 18 of these are currently receiving active management attention in natural areas of the study catchment.

Most naturalised taxa were either tall woody (44%) or herbaceous (25%) (Table 1). More than two-thirds (65%) of the most abundant naturalized plants in towns were introduced for horticultural or ornamental purposes.

Fig. 5 Alien plant taxa recorded within the Berg River Catchment, South Africa. The diagram shows the overlap in numbers of species recorded in four different data sets (SAPIA; Working for Water; CapeNature and the surveys of 12 small towns conducted here). Panel (**a**) shows all 456 species recorded in total across datasets, and panel (**b**) shows a subset of the 149 most abundant alien species of the Town-survey dataset. See Fig. 3 for details of what the various intersections between data-sets mean

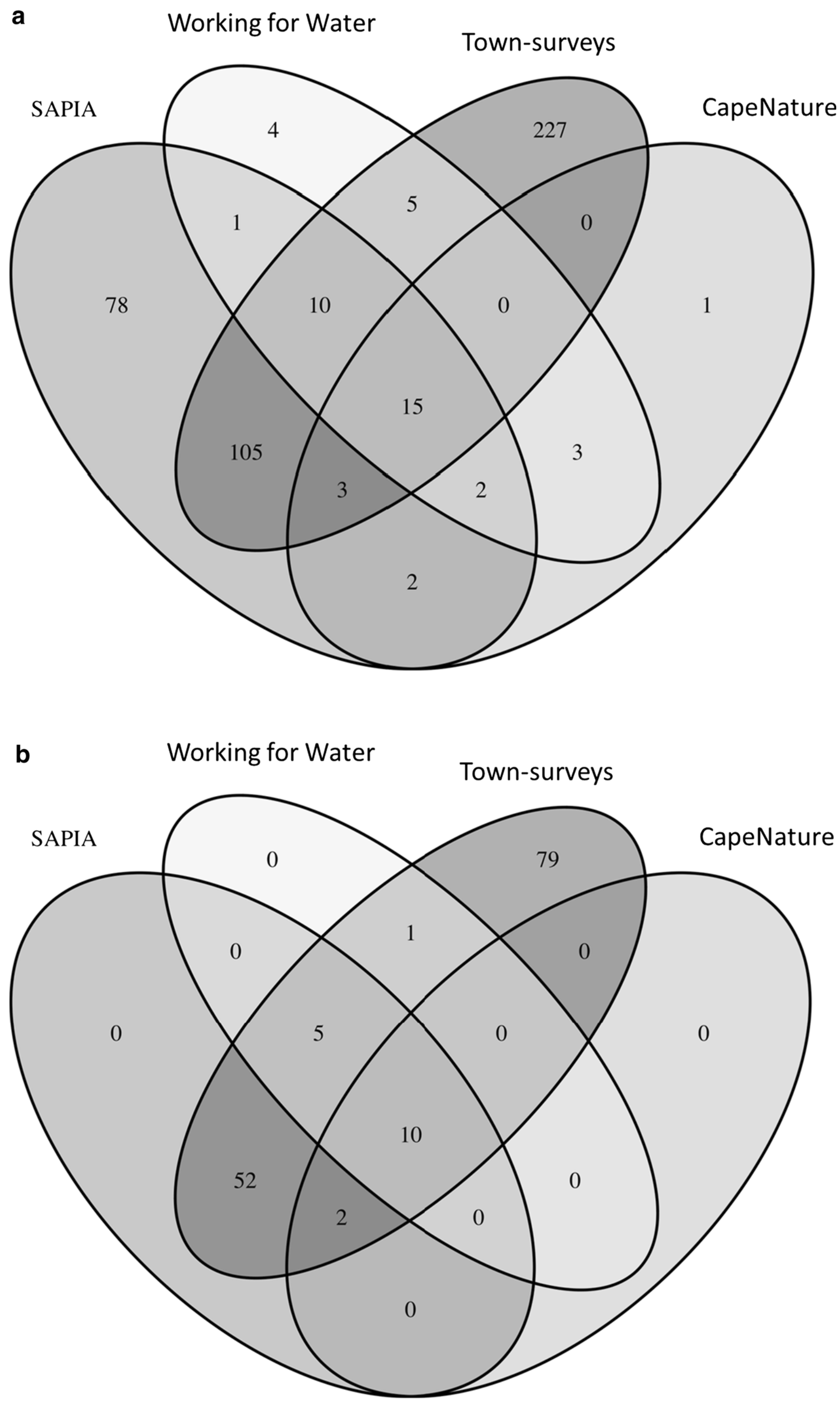

Table 1 Numbers of taxa introduced for ornamental use and non-ornamental use (divided into six growth forms) for the most abundant taxa in towns that were also represented in the SAPIA data set of naturalized taxa (52 taxa from Fig. 5b)

	Tall woody	Short woody	Succulent	Creeper	Grass	Herbaceous	Total
Ornamental taxa	19	2	2	3	1	7	34
Non-ornamental taxa	4	1	1	2	4	6	18
Total records	23	3	3	5	5	13	

We found no significant relationship between total species counts for towns and any environmental parameter (climate and position in the catchment) or the Human Footprint index (proximity to areas of high human disturbance; Supplementary Fig. 1). There was also no significant relationship between these environmental or human disturbance parameters and the proportion of naturalized species in a given town's alien flora (as recognised by the SAPIA database).

The comparison of urban alien plant survey data with records of naturalised as well as invasive populations in the same catchment allow us to revisit and begin to populate the conceptual set of scenarios (Fig. 1). The plants which represent Scenario 1 (Intersection A from Fig. 3) we called "Urban only, not naturalized"; those 227 species occurred only in the town-surveys dataset (around 50% of all species recorded across all datasets) and include non-reproductive species (e.g. *Rosa* spp.). It also includes a subset of species of Scenario 2 or "Urban only, naturalized", which do naturalize within towns but have not yet been detected outside urban areas (e.g. *Breynia disticha*). Species occurring only in invasive or naturalization records and not in towns (Intersection B in Fig. 3) have spread into natural areas from agricultural (therefore not urban) areas (Scenario 8) or were introduced directly into natural areas (Scenario 9, e.g. *Hakea drupacea*). The reason for introduction for each species will explain which scenario applies to which species. The 105 species recorded in both town-surveys and regional naturalization records (SAPIA) are plants which naturalize in towns and in surrounding areas. These species, captured in Scenario 3 (see also Fig. 3 Intersection C), are those potential new invaders which have "Jumped the garden fence" and include many species that were introduced for horticulture (Table 1) (e.g. *Pennisetum setaceum*). Overlap in species' records within towns, regional naturalization as well as regional invasive datasets (Intersection D) indicate that these plants are established invaders in that area and are likely moving from their introduction in agricultural areas (Scenario 6, e.g. *Echium plantagineum*) or from natural areas into agricultural and/or urban areas (Scenario 10, e.g. *Acacia saligna*). Intersection E plants are those few species of Scenario 6 which were introduced into agricultural areas and spread into towns but have remained undetected in natural areas as evidenced by their lack of capture in the regional naturalization database.

Discussion

As expected, a large number of alien plant species enter towns via the horticultural or ornamental trade (Scenarios 1 & 2; Table 1). We also showed that 47% of the most abundant alien species in towns have established naturalized populations outside urban areas (Scenario 3). While some species from this group reflect those with an agricultural origin which are spreading into urban areas (Scenario 6, e.g. *Echium plantagineum*), the majority of the records are of plants which were introduced for ornamental/horticultural purposes (65% from Table 1). This implies they were introduced first into urban environments and their regional naturalization records are an indication of their subsequent spread from urban environments into natural environments. Many authors have highlighted the risk of horticulture as a pathway of invasion (e.g. Hodkinson and Thompson 1997; Reichard and White 2001; Dehnen-Schmutz et al. 2007a, b; Foxcroft et al. 2008; Lambdon et al. 2008; Zenni 2014). Moreover, the invasion risk posed by horticultural trade has recently increased for many reasons, including the expansion in trade through the internet (Lenda et al. 2014) and species selection shifting towards more dry-adapted species in response to climate change. This could be a problem in future as dry-adapted species are more likely to naturalize (Marco et al. 2010). Our results echo these findings (for this catchment) and suggest that the predominant route of invasion in natural areas is that of introduction to towns, and subsequent spread to natural areas and agroecosystems (Scenario 3 from Fig. 1; also Intersection C from Fig. 3). This was somewhat surprising given the harsh environmental conditions in this region, so it would be interesting to repeat this study in other parts of the world. We predict less pronounced patterns in harsher regions such as desert settlements and more pronounced in regions where conditions outside urban settlements are more benign (e.g. tropical regions). The pattern is probably an unwanted side-effect of the practice of preferentially selecting alien garden plant species that are pre-adapted to local environmental conditions.

Our results provide support for previous work that has shown that alien plant species richness is considerably higher within urban settings than in natural areas (Fig. 4). This was expected given the well-established finding that alien species diversity is positively correlated with human population density (van Rensburg et al. 2009; Spear et al. 2013; Aronson et al. 2014a, b). One would expect a high diversity of introduced plants for the mix of horticultural and ornamental use (e.g. roses) and small-scale agricultural use (e.g. lemon trees) to be found in urban ecosystems. We also note how many of these species (227) were only recorded in town surveys (Fig. 5a). These species may require a high degree of human intervention to survive conditions which may be dissimilar to their natural range, or they may even be sterile. This set is considered to be (currently) confined to this modified environment since they do not appear in lists of species that are the focus of agencies involved with invasive plant management (WfW or CapeNature) or in regional records of naturalization (SAPIA). Even if some of these species are naturalized in urban environments, this does not guarantee that they will be able to colonise natural and semi-natural areas outside these urban centres (Reichard and White 2001). Some species in this set are listed invasive taxa in South Africa (e.g. *Tecoma stans*). The fact that they do not yet appear in any of the other datasets implies either that the conditions outside of the urban environments are unsuitable for them to establish, or that naturalized populations have yet to be detected in this catchment. Ideally, a risk assessment should be conducted on these species to determine which could spread.

A large number of species (105) occurred in the towns and were recorded in SAPIA, but do not appear on the WfW or CapeNature lists (Intersection C from Fig. 3). Naturalized species confined to human-dominated ecosystems are underrepresented in SAPIA (L. Henderson, pers. comm.). This means that SAPIA records for our study area indicate records of naturalisation mostly outside of towns—in natural and semi-natural parts of the landscape. Therefore, these 105 species are plants which are found in towns but also have recorded naturalized populations outside of towns in this region. Such species can spread from towns into the surrounding areas notwithstanding the environmental challenges posed by the Cape Floristic Region (fire-prone, summer drought, nutrient poor soils). These species account for 23% of the total species list for the catchment and are identified as likely new invaders (Scenario 3). They thus constitute spread debt as defined by Rouget et al. (2016) and should be of interest to managers in the area. It is important to note that these 105 naturalising alien species are in fact an addition to the 46 species already being treated as invasive in this region (as recognised by their inclusion in CapeNature or Working for Water datasets). This makes the potential invasive species component over 33% of the total recorded alien species for this catchment, which is similar to findings by Tait et al. (2005) for Adelaide and Kowarik et al. (2013) for Berlin, but a little surprising here given the fairly harsh environment.

The finding that more than 70% of the listed invasive species that are receiving expensive management attention at the catchment scale are also found within towns is problematic (Intersection D in Fig. 3). These town-based populations are likely to cause impact not only in the towns, but could also be undermining successful long-term landscape-level clearing operations by providing foci for propagule production and dispersal and therefore re-invasion.

When abundance of plants is considered, the proportion of potentially invasive species (Intersection C in Fig. 3; captured in the town survey data and SAPIA) is much higher (47%, 52 species) than when considering all species, regardless of their abundances (23%; Fig. 5b). These 52 abundant alien plants are thus of particular concern given their proven ability to form naturalized populations outside urban areas in this catchment. Examples of such species in the study area are *Syzygium paniculatum, Schinus terebinthifolius* (both tall woody species), *Bougainvillea* sp. (short woody), *Catharantheus roseus* (herbaceous), *Avena fatua* (grass), and *Agave americana* (succulent). These findings confirm that the invasive species component within these towns is much greater than was assumed, as is the propagule pressure being exerted by small towns into their surroundings.

Trees and shrubs account for many widespread invasions worldwide, and many species have major impacts (Pyšek et al. 2009; Jarošík et al. 2011; Richardson and Rejmánek 2011). Therefore the pattern of dominance by tall woody species in the invasive component of these most abundant plants (Table 1) echoes findings by Kowarik et al. (2013) from Berlin and should raise concern here because the same growth form also accounts for the majority of species that are currently being targeted for management in natural areas in this catchment. Many (65%) of these most abundant naturalized species were introduced for horticulture. This highlights the major importance of this pathway in shaping the invasive species component within these small towns, which agrees with findings of other studies (Downey and Glanznig 2006; Dehnen-Schmutz et al. 2007a, b; Foxcroft et al. 2008; Sanz-Elorza et al. 2008; Marco et al. 2010; Asmus and Rapson 2014; Mayer et al. 2017).

We expected abiotic gradients within the catchment to reveal differences in a given town's ability to host a suite of potentially invasive plant species (Pyšek 1998; Lososová et al. 2012). We found no significant correlates between species richness and either Human Footprint index, mean annual temperature or annual precipitation at a catchment level (Supplementary Fig. 1). This suggests that, within our study area, all urban environments can harbour a suite of species which can naturalize within the same geographical area. Indeed, a third to a half of all urban alien species in each town were also recorded in regional naturalization records (Supplementary Table 1), similar to findings from urban areas in New Zealand (Asmus and Rapson 2014). In other words, our data show that, irrespective of position in the catchment, surrounding environmental conditions or measures of human impact, all towns harbour a similarly high proportion of potentially invasive species, which supports our assertion that small towns act as launching pads of invasions into surrounding areas.

Seebens et al. (2017) found no saturation in the accumulation of alien species across the world. The lack of saturation is also evident at the catchment scale in our study. If similar results emerge from studies of urban areas in other catchments, urban floristic surveys could be an important way of locating potential new invaders and flagging species for early management attention. Risk analyses or assessments of invasion debt (Rouget et al. 2016) are needed to determine which naturalized species need to be targeted for clearing within towns before they begin spreading to surrounding areas. Data for our study area show that tall woody species introduced for horticulture and/or as ornamentals are the most likely to be able to naturalize and spread. Analyses such as those outlined in this paper are needed to elucidate within-country pathways of dispersal of alien plants to provide guidelines for management strategies.

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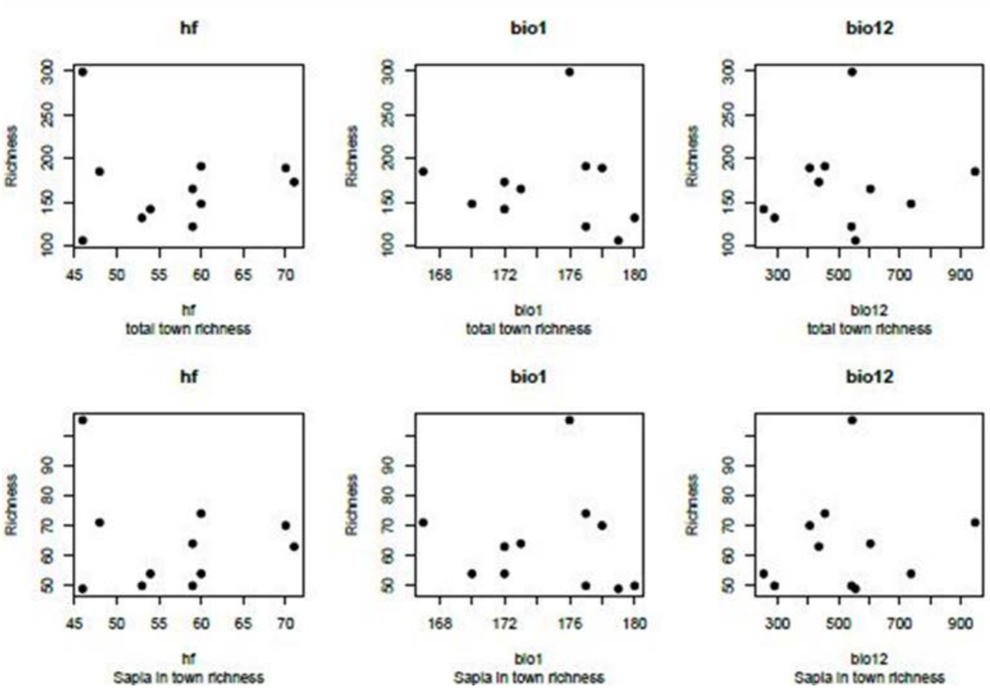
Suppl. Table 1 List of towns located within the Berg River Catchment. The table indicates the total population, population density, number of households and the average household size for each of the towns according to StatsSA census information from 2011. Towns surveyed for this study are indicated with an *. For these towns we indicate the total number of alien species observed from our urban plant surveys as well as the number and proportion of these species which are also included in the regional naturalization database (SAPIA).

Note: No population data were available for the small hamlet of Hermon due to its inclusion in a neighbouring region.

Town	Population	Population Density (people/km^2)	Total number of species	Number and proportion of naturalized species
Aurora	578	356		
Darling	1 073	147		
De Hoek	330	11		
Franschhoek	17 556	2 491		
Geodverwagt	1 979	663		
Gouda *	3 441	450	88	37 (42.0%)
Hermon *	nd	nd	78	36 (46.2%)
Hopefield *	6 460	199	85	34 (40.0%)
Koringberg	1 214	315		
Kylemore	4 328	4 596		
Langebaan	8 297	411		
Langebaanweg	952	134		
Morreesburg *	7 760	285	110	42 (38.2%)
Paarl	112 045	1 734		
Paternoster	1 971	790		
Piketberg *	12 075	910	102	40 (39.2%)
Pniel *	6 264	5 046	100	41 (41.0%)
Porterville *	7 057	884	106	43 (40.6%)
Riebeek Kasteel *	1 144	179	121	48 (39.7%)
Riebeek Wes *	4 350	1 269	106	43 (40.6%)
Saldana	28 142	1 621		
Saron	7 843	3 688		
Tulbagh *	8 969	2 353	106	43 (40.6%)
Velddrif *	11 017	1 242	91	33 (36.3%)
Vredenburg	38 382	2 792		
Wellington	55 543	1 842		
Wittewater	848	1 775		
Wolseley *	1 528	650	100	36 (36.0%)



Suppl. Fig 1 Raw data for the regression analysis of Human Footprint (hf); Mean Annual Temperature (Bio1); Annual Precipitation (Bio12) relative to individual towns by 1) Total Town Species Richness; 2) Town species also noted within SAPIA.

Supplementary Table 2. Complete alien species list for the Berg River Catchment, South Africa when all data sets are combined. Species are listed alphabetically. Their family group is indicated and their presence in the SAPIA, CapeNature, Working for Water and Town-survey data sets is indicated with a "1" in the relevant column. The invasive status of each species in South Africa is indicated by the category under which it is listed. South African legislation, the National Environmental: Biodiversity Act (NEM:BA; Act #10 of 2004), assigns one of four categories to declared invader species: (i) Category 1a species are eradication targets, (ii) Category 1b species may not be traded, must form part of a management plan focussed on their control, and they must be removed where possible, (iii) Category 2 species can only be grown under permit, and (iv) Category 3 species are allowed to remain where found, but may not be propagated or traded. Where a genus containing several listed species is shown, all possible NEM:BA categories for species within this genus are indicated. Some species have different NEMBA category designations depending on their location within the country, so we show only their relevant listing for the Western Cape province of South Africa.

Species	**Family**	**NEMBA Category**	**SAPIA**	**CapeNature**	**Working for water**	**Town-survey**
Abelia sp.	Caprifoliaceae (Linnaeaceae)		0	0	0	1
Abutilon pictum	Malvaceae		0	0	0	1
Acacia adunca	Fabaceae	1a	1	0	0	0
Acacia baileyana	Fabaceae	3	1	1	1	1
Acacia cultriformis	Fabaceae		1	0	0	0
Acacia cyclops	Fabaceae	1b	1	1	1	1
Acacia dealbata	Fabaceae	2	0	0	1	0
Acacia elata	Fabaceae	1b	1	0	1	1
Acacia galpinii	Fabaceae		0	0	0	1
Acacia implexa	Fabaceae	1a	1	0	0	0
Acacia longifolia	Fabaceae	1b	1	1	1	1
Acacia mearnsii	Fabaceae	2	1	1	1	1
Acacia melanoxylon	Fabaceae	2	1	1	1	1
Acacia paradoxa	Fabaceae	1a	1	0	0	0
Acacia podalyriifolia	Fabaceae	1b	1	0	0	1
Acacia pycnantha	Fabaceae	1b	1	1	1	1
Acacia saligna	Fabaceae	1b	1	1	1	1
Acacia sp.	Fabaceae		0	0	1	1
Acalypha wilkensiana	Euphorbiaceae		0	0	0	1
Acanthus mollis	Acanthaceae		0	0	0	1
Acer negundo	Aceraceae	3	1	0	0	1
Acer palmatum	Aceraceae		0	0	0	1
Acer sp.	Aceraceae	3	0	0	0	1
Aechmea spp.	Bromeliaceae		0	0	0	1
Aeonium arboreum	Crassulaceae		0	0	0	1
Agave americana	Asparagaceae		1	0	0	1
Agave attenuata	Asparagaceae		0	0	0	1
Agave sisalana	Asparagaceae	2	0	0	0	1
Agave sp.	Asparagaceae		1	0	0	1
Ageratina adenophora	Asteraceae	1b	1	0	0	1
Ageratum conyzoides	Asteraceae	1b	0	0	0	1
Ailanthus altissima	Simaroubaceae	1b	1	0	0	1
Allium triquetrum	Amaryllidaceae		0	0	0	1
Alnus glutinosa	Betulaceae		0	0	1	1
Alstroemeria sp.	Alstroemeriaceae		0	0	0	1
Ammi majus	Apiaceae		0	0	0	1
Amphilophium buccinatorium	Bignoniaceae		0	0	0	1
Anredera cordifolia	Basellaceae	1b	1	0	0	1
Antigonon leptopus	Polygonaceae	1b	1	0	0	0
Apium graveolens	Apiaceae		1	0	0	0
Araucaria heterophylla	Araucariaceae		0	0	0	1
Araujia sericifera	Asclepiadaceae	1b	1	0	0	1
Arctotheca calendula	Asteraceae		0	0	0	1
Argemone albiflora	Papaveraceae		1	0	0	0
Argemone ochroleuca	Papaveraceae	1b	1	0	0	0
Arum italicum	Araceae		0	0	0	1

Species	Family	NEMBA Category	SAPIA	CapeNature	Working for water	Town-survey
Arundo donax	Poaceae	1b	1	0	1	1
Atriplex lindleyi	Chenopodiaceae		1	0	0	0
Atriplex muelleri	Chenopodiaceae		1	0	0	0
Atriplex nummularia	Chenopodiaceae	2	0	0	0	1
Atriplex sp.	Chenopodiaceae	1b/2	1	0	0	1
Austrocylindropuntia cylindrica	Cactaceae	1a	0	0	0	1
Austrocylindropuntia subulata	Cactaceae	1b	0	0	0	1
Avena sp.	Poaceae		1	0	0	1
Azolla filiculoides	Azollaceae	1b	1	0	0	0
Bambusa balcooa	Poaceae		1	0	0	1
Bauhinia variegata	Fabaceae	3	1	0	0	1
Beaucarnea recurvata	Asparagaceae		0	0	0	1
Betula pendula	Betulaceae		0	0	0	1
Bidens pilosa	Asteraceae		1	0	0	1
Blackiella inflata	Amaranthaceae		1	0	0	0
Boerhavia erecta	Nyctaginaceae		1	0	0	0
Bougainvillea sp.	Nyctaginaceae		1	0	0	1
Brachychiton acerifolius	Malvaceae		0	0	0	1
Brachychiton populneus	Malvaceae		0	0	0	1
Breynia disticha	Phyllanthaceae		0	0	0	1
Briza maxima	Poaceae		1	0	0	1
Bromus catharticus	Poaceae		1	0	0	0
Bromus diandrus	Poaceae		1	0	0	0
Bromus japonicus	Poaceae		1	0	0	0
Bromus pectinatus	Poaceae		1	0	0	0
Bromus sp.	Poaceae		1	0	0	1
Bromus willdenowii	Poaceae		1	0	0	0
Brugmansia x candida	Solanaceae		0	0	0	1
Brunfelsia pauciflora	Solanaceae		0	0	0	1
Bryophyllum delagoense	Crassulaceae	1b	0	0	0	1
Bryophyllum fedtschenkoi	Crassulaceae		0	0	0	1
Buddleja madagascariensis	Buddlejaceae	3	0	0	0	1
Caesalpinia ferrea	Fabaceae		0	0	0	1
Callistemon sp.	Myrtaceae	3	1	0	0	1
Camellia sp.	Theaceae		0	0	0	1
Canna indica	Cannaceae	1b	1	0	0	1
Cardiospermum grandiflorum	Sapindaceae	1b	1	0	0	0
Carduus tenuiflorus	Asteraceae		1	0	0	0
Carica papaya	Caricaceae		0	0	0	1
Carissa macrocarpa	Apocynaceae		0	0	0	1
Carya illinoinensis	Juglandaceae		0	0	0	1
Cascabela thevetia	Apocynaceae		0	0	0	1
Castanea sativa	Fagaceae		0	0	0	1
Casuarina cunninghamiana	Casuarinaceae	2	1	1	0	1
Casuarina equisetifolia	Casuarinaceae	2	1	0	0	0
Casuarina sp.	Casuarinaceae	2	1	0	0	1
Catharanthus roseus	Apocynaceae	1b	1	0	0	1
Celtis sp.	Celtidaceae	3	0	0	0	1
Centaurea cineraria	Asteraceae		0	0	0	1
Centranthus ruber	Caprifoliaceae	1b	1	0	0	1
Cereus hildmannianus	Cactaceae	1b	0	0	0	1
Cereus jamacaru	Cactaceae	1b	0	0	0	1
Cestrum elegans	Solanaceae	1b	0	0	0	1
Cestrum laevigatum	Solanaceae	1b	0	0	1	1
Cestrum sp.	Solanaceae	1b	0	0	1	0
Chamelaucium uncinatum	Myrtaceae		0	0	0	1
Chenopodium album	Chenopodiaceae		1	0	0	1
Cinnamomum camphora	Lauraceae	3	1	0	0	1
Cirsium arvense	Asteraceae		1	0	0	0
Cirsium vulgare	Asteraceae	1b	1	0	0	1

Species	Family	NEMBA Category	SAPIA	CapeNature	Working for water	Town-survey
Cistus x	Cistaceae		0	0	0	1
Cistus x parviflorus	Cistaceae		0	0	0	1
Citharexylum spinosum	Verbenaceae		0	0	0	1
Citrus limon	Rutaceae		0	0	0	1
Citrus sp.	Rutaceae		0	0	0	1
Citrus x	Rutaceae		0	0	0	1
Cleistocactus sp.	Cactaceae		0	0	0	1
Coleonema pulchellum	Rutaceae		0	0	0	1
Colocasia esculenta	Araceae		1	0	0	1
Commelina benghalensis	Commelinaceae		1	0	0	0
Convolvulus mauritanicus	Convolvulaceae		0	0	0	1
Conyza bonariensis	Asteraceae		1	0	0	0
Conyza canadensis	Asteraceae		1	0	0	0
Coprosma repens	Rubiaceae		0	0	0	1
Coprosma sp.	Rubiaceae		0	0	0	1
Cortaderia selloana	Poaceae	1a	1	0	1	1
Cortaderia sp.	Poaceae	1a/1b	0	0	1	0
Corymbia ficifolia	Myrtaceae		0	0	0	1
Cosmos sp.	Asteraceae		0	0	0	1
Cotoneaster pannosus	Rosaceae	1b	1	0	0	1
Cotoneaster vilmorinianus	Rosaceae		0	0	0	1
Cotula turbinata	Asteraceae		0	0	0	1
Crassula tetragona	Crassulaceae		0	0	0	1
Crotalaria agatiflora	Fabaceae	1b	0	0	0	1
Cupressus sp.	Cupressaceae		1	0	0	1
Cuscuta campestris	Convolvulaceae	1b	1	0	0	0
Cydonia oblonga	Rosaceae		1	0	0	1
Cylindropuntia fulgida	Cactaceae	1b	0	0	0	1
Cylindropuntia imbricata	Cactaceae	1b	0	0	0	1
Cynodon dactylon	Poaceae		1	0	0	1
Cytisus scoparius	Fabaceae	1a	1	0	0	0
Datura sp.	Solanaceae	1b	0	0	0	1
Datura stramonium	Solanaceae	1b	1	0	0	1
Disocactus sp.	Cactaceae		0	0	0	1
Dittrichia graveolens	Asteraceae		1	0	0	0
Dolichandra unguis-cati	Bignoniaceae	1b	1	0	0	0
Duranta erecta	Verbenaceae		0	0	0	1
Echeveria gibbiflora	Crassulaceae		0	0	0	1
Echinocactus grusonii	Cactaceae		0	0	0	1
Echinocereus pentalophus	Cactaceae		0	0	0	1
Echinopsis schickendantzii	Cactaceae	1b	0	0	0	1
Echinopsis sp.	Cactaceae	1b	0	0	0	1
Echium fastulosum	Boraginaceae		0	0	0	1
Echium plantagineum	Boraginaceae	1b	1	0	0	1
Echium violaceum	Boraginaceae		1	0	0	0
Echium vulgare	Boraginaceae	1b	1	0	0	0
Eichhornia crassipes	Pontederiaceae	1b	1	0	0	0
Elytrigia repens	Poaceae		1	0	0	1
Erigeron bonariensis	Asteraceae		0	0	0	1
Eriobotrya japonica	Rosaceae	1b	1	0	0	1
Erodium moschatum	Geraniaceae		0	0	0	1
Eschscholzia californica	Papaveraceae		0	0	0	1
Eucalyptus sp.	Myrtaceae	1b/2	1	1	1	1
Eugenia uniflora	Myrtaceae	1b	1	0	0	0
Euphorbia caerulescens	Euphorbiaceae		0	0	0	1
Euphorbia peplus	Euphorbiaceae		1	0	0	0
Euphorbia pulcherrima	Euphorbiaceae		0	0	0	1
Ficus benjamina	Moraceae		0	0	0	1
Ficus carica	Moraceae		1	0	0	1
Ficus elastica	Moraceae		0	0	0	1
Ficus macrophylla	Moraceae		0	0	0	1
Ficus microcarpa	Moraceae		0	0	0	1
Ficus pumila	Moraceae		0	0	0	1

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Ficus rubiginosa	Moraceae		0	0	0	1
Foeniculum vulgare	Apiaceae		0	0	0	1
Fraxinus angustifolia	Oleaceae	3	1	0	0	1
Fuchsia sp.	Onagraceae		0	0	0	1
Fumaria sp.	Fumariaceae		0	0	0	1
Furcraea foetida	Asparagaceae	1a	0	0	0	1
Gaura lindheimeri	Onagraceae		0	0	0	1
Gelsemium sempervirens	Gelsemiaceae		0	0	0	1
Genista monspessulana	Fabaceae	1a	0	0	0	1
Glebionis coronaria	Asteraceae		1	0	0	1
Gleditsia triacanthos	Fabaceae	1b	1	0	0	1
Gnidia squarrosa	Thymelaeaceae		0	0	0	1
Gomphocarpus fruticosus	Asclepiadaceae		0	0	0	1
Gomphrena celosioides	Amaranthaceae		1	0	0	0
Grevillea robusta	Proteaceae	3	1	0	1	1
Grevillea rosmarinifolia	Proteaceae	3	1	0	0	0
Guilleminea densa	Amaranthaceae		1	0	0	0
Hakea drupacea	Proteaceae	1b	1	0	1	0
Hakea gibbosa	Proteaceae	1b	1	1	0	0
Hakea salicifolia	Proteaceae	1b	1	0	0	1
Hakea sericea	Proteaceae	1b	0	1	1	0
Hakea suaveolens	Proteaceae		1	0	0	0
Hedera helix	Araliaceae	3	0	0	0	1
Hedychium sp.	Zingiberaceae	1b	1	0	0	1
Helianthus annuus	Asteraceae		1	0	0	1
Hesperoyucca x whipplei	Asparagaceae		0	0	0	1
Hibiscus sp.	Malvaceae		0	0	0	1
Homalanthus populifolius	Euphorbiaceae	1b	0	0	0	1
Hordeum sp.	Poaceae		1	0	0	0
Hydrangea macrophylla	Hydrangeaceae		0	0	0	1
Hylocereus undulatus	Cactaceae	2	0	0	0	1
Hymenosporum flavum	Pittosporaceae		0	0	0	1
Hypericum perforatum	Hypericaceae	2	1	0	0	0
Hypochaeris radicata	Asteraceae		0	0	0	1
Ilex aquifolium	Aquifoliaceae		0	0	0	1
Inula graveolens	Asteraceae		1	0	0	0
Ipomoea cairica	Convolvulaceae		1	0	0	1
Ipomoea indica	Convolvulaceae	3	1	0	0	0
Ipomoea purpurea	Convolvulaceae	3	1	0	0	0
Ipomoea sp.	Convolvulaceae	1b/3	1	0	0	1
Jacaranda mimosifolia	Bignoniaceae		1	0	0	1
Jasminum humile	Oleaceae		0	0	0	1
Jasminum mesnyi	Oleaceae		0	0	0	1
Jasminum officinale	Oleaceae		0	0	0	1
Juniperus sp.	Cupressaceae		1	0	0	0
Kalanchoe beharensis	Crassulaceae		0	0	0	1
Koelreuteria paniculata	Sapindaceae		1	0	0	0
Lactuca serriola	Asteraceae		1	0	0	1
Lagerstroemia indica	Lythraceae		0	0	0	1
Lagunaria patersonia	Malvaceae		0	0	0	1
Lagurus ovatus	Poaceae		0	0	0	1
Lantana camara	Verbenaceae	1b	1	1	1	1
Lantana montevidensis	Verbenaceae		0	0	0	1
Laurus nobilis	Lauraceae		0	0	0	1
Lavandula sp.	Lamiaceae		0	0	0	1
Lavatera arborea	Malvaceae		1	0	0	1
Lemna gibba	Lemnaceae		0	0	0	1
Lepidium bonariense	Brassicaceae		1	0	0	0
Leptospermum laevigatum	Myrtaceae	1b	1	1	1	0
Leucaena leucocephala	Fabaceae	2	0	0	0	1
Ligustrum japonicum	Oleaceae	1b	0	0	0	1
Ligustrum lucidum	Oleaceae	1b	0	0	0	1
Ligustrum sinense	Oleaceae	1b	0	0	0	1

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Limonium perezii	Plumbaginaceae		0	0	0	1
Limonium sinuatum	Plumbaginaceae	1b	1	0	0	1
Liquidambar x styraciflua	Hamamelidaceae (Altingiaceae)		0	0	0	1
Lonicera japonica	Caprifoliaceae	3	1	0	0	1
Lonicera periclymenum	Caprifoliaceae		0	0	0	1
Lupinus albus	Fabaceae		0	0	0	1
Lycianthes rantonnetii	Solanaceae		0	0	0	1
Lytocaryum weddellianum	Arecaceae		0	0	0	1
Macadamia sp.	Proteaceae		0	0	0	1
Magnolia acuminata	Magnoliaceae		0	0	0	1
Magnolia grandiflora	Magnoliaceae		0	0	0	1
Magnolia sp.	Magnoliaceae		0	0	0	1
Malus sp.	Rosaceae		1	0	0	1
Malva arborea	Malvaceae		1	0	0	1
Malva parviflora	Malvaceae		0	0	0	1
Mammillaria sp.	Cactaceae		0	0	0	1
Mangifera indica	Anacardiaceae		0	0	0	1
Medicago sativa	Fabaceae		1	0	0	1
Melaleuca armillaris	Myrtaceae		0	0	0	1
Melaleuca bracteata	Myrtaceae		0	0	0	1
Melaleuca parvistaminea	Myrtaceae		0	0	0	1
Melaleuca sp.	Myrtaceae		0	0	0	1
Melia azedarach	Meliaceae	1b	1	0	0	1
Metrosideros excelsa	Myrtaceae		0	0	0	1
Mirabilis jalapa	Nyctaginaceae	1b	1	0	0	1
Miscanthus sinensis	Poaceae		0	0	0	1
Monstera deliciosa	Araceae		0	0	0	1
Moringa oleifera	Moringaceae		1	0	0	0
Morus alba	Moraceae	3	1	0	0	1
Myoporum tenuifolium	Myoporaceae	3	1	0	0	1
Myriophyllum aquaticum	Haloragaceae	1b	1	0	0	1
Myriophyllum spicatum	Haloragaceae	1b	1	0	0	0
Myrtus communis	Myrtaceae		0	0	0	1
Nandina domestica	Berberidaceae		0	0	0	1
Nasturtium officinale	Brassicaceae	2	1	0	0	1
Nephrolepis cordifolia	Nephrolepidaceae	1b	0	0	0	1
Nerium oleander	Apocynaceae	1b	1	0	0	1
Nicotiana glauca	Solanaceae	1b	1	0	0	1
Nothoscordum x gracile	Alliaceae		0	0	0	1
Ocimum basilicum	Lamiaceae		0	0	0	1
Odontonema strictum	Acanthaceae		0	0	0	1
Oenothera indecora	Onagraceae		1	0	0	0
Oenothera jamesii	Onagraceae		1	0	0	0
Oenothera rosea	Onagraceae		1	0	0	0
Oenothera sp.	Onagraceae	3	1	0	0	0
Olea europaea	Oleaceae		0	0	0	1
Opuntia elata	Cactaceae	1b	0	0	0	1
Opuntia ficus-indica	Cactaceae	1b	1	0	0	1
Opuntia microdasys	Cactaceae	1b	0	0	0	1
Opuntia monacantha	Cactaceae	1b	1	0	0	1
Opuntia sp.	Cactaceae	1a/1b	1	0	0	1
Opuntia stricta	Cactaceae	1b	0	0	0	1
Orobanche sp.	Orobanchaceae	1b	0	0	0	1
Oxalis corniculata	Oxalidaceae		1	0	0	0
Pachypodium lamerei	Apocynaceae		0	0	0	1
Pandorea jasminoides	Bignoniaceae		0	0	0	1
Papaver sp.	Papaveraceae		0	0	0	1
Paraserianthes lophantha	Fabaceae	1b	1	1	1	1
Parkinsonia x aculeata	Fabaceae	1b	0	0	0	1
Parthenium hysterophorus	Asteraceae	1b	0	1	0	0
Parthenocissus quinquefolia	Vitaceae		1	0	0	1
Parthenocissus tricuspidata	Vitaceae		0	0	0	1

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Paspalum dilatatum	Poaceae		1	0	0	0
Paspalum urvillei	Poaceae		1	0	0	0
Passiflora sp.	Passifloraceae	1b/2	1	0	0	1
Pennisetum clandestinum	Poaceae	1b	1	0	1	1
Pennisetum purpureum	Poaceae		1	0	0	1
Pennisetum setaceum	Poaceae	1b	1	0	0	1
Pennisetum villosum	Poaceae	1b	1	0	0	0
Pereskia aculeata	Cactaceae	1b	1	0	0	1
Persea americana	Lauraceae		1	0	0	1
Persicaria capitata	Polygonaceae	1b	1	0	0	1
Persicaria lapathifolia	Polygonaceae		1	0	0	1
Petrea volubilis	Verbenaceae		0	0	0	1
Phoenix canariensis	Arecaceae		0	0	0	1
Phormium tenax	Asphodelaceae		0	0	0	1
Phyllostachys sp.	Poaceae		0	0	0	1
Physalis peruviana	Solanaceae		1	0	0	1
Phytolacca dioica	Phytolaccaceae	3	1	0	0	1
Phytolacca octandra	Phytolaccaceae	1b	1	1	0	1
Pinus sp.	Pinaceae	1b/2	1	1	1	1
Pistia stratiotes	Araceae	1b	1	0	0	0
Pittosporum undulatum	Pittosporaceae	1b	1	0	1	1
Plantago lanceolata	Plantaginaceae		1	0	0	1
Plantago major	Plantaginaceae		1	0	0	1
Platanus sp.	Platanaceae		1	0	0	1
Plectranthus barbatus	Lamiaceae	1b	1	0	0	1
Plectranthus neochilus	Lamiaceae		0	0	0	1
Plectranthus ornatus	Lamiaceae		0	0	0	1
Plumbago auriculata	Plumbaginaceae		0	0	0	1
Plumeria sp.	Apocynaceae		0	0	0	1
Poa pratensis	Poaceae		1	0	0	0
Podranea ricasoliana	Bignoniaceae		0	0	0	1
Polygonum aviculare	Polygonaceae		1	0	0	0
Polypogon monspeliensis	Poaceae		1	0	0	0
Pontederia cordata	Pontederiaceae	1b	1	0	0	1
Populus alba	Salicaceae	2	0	0	1	0
Populus deltoides	Salicaceae		1	0	0	1
Populus nigra	Salicaceae		0	0	0	1
Populus simonii	Salicaceae		0	0	0	1
Populus sp.	Salicaceae	2	0	1	1	0
Populus x	Salicaceae	2	0	0	0	1
Populus x canescens	Salicaceae	2	1	1	1	0
Portulaca oleracea	Polygonaceae		1	0	0	0
Prosopis sp.	Fabaceae	1b	1	0	0	1
Prunus armeniaca	Rosaceae		1	0	0	1
Prunus domestica	Rosaceae		0	0	0	1
Prunus persica	Rosaceae		0	0	0	1
Prunus sp.	Rosaceae	1b	0	0	0	1
Psidium guajava	Myrtaceae		0	0	0	1
Psidium x cattleianum	Myrtaceae	1b	0	0	0	1
Punica granatum	Punicaceae		1	0	0	1
Pyracantha angustifolia	Rosaceae	1b	1	0	0	1
Pyracantha coccinea	Rosaceae	1b	0	0	0	1
Pyracantha crenulata	Rosaceae	1b	1	0	0	0
Pyracantha rogersiana	Rosaceae		1	0	0	0
Pyrus sp.	Rosaceae		1	0	0	1
Quercus agrifolia	Fagaceae		0	0	0	1
Quercus ilex	Fagaceae		0	0	0	1
Quercus nigra	Fagaceae		0	0	0	1
Quercus palustris	Fagaceae		1	0	0	1
Quercus petraea	Fagaceae		0	0	0	1
Quercus robur	Fagaceae		1	1	0	1
Quercus sp.	Fagaceae		1	0	1	1
Quercus suber	Fagaceae		1	0	1	1

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Raphanus raphanistrum	Brassicaceae		0	0	0	1
Rhaphiolepis indica	Rosaceae		0	0	0	1
Rhododendron indicum	Ericaceae		0	0	0	1
Rhus succedanea	Anacardiaceae		1	0	0	0
Ricinus communis	Euphorbiaceae	2	1	0	1	1
Robinia pseudoacacia	Fabaceae	1b	1	0	1	1
Rosa sp.	Rosaceae		0	0	0	1
Rosmarinus officinalis	Lamiaceae		0	0	0	1
Rubus cuneifolius	Rosaceae	1b	0	1	1	0
Rubus fruticosus	Rosaceae	2	1	1	0	0
Rubus sp.	Rosaceae	1b/2	1	1	1	1
Rumex sp.	Polygonaceae	1b	1	0	0	1
Rumex usambarensis	Polygonaceae	1b	0	0	0	1
Ruscus sp.	Asparagaceae		0	0	0	1
Sagina procumbens	Caryophyllaceae		1	0	0	0
Salix babylonica	Salicaceae		1	0	0	1
Salix caprea	Salicaceae		1	0	0	0
Salix sp.	Salicaceae		0	0	1	1
Salsola kali	Chenopodiaceae	1b	1	0	0	1
Salvia leucantha	Lamiaceae		0	0	0	1
Salvia madagascariensis	Lamiaceae		0	0	0	1
Salvinia molesta	Salviniaceae	1b	1	0	0	1
Sambucus nigra	Caprifoliaceae	1b	1	0	0	1
Sansevieria trifasciata	Asparagaceae		0	0	0	1
Schefflera actinophylla	Araliaceae		0	0	0	1
Schefflera arboricola	Araliaceae		0	0	0	1
Schinus molle	Anacardiaceae		1	0	0	1
Schinus terebinthifolia	Anacardiaceae	3	1	0	0	1
Schizolobium parahyba	Fabaceae		0	0	0	1
Schotia brachypetala	Fabaceae		0	0	0	1
Searsia lancea	Anacardiaceae		0	0	0	1
Senecio tamoides	Asteraceae		0	0	0	1
Senna didymobotrya	Fabaceae	1b	1	0	0	1
Sesbania punicea	Fabaceae	1b	1	1	1	1
Sida rhombifolia	Malvaceae		0	0	0	1
Silybum marianum	Asteraceae		1	0	0	0
Sisyrinchium sp.	Iridaceae		1	0	0	0
Solanum jasminoides	Solanaceae		0	0	0	1
Solanum laxum	Solanaceae		0	0	0	1
Solanum mauritianum	Solanaceae	1b	1	1	1	1
Solanum nigrum	Solanaceae		1	0	0	1
Solanum pseudocapsicum	Solanaceae	1b	1	0	0	0
Sonchus oleraceus	Asteraceae		1	0	0	1
Sorghum halepense	Poaceae	2	1	0	0	0
Spartium junceum	Fabaceae	1b	1	0	0	1
Sphaeropteris cooperi	Cyatheaceae		0	0	0	1
Spiraea cantoniensis	Rosaceae		0	0	0	1
Spirea sp	Rosaceae		0	0	0	1
Stellaria media	Caryophyllaceae		0	0	0	1
Strelitzia alba	Strelitziaceae		0	0	0	1
Strelitzia nicolai	Strelitziaceae		0	0	0	1
Syagrus romanzoffiana	Arecaceae		0	0	0	1
Synadenium cupulare	Euphorbiaceae		0	0	0	1
Syngonium podophyllum	Araceae		0	0	0	1
Syzygium cordatum	Myrtaceae		0	0	0	1
Syzygium jambos	Myrtaceae	3	1	0	0	1
Syzygium paniculatum	Myrtaceae		1	0	0	1
Tagetes minuta	Asteraceae		1	0	0	0
Tamarix ramosissima	Tamaricaceae	1b	1	0	0	0
Tamarix sp.	Tamaricaceae	1b	1	0	0	1
Taxodium distichum	Cupressaceae		0	0	0	1
Tecoma stans	Bignoniaceae	1b	0	0	0	1
Tetrapanax papyriferus	Araliaceae		0	0	0	1

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Thunbergia alata	Acanthaceae		0	0	0	1
Tipuana tipu	Fabaceae	3	1	0	0	1
Torilis arvensis	Apiaceae		1	0	0	0
Trachelospermum jasminoides	Apocynaceae		0	0	0	1
Tradescantia fluminensis	Commelinaceae	1b	0	0	0	1
Tradescantia pallida	Commelinaceae		0	0	0	1
Tradescantia sp.	Commelinaceae	1b	1	0	0	1
Tradescantia zebrina	Commelinaceae	1b	0	0	1	1
Tragopogon dubius	Asteraceae		1	0	0	0
Tribulus terrestris	Zygophyllaceae		1	0	0	1
Trichilia emetica	Meliaceae		0	0	0	1
Trifolium angustifolium	Fabaceae		0	0	0	1
Trifolium sp.	Fabaceae		0	0	0	1
Triticum spp.	Poaceae		0	0	0	1
Tropaeolum majus	Tropaeolaceae		1	0	0	1
Ulmus parvifolia	Ulmaceae		0	0	0	1
Urtica urens	Urticaceae		0	0	0	1
Verbascum virgatum	Scrophulariaceae		0	0	0	1
Verbena bonariensis	Verbenaceae	1b	1	0	0	1
Verbena officinalis	Verbenaceae		1	0	0	0
Verbena rigida	Verbenaceae	1b	1	0	0	0
Verbesina encelioides	Asteraceae		0	0	0	1
Viburnum odoratissimum	Viburnaceae		0	0	0	1
Viburnum tinus	Viburnaceae		0	0	0	1
Vicia sp.	Fabaceae		0	0	0	1
Vinca major	Apocynaceae	1b	1	0	0	1
Vitis sp.	Vitaceae		1	0	0	1
Washingtonia robusta	Arecaceae		0	0	0	1
Westrigia sp.	Lamiaceae		0	0	0	1
Westringia fruticosa	Lamiaceae		0	0	0	1
Wigandia caracasana	Hydrophyllaceae		1	0	0	0
Wigandia urens	Hydrophyllaceae	3	1	0	0	1
Wisteria floribunda	Fabaceae		0	0	0	1
Xanthium spinosum	Asteraceae	1b	1	0	0	0
Xanthium strumarium	Asteraceae	1b	1	1	1	1
Yucca sp.	Asparagaceae		0	0	0	1