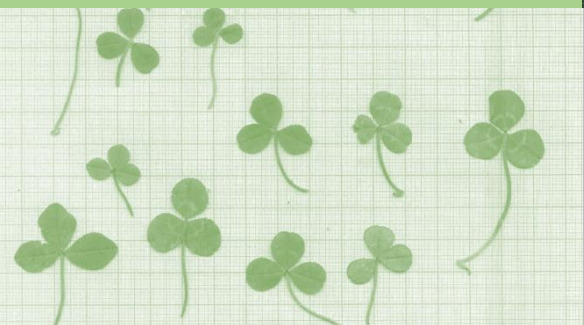




Fine-scale effects of anthropogenic and environmental factors on diversity patterns of spontaneous vascular plants in a medium-sized city in South America (Chile)



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Fine-scale effects of anthropogenic and environmental
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in a medium-sized city in South America (Chile)

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Summary

Urban ecosystems are major hotspots of global biodiversity, the main location of our daily activities and the place in which more than a half of the human population live. However, urban areas are among the most extremely transformed landscapes. They are composed of a heterogeneous matrix of man-made land-use types such as commercial, residential, and green areas, providing a variety of habitat types for urban flora and fauna that lives in them. Despite having been ignored in ecological studies for many years, in the last two decades, a large number of studies have addressed the effects of urbanisation on biodiversity, focusing on species richness and abundance, particularly of plant and bird species. Up to now, general trends of urban plant species around the world show an increase in the introduction of exotic species, a decrease of native habitat specialists, and the emergence of novel species assemblages combining natives and exotics. For plant species richness, several studies have shown strong positive links between the socioeconomic context of urbanisation, habitat types and the diversity of urban green areas. However, research on the effect of urbanisation in other components of plant diversity, such as functional and phylogenetic diversity, remains scarce. In cities, humans modify the environmental conditions in such a way that leads to plant compositional changes, and research in functional diversity could help to understand and predict the consequences of this biotic change. The functional traits research approach has advantages over pure taxonomic approaches as it provides the possibility to make generalisations across sites and communities with no geographical or taxonomical link, and their application provides a tool to link organisms' strategies and ecosystem functioning and ecosystem services. However, compared to species richness, few studies have tried to disentangle the effects of urbanisation on functional diversity in urban areas.

To date, most of the studies about the effects of urbanisation on biodiversity (compositional, functional and phylogenetic) have been carried out in developed countries of the Northern hemisphere, and little has been done in this respect in Latin America, the developing region in the world with the highest degree of urbanisation. Latin American countries host several global hotspots of biodiversity and more than 80% of their population live in urban areas. Furthermore, it is expected that in Latin America the urban population and urban areas will increase in the coming years, especially in small and medium-sized cities, with downstream effects on natural ecosystems and biodiversity. In this context, this thesis aims to study patterns of taxonomical and functional diversity of spontaneous vascular plants that grow in lawns of public green areas of Valdivia, a medium-sized city located in a world hotspot of biodiversity in North Patagonia, Chile. This research is the result of an extensive sampling at the scale of the neighbourhood over 3 years, identifying and measuring all the spontaneous vascular species present in public lawns using 120 plots of 20m². The objective of this work was to contribute to the growing body of knowledge about urban ecology patterns, filling the lack of information that actually exists on the South American continent, assessing the role of factors of anthropogenic and environmental nature as drivers for taxonomic and functional diversity. Moreover, here I develop the first quantitative functional diversity work on the topic of urban floras in Latin America, based on the multivariate analysis of specific anthropogenic and environmental factors to disentangle their role in the patterns of species richness and functional diversity.

In chapter 2 I showed that a medium city in Latin America harbour mainly exotic species plant species (>80%), far surpassing the proportion of exotic species that have been described for cities of the temperate Northern hemisphere

(~20%). Also, I showed how this pattern is not random, as it has a strong positive association with the socioeconomic status of the neighbourhood and the habitat type in which plants grow, linking human factors as drivers of spontaneous species richness beyond the effect of the environment, as reported in other cities worldwide. In addition, Chapter 3 is, according to my extensive literature revision, the first work in Latin America that analyse quantitative traits (plant height, leaf dry matter content-LDMC, and specific leaf area-SLA) in the context of urban areas and give insight on the drivers of species composition of wild plant communities in lawns of residential areas. In general, I found that at the city level trait values showed lower values for functional dissimilarity (FD_Q) over different socioeconomic status (SES). In particular, plant functional strategies for persistence shift differentially, with different anthropogenic (SES, habitat type, percent of exotic species) and an environmental (Nitrogen) mix of drivers modulating the variation in trait values. Thus, the concentration of Nitrogen in the soil and to a minor extent by habitat type drove SLA higher values promoting fast growth and resource use (i.e. acquisitive strategy), whereas SES positively modulate LDMC values promoting a slow growth and higher leaf density (i.e. a conservative strategy), and a complex mix of environmental and anthropogenic factors drives the variation in plant height.

Summing up, the results of this thesis highlight the relevance of anthropogenic factors as habitat type and SES as drivers of species richness and variation in resource-use traits at the fine-scale of the neighbourhood. Additionally, my results suggest the high relevance of bottom-up processes from householders to the top stakeholders, in shaping positively the diversity in urban areas given the relevance of SES as a driving factor of change in species richness and traits. This means that the socioeconomic status of neighbourhoods and the characteristics associated with it (level of education, gardening practices, etc.) influence strongly the way in which the diversity of urban areas is composed, summing up their characteristics at the level of the city.

In this context, the expected human population growth in Latin America sets a priority for more studies about biodiversity in urban areas. As cities are centres for plant species introductions, the knowledge and understanding of the taxonomic and functional urban diversity patterns have high relevance to monitor and protect the diversity of native species in hot-spot areas. Moreover, these areas could serve as a natural classroom to help the people to connect with the native resources and profit from the benefits and services that green areas provide. Hence, overcoming social inequity might be a specific conservation strategy to promote urban biodiversity in Latin American cities.

Resumen

Los ecosistemas urbanos son hotspots globales de biodiversidad, el principal lugar de nuestras actividades diarias, y el lugar donde actualmente vive la mitad de la población humana mundial. Lamentablemente, las áreas urbanas se encuentran dentro de los paisajes con transformación más extrema. Éstas, están compuestas por una matriz heterogénea de tipos de uso del suelo de origen antrópico y semi-antrópico, mezclándose por ejemplo áreas de uso comercial, residencial y áreas verdes, lo que provee una gran variedad de tipos de hábitats para la flora y fauna urbana. La ecología, ha ignorado a lo largo de muchos años las áreas urbanas, sin embargo, en las últimas dos décadas un gran número de estudios han considerado los efectos de la urbanización en la biodiversidad, enfocándose principalmente en la riqueza de especies y su abundancia, particularmente de especies de plantas y aves. Hasta el momento, los patrones generales de especies de plantas urbanas alrededor del mundo, muestran un incremento en la introducción de especies exóticas, una disminución de especies nativas especialistas en cuanto a hábitat, y la emergencia de ensamblajes de especies noveles que combinan especies nativas y exóticas. A nivel de riqueza de especies, diversos estudios han mostrado fuertes relaciones positivas entre el contexto socio-económico de la urbanización, los tipos de hábitat y la diversidad de especies en áreas verdes urbanas. Sin embargo, la investigación sobre el efecto de la urbanización en otros componentes de la diversidad de plantas, como la diversidad funcional y filogenética, sigue siendo escasa. En las ciudades, los seres humanos modifican las condiciones ambientales de tal manera que éstas conducen a cambios en la composición vegetal, en este contexto, la investigación en diversidad funcional podría ayudar a entender y predecir las consecuencias de este cambio biótico. El enfoque de la investigación de rasgos funcionales tiene ventajas sobre los enfoques taxonómicos puros, ya que proporciona la posibilidad de hacer generalizaciones a través de sitios y comunidades sin vínculo geográfico o taxonómico y su aplicación proporciona una herramienta para vincular las estrategias de los organismos y el funcionamiento de los ecosistemas y los servicios ecosistémicos. Sin embargo, en comparación con la riqueza de especies, pocos estudios han intentado desentrañar los efectos de la urbanización sobre la diversidad funcional en áreas urbanas.

Hasta la fecha, la mayor parte de la investigación sobre los efectos de la urbanización en la biodiversidad (composición, funcionalidad y filogenia) se han llevado a cabo en los países desarrollados del hemisferio norte y poco se ha hecho en este sentido en América Latina, zona del mundo con el grado más alto de urbanización. Esto es lamentable, ya que los países latinoamericanos albergan varios hotspots globales de biodiversidad y más del 80% de su población vive en áreas urbanas. Además, se espera que en América Latina la población urbana y áreas urbanas en general, aumenten en los próximos años, especialmente en las ciudades pequeñas y medianas, con un consiguiente efecto sobre los ecosistemas naturales y la biodiversidad. En este contexto, esta tesis doctoral pretende estudiar patrones de diversidad taxonómica y funcional de plantas vasculares espontáneas que crecen en céspedes de áreas verdes públicas de Valdivia, una ciudad de tamaño mediano ubicada en un hotspot mundial de biodiversidad en la Patagonia Norte, Chile. Esta investigación es el resultado de un extenso muestreo a escala de vecindario a lo largo de tres años, identificando y midiendo todas las especies vasculares espontáneas presentes en el césped público de la ciudad utilizando 120 parcelas de 20m². El objetivo de este trabajo fue contribuir al creciente conocimiento de los patrones de ecología urbana, cubriendo la falta de información existente en el continente sudamericano, evaluando el papel de los factores de naturaleza antropogénica y ambiental como causales de cambio en diversidad taxonómica y funcional. Además, desarrollo el primer trabajo de

diversidad funcional cuantitativa sobre floras urbanas en América Latina, basado en el análisis multivariado de factores antropogénicos y ambientales específicos para desentrañar su papel en los patrones de riqueza de especies y diversidad funcional.

En el capítulo 2 se muestra que una ciudad mediana en América Latina (Valdivia, Chile) alberga principalmente especies vegetales exóticas (> 80%), superando ampliamente la proporción de especies exóticas que se han descrito para las ciudades del hemisferio norte templado (~ 20%). Además, se muestra cómo este patrón no es aleatorio, ya que tiene una fuerte asociación positiva con el nivel socioeconómico del vecindario y el tipo de hábitat en el que crecen las plantas, vinculando factores humanos como causales de cambio en la riqueza espontánea de especies más allá del efecto del medio ambiente, lo que concuerda con lo señalado en otras ciudades del mundo. Además, según la extensiva revisión bibliográfica realizada, el capítulo 3 es el primer trabajo en América Latina que analiza los rasgos cuantitativos (altura de la planta, contenido de materia seca de la hoja-LDMC y área específica de la hoja-SLA) en el contexto de las áreas urbanas y da una visión de las causales de cambio de composición de especies dentro de comunidades de plantas silvestres en céspedes de áreas residenciales. En general, a nivel de la ciudad, los valores de rasgos funcionales en disimilitud funcional (FD_Q) fueron bajos en los diferentes estatus socioeconómicos (SES). En particular, las estrategias funcionales de persistencia cambiaron diferenciadamente, con una mezcla de factores antropogénicos (SES, tipo del hábitat, porcentaje de especies exóticas) y un factor medioambiental (nitrógeno) que causaban la variación en los rasgos. Por lo tanto, la concentración de Nitrógeno en el suelo y en menor medida el tipo de hábitat causaron valores más altos de SLA, promoviendo un crecimiento rápido y el uso de recursos (estrategia adquisitiva), mientras que el estado socioeconómico moduló positivamente los valores de LDMC promoviendo un crecimiento lento y una mayor densidad foliar (estrategia conservadora). Aparte, una mezcla compleja de factores medioambientales y antropogénicos impulsó la variación en altura de la planta.

En resumen, los resultados de esta tesis destacan la relevancia de los factores antropogénicos como tipo de hábitat y estatus socioeconómico como causales de variación de la riqueza de especies y los rasgos de uso de recursos a pequeña escala (vecindario). Además, mis resultados sugieren la alta relevancia de procesos “bottom-up”, desde los hogares a las principales partes interesadas, al influir positivamente en la diversidad de las áreas urbanas dada la relevancia del estatus socioeconómico como factor impulsor del cambio en la riqueza y rasgos de las especies. Esto significa que el nivel socioeconómico de los vecindarios y las características asociadas a éstos (nivel de educación, prácticas de jardinería, etc.) influyen fuertemente en la forma en que se compone la diversidad de las áreas urbanas, sumando sus características a escala de ciudad.

En este contexto, al considerar el crecimiento esperado para la población humana en América Latina, urge priorizar más estudios sobre la biodiversidad dentro de áreas urbanas. Como las ciudades son centros para la introducción de especies vegetales, el conocimiento y la comprensión de los patrones taxonómicos y funcionales de diversidad urbana tienen gran relevancia para poder monitorear y proteger la diversidad de especies nativas en hotspots de alto valor ecológico. Por otra parte, estas áreas podrían servir como un aula natural para ayudar a la gente a conectarse con los recursos nativos y beneficiarse de los beneficios y servicios que proporcionan las áreas verdes. Por lo tanto, en ciudades latinoamericanas, superar la desigualdad social podría ser una estrategia específica de conservación para promover la biodiversidad urbana.

Chapter One

General introduction



A fundamental challenge in ecology is to understand what causes the variation in species diversity in a given area. In the case of urban areas, a common but relatively recent ecosystem, in the last 20 years, several advances have been made to disentangle the factors that cause variation in the diversity of flora and fauna in them. However, there are still gaps in the worldwide information available that prevent the generalisation of patterns and drivers in urban biodiversity, as it is in the case of plant diversity. The main purpose of the present doctoral thesis entitled “*Fine-scale effects of anthropogenic and environmental factors on diversity patterns of spontaneous vascular plants in a medium-sized city in South America (Chile)*”, is to contribute to the little known impacts of urbanization on the biodiversity of vascular plants in Latin-American cities, considering their particularities in a biogeographical, climatic (variety of climate zones, from tropical to temperate), and historical context (colonization history and trade). Specifically, I focus on patterns of species richness and functional diversity composition of an intermediate city in Southern of South America, an understudied area with respect to urban biodiversity studies.

1. A new human era and non-analogous ecosystems

For the last two decades, and because of the strong influence of human activities on the global environment and Earth system, the idea of a new century called Anthropocene has become prominent. Although some controversy is held around the beginning of this new era (Hamilton, 2015), it is recognised that anthropogenic effects will continue, given a steady increase of human population with up to 10 billion inhabitants towards 2050 (UN-DESA, 2015). The Anthropocene is characterised by a great magnitude and long-term effects of a series of changes produced by humans (Lewis and Maslin, 2015). Anthropogenic effects on the environment are the land-use change of more than 50% of the earth surface to sustain human population, strong changes in the biogeochemical cycles of Nitrogen, Carbon, and Phosphorous, climate change, overharvesting and the global exchange and invasion to new geographic areas by non-native species (van Kleunen et al., 2015). These effects alter the biodiversity at different scales, from local to global (McGill et al., 2015), and summed up, these new global conditions had produced new interactions of biotic and abiotic components, i.e. *novel*

ecosystems. Morse et al. (2014) define novel ecosystems as a system originated by unintentional or intentional human influence, with a significantly altered and unique species composition, that can sustain itself and can not return to its previous ecosystem state without human agency because of the crossing of ecological thresholds that inhibit it. Thus, new or “novel” (non-analogous) ecosystems are different from degraded ecosystems because they are totally different from the previously existent ecosystem, are new in an ecological and evolutionary context (Jeschke et al., 2013) and affect the diversity of organisms via totally new assemblies of species and changes in species relative abundances.

2. Urban areas as novel ecosystems

In general, cities are characterised by two features: major human-induced changes in the abiotic environment and significant and irreversible changes in the species pool (local extinctions and species introduction), with potential changes in ecosystem functioning (Kowarik, 2011). Given the extreme nature of these changes, the environment changes irreversibly and leads to the generation of novel ecosystems that are considered as small-scale areas of global change (Grimm et al., 2008). Moreover, in cities several of the drivers identified as the causes of biodiversity loss concentrate, that is, habitat loss and the introduction of alien species due to land use change, and ecosystem alteration and creation (Vitousek, 1997). In cities, biotic and abiotic characteristics are influenced by anthropogenic factors, affecting their environmental conditions (Sukopp, 2004). Some abiotic characteristics of urban systems are the increased amount of impervious surfaces; changes in soil moisture (drier in temperate areas and humid in desert areas due to irrigation); nutrient rich soils; heat island effects (temperature increase over the centre of the city); changes in disturbance regimes; soils, water and air pollution; among others (Williams et al., 2009; Pickett and Cadenasso, 2009; Kowarik, 2011). General biotic attributes in urban areas can be the overall increase in species richness; intentional and unintentional species introduction and loss of native species (Klotz and Kühn, 2010); concentration of alien species in the inner part of the city (Wittig et al., 1985); higher proportion of habitat generalist species; increase in food availability for animals and an increase in landscape fragmentation (McDonald et al., 2013; Müller et al., 2013). Urban areas are composed of a heterogeneous matrix of man-made land-use types like commercial, residential, etc., and semi-natural land-use types like gardens, parks and vacant lots, providing several habitat types for the urban assemblies of flora and fauna.

On the whole, the effects of urbanisation go beyond the city level to even a regional scale (Grimm et al., 2008), because of the demand of resources and the pressure that cities exert on surrounding areas for the provision of resources for human consumption, driving habitat loss and fragmentation (Gaston, 2010).

3. The importance urban ecology

Urban ecology is the branch of ecology that studies the processes determining the abundance and distribution of organisms, the interaction between organisms and environmental conditions and the flows energy and biogeochemical elements through urban systems (Gaston, 2010). Under this frame, this thesis focused on the ecological aspects of urban areas rather than the urban planning and social aspects of cities, although it recognises urban ecosystems as socio-ecological systems (Weiland and Richter, 2009).

Studies of species in urban areas date back in time to the 16th century with the first descriptions of plants related to human settlements (Sukopp, 2008). However, urban ecology became an interesting topic of study mainly during the 1970's, after an increasing valuation of nature in Europe (especially in the time post-Second WW) and the USA (Weiland and Richter, 2009). Later, the studies of urban ecology have risen as other effects of cities became evident, like the global increase of human-dominated areas and the subsequent increase in fragmentation and habitat loss, the concentration of human population in cities and the health issues that a higher population density involves (diseases as result of pollution, stressing conditions of life, etc.), as well as the spatial coincidence of cities with naturally species-rich areas (Cressey, 2015). In fact, in 2007, and for the first time in history, most of the world population (>50%) lived in urban areas. As urbanisation increases around the world, the knowledge of the conditions of the urban environment is becoming more relevant (Gaston, 2010). Until now, most urban ecology studies deal with urban areas of the northern hemisphere, specifically from Europe and the USA (Kowarik, 2011; Magle et al., 2012). Paradoxically, most of the megacities (≥ 10 million inhabitants) and large cities (5-10 million inhabitants) are located in areas outside Europe and the USA (UN-DESA, 2014). For instance, Latin America is the second most urbanised region of the world with almost 80% of the population living in cities (UN-DESA, 2014). This area also hosts several hotspots of biodiversity (Figure 1) (i.e. areas with a high proportion of endemism, a high rate of habitat loss and with more than 1500 vascular plant species (Myers et al., 2000). Therefore, research on how

urbanisation may affect those highly biodiverse areas is extremely necessary (Müller et al., 2013). Given the deeply changes that urbanisation process poses on the landscape, most of the studies have focused on the negative impacts that urban areas produce, like species loss and homogenization (McKinney, 2006; McKinney, 2008). However, the ecological relevance of urban green areas is expected to increase, especially because they provide valuable habitats for many plant and animal species (Aronson et al., 2014). Green areas also provide a high variety of ecosystem services and cultural services to the inhabitants such as air filtration, climate regulation, rainwater drainage and flood regulation, water provision, human well-being and health (recreational opportunities, perception of quality of life, decrease in stress and reduction in levels of violence) (Bolund and Hunhammar, 1999, Barton and Pretty, 2010, Gaston et al., 2013). In this context, studying the ecological patterns that define urban diversity and the factors that drive them should be a priority of ecological research, in order to obtain a mechanistic understanding of how patterns of biodiversity are formed in cities.



Figure 1: Biodiversity hotspots from Latin America. Source: United Nations Environment Programme. <http://www.pnuma.org/geo/geoalc3/ing/graficosEn.php>

4. Biodiversity in urban areas

Biodiversity is a multidimensional concept that can be decomposed in three dimensions: taxonomic, functional, and phylogenetic diversity (Naeem et al., 2012, Figure 2). Taxonomic diversity is the number and relative abundance of taxa, from species to genera. Functional diversity is referred as the variation in the range of single traits (i.e. features of species) differences as well as the composition of several traits among species in a given community (Petchey and Gaston, 2002). Phylogenetic diversity addresses the diversity of evolutionary relationships among species based on elapsed time since divergence (Naeem et al., 2012). Each of these dimensions provides insights about the diversity of a community, which can be complemented with temporal and spatial dimensions (McGill et al., 2015)

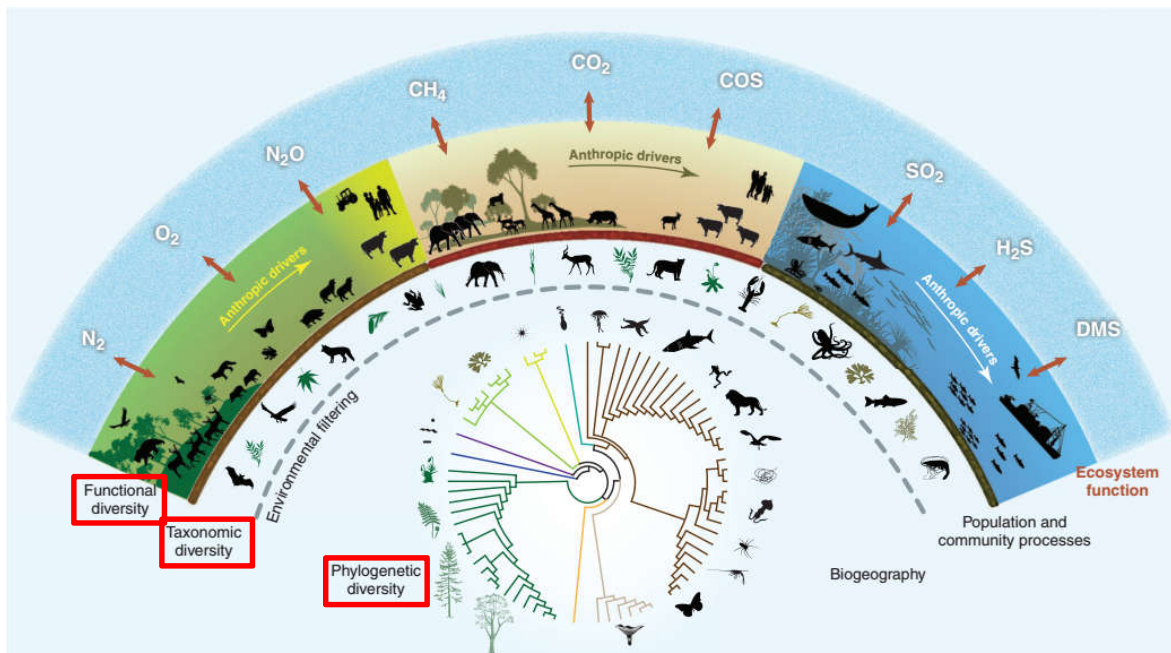


Figure 2: Dimensions of biodiversity. Three levels of diversity are shown (labels on the left side), from Phylogenetic diversity (centre), Taxonomic diversity (middle, after dashed lines), and Functional diversity (gradient of the biota showed in arches) in a given ecosystem affected by anthropogenic drivers. Outermost arch shows the ecosystem functioning as biogeochemical interchanges. From Naeem et al. (2012).

As novel ecosystems, cities provide specific environmental constraints (altered hydric regimes, temperature, etc.), but also artificial constraints (like habitat transformation and fragmentation, species introduction, disturbance regimes, etc.) that finally determine the urban flora. Considering the novel

characteristic of cities, Williams et al. (2009) explain the assembly and development of urban floras suggesting a schematic model of four filters: i) *habitat transformation* from natural or agricultural areas to towns and cities with new environmental characteristics; ii) *habitat fragmentation* creating smaller and isolated areas that lead to eradication of some species while others colonize the new spaces; iii) *environmental changes* leading to an urban environment (increase of temperature in the inner city centre, high loads of Nitrogen, etc.); and iv) *human selection of species* via the introduction of ornamental species and eradication of weeds. These four filters may act simultaneously and are temporally dynamic (i.e. they may occur once and again during city developing process), and include species losses and gains up to the set of species that will persist in the city (Figure 3).

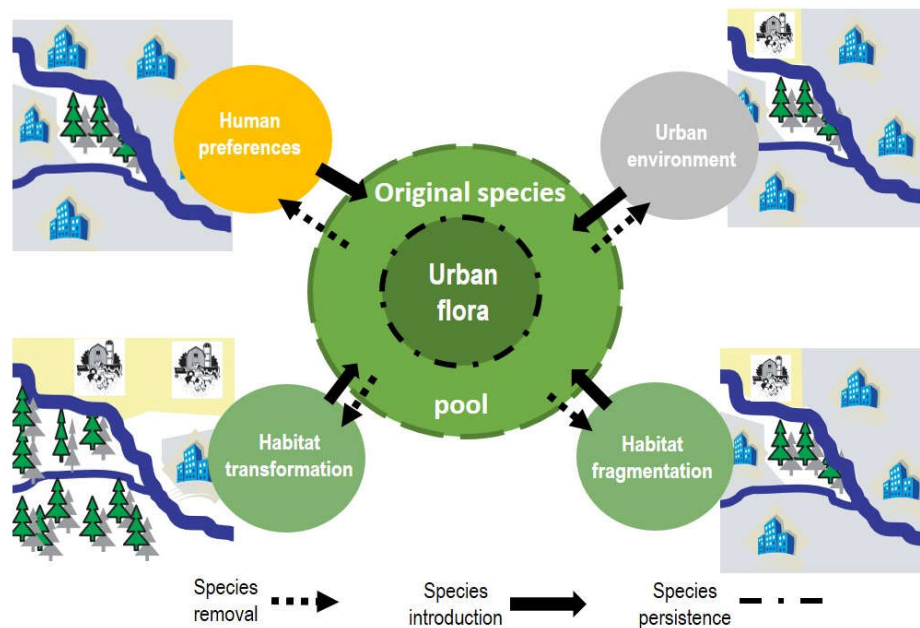


Figure 3: Proposed scheme for the assembly of urban plant communities during urbanisation processes at the city scale. Intentional or unintentional species gains (introduction of species) and losses (species removal) occur as an effect of the four components on the original species pool. These components are dynamically happening in different places and times across the city. These components will select those species capable of coping with the new urban environmental conditions (after habitat and environmental changes) and those selected by humans, setting the urban flora as a subset of original species pool and the new species introduced. Modified from Williams et al. (2009).

Some studies have highlighted the role of human selection as a filter in the composition of urban floras (Hope et al., 2003; Martin et al., 2004; Escobedo et al., 2006; Gavier-Pizarro et al., 2010). Kinzig et al. (2005) proposed the role of cultural characteristics in shaping the urban floras through combined bottom-up and top-down processes. In this framework, bottom-up processes influence the small-scale

of nature in cities at the neighbourhood level. Individual or family behaviour shapes the diversity in gardens, and areas close to houses. Top-down processes are related to the stakeholders' and local government strategies that affect the biodiversity in public spaces via policies and practices (like mowing regime in public areas, regulations about the size and functions of green areas, etc.). Both approaches can be intentional or unintentional. The occurrence or existence of each type of process can be assessed by studying the variation in some ecological patterns and processes: On one hand, if the dominant influences are bottom-up processes then ecological patterns and processes will vary significantly with social and cultural gradients. On the other hand, if top-down processes are dominant, then we will find a weak variation of ecological patterns and processes with socioeconomic and cultural gradients, because of the predominance of the landscape and management strategies at the city level (Kinzig et al., 2005). Finally, it is the mix between ecological and human-mediated processes that determines the species assembly and diversity patterns found in urban areas (Hope et al., 2003; Martin et al., 2004; Knapp et al., 2012).

4.1 Species diversity in urban areas

From the facets of biodiversity, species diversity (taxonomic diversity) is the best-studied one in urban ecology research (Luck and Smallbone, 2010; Fischer et al., 2012). Species richness is a useful assessment of the variety of species that are supported by a certain area because it is direct and intuitive. However, comparisons between geographical areas are difficult due to for example the (sample) size of different studies. Quite some research explored patterns mainly in plant species and birds, and a variety of scales from local (from neighbourhoods to city level), to regional (climatic bioregion), and global (continents, the world) (Aronson et al., 2014).

For plant species, general trends of those studies in urban green areas show an increase in exotic and native species compared with surrounding landscape (Kühn et al., 2004), habitat generalists and long distant dispersers, and a decrease in native species and habitat specialists with short-distance dispersers (Müller et al., 2013). Other authors show a higher species richness in moderate levels of urbanisation (McKinney, 2002). Despite the local and regional increase in species richness (Araújo, 2003; Kühn et al., 2004; Wania et al., 2006), there is evidence of a global decrease of species due to a global homogenization of these environments (McKinney, 2006). At the regional scale, species loss is overcome by species introduction, with a positive balance towards the gain of species (Wania et al.,

2006), and at local scale species richness may increase but there is a decrease in native species due to species loss (Shea, 2002). This pattern changes drastically when observing the global diversity of plant species, because urban areas may share species independent of their geographical range, accounting for the homogenization of urban floras. Cities across the globe are located in different climatic zones, with different socioeconomic realities, different land-planning processes, but despite all these differences, environments select for those species with specific traits or characteristics that help them to survive in the urban environment. Since urban conditions tend to be similar worldwide, the species selected are similar, and therefore cities around the world show a similar composition of plant species (McKinney, 2006; Aronson et al., 2014). Thus, the scale at which the analysis is performed is crucial to understand the effects of urban areas on biodiversity and to draw correct conclusions about patterns and processes. In the urban context, we can define regional (climatic bioregion), city (urban settlement) and local (neighbourhood, street or plot) scales. Each one will present hierarchical filters that contribute to the assembly of urban floras and that influence differently the patterns observed (Aronson et al., 2016). At the regional level, the potential flora sets the species pool for the city, which will be affected by the species introduced by the global exchange of species facilitated by humans (mainly trade activities and historic movement of species at the colonisation of the Americas). In a lower level, cities will be affected by their history of establishment (age of the city, the legacy of the previous land uses), socioeconomic and cultural characteristics (density of the neighbourhoods, classification as developed, developing etc.). Finally, the local scale is set by the species biotic interactions mediated by their traits (competition, mutualism, etc.) and local scale habitat characteristics. Till now, there is a need for quantitative assessment of the fine-scale patterns of community assemblies, which are still scarcely known (Aronson et al., 2016).

4.2 Functional diversity in urban areas

Functional traits are morpho-physio-phenological traits which impact fitness indirectly via their effects on growth, reproduction and survival, the three components of individual performance (Violle et al., 2007). According to this definition, traits can be categorised as morphological, physiological, behavioural or phenological, and are measured at the level of the individual (Cadotte et al., 2011; Pérez-Harguindeguy et al., 2013) (Table 1). Those features can be at different levels, from the cell to the organism. They can be categorical (e.g. growth form, pollination mode), or numerical (e.g. leaf area,

height, seed size). Functional diversity emphasises the phenotypic differences among taxa because it represents the range of functional trait differences among species (Violle et al., 2007). Therefore, a community is functionally richer if it has a larger variety of trait states and/or traits. Moreover, functional diversity is independent of taxonomic identity and generally from phylogenetic relatedness, allowing comparisons among different species and geographical areas (Weiher, 2010; Williams et al., 2015). Environmental factors constrain which individuals bearing specific traits values are able to be sorted out and persist in a community (Keddy, 1992). In the urban context, environmental conditions change towards a dryer and fragmented, plant traits shift in frequency and identity (Díaz and Cabido, 1997). Moreover, due to common characteristics of the urban environment, functional homogenization may be an outcome from urbanisation. Studying the variation of plant traits due to urbanisation may help to understand the effects of urbanisation on ecosystem functioning because functional traits allow the link between the strategies that organism have to persist and thrive and the functioning of the ecosystem (Loreau et al., 2001).

Table 1: Categories of plant traits and some examples of traits for each category. Data from Knapp et al. (2008); Cadotte et al. (2011); Pérez-Harguindeguy et al. (2013).

<i>Trait category</i>	<i>Physical</i>	<i>Physiological</i>	<i>Phenological</i>
<i>Trait examples</i>	Plant branching architecture	Plant photosynthetic pathway	Flowering time
	Leaf anatomy	Presence of secondary metabolites	Leaf life span
	Life form	Leaf Nitrogen concentration	
	Plant height	Leaf water potential	
	Specific leaf area (SLA)		
	Leaf dry matter content (LDMC)		
	Root morphology		

Thus far, most urban functional trait studies have focused on categorical traits in urban-rural gradient (Lososová et al., 2006; Knapp et al., 2008; Williams et al., 2015). General results of these studies showed a trend of plants species that are wind-pollinated, blooms in mid-summer, are vegetatively reproduced, and wind or human dispersed. However, these trends are from city to country scale and there is a lack of information at the fine-scale (Aronson et al., 2016).

5. Urban areas in temperate ecosystems in South America

Chile, in the South-West of South America, hosts the temperate evergreen “winter rainfall-Valdivian forests” world biodiversity hotspot (Figure 1), in the south part of the country. This hotspot is relevant in the context of its biogeographic isolation to other areas with similar flora and fauna in the world. Moreover, it holds high levels of endemism in South America (Scherson et al., 2014) and high mutualism with more than 50% of the plant species in temperate forests in Chile need a specific biotic pollinator or seed disperser (many species of the flora depending on few animals) (Aizen et al., 2002; Smith-Ramírez et al., 2005), a level comparable to the mutualism relations founded in tropical forest (Rodríguez-Cabal et al., 2008). These unique characteristics set the priority for conservation of this hotspot, and highlight the relevance of conservation strategies which, in this case, depends upon a single government policy (Scherson et al., 2014). Given the role that cities play in the species introduction (Klotz and Kühn, 2010), the conservation strategies should be extended to the cities within this biodiversity hotspot, as is the case of the city of Valdivia (39°48'30"S, 73°14'30"O). Thus, understanding the patterns of diversity in the cities is relevant to the hotspot conservation. For example, to develop strategies to manage green areas in the city because they provide habitat for pollinators and seed dispersers that are essential for ecosystems functioning, and could be habitat islands for biodiversity within a matrix of a progressively more homogenous landscape under anthropic pressure. Rapid changes related to habitat loss and fragmentation due to anthropogenic pressure is a significant problem in this territory. From the total area of temperate forest in both, Chile and Argentina, more than 90% of the area of greatest value for conservation is unprotected (Rodríguez-Cabal et al., 2008) and annually more than 120,000ha of this forest type are degraded or destroyed (Lara et al., 1996). The economic growth that Chile experienced over the last three decades promoted the migration of rural population to cities. With almost 90% of the population living in urban areas (INE, 2005), the rapid and unplanned development of urban centres exerts new pressures over natural and semi-natural landscapes. However, the potential effects of this rapid urban growth remain unknown (Cursach and Rau, 2008). Thus far, in Chile few studies addressed the diversity of urban areas. These studies focused specifically on phytosociological description of plant species (Oberdorfer, 1960; Gunckel, 1963; Finot and Ramírez, 1996; Hoffmann, 1998; De la Maza et al., 2002; Rozzi et al., 2003; Pauchard et al., 2006; Escobedo et al., 2006; Finot and Ramírez, 2010), species richness (Ardiles and Peñaloza, 2013 for bryophytes; Díaz and Armesto, 2003; Kramer-Hepp and Gómez-Unjidos, 2012; Cursach and Rau, 2008; Silva et al., 2015 for birds), or landscape characteristics, such as urban form and

connectivity between green areas (Romero and Vásquez, 2005; Reyes-Päcke and Figueroa-Aldunce, 2010; Banzhaf et al., 2013; Krellenberg et al., 2014). Also, most of these studies are based on Santiago de Chile, a megacity (> 6 millions of inhabitants) located in central Chile, and information based on small or mid-sized cities in other biogeographical areas of the country are scarce or even inexistent, although they should growth the most in size and population in the coming years (Pauchard and Barbosa, 2013). Also, there are gaps in information in the abundance of species in a given area, and on the range of traits values that the species present in the area can have. With this information, we can evaluate with greater power changes in diversity given a gradient of predictors, either environmental ones or anthropogenic ones, and derive a mechanism to explain present patterns of the distribution of species.

6. General and specific objectives

To date, several studies have shown strong links between the socio-economic context of urbanisation, habitat types and the diversity of urban green areas. Around the world, lawns (i.e. cultivated, mown ornamental grasslands) are a dominant land cover class in green areas (Ignatieva and Stewart, 2009). They are ubiquitous in private gardens, private and public parks, and road verges, and therefore they are the closest vegetation type for people in their everyday life (Weber et al., 2014). The variety of geographical and habitat conditions in which lawns grow make them an interesting and relevant place to study the human effect on urban plant communities. On the other hand, in urban areas of the Northern hemisphere, Australia and New Zealand, household income has been linked with plant species diversity with a positive relationship between human wealth and species richness (e.g. Hope et al., 2003, Luck and Smallbone, 2010). Therefore, this thesis aims to study patterns of taxonomical and functional diversity of vascular plants in lawns of public green areas of Valdivia, a medium-sized city located in a world hotspot of biodiversity in North Patagonia, Chile (Dinerstein et al., 1995; Olson and Dinerstein, 2002).

I will compare the findings of this thesis with the expected floristic changes predicted by Williams et al. (2009) (table 2), to summarise the results and compare them in a broad context.

Table 2: Predictions of changes in floristic composition and functional traits associated with four urbanisation filters proposed by Williams et al. (2009). *Italics letters show the expected dominant response to each filter. Modified from Williams et al. (2009).*

Filtre	Floristic composition	Functional traits
<i>1. Habitat transformation</i>		
Habitat loss	<i>Loss</i>	<i>Narrowing</i>
Novel habitat creation	Gain	Broaden
<i>2. Fragmentation</i>		
Extirpation	<i>Loss</i>	<i>Narrowing</i>
Invasion	Gain	Narrowing
<i>3. Urban environment</i>		
Stressor on natural habitat	<i>Loss</i>	<i>Narrowing</i>
Novel urban habitat	Gain	Shift
<i>4. Human preferences</i>		
Introductions	<i>Gain</i>	<i>Shift</i>
Eradications	Loss	Narrowing

Against this background, this doctoral thesis specifically aims to:

- Describe taxonomic and functional diversity composition of spontaneous vascular plants communities growing in public lawn areas in an intermediate city of Latin-America.
- Determine the influence at fine-scale of anthropogenic factors on the shaping of vascular plant composition in both facets of diversity.
- Compare patterns of taxonomic and functional diversity found in a city in South America with other areas of the world.

Accordingly, in **chapter 2**, entitled “*Socio-economic status drives wild plant diversity in urban public green areas of a South American city (Valdivia, Chile)*”, this doctoral thesis focuses on taxonomical diversity using an approach that combines human-mediated (anthropogenic) factors and environmental characteristics, in order to answer: a) What is the origin of species in urban lawns of Valdivia and from which families are they? b) Which differences exist in plant species richness and plant evenness among different lawn habitat types and socioeconomic status?, and c) are there other anthropogenic (*i.e.* disturbance by trampling), and environmental factors (C/N ratio), driving the diversity as species richness in the sampled communities? Considering the history of colonisation of Valdivia (over 460 years of European settlers), we expect that urban green areas have a high proportion of exotic species, mainly from Europe, and a high proportion of well-dispersed species (opportunistic species).

Based on the results of chapter 2, in **chapter 3**, entitled "*Multiple human-mediated factors drive plant functional strategies in a city in Southern South America*" I focus on the functional diversity of wild plant communities in lawns of residential areas, to test the effect of multiple predictors of anthropogenic factors (socioeconomic status, habitat type, disturbance, proportion of exotic species), and environmental nature (C/N ratio in soil). This included the proportion of exotic species as another predictor of the functional response, because exotic species may have a significant effect on resource availability affecting the persistence of plant species and changing the community assembly (Didham et al., 2005). I will answer the following questions: a) which are the characteristics of the functional diversity in terms of composition (community-weighted means, CWM) and structure (Rao's quadratic entropy, FD_Q). b) What are the anthropogenic and environmental factors driving functional diversity? I expect to find a poor functional diversity in the area expressed as a narrow set of CWM values and low FD_Q values because of the effect of different filters on the urban community.

Finally, **chapter 4** synthesises the previous chapters, discusses the main results, emphasises the links between them and compares the findings with other areas of the world. Lastly, it encompasses the findings of both chapters towards answering the general research question: how do humans change plant communities in urban areas. I discuss implications of the work in a global context and summed up a general conclusion.

Chapter Two

Socio-economic status drives wild plant diversity in urban public green areas of a South American city (Valdivia, Chile)

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Abstract

Urban areas provide different habitat types for urban flora and fauna. The effects of urbanisation on ecological systems cannot be isolated from the socio-economic context in which it is embedded. Little information exists on how different factors such as habitat types, socioeconomic status, and environmental characteristics affect species richness and composition in public urban green areas of the world, especially in Latin American countries and the Southern Hemisphere. In this study, we investigated patterns of plant diversity of public lawns in Valdivia, an intermediate sized city of Chile located within a global biodiversity hotspot. With a stratified random sampling design over neighbourhoods and habitat types of the city that included 120 plots of 20 m², each, we wanted to answer: a) What is the origin of species in urban lawns and from which families are they? b) Which differences exist in plant species richness and plant evenness among different socioeconomic status (SES) of the resident human population and habitat types (lawns in road verges, broad road verges, and squares)? And c) are there other anthropogenic and environmental factors driving the diversity as species richness in the sampled communities? Our results show communities strongly dominated by exotic species, with only 20% of native vascular plant species. This corroborates an opposite trend in the Southern Hemisphere compared to Northern Hemisphere. Habitat type and SES had significant effects on species richness, with higher values in narrow verges and richer SES. In contrast, we found low and uniform values of evenness across all lawn habitat types and SES. Disturbance by trampling was an additional factor negatively related with species richness, which shaped urban communities. In this context, the positive relation between species richness and SES could have a predictive value to locate areas of low or high diversity in cities knowing their SES. Our analyses promote the relevance of bottom-up processes in shaping the diversity in urban areas. The expected population growth in Latin America sets a priority for more studies about

general patterns of biodiversity in urban areas. Hence, overcoming social inequity might be a means to promote urban biodiversity and specific conservation strategies to promote native species should be taken.

Keywords

Anthropogenic filters, bottom-up processes, species richness, temperate ecosystems, urban ecosystems.

1. Introduction

Cities are among the most extremely transformed landscapes (McKinney, 2002). Nevertheless, despite being “novel ecosystems” (Hobbs et al., 2006), they can provide valuable habitats for many plant and animal species (Aronson et al., 2014). Still, the importance of cities in this respect has been largely overlooked (Perring et al. 2013). Urban areas are composed of a heterogeneous matrix of man-made land-use types such as commercial, residential, and green areas, among others, providing many different habitat types for the urban flora and fauna.

In cities, biotic (e.g. alien species, i.e. non-native) and abiotic (e.g. water supply, temperature and nutrients) conditions are largely influenced by human actions (Sukopp, 2004). The effects of urbanisation on ecological systems can thus not be isolated from the socio-cultural context in which it is embedded. Kowarik (2011) reviewed studies from urban areas in Europe and North America and listed drivers of biodiversity change such as habitat degradation, fragmentation or loss, as well as socioeconomic factors impacting biodiversity, such as income, ornamental trade, and management of urban green spaces. Kinzig et al. (2005) proposed a bottom-up, top-down strategy of anthropogenic effects to modulate the patterns of biodiversity for perennial plants and birds in cities. At the bottom-up level, neighbours and their particular socioeconomic and cultural characteristics will influence patterns of biodiversity with their individual decisions; at the top-down level, local government policies and practices will influence biodiversity at the scale of the city. In this context, management decisions and biodiversity selection could create unnatural conditions, such as land development or the introduction of exotic species favoured by humans (McKinney, 2002, 2008).

Previous studies have linked household income and plant species diversity patterns in urban areas of the Northern Hemisphere, Australia and New Zealand, and found a positive relationship between human wealth and species richness of plants and birds (e.g. Hope et al., 2003; Luck and

Smallbone, 2010; Stewart et al., 2009). Moreover, wealthy areas were shown to have a higher proportion of exotic species introduced for landscaping, as well as recently naturalised species in New Zealand (Oceania) and Burundi (Africa) (Sullivan et al., 2004; Bigirimana et al., 2012; respectively). Low-income areas may have a high proportion of exotic species due to the presence of vacant lots that represent suitable habitat for invasive species (Gulezian and Nyberg, 2010). Overall, all these studies show strong links between the socio-economic context of urbanisation and biodiversity. In addition, habitat types can also influence the diversity of urban green areas because the heterogeneous conditions that they hold may provide different habitat for the species in the city (Grimm et al., 2008). Around the world, and especially in Western-influenced countries, lawns of different shapes and sizes are frequent elements in green areas (Henderson et al., 1998; Ignatieva, 2010; Fraser et al., 2013; Runfola et al., 2013). Garden lawns of the UK are dominated by native plant species (Thompson et al., 2004), while those in New Zealand are dominated by exotic plant species (Ignatieva and Stewart, 2009), *i.e.* those native to Britain and Europe. Bertocini et al. (2012) found in Paris, France, a high native species richness in lawns privately managed (*i.e.* disturbed by mowing, and managed by fertilisation, etc.) with low public access, as well as in small public lawns. In comparison with species richness, species evenness has largely been overlooked in urban studies, although an increase in plant evenness relative to rural areas has been reported (Hope et al., 2003; Grimm et al., 2008; Walker et al., 2009). However, most of the urban studies relied on one factor to explain plant species patterns (Fischer et al., 2016), and little information exists on how a combination of factors may interact and affect the patterns observed in plants diversity. Factors such as habitat types, socioeconomic status, and environmental characteristics affect species richness and composition in public urban green areas of the world and their interaction may lead the patterns found worldwide.

To date, most of the studies have been carried out in developed countries of the northern hemisphere, and little has been done in this respect in Latin America (Aronson et al., 2014; La Sorte et al., 2014; but see Pauchard et al., 2006; Fischer et al., 2016; Silva et al., 2015). Latin American countries host several global hotspots of biodiversity (Myers et al., 2000) and more than 80% of their population live in urban areas. Furthermore, it is expected that in Latin America the urban population and urban areas will increase in the coming years (UN-DESA, 2010), especially in small and medium-sized cities, with downstream effects on natural ecosystems and biodiversity. Here, we investigate local patterns of plant diversity of public urban green areas in an intermediate sized city of a Latin American country, namely Valdivia (Chile), placed in a global hotspot of biodiversity (Dinerstein et al., 1995; Olson and Dinerstein, 2002). Valdivia is a city surrounded by

wetlands, but many of them have been under severe pressure from urban sprawl, disappearing due to the need of areas for housing development or as a consequence of their transformation into wastelands (Skewes et al., 2012; Pauchard and Barbosa, 2013). In this context, we analyse the patterns of native and alien plant species diversity of the neighbourhoods of Valdivia, namely richness (species numbers) and evenness (i.e. the equitability of the proportional abundances of species; Smiths and Wilson, 1996). We use an approach that combines anthropogenic factors like habitat type, socioeconomic status, and disturbance, and environmental factors (C/N ratio) in order to answer: a) What is the origin of species in urban lawns of Valdivia and from which families are they? b) Which differences exist in plant species richness and plant evenness among different lawn habitat types and socioeconomic status? And c) are there other anthropogenic and environmental factors (i.e. disturbance by trampling, soil C/N ratio), driving the diversity as species richness in the sampled communities?

Given the general pattern of high species richness in urban areas worldwide, it may be expected to find a high proportion of both, native and exotic species in the city (Aronson et al., 2014). However, considering the history of colonization (over 460 years of European settlers), trading history of Valdivia as a Spanish port in the Pacific area, and the particular isolated biogeographical conditions of the temperate forest area in which the city lays (Amesto et al., 1996), we expect that urban green areas have a higher proportion of exotic species, mainly from Europe, and a high proportion of fast-growing opportunist plants species, accordingly with patterns found in New Zealand (Stewart et al. 2009, Aronson et al. 2014) and in Santiago, Chile (Fischer et al., 2016). Also, we suppose to find lower species richness in low-income areas (Martin et al., 2004) and high values of evenness given the effect of human preferences linked to socioeconomic status. Moreover, we expect to find a reduced species richness in highly disturbed areas, as the result of a selection of disturbance –tolerant species, and a reduction in evenness values given the dominance that some disturbance tolerant species may display.

Our findings should light into local and regional knowledge on biodiversity in urban areas, and contribute to a better understanding of the patterns and processes in Latin America.

2. Methods

2.1 Study area

We selected public green areas in residential sectors in the growing medium-sized city of Valdivia (39°48'30"S, 73°14'30"O), South America. The city is located at the confluence of three rivers (*Calle-*

Calle, *Cruces* and *Valdivia*), and about 15km east of the Pacific Ocean, in the Valdivian Rainforest Ecoregion in North Patagonia, a world hotspot of biodiversity (Dinerstein et al., 1995; Olson and Dinerstein, 2002). The climate is wet-temperate with a strong oceanic influence (Di Castri and Hajek, 1976), with a mean annual temperature of 12.2°C and a range of monthly average of 4.6°C in August (minimum) and 23°C in January (maximum). Annual precipitation is around 2500 mm, with rainfall throughout the year but with a peak in winter months (June-August) (Fuenzalida, 1965; Amigo and Ramírez, 1998). Relative air humidity ranges between 67-89% (Gerding et al., 2006). Soils are well-drained Ultisols (red clay soils) of volcanic origin placed on metamorphic bedrock (Gerding et al., 2006).

Valdivia is characterised by detached houses and low buildings scattered on both banks of the *Calle* and *Valdivia* rivers, with buildings <4 stories mainly in the city centre and new neighbourhoods in the periphery (Figueroa et al., 1998). About a half of the surface of the city are green areas (51%), with ~12% under municipal stewardship. Most of the tree cover is located in private areas (50%), and about 30% of the surface of municipal areas (Silva et al., 2015). Near the city, rural areas are dominated by exotic tree plantations and to a minor degree by small owners developing agroforestry activities (Seis et al., 2014).

The city was founded in 1552 by Spanish colonists, based on a grid plan, in an area with a long history of human settlement by Native American people. The number of inhabitants of Valdivia was nearly 130,000 in the last national census (2002), with a density of 151.22 persons per square kilometre (w. It hence is classified as a mid-size city (UN-Habitat, 2015).

2.2 Sampling

2.2.1 Anthropogenic and environmental factors

We looked for proxies representing the social aspects of cities as well as those classifying the human-made habitat type in which our study sites are embedded, within public lawn areas. Therefore we chose socioeconomic status, lawn habitat type and trampling disturbance as anthropogenic variables potentially influencing the diversity of the urban greens of Valdivia. We also considered the possibility of other environmental factors co-varying with habitat type or SES, such as soil C/N ratio.

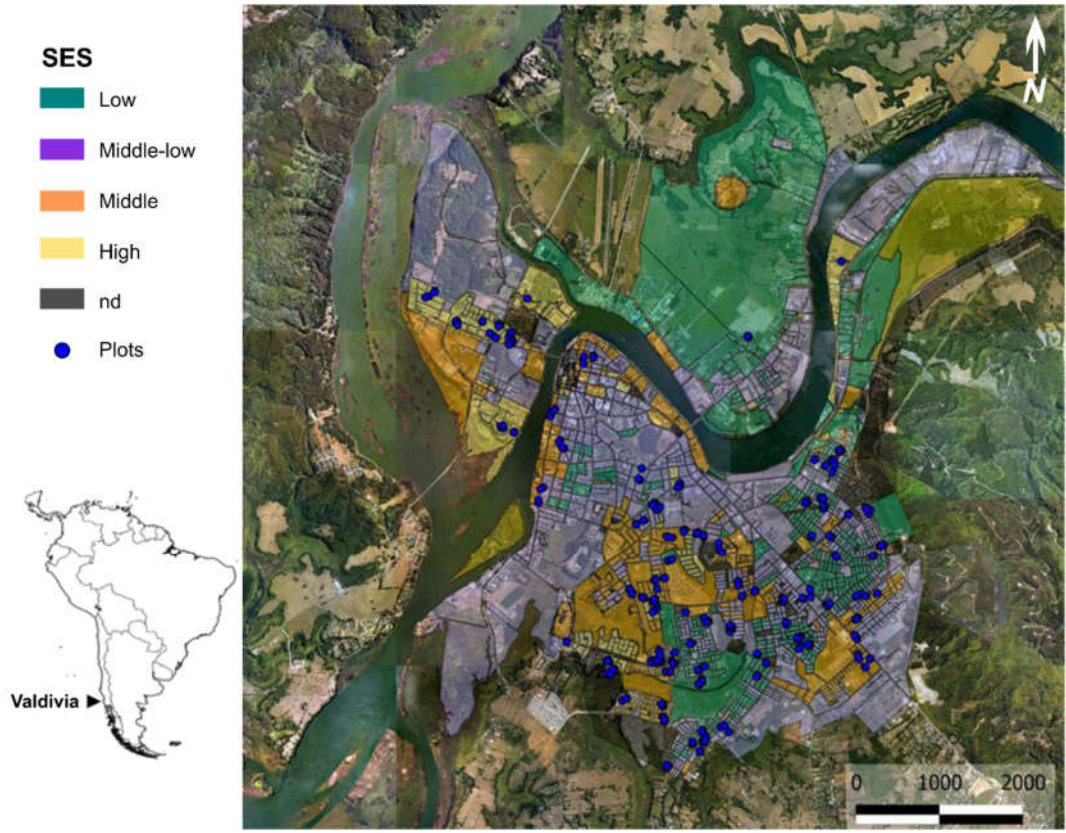


Figure 1: Administrative area of the city of Valdivia (39°48'S, 73°14'O). Colour scale polygons show the city blocks and their socioeconomic status, blue dots marks sampled areas of the city. Scale in meters. The inset shows the position of the study area in South America. SES= Socioeconomic status; nd = no socioeconomic data available for the block, inhabited areas. Satellite image: courtesy of O. Barbosa, Universidad Austral de Chile.

Table 1: Habitat types selected, including their general characteristics and main differences. All habitat types belong to public areas, although unclear regulations and social factors may affect their maintenance.

Habitat type	Description	Area	Vegetation type	Management	Public role/use
Road verges (NV)	Narrow lawns between sidewalk and road, or sidewalk and front house.	0.5 - 2 m wide, variable length	Lawns with trees or other vegetation planted by the municipality or by neighbours. Spontaneous herbs and shrubs.	Stewardship (mowing) shared between municipality and residents. No clear regulations.	Ornamental or domestic use (provisional storing of firewood or garbage).
Broad road verges (BV)	Lawns between sidewalk and road of more than 2m breadth and commonly located close to houses entrance.	40-20000m ²	Lawns with trees or other vegetation planted by the municipality or by neighbours. Spontaneous herbs and shrubs.	Stewardship (mowing) shared between municipality and residents. No clear regulations.	To delimitate properties, to store provisionally firewood or garbage or to improve the appearance of the front house area and neighbourhood. Car parking.
Square and "pocket" parks (SQ)	Lawns areas generally provided with playground and benches. In general have a square shape. "Pocket" parks are small squares with minimum facilities	300-20000 m ²	A mix of lawns and areas with flower beds and/or trees.	Municipal stewardship (mowing, general maintenance)	Playground and meeting point for leisure or other activities.

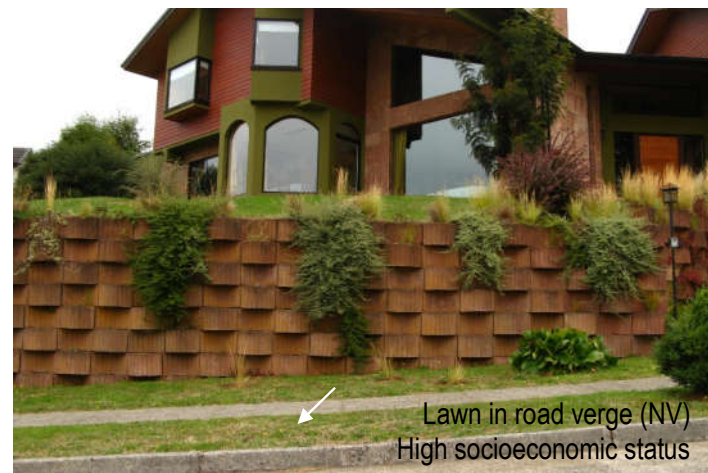


Figure 2: Examples of the green areas associated with lawn habitat types sampled around the city of Valdivia: a) Lawns in broad road verge (RV), b) Lawns in road verge (NV). Formal green space: c) Lawns in squares (SQ). The pictures show three of the four socioeconomic statuses in which the habitat types were sampled.

In this context, first, we chose a proxy for socioeconomic status (“SES” hereafter) of each residential area in the city. We hence applied the index for welfare classification of the National Agency for

Statistics of Chile (INE). The information available was georeferenced at the resolution of street blocks of residential neighbourhoods from the latest National Census (year 2002). Later, the data was updated by the *Observatorio Urbano* bureau, which is part of the Ministry of Housing and Urban Development (MINVU), with information of the MINVU up to the year 2005. The index for welfare classification is divided into five equally sized quintiles (Instituto Nacional de Estadísticas, 2005), based on characteristics of the household, head of the household, and housing (see Appendix A1 for details). We selected the four upper socioeconomic quintiles (2nd=low, 3th=middle-low, 4th=middle and 5th=high SES) for a gradient of socioeconomic conditions throughout the city. The first quintile (1st=lowest SES) was not selected due to the low number of replicates (Figure 1).

Our second factor was “habitat type” considering lawns in different public green areas (Table 1). Common green areas in residential streets are road verges. A road verge is a strip of land between road and sidewalk, between the sidewalk and front garden, or in front of houses. Road verges are of public use and of municipal ownership. They can have turf grasses, herbs, shrubs or trees. Their name varies depending on the country, for example, easement gardens (USA), street lawns or grass verges (The UK and New Zealand). In this study, we identified two types of road verges, according to the area that they cover and the position and use that they have. Other common green areas typical in Latin-American countries are squares (in Spanish “plaza”). Thus, we defined three habitat types in public green areas: lawns in road verge along sidewalks (NV), lawns in broad road verges along sidewalks (BV), and lawns of squares (SQ) (Figure 2).

We selected disturbance as another anthropogenic predictor (“disturbance”) as urban areas have high levels of man-made disturbance, influencing and selecting the species with traits that allow them to survive (Brunzel et al., 2009). The three habitat types reflect a gradient of intensity of disturbance, according to their use by pedestrians (“trampling”). We estimated visually the degree of disturbance as the proportion of bare soil due to trampling over each patch of lawn in a green area in the surveyed patches.

Finally, we measured Nitrogen and Carbon content and estimated the C/N ratio in the soil as environmental covariates. These factors are the most likely to vary among sampled sites (Pickett et al., 2009), are simple to measure, and previous studies had shown their effects on structure and composition of plants in urban areas (Hill et al., 2002; Godefroid et al., 2007), given their relevance to plants growth (Garnier and Navas, 2011).

2.2.2 Plot selection and sampling

We crossed SES of neighbourhoods with habitat type to select sampling areas. We selected only those neighbourhoods which were already present by 2002 to avoid areas in early successional

stages, in which most of the species could be annuals, Then, we performed a stratified random sampling over neighbourhoods selecting specific blocks for a certain habitat type, excluding all sites with a distance of ≤ 130 m to wetlands or urban forests to avoid the effect of other green areas as a potential propagule source of species. Next, in each block, we arbitrarily selected ten plots and georeferenced each plot with a Garmin Oregon 400t GPS. Hence, we surveyed 120 plots of 20 m² after visually checking for homogeneity of conditions (e.g. avoiding large portions of concrete or recently mown sites).

Vegetation surveys were performed during the summers of 2010-2012. We noted all spontaneously growing plants present on each plot. Each individual was identified if possible at the species level (3% could only be identified at the genus level) following the taxonomic references of Zuloaga *et al.*, (2008) and Matthei *et al.*, (1995). The native range of the species was determined following the “Flora del Cono Sur” and the “Grin database” (Zuloaga *et al.*, 2008; USDA, ARS, National Genetic Resources Program, 2013). We estimated the abundance of each species following Londo’s scale (Londo 1976, Table S1). This classification offers a scale that allows a more detailed cover estimate, as it refines the scales proposed by Kraft (1954) and Braun-Blanquet (1964).

To assess soil C/N in each plot, we collected one equal-sized full teaspoon of soil sample (approximately 5 grammes) from the upper soil layer at five different points in each plot, and we combined them to a single sample per plot. Afterwards, we stored the soil samples in plastic bags and froze them in a refrigerator firstly, then dried in an oven at 60° C for at least 72 hours. Soil samples were homogenised and sieved prior to the determination of the element content for each sample with a Vario EL III CNS Elemental Analyzer at 950°C.

2.3 Data analysis

2.3.1 Taxonomic diversity analysis: species richness and evenness

As measures of diversity, we calculated species richness and species evenness. Species richness was calculated as the number of different species per plot. Species evenness is defined as the equitability of the proportional abundances of species. We applied the E_{var} index [1] proposed by Smiths and Wilson (1996), because, unlike the frequently used Pielou evenness, it is not influenced by species richness (Smith and Wilson, 1996; Heip *et al.*, 1998).

$$Evar = 1 - \frac{2}{\pi} \arctan \left\{ \frac{\sum_{s=1}^S (\ln(x_s) - \sum_{t=1}^S \ln(x_t) / S)^2 / S}{\sum_{t=1}^S \ln(x_t) / S} \right\} \quad [1]$$

, where S =number of species in the sample, X_s = abundance of the s^{th} species.

E_{var} is based on the variance of the log abundance over the species, and ranges from >0 to 1, with 1 indicating a completely even distribution of the species abundances.

We analysed the influence of habitat type and SES on evenness and richness using a two-way ANOVA, checking for normality, homoscedasticity and independence of the residuals. Evenness and species richness were hence log and square root transformed, respectively.

2.3.2 Drivers of species richness

To assess the drivers of diversity, we explored the relationship between species richness (square root transformed), environmental (soil C/N) and anthropogenic variables (habitat type, SES and disturbance) previously recorded on the field. We tested the relation with general linear mixed-effects models (GLMMs), having SES, habitat type (Habitat), disturbance, and soil C/N. We considered “sampling year” as a random effect to account for the variability of weather conditions among years. We compared different models employing a top-down strategy (Zuur, 2009), first fitting the best random structure (e.g. having “year” or not as the random factor) and then creating biologically meaningful models with different combinations of fixed effects. We used backwards selection based on the Akaike Information Criterion corrected for small sample size (AIC_c). From the 32 combinations computed, we ranked the best models considering their AIC_c scores. Models with low AIC_c indicate better fit and statistical support than those with higher scores. Delta AIC_c (Δi) indicates the difference between the model with the smallest AIC_c score and the i^{th} model. We chose $\Delta i \leq 5$ as the limit for model selection, following Burnham (2002) and Burnham et al. (2010), and discarded models with $\Delta i > 5$. Models with given values $\Delta i < 2$ are considered to be equally good with the best empirical support, while those with $\Delta i < 5$ have little support. Akaike weights (ω_i) provide the relative likelihood of a model to be the best one for the data among the evaluated models. Best fit models score close to $\omega_i = 1$. For model selection, we used the function “dredge” from the package MuMIn (ver. 1.9.5) (Barton, 2012). We checked for spatial autocorrelation of the residuals among sites using Moran’s I coefficient, tested for statistical significance using 1000 permutations as implemented in the package “ncf” (Bjornstad, 2013). Afterwards, we corrected for multiple testing using Holm’s (1979) method. We did not find a signal of spatial autocorrelation, though. All analyses were performed using R 3.0.1 (R Core Team, 2016).

3. Results

3.1 Origin and taxonomic composition of urban lawns of Valdivia

We found a total of 112 species in public green areas of the study area (Table S3), with a high proportion of exotic species (~80%, 93 species), mainly of European origin (54 species, Figure 3). In general, there were 13.3 (± 4.0) exotic species per plot and 2.2 (± 1.8) native species per plot (Table S4). The most common families found in the study area were the easily dispersed *Poaceae* and *Asteraceae* (26% and 24%, respectively, Figure 4). At the species level, the five most frequent species in the study area were exotic species (*Trifolium repens*, *Lolium sp.*, *Plantago lanceolata*, *Leontodon saxatilis*, and *Hypochaeris radicata*). The only native species that was inside the group of the ten most frequent species in the study area (rank 9) was *Dichondra sericea* (3.2%) (Table S5). Exotic species dominated the communities independent of SES and habitat types (Figure 5, Table S4).

3.2 Species richness and evenness among different habitat types and SES

Habitat type showed a significant effect on species richness with highest species richness in narrow verges (NV, Table 2, and Figure 6a). There was also a significant effect of SES on species richness with a steady increase in species richness from low to high SES. However, the interaction was not significant (Table 2, Figure 6a).

Evenness values were low and showed no significant variation among plots from different SES or habitat type (Table 2, Figure 6b). We found no relation between evenness and species richness regarding diversity patterns. Evenness values varied little compared to species richness, showing that with high or low values of species richness, the evenness values remains around a mean value of 0.22 (± 0.07) (Figure 7).

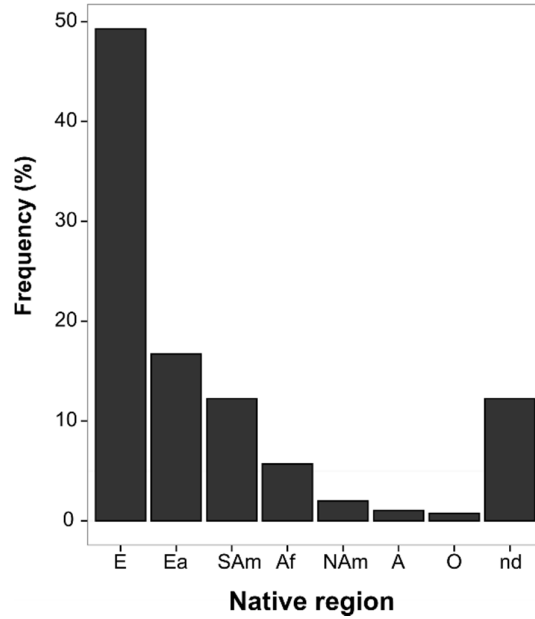


Figure 3: Original geographical range of the 113 species of vascular plants that spontaneously grew in public lawns in Valdivia. A= Asia; E= Europe; Af= Africa; NAm= North America; SAm= South America; Ea= Eurasia, O= Other, nd= non-determined. Note the high proportion of individuals with European origin in this assemblage over the total number of plants (1308 of a total of 2017 individuals).

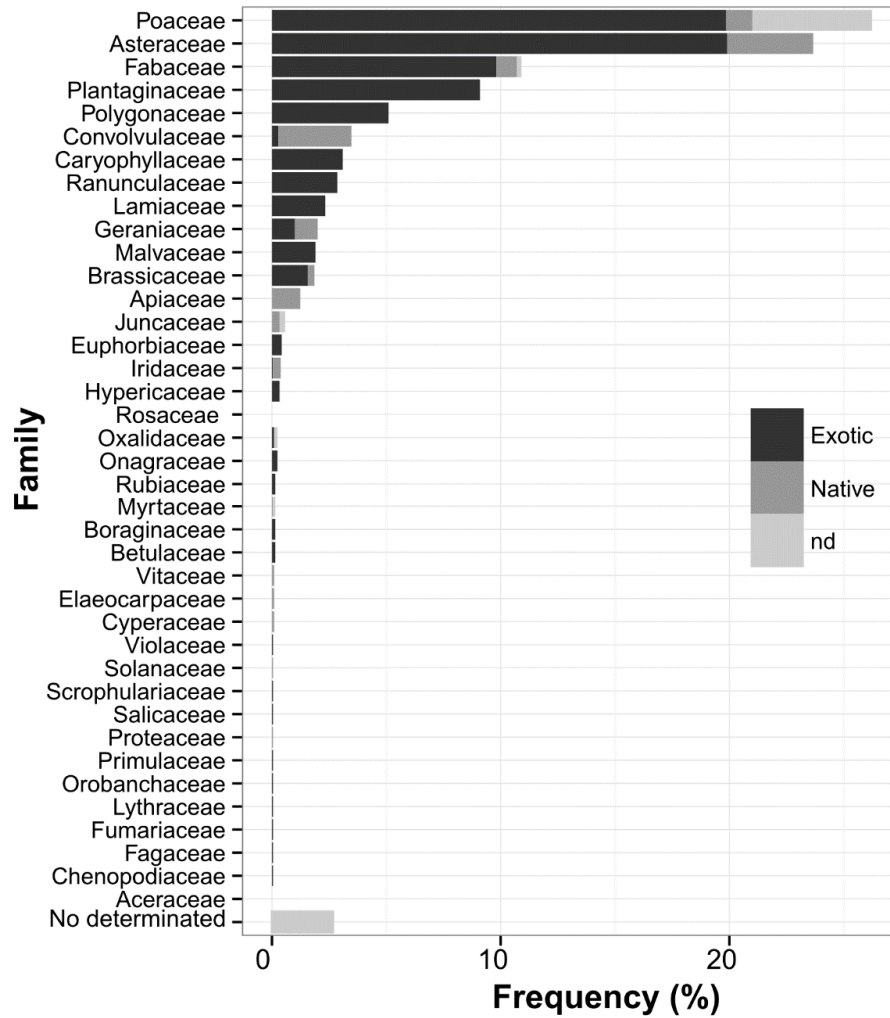


Figure 4: Frequency of occurrence of the 39 families of vascular plant species found in public lawns in Valdivia, Chile. Plant status (exotic, native, nd: non-determined) is indicated for each family in grayscale. 3% of the total individuals could not be identified (nd).

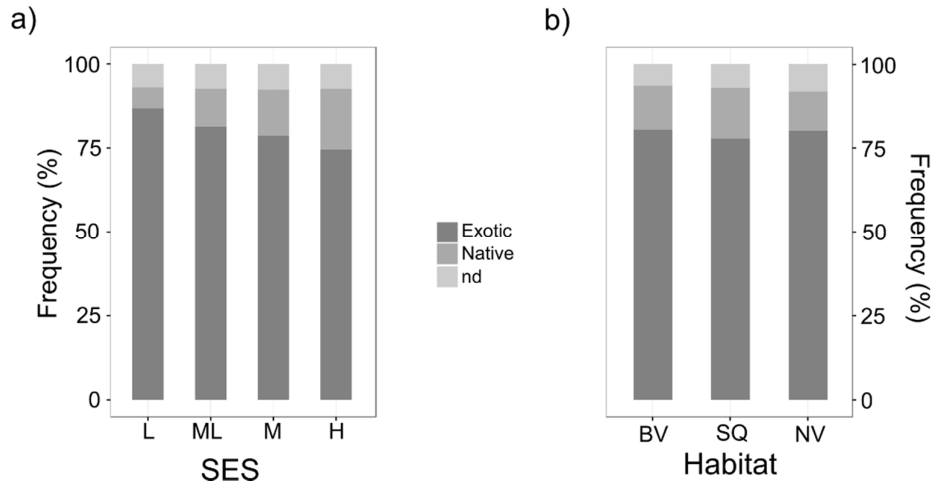


Figure 5: Percentage of exotic and native plants species in the different socioeconomic statuses (SES) (a), and habitat type (b) in public lawns of Valdivia (Chile). SES codes: L=low SES, ML= Middle-low SES, M= Middle SES, H=High SES. Habitat type codes: BV= Lawn in broad road verge, NV= Lawn in road verge, SQ= Lawn in square. Nd= non-determinate species.

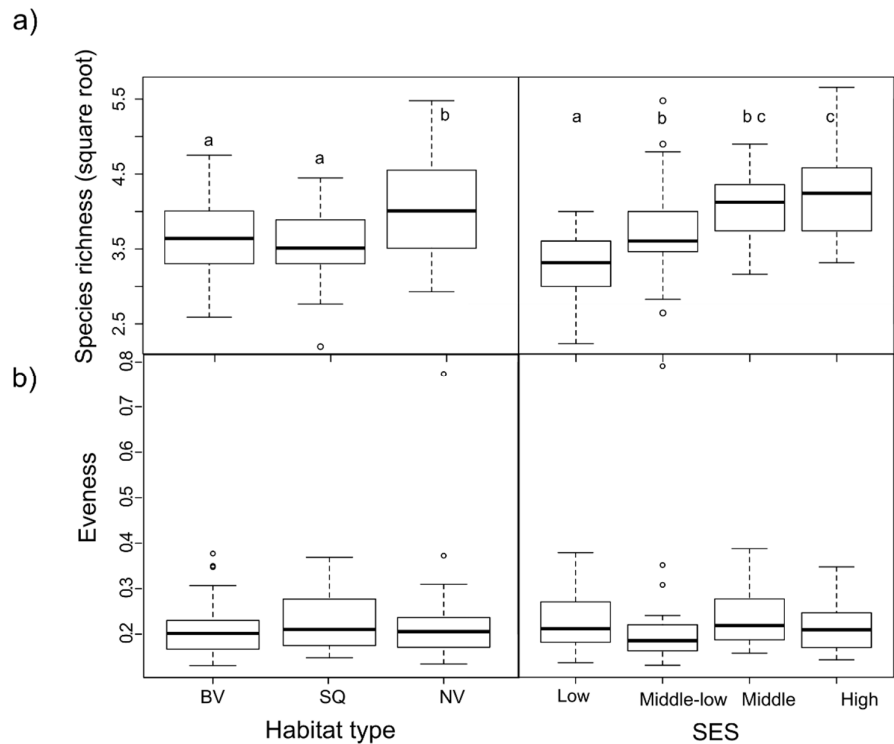


Figure 6: Components of diversity in relation to habitat type and SES without interaction. a) Species richness in relation to lawn habitat type and SES. Significant differences among categories are indicated by letters after Tukey HSD posthoc test; b) Evenness as Smith and Wilson (1996) E_{var} in relation to habitat type and SES. No significant difference was found, neither an interaction. Habitat type: BV= Broad road verge; NV= Road verge; SQ= Square.

Table 2: ANOVA results of the influence of socioeconomic status (SES) and habitat type (Habitat) on (a) species richness, and (b) evenness of spontaneously growing vascular plants in public lawn areas of Valdivia, Chile. Species richness and evenness were square root and log transformed before the analyses to achieve normality.

a) Species richness

Predictors	d.f.	SS	Mean	F-stat	P value	
SES	3	15.50	5.17	19.84	<0.001	***
Habitat	2	6.86	3.43	13.17	<0.001	***
SES * Habitat	6	0.9	0.15	0.58	0.75	n.s.
Residuals	108	28.12	0.26			

b) Evenness

Source of variation	d.f.	SS	Mean	F-stat	P value	
SES	3	0.32	0.10	1.44	0.24	n.s.
Habitat	2	0.17	0.08	19.84	0.32	n.s.
SES * Habitat	6	0.68	0.11	1.56	0.17	n.s.
Residuals	108	7.86	0.07			

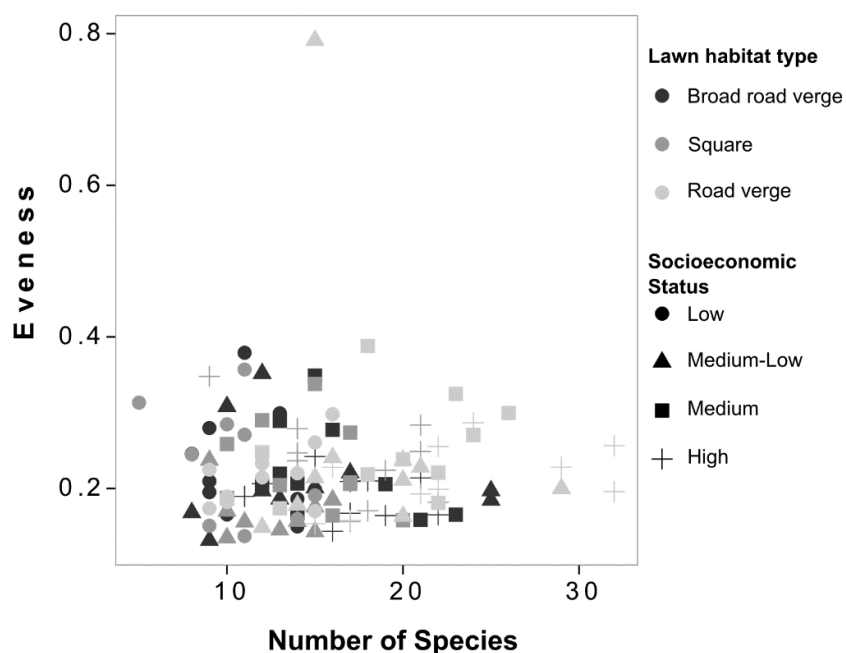


Figure 7: Diversity broke down into species evenness and species richness per plot. Each plot is characterised by grayscale (lawn habitat type) and symbol (SES). Note that the abundance of species does not change significantly over the different conditions, remaining around 0.2. Evenness was calculated according to Smith and Wilson (1996) E_{var} index.

3.3 Drivers of species richness

The combination of SES, habitat type and the percentage of soil disturbance were the best predictors for species richness per plot (Table 3). The percentage of disturbance in the sampled habitat types was negatively related with species richness, while habitat type and SES positively affect species richness (Table 3, Figure 8). Thus, the higher species richness was found in NV lawns close to sidewalks, located in high SES with a low percentage of disturbance. The second, almost as good model (Table 3) additionally contained soil C/N (with a negative effect on species richness) and another just slightly worse model only contained SES and habitat type.

Table 3: GLMM (Generalized Linear Mixed-effect Model) selection of factors correlated to species richness based on Akaike Information Criterion with a correction for small sample size (AIC_c). Akaike Information Criterion delta (Δi) shows the difference between the best model ($\Delta i=0$) and the model with lowest AIC_c score, considering the loss of information of each model. From the 32 models analysed, the table shows the ones with $\Delta i < 5$. Akaike weights (ω_i) gives the normalised likelihoods of each model. "Sampling year" was considered as a random effect in every model. No correlation was found between the amount of soil disturbance and proportion of Carbon and Nitrogen in soil samples (C/N).

Model	Intercept	bare	C/N	Habitat	SES	df	logLik	AIC _c	Δi	ω_i
SES+ Habitat+ disturbance	3.623	-0.73		+	+	9	-85.07	175	0	0.713
SES+Habitat+disturbance+C/N	3.901	-0.71	-0.021	+	+	10	-87.42	176	1.82	0.287
SES+Habitat	3.339			+	+	8	-88.13	179	4.68	0.064

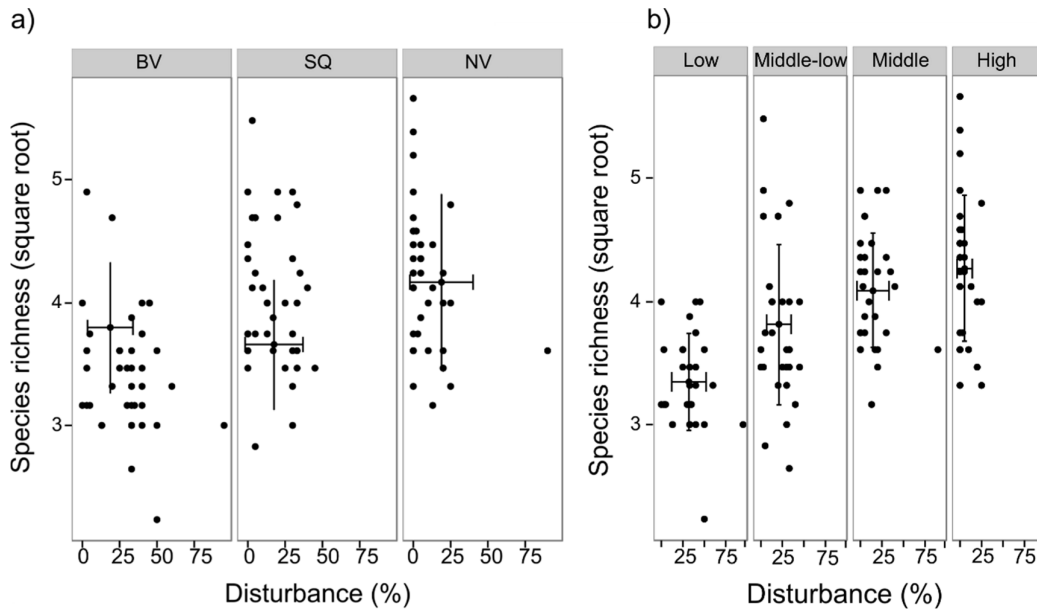


Figure 8: Drivers of species richness used in a GLMM (original values). a) Species richness and soil disturbance considering three different habitat type: BV= Broad road verge; NV: Road verge; SQ: Square; and b) species richness and soil disturbance considering different SES.

4. Discussion

4.1 Origin and taxonomic composition of urban lawns of Valdivia

Our analysis of public lawns revealed communities strongly dominated by exotic species, with only 20% of native vascular plant species, a high amount considering worldwide trends and according to our expectations. A recent global review, that considers the complete flora of cities, found that 28% of urban plant species are exotic (Aronson et al., 2014). At small scale, Thompson et al. (2004) found a higher percentage of native species in garden lawns of Sheffield, UK (159 species, 94% native). Furthermore, Bertoni et al. (2012) found less than 10% of exotic species in private and public lawns in Paris. In contrast, our findings as well as the ones of Fischer et al. (2016) and Stewart et al. (2009) support an opposite trend in the Southern Hemisphere, with exotic species dominating lawn like habitats (as suggested also by Ignatieva and Stewart, 2009). In particular, Fischer et al. (2016) found that 95% of the species in wild grassland of parks in Santiago, Chile, were exotic. The long history of thousands of years developing agricultural areas and pastures in Europe and west Asia areas gives time for plant species to adapt to this kind of land use by co-evolution and breeding from a native species pool (Eriksson et al., 2002). South-America has a

different history of development, lacking these long temporal processes related to land use history that helped native species to adapt to new lawn conditions in the Old World. So, in contrast, the South American sites are well suited for the introduction and establishment of European species pre-adapted to habitat conditions similar to those of the Old World, but without equivalent in the New World prior to the colonisation by European settlers.

In Valdivia, the continuous and fast land transformation has led to the displacement of the native flora that grew on wetlands and adjacent areas by species adapted to drier habitats in residential areas. Through processes related to colonialism, European plant species from temperate areas arrived, first with settlers from Spain, and later from The Netherlands, Ireland, Germany and other countries (Montt Pinto, 1971). Moreover, through the increase in human-mediated transport and trading activities of goods and ornamental plants, new species were accidentally or deliberately introduced (Fuentes et al., 2008, 2013). Some of those new plant species found suitable climatic conditions under the wet temperate climate of Valdivia and outcompeted the native ones, by being better able to thrive in the newly created habitats of urban areas.

The high proportion of European plant species from temperate areas in the temperate climate in Valdivia can be explained by climate matching, or the capacity of invasive species to conserve their climatic niche in the invaded ranges (Broennimann et al., 2007). However, it is also possible that in principle some species might have experienced shifts in their ecological niche, as a result of the release from biotic constraints (competitors or predators), through the availability of empty niches in the new range or by evolving in the new range (Broennimann et al., 2007). Though, this is a rather uncommon process (Petitpierre et al., 2012).

Of the 39 families presented in the study area, the dominant ones were *Poaceae*, *Asteraceae* and *Fabaceae*. These results are similar to what Finot (1993) found in a vegetation analysis through different habitat of the city (including wetlands) more than 20 years ago (*Poaceae* 18.5%, *Asteraceae* 11.7%, *Fabaceae* 9.9%). The same exotic families are the most common in central Chile (Jiménez et al., 2008). At a worldwide scale, grasses and perennial forbs dominate in urban lawns of Europe, North America and New Zealand (Ignatieva and Stewart, 2009), and are sold as lawn seed mixtures for landscaping (Stewart et al., 2009). As lawns are a globally wide-spread type of green area of European origin, we could expect that these species will be present and spread worldwide, supporting the idea of a homogenization of urban areas (McKinney, 2006). Fischer et al. (2016) found quantitative support for homogenization for lawns in Santiago, Chile, as we do, and shows that lawns in urban areas of a temperate city in South America do not reflect the biogeographic species pool, opposite to the findings of Aronson et al. (2014).

The specific composition of lawn plant species could reflect the suitability (and hence human preference) of certain types of species for these habitats. In our case, the most frequent species were *Trifolium repens* (Fabaceae), *Lolium sp.* (Poaceae), *Plantago lanceolata* (Plantaginaceae), *Leontodon saxatilis* and *Hypochaeris radicata* (Asteraceae). In the case of native species, we only found one species that was explicitly selected and maintained by gardeners for its appeal as ground cover (*Dichondra sericea*). This species was found mainly spontaneously growing, but it also propagates generatively, especially in front gardens (Hernán Céspedes, gardener, personal communication). *Dichondra sericea* (Convolvulaceae), *Gamochaeta americana* (Asteraceae), and *Hydrocotyle indecora* (Apiaceae) were the most commonly observed native species. Both, *Dichondra sericea* and *Hydrocotyle indecora*, are small size, creeping species with the ability of vegetative sprouting via stolons, helping them to persist and spread (Pérez-Harguindeguy et al., 2013). Interestingly, the same genera were also reported in lawns of Christchurch (New Zealand), in which the three most common native species were forbs of the genera *Hydrocotyle* and *Dichondra* (Stewart et al., 2009), suggesting to extend the concept of biotic homogenization to genus level.

4.2 Species diversity patterns

Species richness and evenness showed contrasting patterns. Habitat type and SES had significant effects on species richness, with higher values in NV and richer SES. In contrast, we found low and uniform values of evenness across all lawn habitat types and SES. These contrasting findings highlight the need to use several metrics to describe patterns in diversity, even if only considering taxonomic aspects and ignore other aspects of diversity (Winter et al., 2013).

It is interesting to note that evenness is not influenced by SES or habitat type, and our expectation of different values of evenness across the city was not supported. We expected to find higher values of evenness in higher SES as the result of human preferences (“one of everything” effect by ornamental species introduction, Walker et al., 2009), and low values of evenness in lower SES by effect of dominant species (Hillebrand et al., 2008) was not supported. It may suggest that the abundance of species is less sensitive to these anthropogenic factors, or that factors affecting species are more homogeneous. In public green spaces and particularly in NV and BV, neighbours share the maintenance of lawns in front of their homes, weeding those with undesirable traits, such as spines (personal communication with householders). Thistles (*Cirsium vulgare*, *Sonchus oleraceus*) and other spiny plant species are actively removed from lawns, so they remain in low

abundance. Low evenness relates to uneven communities, with a few dominant species and many rare or less abundant ones, suggesting a strong competition between the species (Maurer and McGill, 2011). This can have at least two reasons: (i) the direct influence of humans, promoting a few species with the occasional weeds in between and (ii) indirectly via the introduction of exotic species and natives from other areas that may become dominant in the new habitat. Moreover, evenness may reflect changes faster than species richness (Hillebrand et al., 2008) and could be more helpful for monitoring conservation projects in urban areas.

4.3 Factors driving species richness

4.3.1 Socioeconomic status (SES)

SES shows an interesting and direct effect on species richness supporting our expectations of higher species richness in high SES areas and lower species richness in low SES. Wealthier areas had a significantly larger number of spontaneous species than poorer ones. Several studies had noted the relation between species richness and SES in different cities around the world (e.g. Hope et al., 2003; Martin et al., 2004; Luck et al., 2009; Bigirimana et al., 2012). Hope et al. (2003) refer to the “luxury effect” as the preference of high SES families for settling in areas that are species-rich, either by creating a more diverse landscape or by selecting those areas already diverse in species (Kühn et al., 2004). The same effect could explain the positive relationship between SES and plant richness that we found in Valdivian lawns. People of higher SES have the possibility and willingness to invest in gardening species, increasing the likelihood of species escaping from gardens into the adjacent public green areas (Sullivan et al., 2004; Bigirimana et al., 2012). Then, human stewardship could explain the higher amount of species richness in them via a bottom-up influence (Kinzig et al., 2005). Families in high socioeconomic areas invest time and money to maintain the aesthetic value of the neighbourhood by planting and watering, especially those close to sidewalks (NV and BV). They also put pressure on the municipality to keep squares and pocket parks clean, trees and shrubs trimmed and grass mowed in a top-down influence of the government to the state of the green areas. Previous studies have shown the social role of lawns and front gardens and the high symbolism that they have for gardening practices, especially in higher SES neighbourhoods (Whitney and Adams, 1980; Zmyslony and Gagnon, 1998; Marco et al., 2010; Fraser et al., 2013). Additionally, there are more indirect effects: watering gardens also increase water availability in adjacent lawns, and therefore lawns located in wealthier areas have a better

water supply (less drought), are less utilised and hence less disturbed, and can thus also promote more sensitive species.

Low SES areas were poor in species richness, and the proportion of natives was remarkably low or they were even absent. These areas were mainly under the stewardship of the municipality, with less participation of neighbours in the maintenance practices. The bottom-up influence of increasing the aesthetic values of the public areas is almost inexistent. Thus, the vegetation in this areas may be under higher environmental pressure (lack of watering during the dry summer season) compared to the pressure that human stewardship practices may produce (weeding, watering, fertilisation).

Finally, we faced in this low SES areas simple communities in terms of species richness, characterised by a novel suite of species of mainly exotic origin (species gain and loss of native ones) that are able to survive in the new environmental conditions. On the contrary, higher SES will have a stronger effect of human preferences on their green areas, outpacing some environmental constraints (water availability, species competence) and generating new assemblies of native and exotic species, as Williams et al. (2009) proposed in their framework for predicting the effects on urban flora.

4.3.2 Other factors driving species richness

Our analysis of co-variables that may affect species richness showed the relevance of habitat type and disturbance by trampling. Species richness in habitat types did not have higher diversity in the habitat types that should have a lower human impact, namely BV and SQ. NV had significantly higher species richness than BV and SQ. There might be a lower rate of seed dispersal across different habitat types in the city, but NV. Among the three studied habitat types, NV is the one with more pedestrian traffic, hence highest propagule pressure, and therefore, it is more exposed to human movement and impacts. Humans and their means of transport are vectors of seed dispersal and NV could receive the seed pools easily. Seeds can be attached to clothing and footwear and reach lawns from different places (Auffret et al., 2014). Vehicles can transport seeds from and to cities in large quantities accelerating plant invasions due to the transport of invasive seeds (von der Lippe and Kowarik, 2007, 2008). NV habitats are close to roads, thus they could receive the seeds attached to vehicles increasing the pool of species present in them. Hence seed dispersal is facilitated by human activities and increases the species richness on those habitats. Additionally, NV may have different micro-site conditions, due to disturbances such as trampling and the input of nitrogen via dog faeces and garbage in lower income areas, facing the heterogeneity of

landscape and giving the conditions to persist to some small species (McKinney, 2008). Another explanation to the high species richness in NV is related to our sampling method. Due to the area available to sample in the public green spaces most of the plots located in BV and SQ were squared shaped, while the plots in road verges (NV) were suited to fit in the 20m², being more rectangular and thus representing a potentially longer environmental gradient. The outcome is a longer section for sampling species than the other two habitat types and a potentially better performance in sampling species richness (Stohlgren et al., 1995).

According to our best model, disturbance by trampling was an additional force that shapes urban communities and interacts with habitat type and SES. The percentage of disturbance in the sampled habitats was negatively related with species richness, while habitat and SES affected positively. Additionally, soil C/N was selected among the best models. Public urban green areas are under constant pressure of trampling that may deteriorate plant species until the soil is bare and compacted. Trampling would filter those native and exotic species able to cope with continuous disturbance, with traits that allow them to survive and thrive, decreasing diversity (Niemelä, 1999; McKinney, 2002). Bertoncini et al. (2012) found that public lawns in Paris have fewer species than private lawns due to the impact of trampling during the summer days. In this context, NV in high SES neighbourhoods had less human traffic, and since they have probably more often car trips, the trampling effect is less intense and seed dispersal could be facilitated by cars, explaining the higher amount of plant species. As Williams et al. (2009) state, several factors (or filters) of urbanisation act simultaneously as the city develops, and even if they do not interact, as in our case, they are difficult to isolate as drivers of biodiversity changes.

In this study, soil C/N is the only strict environmental factor that we analysed. Other studies have correlated urban flora with the light condition, soil moisture and nitrogen reaction (Godefroid and Koedam, 2007). This was done, though, rather indirectly by using plants' preferences (Ellenberg indicator values) rather than direct measurements. Exploring these factors by direct measurement can be a fruitful avenue for future research. Several works highlight the relevance of mowing frequency as a variable that decreases diversity in lawns (McKinney, 2002). We did not evaluate this factor because retrieving reliable information about the frequency of mowing was not possible.

5. Conclusions

As a result of colonialism, international and national trade, land use history, and climate matching, our findings support a trend in the Southern Hemisphere, with much higher proportions of exotic

plant species over natives in urban lawn habitats, which do not reflect the biogeographic species pool of the natural non-urban areas. However, ecological studies are still underrepresented on the Southern Hemisphere and more evidence is needed to support this trend.

SES was an important driving factor of species richness. Our analyses promote the relevance of bottom-up processes, from householders to the top stakeholders in shaping the diversity in this urban area. The positive relation between species richness and SES has been reported in different countries around the world and could have a predictive value to locate areas of low diversity in cities knowing their SES. Moreover, identifying the mechanisms behind such relationship would allow management strategies to protect and increase biodiversity in urban areas.

Specifically for Latin America, in which high inequity of income and extremes in social status are common and the proportion of the population living in poor areas is high, we could expect a rather negative scenario for species richness in cities. In low-income urban settlements we may find literally deserts of biodiversity, and consequently, population detached from nature. It could be that the rapid pace of urban change in Latin America could add higher pressure to natural communities, not giving them enough time to evolve and adapt to the newcomer species. This could jeopardise areas of high diversity located near to cities. The expected population growth in this continent sets a priority for more studies about general patterns of biodiversity in urban areas. Hence, overcoming social inequity might be a means to promote urban biodiversity, as well.



Supplementary material

Table S1: Cover-abundance estimation of species with Londo's decimal scale. A comparison of Londo scale for coverage recording in vegetation analysis and Braun-Blanquet scale is shown. Londo developed a fine scale to account for small changes in species cover, expanding Braun-Blanquet classification. This scale adds the decimal point and a description of the coverage characteristics on the field. Symbols as “·, +, -” have no mathematical significance. Source: Londo 1976.

Symbol	Coverage	Supplementary symbols	Braun-Blanquet scale
·1	<1%	· = r = rare, sporadic	+
·2	1-3%	p = rather sparse	1
·4	3-5%	a = plentiful	
		m = very numerous	
1	5-15%	1 - = coverage 5-10%	2
		1 + = coverage 10-15%	
2	15-25%		
3	25-35%		
4	35-45%		3
		5 - = coverage 45-50%	
5	45-55%	5 + = coverage 50-55%	
6	55-65%		4
7	65-75%		
8	75-85%		
9	85-95%		5
10	95-100%		

Table S2: List of variables and its characteristics considered in the measurement of socioeconomic status in Chile (Instituto Nacional de Estadísticas 2005). The combination of those variables, analysed with a PCA (PRINCALS) grouped the population in five classes, from low to high status. Translated from Instituto Nacional de Estadísticas 2005.

Housing characteristics	Household characteristics	Head of the household's characteristics
- Household type	- Overcrowded housing (YES/NO)	- Age
- Tenancy type	- Number of people in the household	- Level of education
- Wall cladding type	- Number of sleeping rooms	- Years of education
- Floor covering type	- Employment rate	- Occupational category
- Roof covering type	- Household equipment	
Provision of basic services:		
- sanitary, water, and electricity supplies	- Number of private cars	

Table S3: Species list of spontaneously growing vascular plants on public green areas in the city of Valdivia, Chile (# families= 39, # species= 112) sampled during summers 2010-2012 in 120 plots of 20m², each. Native range of distribution: A= Asia; E= Europe; Af= Africa; NAm= North America; SAm= South America; Ea= Eurasia, O= Other, nd= No data. The native range of the species was determined following the “Flora del Cono Sur” and the “Grin database” (Zuloaga et al. 2008, USDA, ARS, National Genetic Resources Program 2013).

Family	Species	Status	Native range
Aceraceae	<i>Acer pseudoplatanus</i>	Exotic	Ea
Apiaceae	<i>Hydrocotyle indecora</i>	Native	SAm
Asteraceae	<i>Achillea millefolium</i>	Exotic	E
	<i>Bidens aurea</i>	Exotic	NAm
	<i>Calendula officinalis</i>	Exotic	nd
	<i>Chevreulia sarmentosa</i>	Exotic	SAm
	<i>Cichorium intybus</i>	Exotic	E
	<i>Cirsium vulgare</i>	Exotic	E
	<i>Crepis capillaris</i>	Exotic	E
	<i>Erigeron karvinskianus</i>	Exotic	NAm
	<i>Gamochaeta americana</i>	Native	SAm
	<i>Hypochaeris radicata</i>	Exotic	E
	<i>Leontodon saxatilis</i>	Exotic	E
	<i>Leucanthemum vulgare</i>	Exotic	E
	<i>Matricaria matricarioides</i>	Exotic	A
	<i>Soliva sessilis</i>	Native	SAm
	<i>Sonchus oleraceus</i>	Exotic	E
	<i>Taraxacum officinale</i>	Exotic	E
Betulaceae	<i>Betula pendula</i>	Exotic	Ea
Boraginaceae	<i>Myosotis sp</i>	Exotic	nd
Brassicaceae	<i>Brassica nigra</i>	Exotic	E
	<i>Capsella bursa-pastoris</i>	Exotic	E
	<i>Lepidium didymum</i>	Native	SAm
	<i>Raphanus sativus</i>	Exotic	E
	<i>Sisymbrium officinale</i>	Exotic	E
Caryophyllaceae	<i>Cerastium fontanum</i>	Exotic	E
	<i>Polycarpon tetraphyllum</i>	Exotic	E
	<i>Sagina procumbens</i>	Exotic	Af
	<i>Sagina sp</i>	Exotic	nd
	<i>Spergula arvensis</i>	Exotic	E
	<i>Spergula rubra</i>	Exotic	E
	<i>Stellaria media</i>	Exotic	E
Chenopodiaceae	<i>Chenopodium murale</i>	Exotic	A
Convolvulaceae	<i>Calystegia sepium</i>	Exotic	E
	<i>Convolvulus arvensis</i>	Exotic	E
	<i>Dichondra sericea</i>	Native	SAm
Cyperaceae	<i>Cyperus rigens var. rigens</i>	Native	SAm
Elaeocarpaceae	<i>Aristotelia chilensis</i>	Native	SAm
Euphorbiaceae	<i>Euphorbia peplus</i>	Exotic	E

Fabaceae	<i>Cytisus scoparius</i>	Exotic	E
	<i>Lotus corniculatus</i>	Exotic	E
	<i>Lotus subpinnatus</i>	Native	SAm
	<i>Medicago lupulina</i>	Exotic	E
	<i>Ornithopodium perpusillum</i>	Native	SAm
	<i>Robinia pseudoacacia</i>	Exotic	NAm
	<i>Trifolium campestre</i>	Exotic	E
	<i>Trifolium dubium</i>	Exotic	E
	<i>Trifolium fragiferum</i>	Exotic	Ea
	<i>Trifolium pratense</i>	Exotic	E
	<i>Trifolium repens</i>	Exotic	Ea
Fagaceae	<i>Quercus robur</i>	Exotic	Es
Fumariaceae	<i>Fumaria sp.</i>	Exotic	nd
Geraniaceae	<i>Erodium cicutarium</i>	Exotic	Af
	<i>Erodium moschatum</i>	Exotic	Af
	<i>Geranium core core</i>	Native	SAm
Hypericaceae	<i>Hypericum humifusum</i>	Exotic	O
Iridaceae	<i>Crococsmia x crocosmiiflora</i>	Exotic	Af
	<i>Olsynium biflorum</i>	Native	SAm
Juncaceae	<i>Juncus bufonius</i>	Exotic	O
Lamiaceae	<i>Prunella vulgaris</i>	Exotic	E
Lythraceae	<i>Lythrum hyssopifolia</i>	Exotic	E
Malvaceae	<i>Malva nicaeensis</i>	Exotic	E
	<i>Modiola caroliniana</i>	Exotic	NAm
Myrtaceae	<i>Luma apiculata</i>	Native	SAm
Onagraceae	<i>Epilobium sp</i>	Exotic	nd
Orobanchaceae	<i>Parentucellia viscosa</i>	Exotic	E
Oxalidaceae	<i>Oxalis articulata</i>	Exotic	SAm
	<i>Oxalis corniculata var. atropurpurea</i>	Exotic	E
Plantaginaceae	<i>Plantago lanceolata</i>	Exotic	E
	<i>Plantago major</i>	Exotic	Ea
	<i>Veronica persica</i>	Exotic	E
	<i>Veronica serpyllifolia</i>	Exotic	Ea
Poaceae	<i>Agrostis capillaris</i>	Exotic	E
	<i>Aira caryophyllea</i>	Exotic	E
	<i>Anthoxanthum odoratum</i>	Exotic	E
	<i>Apera interrupta</i>	Exotic	E
	<i>Arrhenatherum elatius var. bulbosum</i>	Exotic	E
	<i>Briza minor</i>	Exotic	E
	<i>Bromus catharticus</i>	Native	SAm
	<i>Bromus lithobius</i>	Native	SAm
	<i>Cynodon dactylon</i>	Exotic	Af
	<i>Dactylis glomerata</i>	Exotic	E
	<i>Festuca arundinacea</i>	Exotic	E
	<i>Foeniculum vulgare</i>	Exotic	E
	<i>Holcus lanatus</i>	Exotic	E

	<i>Hordeum murinum</i>	Exotic	E
	<i>Hordeum murinum</i> L. ssp. <i>leporinum</i>	Exotic	E
	<i>Leptochloa virgata</i> (L.) P. Beauv.	Native	SAm
	<i>Lolium multiflorum</i>	Exotic	E
	<i>Lolium perenne</i>	Exotic	E
	<i>Lolium temulentum</i>	Exotic	E
	<i>Paspalum dasypleurum</i>	Native	SAm
	<i>Poa annua</i>	Exotic	E
	<i>Poa pratensis</i> ssp. <i>angustifolia</i>	Exotic	Ea
	<i>Setaria parviflora</i>	Exotic	SAm
	<i>Setaria pumila</i>	Exotic	Ea
	<i>Vulpia bromoides</i>	Exotic	E
Polygonaceae	<i>Polygonum aviculare</i>	Exotic	E
	<i>Rumex acetosella</i>	Exotic	Ea
	<i>Rumex obtusifolius</i>	Exotic	E
Primulaceae	<i>Anagallis arvensis</i>	Exotic	Af
Proteaceae	<i>Embothrium coccineum</i>	Native	SAm
Ranunculaceae	<i>Ranunculus repens</i>	Exotic	Af
Rosaceae	<i>Cotoneaster coriaceus</i>	Exotic	A
	<i>Cotoneaster</i> sp	Exotic	nd
	<i>Rubus</i> sp	Exotic	nd
Rubiaceae	<i>Sheardia arvensis</i>	Exotic	E
Salicaceae	<i>Populus alba</i>	Exotic	Ea
Scrophulariaceae	<i>Verbascum</i> sp	Exotic	nd
Solanaceae	<i>Solanum tuberosum</i>	Native	SAm
Violaceae	<i>Viola x wittrockiana</i> *	Exotic	O
Vitaceae	<i>Cissus striata</i>	Native	SAm

*Horticultural hybrid

Table S4: Summary of descriptive statistics values of species richness per plot for each habitat type and socioeconomic status (SES) in vegetation plots of Valdivia, Chile. General total values are given at the bottom of the table.

Factor	Categories	Mean Native species	SD	Mean Exotic species	SD	Mean total species	SD
Habitat type	Broad road verges-BV	2.1	1.5	12.5	3.2	14.7	4.1
	Road verges-NV	2.1	1.5	11.6	3.1	13.7	3.8
	Squares and pocket parks-SQ	2.3	2.2	15.6	4.3	17.9	6.0
SES	Low	0.8	0.9	10.6	2.4	11.3	2.5
	Middle-low	1.8	1.4	13.2	4.4	14.9	5.2
	Middle	2.6	1.4	14.4	3.4	16.9	3.8
	High	3.5	2.0	14.9	3.9	18.4	5.1
	Total	2.1	1.8	13.2	4.0	15.4	5.0

Table S5: List of the ten most frequent plant species in the city of Valdivia. Status refers to the original geographical range of the species and their status as native/ exotic to the study area. Frequency is calculated as a measure of abundance.

#	Family	Species	Status	<i>n</i>	%
1	Fabaceae	<i>Trifolium repens</i>	Exotic	116	5.5
2	Poaceae	<i>Lolium sp</i>	Exotic	107	5.0
3	Plantaginaceae	<i>Plantago lanceolata</i>	Exotic	103	4.9
4	Asteraceae	<i>Leontodon saxatilis</i>	Exotic	100	4.7
5	Asteraceae	<i>Hypochaeris radicata</i>	Exotic	99	4.7
6	Asteraceae	<i>Taraxacum officinalis</i>	Exotic	92	4.4
7	Poaceae	<i>Poa annua</i>	Exotic	75	3.6
8	Poaceae	<i>Agrostis capillaris</i>	Exotic	73	3.5
9	Convolvulaceae	<i>Dichondra sericea</i>	Native	67	3.2
10	Plantaginaceae	<i>Plantago major</i>	Exotic	62	2.9

Chapter Three

Multiple human-mediated factors drive plant functional strategies in a city in Southern South America



Chapter Three

Multiple human-mediated factors drive plant functional strategies in a city in Southern South America

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Abstract

Studies of functional diversity are a tool to understand and predict the consequences of biotic change. This holds especially true in cities where humans altered the environmental conditions leading to plant compositional changes. However, compared to species richness, few studies have tried to disentangle the effects of urbanisation on functional diversity. Here, we explore patterns of functional diversity of wild vascular plants, in terms of functional composition (community-weighted mean, CWM) and structure (Rao's quadratic entropy index, FD_Q), to disentangle how anthropogenic and environmental factors affect the persistence and performance of plants in public green areas of Valdivia, a city located within a global hotspot of biodiversity in Chile. We used an approach that focusses on the response of three functional traits related to wild plant persistence in lawns of residential areas: plant height, leaf dry matter content (LDMC) and specific leaf area (SLA). We evaluated their response against a set of multiple predictors of anthropogenic (socioeconomic status, habitat type, disturbance, the proportion of exotic plant species) and environmental nature (soil C and N). Valdivian lawns represent communities with a homogeneous composition of mean traits (CWM), low evenness, and low dissimilarity (FD_Q) of traits related to plant persistence and performance (LDMC, SLA and plant height). However, anthropic (socioeconomic status, habitat type, disturbance and proportion of exotics plant species) and environmental factor (N) showed a relevant role as drivers of composition and structure in the urban lawns. We found that structure but no composition of persistence traits was driven by anthropogenic factors at the local scale. Moreover, we found the combined effects of factors explained the variation in traits. The results of this research will help to understand local scale patterns and mechanisms of urbanisation on functional traits, disentangling the effect of factors acting on urban

floras, and contribute to broad-scale patterns and mechanisms of urbanisation in wild plants communities. Our work is a contribution to fill the regional gap of urban ecology studies in fast growing cities of Latin America.

Keywords

Temperate ecosystems, functional diversity, leaf, SLA, Rao's entropy, CWM

1. Introduction

Urban ecosystems are major hotspots of global biodiversity (Aronson et al., 2014), the main location of our daily activities and the place in which more than a half of the human population live (UN-DESA, 2014). Despite been ignored in ecological studies for many years (McDonnell, 1997), in the last decades a large number of studies have addressed the effects of urbanisation on biodiversity, focusing on species richness and abundance, particularly of plant and bird species (Kowarik, 2011; Williams et al, 2015). Moreover, there is a lack of research in urban ecosystems in geographical areas like Latin America (Pauchard et al., 2006; Kowarik, 2011), the developing region in the world with the highest degree of urbanisation (UN-DESA, 2014). Up to now, general trends of urban plant species around the world show an increase in the introduction of exotic species, a decrease of native habitat specialists, and the emergence of novel species assemblages combining natives and exotics. For plant species richness there is evidence of a decrease in species with the age of the neighbourhood (time since establishment) and an increase of species on wealthy neighbourhoods (Hope et al., 2003; Martin et al., 2004; Chapter 2), and previous land use (Luck and Smallbone, 2010; Cook et al., 2012). However, research on the effect of urbanisation in other components of plant diversity, such as functional and phylogenetic diversity, remain scarcely know (Lososová et al., 2006; Knapp et al., 2012; Williams et al., 2015).

Functional diversity is the range of functional trait differences among species in a given community (Petchey and Gaston, 2002). Violle et al. (2007) defined functional trait as any morphological, physiological, or phenological feature measured at the individual level with no reference to the environment or any other level of organisation, which strongly influences the individual fitness and performance at given environmental conditions. Practical attributes of functional traits are the possibility to build generalisations across sites and communities with no geographical or taxonomical link (Reich et al., 1997), and its application as a tool to link organisms' strategies and ecosystem functioning (Loreau et al., 2001) and ecosystem services (Diaz and Cabido, 2001; Harrison and Winfree, 2015).

A way to measure functional diversity is through a compositional and structural perspective. According to this, the functional composition is the mean trait value weighted by species abundance, also known as community-weighted mean (CWM). It represents the biomass-ratio hypothesis of Grime (1998), where the most abundant species in the community will drive the ecosystem functions. Moreover, functional structure is the composition and range of dissimilarities of functional traits (Garnier and Navas, 2012). Rao's quadratic entropy index (hereafter FD_Q , Rao, 1982) is one of the indices that account for traits dissimilarities (Cadotte et al., 2011). It is the abundance-weighted pairwise distance between species in the functional trait space (Mason and Mouillot, 2013). In addition, FD_Q involves two of the three components of functional diversity stated by Mason et al. (2005): functional richness (i.e. the functional space occupied by species), and functional divergence (i.e. the degree of which abundance is distributed towards the extremes of functional space), which make it a convenient index to be used. Thus, the combination of functional composition (CWM) and range dissimilarities (FD_Q) can measure different aspects of functional diversity in a given community and can explain key ecosystem processes (Mouillot et al., 2011).

We can assess the response of plants to the environmental conditions with the variation in functional traits since they represent the strategy of plant survival in a given environment. Those strategies are reflected in sets of plant traits (syndromes) that explain why some species thrive in a given environment (Pérez-Harguindeguy et al., 2013). Westoby (1998) proposed the LHS strategy (leaf, height, seed) to explain how plants establish, persist and disperse. Plant height, a whole-plant trait, has been linked positively with resource acquisition, reproductive success (as reproductive size), and competitive advantage (Díaz et al., 2013). Leaf dry matter content (LDMC) and specific leaf area (SLA) are leaf traits linked to resource acquisition and allocation, accounting for the performance of individuals *in situ* (Díaz et al., 2013), and resistance to disturbance. LDMC, a proxy for tissue density in plants, is associated positively with leaf lifespan, and resistance to physical disturbance. SLA, a ratio of leaf area and dry mass, is strongly associated with plants' functions as photosynthetic rate growth (positively), and leaf lifespan (negatively). Moreover, leaf traits give insights on nitrogen and carbon content in plants, because plants incorporate those elements in their tissues, and may increase rates of cycling in the ecosystem if the dominant ones have a high content of them (Laughlin et al., 2015). Thus, their variation helps to predict decomposition rates, linking this process with the carbon cycle at the ecosystem level. Both traits capture different aspects of plant resource acquisition and resource cycling via litter decomposition (Garnier and Navas, 2012).

Cities are socio-environmental systems because they have modified environmental conditions because of human activities (Sukopp, 2004; Kinzig et al., 2005). As functional traits respond to

environmental conditions, functional diversity is a tool to understand and predict the consequences of biotic change produced by humans in cities because it explains plant compositional changes in these new environmental gradients (Petchey and Gaston, 2006). Williams et al. (2009) proposed a set of four filters that shape plant communities persistence in cities: habitat transformation, habitat fragmentation, urban environment, and human preferences. These filters act simultaneously, and normally they change environmental conditions within urban areas, by modifying the natural environment towards a warmer and drier habitat (Sukopp, 2004). These changes allow the gain of more suitable species (native or exotic), the loss of less suitable species (usually native ones), and thus creates new biotic communities (Williams et al., 2009).

Public green areas in city neighbourhoods are especially prone to display the combined effect of both environmental and anthropogenic factors, given the influence of the environmental gradient (McDonnell et al., 2012), neighbour area, and the different strategies of stewardship that they have (bottom-up/top-down strategies, *sensu* Kinzig et al., 2005). Moreover, public areas combine spontaneously growing plants (wild plants), some cultivated ornamental plants (e.g. trees and shrubs), and ornamentals escaped from surrounding house gardens. Ornamental species are strongly determined by citizens' and public administrators' (Larson et al., 2009; Kendal et al., 2012) while those with traits to thrive in urban areas will persist and grow spontaneously (Williams et al., 2009; Bigirimana et al., 2012; Maurel et al., 2016). However, little information exists on how different anthropogenic factors (such as habitat type, socioeconomic status, disturbance, the proportion of exotic plant species), and environmental characteristics (like soil C/N) affect functional diversity in its composition and structure.

In a review in plant functional diversity, Williams et al. (2015) found that most of the research focused on indicators (such as Ellenberg's numbers) (Knapp et al., 2008), Grime's CSR classification (1988) (Lososová et al., 2006), qualitative whole-plant traits (like growth and life form) (Dolan et al., 2011), and qualitative regenerative traits (such as pollination, dispersal mode, etc.) (Duncan et al., 2011; Knapp et al., 2012). In this context, it has been suggested that urbanisation shifts the conditions of the realised ecological niche of plants towards light demanding, warmer, drought tolerant, alkaline, and nutrient rich soil conditions (Williams et al., 2015), narrowing the functional diversity of the urban communities. Nevertheless, environmental and anthropogenic effects have been hard to separate from each other as filters of plant trait variation (Knapp et al., 2012) because, their effect may vary at the local scale (Lefcheck et al., 2015) and affect functional traits simultaneously (Williams et al., 2009).

In this study, we explore patterns of functional diversity of wild vascular plants in lawns of public green areas Valdivia, a medium-sized city, and hotspot of biodiversity in North Patagonia

(Dinerstein et al., 1995; Olson and Dinerstein, 2002). Lawns are a dominant land cover in green areas of cities around the world, mainly in those with occidental influence (Ignatieva and Stewart, 2009). Lawns are ubiquitous in private gardens, private and public parks and road verges (also known as easement garden, street-side garden, etc.). Thus, they are the closest vegetation type for people in their everyday life (Weber et al., 2014). The variety of conditions in which lawns grow made them an interesting and relevant vegetation cover to study the human effect on urban plant communities. In this context, we explore three functional traits related to species persistence and performance (height, LDMC and SLA), of wild plant communities in lawns of residential areas. We evaluate the trait response to multiple predictors of anthropogenic (socioeconomic status, habitat type, disturbance, proportion of exotic plant species,) and environmental nature (soil C and N content), in order to know how these factors affect the persistence and performance of plants in the public green areas of Valdivia. Specifically, we aim to: a) Assess the persistence and performance response of plants to socio-environmental conditions, as the patterns of functional composition (CWM) and structure (FD_Q) of the community. b) Disentangle which factors (anthropogenic or environmental ones, single or multiple) drive the patterns of functional diversity composition and structure for persistence and performance traits and the strength of that relation. We expect to find a poor functional diversity in the area by a narrow set of CWM values and low FD_Q values in general and in particular, due to the habitat filtering mechanisms described above.

2. Methods

2.1 Study area

We selected the city of Valdivia (39°48'30"S, 73°14'30"W) as an example of a growing medium-sized urban area in South America (Figure 1). The city is located about 15km east of the Pacific Ocean, at the confluence of three rivers (*Calle-Calle*, *Cruces*, and *Valdivia*). The climate is wet-temperate with a strong oceanic influence (Di Castri and Hajek, 1976). The mean annual temperature is 12.2°C with a maximum mean monthly average of 23°C in January and a minimum mean monthly average of 4.6°C in August. There is rainfall throughout the year with peaks in winter months (June-August). The mean annual precipitation is ~2500 mm and the relative humidity ranges between 67 and 89% (Fuenzalida, 1965; Amigo and Ramírez, 1998). The city is in a geological area of well-drained Ultisols (red clay soils) of volcanic origin on metamorphic bedrock (Gerding et al., 2006).

Valdivia is one of the oldest cities in Chile. Founded in 1552 by the Spanish colonisers, the city set up based on a grid plan in an area with a long history of human settlement by indigenous people

(Montt Pinto, 1971; Navarro, 2012). With nearly 130,000 inhabitants in 2002, Valdivia is a mid-size city (Instituto Nacional de Estadísticas, 2005; UN-Habitat 2015), with a density of 151.22 inhabitants per square kilometre (Instituto Nacional de Estadísticas, 2010). The city is located in the north-temperate biogeographic region of Chile (Bannister et al., 2012) and it is surrounded by wetlands under severe pressure from urban sprawl, due to areas needed for housing development and/or informal wastelands (Skewes et al., 2012; Pauchard and Barbosa, 2013). More than half of the surface in Valdivia is covered by green areas (51%), of which around 12% are under municipal stewardship (Silva et al., 2015). Exotic tree plantations and to a minor degree agroforestry activities of small owners dominate the rural areas near to the city (Seis et al., 2014). Detached houses and low buildings are scattered on both banks of Calle-Calle and Valdivia Rivers and are characteristic of the city. Historical buildings and buildings over four-story are located in the city centre, and new neighbourhoods in the periphery (Figueroa et al., 1998).

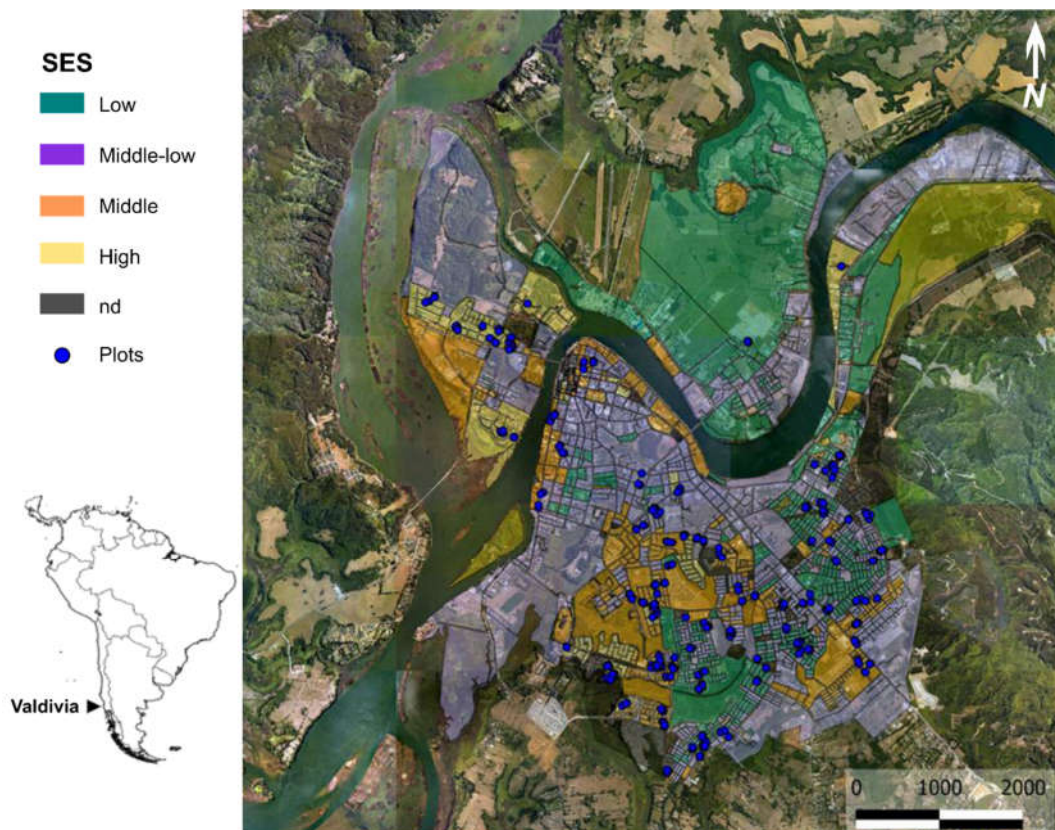


Figure 1: Administrative area of the city of Valdivia (39°48'S, 73°14'O), Chile. Colour polygons show the socioeconomic status classification. Blue dots mark sampled areas of the city. The inset shows the position of the study area relative to South America. Satellite image: courtesy of O. Barbosa.

2.2 Sampling

We selected anthropogenic and environmental direct factors that represent the social aspect of cities and human-made public green areas to explain trait variation and persistence of vascular plants in the city. Accordingly, we chose an approach that includes multiple predictors, as an index for socioeconomic status, lawn habitat type, disturbance, Nitrogen content in soil, Carbon content in soil, and soil C/N ratio (Table 1).

Table 1: List of variables selected for this study and their descriptions.

Type of variable	Variable		Description
Response	Community weighted mean	CWM	Abundance-weighted mean trait values by species present in a community.
	Rao's Q	FD _Q	Quadratic entropy index per plot for each lawn habitat type and socioeconomic status.
Predictor	Socioeconomic status	SES	A five quintiles classification from the National Agency for Statistics of Chile (INE) based on characteristics of the household, head of the household, and housing
	Habitat type	HT	Classification of lawn habitat according to their structure, ownership, and use. Three types of habitat type recognised for this study.
	P _{exo}	Proportion	Proportion of exotic vascular plants present in each plot based on the total number of plant species. The classification of plants species is relative to their geographical origin and the presence in the study area.
	N	Percentage	Average of the percentage of Nitrogen content in the upper layer of soil (10cm).
	C	Percentage	Average of the percentage of Carbon content in the upper layer of soil (10cm)
	C/N	Proportion	Proportion of total Carbon and Nitrogen present in the upper 10cm of soil.
	Disturbance	Percentage	Percentage of bare soil in sampled lawn patches due to disturbance by trampling by pedestrians.

2.2.1 Anthropogenic predictors

We explore the anthropogenic factors affecting urban biodiversity (Kowarik, 2011), such as socioeconomic and related factors to represent the socio-environmental aspects of cities. First, we selected a proxy for socioeconomic status ("SES" hereafter) of each residential area in the city. We hence applied the index for welfare classification of the National Agency for Statistics of Chile (INE). This index is based on characteristics of the household, head of the household, and housing (Table S1) collated by the INE with a nonlinear principal component analysis (*the Gifi System of Descriptive*

Multivariate Analysis, details in Instituto Nacional de Estadísticas, 2005). All data were georeferenced, gathered at the resolution of street blocks of residential neighbourhoods from the latest National Census (year 2002), and updated by the *Observatorio Urbano* bureau to the year 2005 with information of the Ministry of Housing and Urban Development (MINVU). Five quintiles size were classified by the National Agency for Statistics of Chile (Instituto Nacional de Estadísticas, 2005). We selected the four upper socioeconomic quintiles (2nd=low, 3th=middle-low, 4th=middle and 5th=high status) to represent a gradient of socioeconomic conditions throughout the city (Kinzig et al. 2005). The first quintile (1st= lowest SES) was not selected due to the low number of replicates (Figure 1).

As a second factor, we defined lawn habitat types in public green areas (“habitat types” hereafter). Common green areas in residential streets are road verges. A road verge is a strip of land between the road and the sidewalk, a strip of land between sidewalk and front garden, or in front of houses. Road verges are of public use and municipal ownership. They can have turf grasses, herbs, shrubs or trees. Their name varies depending on the country, for example, easement garden (USA), street lawns or grass verge (the UK and New Zealand). We identified two types of road verges, according to the area that they cover and the position and use that they have (Table 2). Other common green areas typical in Latin-American countries are squares (“plazas”). Accordingly, we defined three habitat types in public green areas: narrow lawns in road verge along sidewalks (NV), broad lawns in road verges along sidewalks (BV), and lawns of squares (SQ) (Figure 2).

We selected disturbance as our third anthropogenic predictor, as it is a habitat-related factor. Urban areas have high levels of man-made disturbance, which can have an effect selecting the species with traits that allow them to survive (Brunzel et al., 2009). The three habitat types defined previously should reflect a gradient of intensity of disturbance, according to their use by pedestrians. We estimated disturbance visually as a percentage of bare soil due trampling in the surveyed patches.

Lastly, we considered the proportion of exotic plant species as an additional predictor for trait variation. Previous studies noted a high proportion of exotic species in urban areas (Kühn et al., 2004; Lososová et al., 2012). Moreover, Palma et al. (2016) showed for 11 cities in North America, Asia and Oceania the prevalence of exotic species with traits that allow them to cope with the new environmental conditions. Therefore, we included the proportion of exotic plant species as a relevant factor that may explain the composition of functional traits in this city.

2.2.2 Environmental predictors

We selected content of Nitrogen, and Carbon in soil, and estimate the C/N ratio as environmental factors considering their relevance to plant growth (Garnier and Navas, 2012), simplicity to measure, and their effects on structure and composition for plants in urban areas (Hill et al., 2002; Godefroid et al., 2007; Knapp et al., 2009). We collected one equal-sized full teaspoon soil sample (approximately 5 grammes) from the upper soil layer at five different points in each plot, and we combined them to have one sample per plot. Afterwards, we stored the soil samples in plastic bags and frozen them in a refrigerator firstly, then dried in an oven at 60° C for at least 72 hours. Then, we homogenised and sieved each sample and determined the element concentration (%) of N and C, and the proportion of Carbon and Nitrogen (C/N) for each soil sample with a Vario EL III CNS Elemental Analyzer at 950°C.

2.2.3 Plot selection

We crossed SES of neighbourhoods and habitat type to select sampling areas. First, we did a stratified random sampling over neighbourhoods to select specific blocks for a certain habitat type. In order to control the time since neighbourhood establishment and avoid areas in early successional stages, in which most of the species could be annuals, we selected only those who were already present by 2002. We excluded all sites with a distance of ≤ 130 m to wetlands or urban forests prevent a potential effect of green areas than the selected as a potential propagule source of species. Next, in each block, we selected arbitrarily ten plots in habitat like areas and georeferenced each plot with a Garmin Oregon 400t GP. We surveyed 120 plots of 20 m² after visually checking for homogeneity of conditions (e.g. avoiding large paved areas or recently mown sites).

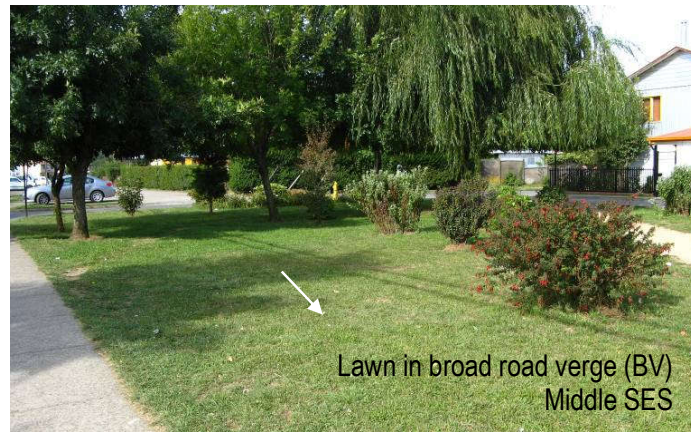


Figure 2: Examples of the green areas associated with habitat types sampled around the city of Valdivia: a) narrow lawns in road verge (NV) in high SES, b) broad lawns in road verge (BV) in middle SES, and c) lawns in square (SQ) in low SES. The pictures show three of the four SES in which the habitat types were sampled.

Table 2: Habitat types selected, including their general characteristics and main differences. All habitat types belong to public areas, although unclear regulation and social factors may affect their maintenance.

Habitat type	Description	Area	Vegetation type	Management	Public role/use
Road verges (NV)	Narrow lawns between sidewalk and road, or sidewalk and front house.	0.5 - 2 m wide, variable length	Lawns with trees or other vegetation planted by the municipality or by neighbours. Spontaneous herbs and shrubs.	Stewardship (mowing) shared between municipality and residents. No clear regulation.	Ornamental or domestic use (provisional storing of firewood or garbage).
Broad road verges (BV)	Lawns between sidewalk and road of more than 2m broad and commonly located close to houses entrance.	40-20000m ²	Lawns with trees or other vegetation planted by the municipality or by neighbours. Spontaneous herbs and shrubs.	Stewardship (mowing) shared between municipality and residents. No clear regulation.	To delimitate properties, to store provisionally firewood or garbage or to improve the appearance of the front house area and neighbourhood. Car parking.
Square and "pocket" parks (SQ)	Lawns areas generally provided with playground and benches. Generally have a square shape. "Pocket" parks are small squares with minimum facilities	300-20000 m ²	Mix of lawns and areas with flowerbeds and/or trees.	Municipal stewardship (mowing, general maintenance)	Playground and meeting point for leisure or other activities.

2.2.4 Trait sampling

Based on Kleyer et al. (2008), we chose *a priori* a set of traits related to persistence: plant height, leaf dry matter content (LDMC), and specific leaf area (SLA). We collected plant leaves samples during summers of 2010-2012. We surveyed and identified to species level all spontaneous (i.e. wild) vascular plants (those that arrived at a very location, germinated and grew on their own account) inside each plot, following Zuloaga et al. (2008) and Matthei et al. (1995). Then, we estimated cover-abundance for each species with Londo's scale of vegetation (Londo, 1976). In each plot, we sampled leaf traits collecting two leaves (incl. petioles, if applicable) exposed to the light of each of ten randomly selected individuals per species, and stored them in hermetic plastic bags on coolers to keep them turgid, following LEDA standards as far as possible throughout all following stages (Kleyer et al., 2008). In the case of rare species (three individuals of the same species per plot), we sampled a minimum of three individuals (two leaves from each). For small leaves, we collected a branch of the plant separating the leaves before other measures in the lab. In case of heterophyllous species (plant species with dissimilar leaves on one plant), we collected two leaves from the base and the stem. For plants with compound leaves, we included the rachis in all measurements. We sampled at mornings and near sunsets to avoid loss of weight due to summer day temperatures.

We measured plant height (hereafter "height") of each individual from the base to the highest photosynthetic tissue of the plant and then averaged per species ('Canopy height' in Kleyer et al., 2008). Leaf dry matter content (LDMC), and specific leaf area (SLA) were calculated after measurement of leaf area and leaf weight averaged per species present per plot (Table 3). We weighted leaf samples in a digital scale with a range of 0.01g, and with an analytical scale with a sub-milligram range for those small leaves with weight ≤ 0.01 g. We scanned all leave samples on a flatbed scanner (HP Scanjet Photo Scanner) at 300dpi, and for small leaves (<1 cm) at 600 dpi. In the case of very large leaves (>30 cm), we cut them into pieces to fit the scanner size and measured immediately. We measured leaf area with *ImageJ* software, which allowed us to automatize the image analysis (Schneider et al., 2012). Finally, we measured leaf dry mass with the leaves samples stored in paper bags identified with species and plot names and then dried in an oven at 60°C for at least 72 hours. We sampled ~ 15,600 individual plants in total. We were not able to identify to species level those hybrid species and species that were in vegetative state at the moment of the sampling. Therefore, we ended up with a reduced set of species to analyse and we did not consider part of the total community (Májeková et al., 2016).

Table 3: Overview of plant functional traits selected and their links with environmental variables and ecosystem processes (EP) and services (ES). For details about trait and ecosystem services, see Díaz et al. (2013)

Trait	Description	Related environmental variables	Ecological strategy	Life- history processes	Influenced EP	Relation with EP	Influence on ES
Height (cm)	Plant height, considering the distance between the base of the plant to the highest photosynthetic structure	-Nutrients -Soil moisture -Temperature	-Plant resource acquisition -Disturbance response	-Reproductive success -Competition	-Plant transpiration	+	-Ecosystem hydrological regulation & climate buffering
Leaf dry matter content (LDMC) (mg/g)	Ratio of leaf dry mass to leaf fresh mass	-Nutrients -Temperature	-Plant resource use -Plant resource conservation -Disturbance response	-Establishment -Competition -Plant growth	-Litter decomposability	-	-Nutrient availability & soil fertility
					-Plant palatability to herbivores	-	-Trophic transfer as food for other organisms
					-Plant flammability	+	-Ignition risk and fire propagation Soil fertility -Risk of fire for human settlements
Specific leaf area (SLA) (mm ² /mg)	Ratio of leaf area to leaf dry mass	-Light -Soil moisture -Temperature -Nutrients	-Plant resource use -Plant resource conservation -Disturbance response	-Establishment -Competition -Plant growth	-Litter decomposability	+	-Nutrient availability & soil fertility
					-Plant potential relative growth rate	+	-Primary productivity and food provision
					-Plant palatability to herbivores	+	-Trophic transfer as food for other organisms

2.3 Data analysis

2.3.1 Functional diversity assessment

We chose community-weighted mean trait values (Garnier et al., 2004), and Rao's quadratic entropy (Botta-Dukát, 2005) to describe the functional diversity of the community. CWM informs about the central tendency of trait value in a community, whereas FD_Q express the dissimilarity between trait compositions in a given and among different communities. Thus, these indices complement each other in the measurement of trait structure in plant communities (de Bello et al., 2010; Ricotta and Moretti, 2011) and account for species abundance.

We estimated the functional composition of sites with the community-weighted mean value per trait (CWM) as [1]:

$$CWM = \sum_{i=1}^S p_i x_i \quad [1]$$

, where p is the relative abundance of species i , S is species richness, and x is the trait value of species i (Garnier et al., 2004). The fundament of this approach is the mass-ratio hypothesis of Grime (Grime, 1998), which states that most abundant species will influence strongly ecosystem properties. To express that influence, trait values per species are weighted by their relative abundance.

We aimed to identify the major sources of variation of CWM traits using a principal components analysis (PCA) (function *prcomp*, ver.3.2.4; (R Core Team, 2016), with mean-trait values per species, per site as replicates (120 replicates in total). CWM trait values were standardized (mean=0, variance=1) before the analysis. Subsequently, considering the SES and habitat type as predictors, we analysed the scores of the distribution of trait values per site in the first principal component (PC1) with a two-way ANOVA. To determine significant differences between the groups, we applied a posthoc Tukey's honest significant difference (Tukey HSD, Tukey, 1949).

We calculated the Rao's quadratic entropy index (FD_Q) as a measure of functional dispersion (Rao, 1982b; Botta-Dukát, 2005). This index is based on dissimilarity measured as the sum of the distances between pairs of species in a given community and accounts for the relative abundance of species (Weiher, 2010). Contrary to other proposed functional indices, such as functional richness (FRic), functional evenness (FEve) (Villéger et al., 2008), and functional dispersion (FDis) (Laliberté and Legendre, 2010), FD_Q is independent of species richness. FD_Q and FDis estimate the dispersion of traits and thus are highly correlated. However, they differ, as FD_Q is the expected dissimilarity between the weighted traits of two randomly selected individuals from a given assembly (Ricotta and Moretti, 2011), while FDis measures the distance of weighted trait per species to a weighted centroid (Laliberté and Legendre, 2010). In addition, if the distance method used is the same, FD_Q allows comparisons of various facets of biodiversity as taxonomic, functional, and phylogenetic diversity. Moreover, FD_Q combines measures of functional richness and functional divergence covering a broad spectrum of the three components of functional diversity (Mouchet et al., 2010).

To calculate FD_Q , we need three matrices: trait values per species, species abundances per site, and trait distances. Then, we calculated Rao's Q with the following equation [2] (Rao, 1982a; Botta-Dukát, 2005):

$$Q = \sum_{ij}^S d_{ij} p_i p_j \quad [2]$$

, where d is the difference between trait values of species i and j , S is the number of species, and p is the weighted relative abundance of species. The difference between species in the trait distance matrix gives information about the occupied volume of trait space (Weiher et al., 1998), thus FD_Q values are close to zero when species have the same trait values. In contrast, high FD_Q values indicate higher trait community dissimilarity. Species with different trait values will hence be more distant to each other and thus will have higher values of FD_Q (Pavoine et al., 2005). Additionally, FD_Q increases when the most abundant species have extreme trait values.

To assess the amount of trait diversity, we computed a multi-trait FD_Q index for the three log transformed traits in each of residential public lawns sampled (120 sites in three habitat types by four SES, pooled together). We also computed the index for functional evenness (FEve) to fully cover other aspects of functional diversity and characterise the functional diversity of the community. For both indices, we used the function *dbFD* from the R package *FD* (ver.1.0-12) (Laliberté and Legendre, 2010), and a Euclidean distance. Then, we analysed the variation of each functional diversity index with a two-way ANOVA, considering as explanatory variables SES and habitat type. If there were significant effects, we applied a posthoc Tukey's HSD test ($\alpha=0.05$) to detect group differences.

Further, we analysed leaf traits and height separately to disentangle the different drivers on each trait and to assess the effects on ecosystem processes (Weiher, 2010). A single trait approach exposes any effect that could be masked by the multi-trait approach (e.g. due to trade-offs), giving the chance to analyse each trait case by case. In addition, we can take a detailed look on the variation for each trait. This is especially relevant for LDMC and SLA, as their opposite tendencies could annulated each other. We computed separately Rao's Q values for each of the three traits selected with the function *dbFD* from the R package *FD* (ver.1.0-12) (Laliberté and Legendre, 2010), with standardised trait data (mean=0 and variance = 1), and a Euclidean distance for the distance matrix.

2.3.2 Drivers of functional diversity

To assess which factors drive the functional composition of urban plant communities, we explored the variability of CWM values and FD_Q by a set of environmental and anthropogenic variables (table 1) with generalised linear mixed-effects models (GLMMs). This method allows the analysis of fixed effects (i.e. the levels of interest for the study), and random effects to control for random (or unwanted) covariates (Bolker et al., 2009). We tested for correlation between pairs of explanatory variables with a Pearson's product-moment correlation test to avoid model distortions due to collinearity. From the seven predictors selected (table 1), only average content of soil Carbon and average content of soil Nitrogen correlate (0.93, $p < 2.2e^{-16}$), so we kept Nitrogen in our models as a sensitive predictor.

We generated seven global models with the function *lmer* of the package *lme4* (ver. 1.1-12) (Bates et al., 2015), with a different combination of all the relevant explanatory variables for trait CWM (three models), and Rao's Q (four

models). We standardised all explanatory variables to zero mean and unit standard deviation to obtain comparable standardised coefficient estimates (Schielzeth, 2010). To consider the variability of weather conditions among sampling years we choose "Sampling year" as a random intercept (random effect) (Zuur et al., 2009). We created a model set for each response variable based on a multimodel inference approach (Burnham and Anderson, 2003). For that, all possible fixed effect structures were fitted automatically via a stepwise inclusion of fixed effects with the function *dredge*, package MuMIn (ver. 1.15.6) (Barton, 2012). We selected the best-fitted models based on Akaike Information Criterion corrected for small sample size (AICc), ranking as best model those with smallest AICc. AICc is recommended when there are less than 40 observations per parameter (Anderson et al., 2001). AIC values rank competing models in terms of information loss. Next, we set a selection criteria based on $\Delta AICc$ to rank and selected models set to perform model averaging. $\Delta AICc$ indicates how much better a model is than the following one with $\Delta AICc$ close to zero as better-supported ones than those with higher values. Models with a value of $\Delta AICc \geq 9$ have little support, thus we define $\Delta AICc \leq 2$ as the limit criteria for our model selection, following Burnham et al. (2010). Once the model set for each response variable was defined, we performed the model averaging of predictors with the function *model.avg*, package MuMIn (ver. 1.15.6) (Barton, 2012), to obtain the coefficient estimates for each predictor and their interactions with a full average ("zero method") method (Burnham and Anderson, 2003; Grueber et al., 2011). Since differences in $\Delta AICc$ between models can be small, for each set of models selected we assess the probability of model to be the best-approximating model with Akaike weights (ω_i). ω_i ranged between zero, for models with poor fit, and one indicating those with the best fit. With the ω_i values, we estimated the evidence ratio (ER = ω_i/ω_j) as an empirical value to evaluate how much more likely the best model is compared to another. The relative importance of each predictor was calculated as the sum of ω_i for each model in which the variable appears, with the highest importance scoring close to 1. This measure is relevant as variables not included in the best model may have an important role that is quantified with the relative importance (Anderson et al. 2001). For complex systems as a city, in which we may have a mix of explanatory variables and with interactions, ω_i assess the relevance of each variable rather than a single model, especially if there is no model with a strong evidence for its selection ($\omega_i > 0.9$) (Symonds and Moussalli, 2010).

We performed all statistical analyses with the software R 3.2.4 (R Core Team, 2016), and transformed trait values to normalise them. Before analyses, we checked for spatial autocorrelation of the residuals among sites using Moran's I coefficient, tested for statistical significance using 1000 permutations as implemented in the package "ncf" (Bjornstad, 2013). Afterwards, we corrected for multiple testing using Holm's (1979) method. We did not find a signal of spatial autocorrelation, though.

3. Results

3.1 Characterization of functional diversity composition and structure

3.1.1 Functional diversity composition

In the PC analysis of CWM trait values, the first two components extracted the most relevant information of the trait space (84% of the trait variability). The PCA biplot showed for the first axis opposing trends of the two leaf traits (LDMC and SLA), which are almost perpendicular on height, hence capturing different aspects of the trait space. Moreover, height explained most of the variation in the second component (Figure 3). PCA scores of persistence and performance traits mean values (CWM) were similar within the gradient of anthropogenic factors. They showed no significant differences with respect to SES (two-way ANOVA, $F_{3, 108} = 1.23$, n.s., Table S2), habitat type ($F_{2, 108} = 1.68$, n.s.), nor for the interaction between SES and habitat type ($F_{6, 108} = 1.28$, n.s., Table S2). Thus, the composition of traits did not vary across the gradient of anthropogenic factors.

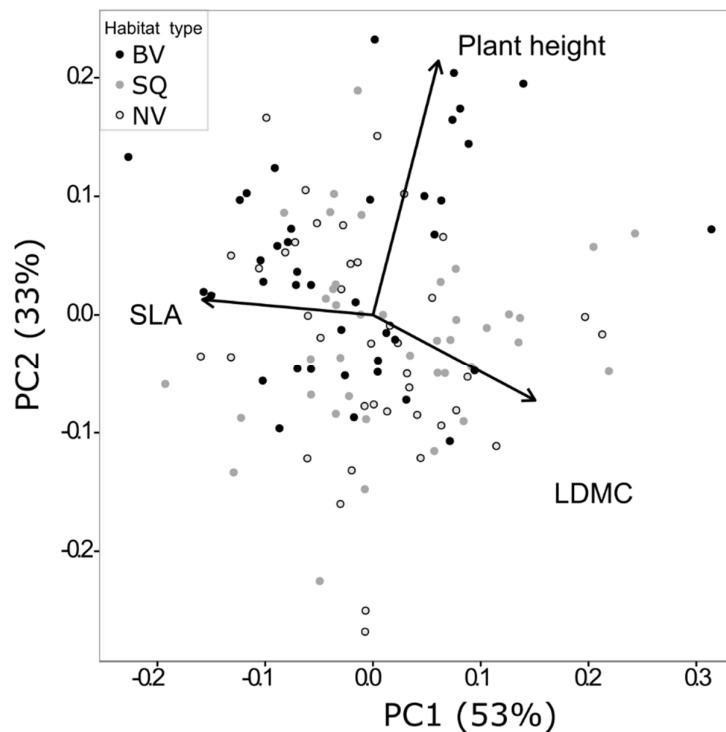


Figure 3: PCA biplot representing the principal sources of variation in the functional composition of the community, based on CWM trait values per site for LDMC, height and SLA at the plot level, sampled across different SES and habitats types in the city of Valdivia (Chile). Arrows represent gradients of leaf dry matter content (LDMC), specific leaf area (SLA) and height on the first two principal components. Grey scale identify the three habitat types evaluated: BV= broad lawns in road verge, NV= narrow lawns in road verges, and SQ= lawns in squares.

3.1.2 Functional diversity structure

FD_Q differed significantly among SES. FD_Q values in the high SES were significantly higher than in the lower SES (Tukey HSD test, figure 4, table 4,). This suggests that the “high” SES is functionally more diverse than the lower SES, having a wider variety of traits values. On the contrary, FEve showed no significant relations neither with SES nor with habitat type (two-way ANOVA, n.s., table 4 and figure 4). Finally, the three indices showed in general a community with no variation in their composition (mean values, CWM) across neighbourhoods, neither across habitat, but with a heterogeneous abundance distribution (FEve) not related to the anthropogenic gradient, and a divergence (FD_Q) pattern between communities related to the SES.

Table 4: Two-way ANOVA on the responses of functional diversity indices Rao’s Q (FD_Q), and functional evenness (FEve) to socioeconomic status (SES) and habitat type across sample sites plots of public lawns in Valdivia (Chile).

Factor	d.f.	FD _Q			FEve		
		F-stat	P value		F-stat	P value	
SES	3	8.846	2.70E-05	***	1.47	0.226	n.s
Habitat	2	0.548	0.58	n.s.	0.74	0.478	n.s.
SES * Habitat	6	1.564	0.165	n.s.	0.52	0.792	n.s.
Residuals	108						

n.s.= $p>0.05$, *= $p<0.05$; **= $p<0.01$; ***= $p<0.0001$

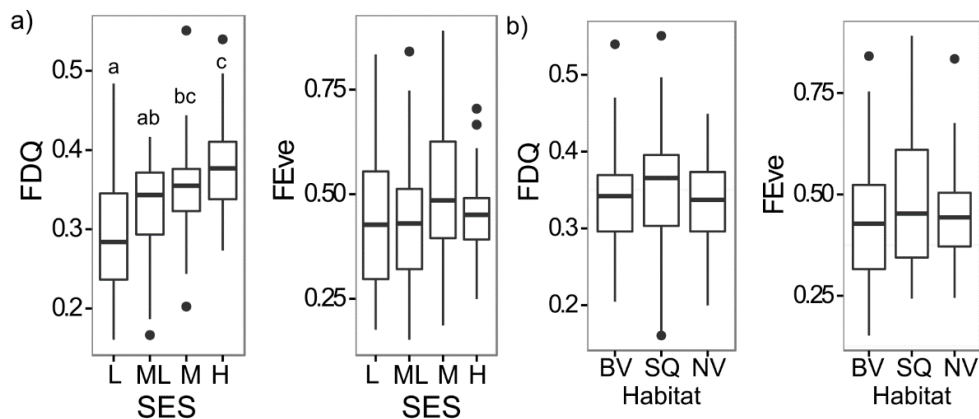


Figure 4: Boxplot of the effect of anthropogenic factors on functional diversity indices (FD_Q and FEve) per site, showing the standard error as a box (SE), median values as a horizontal line, and standard deviation as whiskers. a) FD_Q values differ across neighbours' socioeconomic status (two-way ANOVA, $F_{3,108} = 5.96$, $p < 0.001$). FEve values have no significant differences between groups. b) There is no significant relation of both indices with Habitat type. Groups identified with the same letter are not significantly different considering $\alpha = 0.005$. Legend for socioeconomic status (SES): L=Low, ML= middle-low, M= middle, H= high.

3.2 Drivers of functional diversity composition and structure

3.2.1 Drivers of functional diversity composition: CWM

We applied full model averaging across all plausible model. The multi-model inference approach showed the complex relation of predictors driving CWM trait responses, as there was not a single driver that could explain CWM traits variation in the study site (Table 5). C/N content in soil was not relevant for the subset of models, indicating minor importance as a driver in our model's sets, as well as several interactions considered in global models.

In the case of LDMC^{CWM}, the analysis showed that the anthropogenic factors SES, HT, and their interactions were the most influential variables for LDMC^{CWM}. Both factors appeared in all the models for this trait (relative importance=1), suggesting a strong relationship between anthropogenic drivers and LDMC values. Moreover, three of the four relevant interactions of factors detected for the models were relevant for LDMC^{CWM} (Table 5 and 6). Disturbance had a 65% of relative importance to HT and SES and appeared in three of the four models selected for LDMC^{CWM} (Table 6). High SES had the highest parameter estimated value; affecting positively LDMC^{CWM}, while the interactions between HT: NV and every level of SES resulted in negative estimates (Table 7).

For SLA^{CWM}, N and HT: N had the highest relative importance for the models (1), followed by a 24% of HT and P_{exo} (Table 5). The best model for SLA had a *wi* of 0.52, the best of all the set models obtained for CWM traits. However, all confidence intervals of the estimates included zero, therefore there was little evidence that the predictors analysed affect the SLA^{CWM} (Table 7).

Finally, for height^{CWM}, P_{exo} was the most important driver for the model subset (1), followed by an 81% of N, 68% for SES, and HT (66%) relative to P_{exo} (Table 5). Disturbance had a minor importance in the subset of models (11%, Table 6). P_{exo} had the highest coefficient estimate value, affecting positively height^{CWM}, followed by habitat type NV. SES had a negative effect on height^{CWM}, as suggested by estimate parameters (Table 7).

Table 5: Importance values for parameters in candidate models for CWM traits values and FD_Q for multiple and single traits. Importance values are calculated considering the final model subset, after model averaging.

Model parameter	LDMC ^{CWM}	SLA ^{CWM}	height ^{CWM}	FD _Q	LDMC ^{FD_Q}	SLA ^{FD_Q}	height ^{FD_Q}
HT	1	0.24	0.66	-	1	0.39	0.23
SES	1	-	0.68	1	1	-	1
Disturbance	0.65	-	0.11	0.21	-	0.37	1
N	-	1	0.81	0.23	0.87	1	1
P _{exo}	0.14	0.24	1	1	-	-	1
HT:N	-	1	-	-	0.41	-	0.37
HT:SES	1	-	-	-	1	-	-
SES:Disturbance	0.5	-	-	-	-	-	-
SES:P _{exo}	0.14	-	-	-	-	-	-

HT: Habitat type; SES: Socioeconomic status; N: average proportion of Nitrogen; C/N: proportion C and N in soil; P_{exo}: proportion of exotic plant species.

Table 6: Most parsimonious linear mixed models of CWM traits. The table shows only models with substantial support ($\Delta AICc < 2$) (K. P. Burnham and Anderson 2004). "Sampling year" was the random effect in every model. ω_i = Akaike weights for models fit; ER= evidence ratio; acc ω_i = accumulative ω_i .

Response variable	#	Fixed explanatory variables	K	LogL	AICc	$\Delta AICc$	ω_i	ER	acc ω_i
LDMC ^{CWM}	1	HT*SES+ Disturbance+ SES:Disturbance	18	-148.95	324.95	0	0.36	1.0	0.36
	2	HT*SES	14	-151.15	324.98	0.03	0.35	1.0	0.71
	3	HT*SES+ Disturbance	15	-152.16	326.66	1.72	0.15	2.4	0.86
	4	HT*SES+Disturbance+P_exo+SES:Disturbance+SES:P_exo	22	-147.48	326.86	1.91	0.14	2.6	1
SLA ^{CWM}	1	N+HT:N	6	-168.25	340.8	0	0.52	1.0	0.52
	2	N+HT:N+P_exo	7	-169.38	342.33	1.53	0.24	2.2	0.76
	3	HT*N	8	-168.11	342.34	1.54	0.24	2.2	1
height ^{CWM}	1	HT+SES+N+P_exo	10	-142.53	307.09	0	0.24	1.0	1
	2	N+P_exo	5	-148.49	307.51	0.42	0.2	1.2	0.44
	3	HT+SES+P_exo	9	-143.97	307.6	0.51	0.19	1.3	0.63
	4	SES+P_exo	8	-145.41	308.13	1.04	0.14	1.7	0.77
	5	HT+N+P_exo	7	-146.71	308.42	1.34	0.12	2.0	0.89
	6	HT+SES+N+P_exo+Disturbance	11	-142.13	308.73	1.64	0.11	2.2	1

HT: Habitat type; SES: Socioeconomic status; N: average proportion of Nitrogen; C/N: proportion C and N in soil; P_exo: proportion of exotic plant species.

Table 7: Summary parameter estimates and standardised effects sizes for models with $\Delta_i \leq 2$ after model averaging for the effect of each predictor on the respective CWM traits evaluated. For categorical predictors "SES" "Low socioeconomic status" is the reference category. For categorical predictor "Habitat type", the reference is "Broad road verge" (BV). C.I.: Confidence interval. Relative importance (I_{ω_i}) is the sum of the AICc weights (ω_i) of the models after model selection and averaging.

#	Parameter	LDMC ^{CWM}					SLA ^{CWM}					height ^{CWM}				
		β	S.E.	C.I.	C.I.	I_{ω_i}	β	S.E.	C.I.	C.I.	I_{ω_i}	β	S.E.	C.I.	C.I.	I_{ω_i}
1	Intercept	-0.81	0.32	-1.44	-0.19	-	-0.05	0.11	-0.28	0.17	-	0.10	0.23	-0.36	0.56	-
2	Habitat type SQ	0.58	0.40	-0.20	1.37	1.00	-0.06	0.15	-0.67	0.21	0.24	0.08	0.16	-0.24	0.49	0.66
3	Habitat type NV	0.92	0.39	0.15	1.69	1.00	0.04	0.13	-0.30	0.59	0.24	0.33	0.28	0.13	0.87	0.66
4	SES Middle-low	0.58	0.42	-0.26	1.41	1.00	-	-	-	-	-	-0.14	0.20	-0.64	0.22	0.68
5	SES Middle	0.54	0.41	-0.28	1.36	1.00	-	-	-	-	-	-0.35	0.31	-0.97	-0.06	0.68
6	SES High	1.92	0.48	0.98	2.86	1.00	-	-	-	-	-	-0.44	0.37	-1.16	-0.14	0.68
7	Disturbance	0.18	0.19	-0.06	0.63	0.65	-	-	-	-	-	-0.01	0.04	-0.25	0.09	0.11
8	N	-	-	-	-	-	0.20	0.20	-0.18	0.59	1.00	-0.13	0.09	-0.31	0.00	0.81
9	P_exo	-0.07	0.19	-0.92	-0.07	0.14	0.02	0.06	-0.11	0.26	0.24	0.37	0.10	0.17	0.57	1
10	Habitat type SQ:N	-	-	-	-	-	0.07	0.24	-0.40	0.54	1.00	-	-	-	-	-
11	Habitat type NV:N	-	-	-	-	-	-0.50	0.26	-1.01	0.02	1.00	-	-	-	-	-
12	Habitat type SQ:SES Middle-low	0.15	0.55	-0.95	1.25	1.00	-	-	-	-	-	-	-	-	-	-
13	Habitat type NV:SES Middle-low	-1.63	0.55	-2.72	-0.55	1.00	-	-	-	-	-	-	-	-	-	-
14	Habitat type SQ:SES Middle	0.05	0.57	-1.08	1.18	1.00	-	-	-	-	-	-	-	-	-	-
15	Habitat type NV:SES Middle	-1.17	0.55	-2.26	-0.08	1.00	-	-	-	-	-	-	-	-	-	-
16	Habitat type SQ:SES High	-0.96	0.58	-2.12	0.20	1.00	-	-	-	-	-	-	-	-	-	-
17	Habitat type NV:SES High	-1.27	0.57	-2.39	-0.14	1.00	-	-	-	-	-	-	-	-	-	-
18	SES Middle-low: Disturbance	-0.27	0.33	-1.07	-0.04	0.50	-	-	-	-	-	-	-	-	-	-
19	SES Middle: Disturbance	-0.21	0.27	-0.88	0.02	0.50	-	-	-	-	-	-	-	-	-	-
20	SES High: Disturbance	0.16	0.32	-0.46	1.11	0.50	-	-	-	-	-	-	-	-	-	-
21	SES Middle-low: P_exo	0.08	0.23	-0.07	1.19	0.14	-	-	-	-	-	-	-	-	-	-
22	SES Middle: P_exo	0.12	0.32	0.25	1.46	0.14	-	-	-	-	-	-	-	-	-	-
23	SES High: P_exo	0.06	0.17	-0.11	0.94	0.14	-	-	-	-	-	-	-	-	-	-

HT: Habitat type; SES: Socioeconomic status; N: average proportion of Nitrogen; P_exo: proportion of exotic plant species.

3.2.2 Drivers of FD_Q : multi-trait and single-trait approach

FD_Q showed a different tendency in the relevance of the predictors. For the multi-trait approach, the most influential predictors of FD_Q were SES and P_exo. On the contrary, at evaluating the three traits separately, N and SES were the most relevant predictors (value of 1 of relative importance in two traits of the three evaluated). HT appeared in three models selected with a different degree of relevance ranging from 0 to 0.23 (Table 6). For the evaluated model subset, C/N content in soil and the interactions between different predictors were irrelevant, (Table 6). Moreover, the single trait assessment of FD_Q gave us insights in the particular dynamics of each trait. We found that different patterns of drivers for functional composition drove the variability in functional structure. Thus, $LDMC^{FD_Q}$ drivers were anthropogenic factors (HT and SES) and their interaction. Nitrogen (environmental factor) drove SLA^{FD_Q} and height had as predictors of variation a mix of environmental and anthropogenic factors (SES, disturbance, N, and P_exo).

3.2.2.1 FD_Q for multiple traits

Model selection showed that SES and P_exo account for the highest ω_i valued model (0.55) which was 2.4 times better than the next models according to the evidence ratio (Table 8). Middle and high SES categories had a positive effect on the FD_Q values as seen in the parameter estimates and confidence intervals. However, there was a poor support for the effect of P_exo on this index (Table 9).

3.3.2.2 FD_Q for single trait values

As with the multi-trait approach and given the low values of ω_i for each model of the subset after model averaging, we had a low level of support for the FD_Q models (Table 8). In the case of $LDMC^{FD_Q}$, the main parameters were HT, SES and their interaction, followed by N and the interaction HT: N (87% and 41 % of relative importance to the main parameters, Table 5). All SES levels had a positive effect over $LDMC^{FD_Q}$, as well as for every interaction between HT and N. Parameter estimate values showed that the highest values of $LDMC^{FD_Q}$ were in squares of the middle SES, as well as the lowest values in squares in the middle-low SES (Table 8). For SLA^{FD_Q} , there was a low weight of evidence for models in this set, with a ω_i of 0.26 and 0.24 as maximum values (Table 8). Main parameters were N, followed by HT and Disturbance (39 and 37% of relative importance to N, Table 5). From the parameter estimates, SQ had a positive effect on the SLA^{FD_Q} values. Other relations had little evidence for an effect (Table 9). Finally, in the case of height FD_Q , four parameters showed to be important: SES, Disturbance, N, and P_exo (Table 5). This contrast highly with a number of parameters relevant for Height CWM (only one, Table 5). Best models ranked closely by ω_i , without a strong evidence for a single best model in the set (Table 8). Middle and high SES, as well as Disturbance and N, affected positively height FD_Q , while P_exo affected negatively the values of height FD_Q (Table 9).

Table 8: Selection of the most parsimonious linear mixed models of FD_Q ($\Delta AICc < 2$). (Burnham and Anderson, 2004). For each model, “Sampling year” was the random effect. ω_i = Akaike weights for models fit; ER= evidence ratio; $acc \omega_i$ = accumulative ω_i .

	Model	Fixed explanatory variables included	df	LogL	AICc	$\Delta AICc$	ω_i	ER	$acc \omega_i$
FD_Q	1	SES+P_exo	7	201.61	-388.2	0	0.55	1.0	0.55
	2	SES+Disturbance+P_exo	8	201.90	-386.5	1.71	0.23	2.4	0.78
	3	SES+N+P_exo	8	201.82	-386.3	1.89	0.21	2.6	0.99
LDMC FD_Q	1	HT*SES+N	15	256.29	-477.9	0	0.32	1.0	0.32
	2	HT*SES+N+HT:N	17	258.87	-477.7	0.25	0.29	1.1	0.61
	3	HT*SES+N+P_exo	16	256.78	-476.2	1.7	0.14	2.3	0.75
	4	HT*SES	14	254.08	-476.1	1.81	0.13	2.5	0.88
	5	HT*SES+N+P_exo+HT:N	18	259.41	-476	1.95	0.12	2.7	1.00
SLA FD_Q	1	N	4	138.97	-269.6	0	0.26	1.0	0.26
	2	N+Disturbance	5	139.99	-269.5	0.14	0.24	1.1	0.50
	3	HT+N	6	140.64	-268.5	1.06	0.15	1.7	0.65
	4	HT+N+Disturbance	7	141.64	-268.3	1.33	0.13	2.0	0.78
	5	N+HT:N	6	140.4	-268.1	1.53	0.12	2.2	0.90
	6	HT*N	8	142.55	-267.8	1.81	0.10	2.6	1.00
height FD_Q	1	SES+N+Disturbance+P_exo	9	207.01	-394.4	0	0.40	1.0	0.4
	2	SES+N+Disturbance+P_exo+HT:N	11	209.34	-394.2	0.15	0.37	1.1	0.77
	3	HT+SES+N+Disturbance+P_exo	11	208.84	-393.2	1.16	0.23	1.7	1.00

HT: Habitat type; SES: Socioeconomic status; N: average proportion of Nitrogen; P_exo: proportion of exotic plant species

Table 9: Summary parameter estimates and standardised effects sizes (models with $\Delta i \leq 2$ after model averaging) for the effect of each predictor on FD_Q (multi-trait approach), and individual trait FD_Q . For categorical predictors SES, “Low socioeconomic status” was the reference category. For categorical predictor HT, the reference was “Broad road verge” (BV). C.I.: Confidence interval. Relative importance (I_{wi}) is the sum of the AICc weights (w_i) of the models after model selection and averaging.

Parameter	FD_Q					$LDMC^{FD_Q}$					SLA^{FD_Q}					$height^{FD_Q}$				
	β	S.E.	C.I.		I_{wi}	β	S.E.	C.I.		I_{wi}	β	S.E.	C.I.		I_{wi}	β	S.E.	C.I.		I_{wi}
(Intercept)	0.10	0.01	0.08	0.12		0.06	0.01	0.03	0.09		0.10	0.01	0.08	0.12		0.05	0.02	0.01	0.08	-
Habitat type SQ	-	-	-	-	-	-0.01	0.01	-0.04	0.01	1.00	0.01	0.02	0.00	0.06	0.39	0.00	0.00	-0.02	0.01	0.23
Habitat type NV	-	-	-	-	-	0.01	0.02	-0.03	0.04	1.00	0.00	0.01	-0.02	0.05	0.39	-0.01	0.01	-0.05	0.00	0.23
SES Middle-low	0.01	0.01	-0.01	0.04	1.00	0.03	0.01	0.00	0.06	1.00	-	-	-	-	-	0.01	0.01	-0.02	0.03	1.00
SES Middle	0.03	0.01	0.00	0.05	1.00	0.03	0.01	0.01	0.06	1.00	-	-	-	-	-	0.03	0.01	0.00	0.05	1.00
SES High	0.04	0.01	0.02	0.07	1.00	0.03	0.01	0.00	0.05	1.00	-	-	-	-	-	0.04	0.01	0.01	0.07	1.00
Disturbance	0.00	0.00	-0.01	0.01	0.23	-	-	-	-	-	0.00	0.01	-0.02	0.00	0.37	0.01	0.00	0.00	0.02	1.00
N	0.00	0.00	-0.01	0.01	0.21	-0.01	0.01	-0.03	0.00	0.87	-0.01	0.01	-0.03	0.01	1.00	0.01	0.01	0.00	0.03	1.00
P_exo	-0.01	0.00	-0.02	0.00	1.00	0.00	0.00	0.00	0.01	-	-	-	-	-	-	-0.02	0.00	-0.03	-0.01	1.00
Habitat type SQ:N	-	-	-	-	-	0.01	0.01	0.00	0.03	0.41	0.00	0.01	-0.06	0.01	0.22	0.00	0.01	-0.02	0.02	0.37
Habitat type NV:N	-	-	-	-	-	0.01	0.01	0.00	0.03	0.41	0.00	0.01	-0.03	0.04	0.22	-0.01	0.01	-0.04	0.01	0.37
Habitat type SQ:SES Middle-low	-	-	-	-	-	-0.04	0.02	-0.07	0.00	1.00	-	-	-	-	-	-	-	-	-	-
Habitat type NV:SES Middle-low	-	-	-	-	-	0.00	0.02	-0.04	0.04	1.00	-	-	-	-	-	-	-	-	-	-
Habitat type SQ:SES Middle	-	-	-	-	-	0.04	0.02	0.00	0.07	1.00	-	-	-	-	-	-	-	-	-	-
Habitat type NV:SES Middle	-	-	-	-	-	-0.03	0.02	-0.07	0.00	1.00	-	-	-	-	-	-	-	-	-	-
Habitat type SQ:SES High	-	-	-	-	-	0.02	0.02	-0.02	0.05	1.00	-	-	-	-	-	-	-	-	-	-
Habitat type NV:SES High	-	-	-	-	-	0.02	0.02	-0.01	0.06	1.00	-	-	-	-	-	-	-	-	-	-

HT: Habitat type; SES: Socioeconomic status; N: average proportion of Nitrogen; P_exo: proportion of exotic plant species.

4. Discussion

In this study, we focused on the functional composition and structure of a set of traits (LDMC, SLA and height) related to plant performance and persistence strategies that may explain the community observed in urban lawns of Valdivia. Williams et al. (2015) highlight the relevance of local factors and disturbances on shaping trait composition in a particular location; in this context, we evaluated the local characteristics of the neighbourhood to assess the variation at a finer scale. In general, we found that functional structure but not functional composition is explained by anthropogenic factors. Furthermore, we found that multiple factors drive traits related with plant persistence and performance.

4.1 Functional diversity of traits related to plant persistence and performance in neighbourhoods of Valdivia

Valdivia is characterised by communities with homogeneous composition of mean traits (CWM), low evenness and low dissimilarity (FD_Q) of evaluated traits. The invariant functional composition across the neighbourhoods with different SES and HT factors may suggest a stronger effect of the environmental factors than the anthropogenic ones on the persistence and performance traits. Therefore, leaf traits and plant height had similar patterns across the city. Although functional evenness did not vary with anthropogenic factors like SES and habitat type, the low values suggest a heterogeneous abundance distribution in the city. An interpretation to this heterogeneous abundance is an uneven distribution of resources across the neighbourhoods not related to the anthropogenic factors analysed and that may potentially increase the risk of invasion by exotic species in the area (Mason et al., 2005).

Regarding FD_Q patterns, we found low values suggesting a narrow range of the evaluated traits. As FD_Q account for trait dissimilarity, moderated FD_Q values occur when the abundance of the evaluated species are similar and the distance between species is small. Higher values of FD_Q are a consequence of both extreme abundance values (abundance heterogeneity) and the moderate distance between species, or by an even distribution of abundances and the high distance between species (Mason and Mouillot, 2013). These results support the hypothesis of a community with a narrow suite of plant traits filtered by the urban environmental conditions (Williams et al., 2009). The environmental filtering concept states that abiotic factors select a suite of traits that allow species to acquire resources in competition with co-occurring species, generating patterns of similarity between species as the niche differences decrease (Kraft et al., 2015). Hence, the most abundant species will display similar trait values as they use similar niches. The environment filters the species, selecting those with traits that allow them to survive and thrive in it. Consequently, communities with similar traits (like those of this study) will be functionally similar but poorer than those with a dissimilar composition of traits because they have narrower traits range to respond to environmental gradients (Mason et al., 2005). Further research on community assembly rules that model observed and expected

trait values in this urban community could confirm whether environmental filtering explains species coexistence (Ricotta and Moretti, 2011; de Bello, 2012).

4.2 Drivers of functional diversity composition and structure

Our analyses showed a relevant role of both anthropic and environmental variables, as multiple drivers of composition and structure in the urban communities of Valdivia. Moreover, we found a pattern where the drivers for composition were almost the same that the drivers for dissimilarity of traits. In detail, for the leaf traits, LDMC drivers were anthropogenic, while a mix of environmental (N) and anthropogenic (HT) factors drove SLA. For plant height, we found a mix of anthropogenic and environmental factors drove composition and structure. When assessing the relevant predictors for functional diversity structure as trait dissimilarity (FD_Q), the multi-trait approach gave us a general idea of the tendency in trait dissimilarity, with a mix of environmental and anthropogenic factors driving those relations. Namely, SES and P_exo where the most relevant factors to explain such variation. As proposed by Williams et al. (2009), in this case, the high proportion of exotic plant species in lawn habitats overcame several environmental filters (see Chapter 2). Those filters may narrow the variety of trait values, and thus, produce a homogeneous urban community, with similar values of CWM and low dissimilarity (FD_Q). It is interesting to note that the status of plant species (exotic or native to the area of study) appears as a relevant factor to drive traits, as showed by the work of Knapp and Kühn (2012). It may imply that the taxonomic composition of the community have indirect effects on ecosystem processes as the nutrient cycling, in our case, and highlight the relevance of the species status as a characterization to take into account for future studies.

4.2.1 Specific leaf area (SLA)

For SLA^{CWM} the drivers were N and the interaction between HT and N, while for SLA^{FD_Q} N was the only driver. However, we did not have a strong evidence for driving factors on SLA. Previous studies in urban areas documented a variety of responses for SLA, but not a unique defined trend for this trait (Thompson and McCarthy, 2008; Knapp et al., 2009). In a review of functional diversity in urban areas, Williams et al. (2015) suggested that the lack of a unique pattern in SLA is the results of the action of several abiotic factors affecting the trait in different directions (positive or negative effects) through the city and therefore the final outcome is an inconsistent pattern. Those factors act in a directional or no directional way, according to its context dependency. In our case, N content in soil was the main driver of SLA^{CWM} . Nitrogen is a relevant nutrient that promotes fast-growing species with high SLA through the exploitation of resources (Lavorel and Garnier, 2002). Urban areas are known to be nitrate-rich environments (Pellissier et al., 2008), and this characteristic may drive the mean values that SLA. When considering the second driver, N interacting with HT, we found that NV habitats had higher values of SLA and thus higher growth rates. In Germany, Knapp et al. (2008) found that urbanisation shift species traits due to the novel urban conditions. Specifically, they found that intensive and regular disturbances favour the presence of species with high SLA and low LDMC. NV habitat are located on the most exposed side to the roadside, and was exposed to several

disturbances and changes in soil composition, as dog faeces in the street, that may increase the concentration of soil N. Moreover, nutrient rich habitats promote fast-growing species (Lavorel and Garnier, 2002) and thus explain the higher values of SLA that we found in this habitat type. Further, N as a driver of SLA FDQ promotes the divergence between species values of SLA as its content may vary across the city. Habitat heterogeneity could provide different N conditions through the neighbourhoods (Niemelä, 1999), allowing both non-nitrophilous and nitrophilous species to establish in them. Finally, the species abundances could be affected and this variance is reflected in the FDQ values obtained, promoting dissimilarity.

4.2.2 Leaf dry matter content (LDMC)

Anthropogenic factors drove both, composition and structure of LDMC. We found that middle and high SES had more dense leaves (higher community-mean values of LDMC) than in the two lower SES. Parallel, we found the highest dissimilarity, and thus a higher divergence and functional diversity in the middle-low to high SES compared with the lower SES. In relation to habitat type, as was expected, LDMC mean values were lower in the NV habitat, contrasting with the high values found for SLA according to Westoby et al., (2002) who proposed a negative relation between both leaf traits. Moreover, NV lawns in middle SES and SQ lawns in middle-low SES had the tendency of being more similar in $LDMC^{FDQ}$, and thus had lower values of $LDMC^{FDQ}$. The most dissimilar community was in squares (SQ) in middle SES, highlighting the heterogeneity of these habitat types in those SES areas.

In a study on small urban parks and their surrounding neighbourhoods in U.S.A, Kinzig et al. (2005) described the mechanisms behind anthropogenic factors as a "bottom-up" and "top-down" strategies, explaining the selection of plant and bird species by human preferences. According to it, in a bottom-up situation neighbours will influence patterns of biodiversity with their preferences, scaling from the individual to the neighbourhood level. In contrast, the local administration (management at the city level) will influence the biodiversity at a city scale via policies and management practices (top-down), shifting trait distributions and affecting the abiotic responses (Williams et al., 2015). Thus, ecological patterns will show the influence of both strategies according to the strength of each one. In our results, we found evidence of bottom-up mechanisms to explain the variation in LDMC (composition and structure) by the relevance of anthropogenic drivers. The effect of bottom-up mechanism showed high mean values of LDMC for the upper SES and for the divergence (FDQ) across middle-low to high SES. Moreover, as Kinzig et al. (2005) suggested, habitat type interacts with SES and thus presented different patterns across the combination of both anthropogenic factors.

The neighbours' management can explain the highest mean values for $LDMC^{CWM}$ at highest SES because lawn care is under neighbours' stewardship, especially in middle and high SES areas (Hernán Céspedes, a local gardener, personal communication). They will water, weed, and mow lawns to keep their green areas tidy and the aesthetics of the neighbourhood. Income of the householder has been pointed as a relevant factor explaining patterns in species richness (Martin et al 2004), as well as educational level (Pham et al., 2013). Thus, it is possible that gardening practices in these SES, as mowing, will affect the performance of plants (Loram et al., 2011). We evaluated the

disturbance as trampling pedestrians and users in lawns, which appear to be of minor relevance as a single factor, but appears as a factor in our models of trait variation. However, we did not cover mowing frequency in the areas surveyed, that could give a better estimation of LDMC related with plant performance and not with human behaviour. Moreover, we did not have systematic records of the use of fertilisation or frequency of visit, as it has been done in other lawn studies (Bertoncini et al., 2012). Several studies in grasslands show the effect of mowing (defoliation) on plant traits, increasing species diversity by restraining the dominant species and benefiting the suppressed ones (Benot et al., 2014). A similar mechanism could explain the higher LDMC FDQ values found in the higher SES, which appears to be the most intensely managed. However, these relationships remain context dependent and we need specific studies to assess the relation between mowing and LDMC as a leaf trait.

4.2.3 Plant height

The main factor that drives both height CWM and FDQ was the proportion of exotic species (P_{exo}). Several studies note that urban areas are rich in exotic species because they are adapted to the urban environmental conditions (Palma et al., 2016). Under this frame, the environment filters for the species with traits giving them a competitive advantage, like rapid growth, taller maturity height, among others. Furthermore, this selection of species will promote an optimal mean value, generating a set of species that are similar in their mean trait values, with most abundant species tending to occupy similar niches (Mason et al., 2011), and narrowing also the functional diversity range. According to our results on height FDQ , we found that the more exotic species, the more similar were the communities. Probably, since environmental filtering will be less severe and the community could harbour a broader variety of species, in this study a lower proportion of exotic species promotes height dissimilarity (FDQ).

Contrary to Europe, the southern hemisphere hosts a high proportion of exotic species in urban areas (Stewart et al., 2009), which has been seen in previous studies in other Chilean cities (Pauchard et al., 2006; Fischer et al., 2016). Particularly, we found that lower SES had a higher proportion of exotic species compared to the wealthier ones (middle and high SES, Chapter 2) and that higher SES favoured shorter plant species. Kinzing et al. (2005) considered that a city is like a mosaic of socio-cultural conditions, with ethnic, cultural, economic and educational characteristics that interact and influence a given area, including the nature in it. Such socio-cultural heterogeneity could explain that higher SES (Middle, High) had shorter plants. Neighbours' stewardship regimes (bottom-up) will predominate in the wealthier areas because their sociocultural characteristics and their capacity to invest and take care of green areas modify the direction of trait changes. Thus, the effects of the presence of exotic species on traits due to environmental filtering will be out passed by human actions. Furthermore, we found taller plants in areas that are managed by the municipality, i.e. where there is a lack of mowing, like areas with low and middle-low status. These are areas, where the management is less intense, there is a chance for tall species to establish and thrive. Other drivers of dissimilarity in plant height found in this study were N content and disturbance by trampling, but with lower effects. Plant height is positively related to nutrient rich environments, as they promote a resource acquisitive strategy and rapid growth of the plant species (da Silveira Pontes et al., 2015). Thus, variation in the content of

nitrogen in the soil will affect the variation in plant capacity to growth, and areas with higher content of nitrogen will have taller plants because of the increased photosynthetic rate and growth rate (Garnier and Navas, 2012). The milder response of plant height to disturbance by trampling could be explained by the relation of plant height with two opposite strategies: tolerance to disturbance via shorter plants, or competitive advantage by producing fast-growing and taller plants (Díaz et al., 2001; Mason et al., 2011). Both patterns have been found in urban areas (Thompson and McCarthy, 2008; Knapp et al., 2008). In our case, the higher the disturbance by trampling, the more dissimilar the height of the plants was. Studies in woodland paths in Finland showed that trampling increases the proportion of exotic plant species and trampling tolerating species (Hamberg et al., 2010), thus disturbance could be a factor that promotes the presence of exotic plants in a site, and may explain the combined effect of the drivers that we found. Finally, in order to understand patterns and trends in plant communities, as relevant as quantitative traits are qualitative ones. For example, the analysis of trends in life history traits (i.e. annual, perennial) and growth form traits could improve the comprehension of the lawn habitats included in this study. Moreover, understanding of the biotic relations and trophic chain in urban communities will complement and complete the conceptual model of the functioning of urban communities, their mechanism, and processes.

5. Conclusion

The public green areas of Valdivia present communities with homogeneous composition of mean traits (CWM), low evenness, and low dissimilarity (FD_Q) of traits related to plant persistence and performance (LDMC, SLA and plant height). However, anthropic (SES, habitat type, proportion of exotic plant species) and environmental factors (Nitrogen content in soil) showed a relevant role as multiple drivers of composition and structure in the urban lawns.

When assessing the response of traits selected to the socio-environmental conditions of the city, we found that in general the structure, but not the composition of traits related to persistence and performance was driven by anthropogenic factors, specifically socioeconomic ones, showing the facilitation role of humans in urban habitats. However, a detailed look into the patterns showed a complex relation of multiple factors driving differentially each trait. The composition and structure (divergence) of LDMC and height were driven by anthropogenic factors (SES, habitat type and proportion of exotic plant species) while SLA composition was mainly driven by environmental factor. Plant height showed a heterogeneous pattern in the composition drivers and divergence drivers, as for the latest, a mix of anthropogenic and environmental factors explained the patterns found.

Finally, in Valdivia, we see that lawns in the upper SES had a high LDMC and short size, thus will look tidy and decompose slowly and will be functionally divergent compared to the other SES. Additionally, plants that perform an acquisitive strategy, growing fast and decomposing easily, compose the lawns in narrow verges. As we expected, we found a narrow structure and composition of functional diversity, as the result of the multiple filters affecting public areas.

In particular, the recent events of extreme long dry summers and short but intense rains in winter in the south of Chile sets the alarm to think about the nature of our urban areas, in which 85% of the population lives. Moreover, it highlights the steps that the government, city planners, and the local community have to take in order to keep a resilient city. Top down and bottom up actions are needed to enhance the functional diversity and thus the ecosystem functioning in these habitats. In general, the results of this research will help to the understand broad-scale patterns and mechanisms of urbanisation in wild plants communities and are a contribution to fill the regional gap of urban ecology studies in Latin America and is a contribution to the general understanding of global change.



Supplementary material

Table S1: Housing and household variables and characteristics considered by Instituto Nacional de Estadísticas (Chile), making up the in the elaboration of the index of welfare. All the information gathered at the household level, then collated, analysed with a non-linear PCA (PRINCALS method) and subsequently grouped the population into five classes, from low to high status. Translated from Instituto Nacional de Estadísticas 2005.

Housing characteristics	Household characteristics	Head of the household's characteristics
- Household type	- Overcrowded housing (Y/N)	- Age
- Tenancy type	- Number of people in the household	- Level of education
- Wall cladding type	- Number of sleeping rooms	- Years of education
- Floor covering type	- Employment rate	- Occupational category
- Roof covering type	- Household equipment	
- Provision of basic services: sanitary, water and electricity supplies	- Number of private cars	

Table S2: Two-way ANOVA results of PCA1 scores of community weighted trait means (CWM).

Factor	d.f.	CWM traits		
		F-stat	P value	
SES	3	1.23	0.30	n.s.
Habitat	2	1.68	0.19	n.s.
SES * Habitat	6	1.28	0.27	n.s.
Residuals	108			

n.s.=p>0.05

Table S3: Descriptive statistics values for the functional diversity indices analysed: Rao's Q (FD_Q) and functional evenness (FEve). Socioeconomic status (SES) is in increasing order. Values of FD_Q are square transformed, as used for the ANOVA test.

Factors	FD _Q			FEve			
	Median	Mean	SD	Median	Mean	SD	
SES	Low	0.28	0.30	0.08	0.43	0.44	0.17
	Middle-low	0.34	0.33	0.07	0.43	0.44	0.16
	Middle	0.35	0.35	0.06	0.48	0.51	0.17
	High	0.38	0.38	0.06	0.45	0.44	0.11
Habitat	Broad sidewalk	0.34	0.34	0.07	0.43	0.44	0.17
	Narrow sidewalk	0.37	0.35	0.09	0.45	0.48	0.16
	Square	0.34	0.33	0.06	0.44	0.45	0.13

Figure S4: Relevant relationships for GLMM for CWM trait values: a) LDMC, b) SLA, c) Height. Values depicted are transformed when indicating in parentheses. For Habitat type: BV: broad road verge; SQ: Square; NV: narrow road verge. For Socioeconomic status (SES): L=low; ML: middle-low; M: middle; H: high.

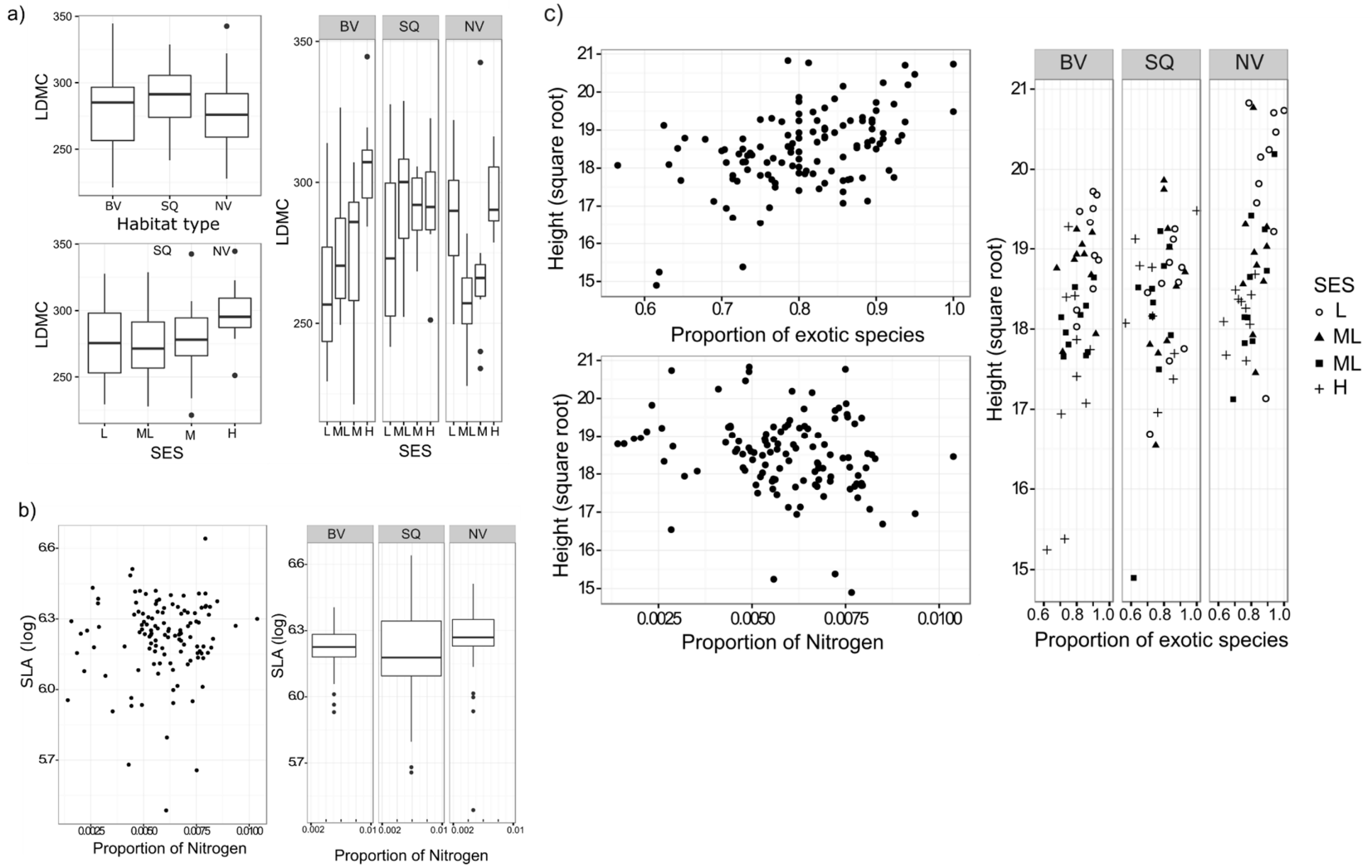


Figure S5: Relevant relationships of the GLMM for FDQ multi-trait. a) For Socioeconomic status (SES): L=low; ML: middle-low; M: middle; H: high. b) For the proportion of exotic plant species (P_exo).

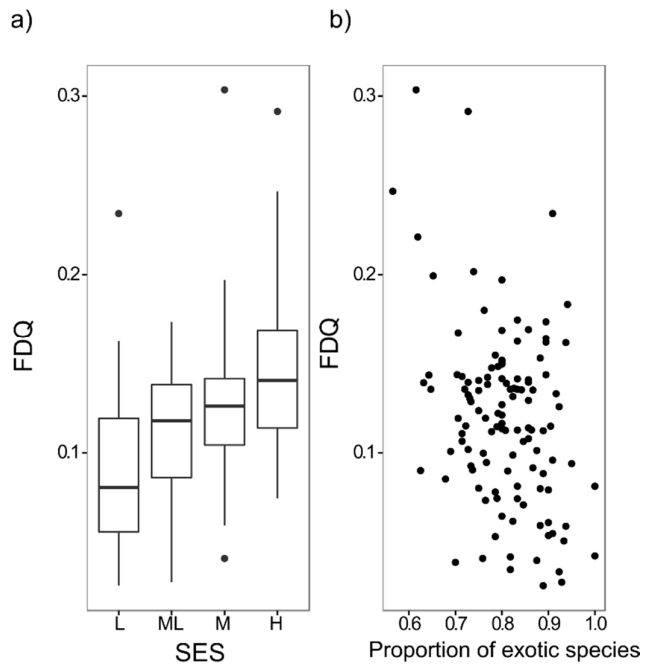
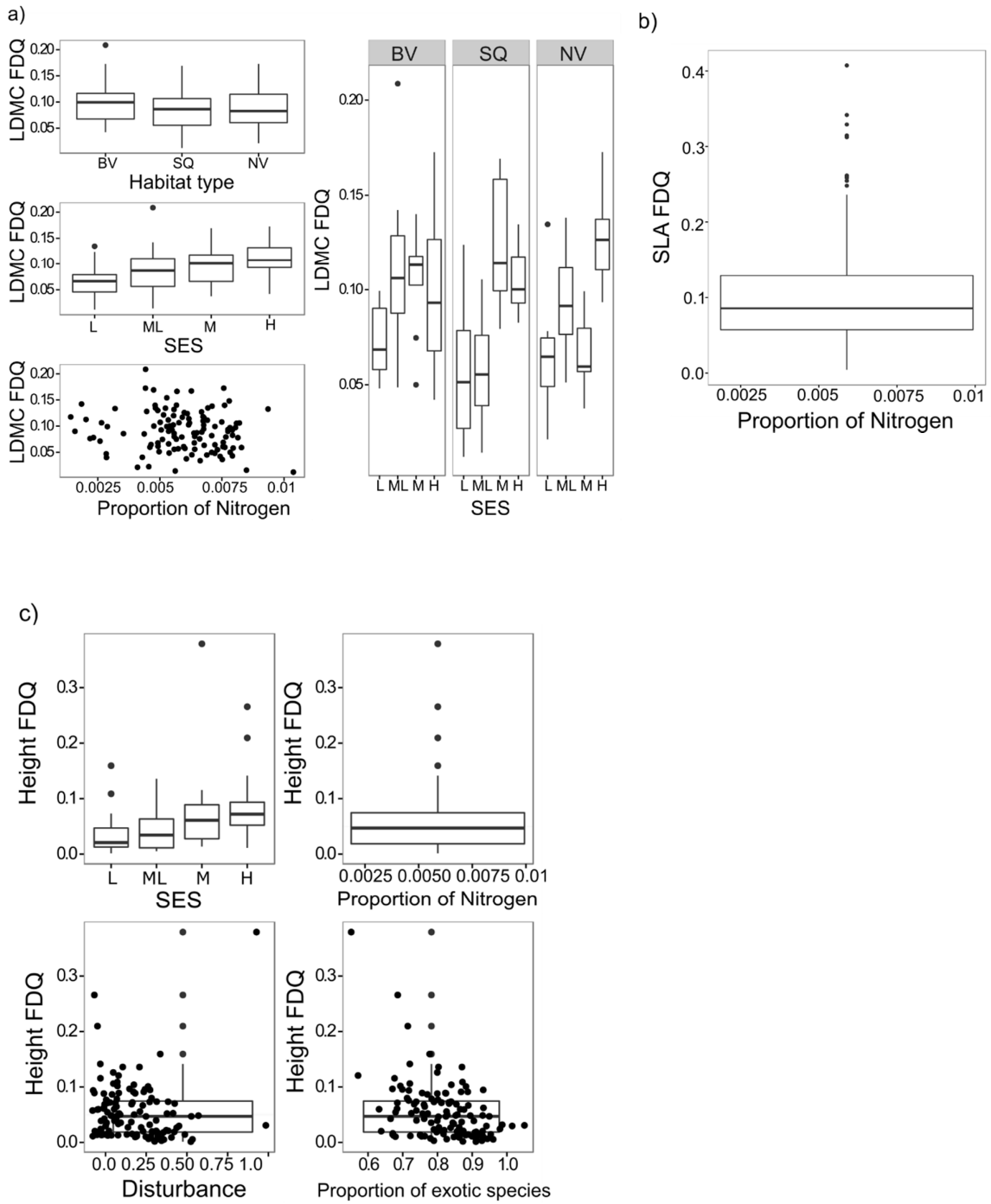


Figure S6: Relevant relationships for GLMM for FD_Q trait values: a) LDMC, b) SLA, c) Height. For Habitat type: BV: broad road verge; SQ: Square; NV: road verge. For Socioeconomic status (SES): L=low status; ML: middle-low status; M: middle status; H: high status.



Despite many years in which ecologists have neglected the urban ecosystem as a research area, in the few last decades the awareness of the relevance of urban areas has been increasingly recognised, with a rise of research in cities. Even though many advances have been made to understand how urban areas and particularly urban floras develop, there are still gaps that prevent a general conceptualization. As Aronson et al. (2016) pointed out in a review about urban floras worldwide, there is still a bias on the development of urban ecology studies towards cities in temperate environments located in developed areas of the Northern hemisphere. Moreover, most of the research up to date is based principally on species richness lists of flora, and quantitative research that accounts for patterns in Latin America is scarce and urgently needed.

In the present doctoral thesis, I described, at a fine scale, the taxonomic and functional diversity of the spontaneous vascular flora of Valdivia, a medium-size in Chile, South America. This work is the result of an extensive 3 years sampling at the scale of the neighbourhood, identifying and measuring all the spontaneous vascular species present in public lawns using 120 plots of 20m² over an area of ~2,000 ha (Maturana and Muñoz, 2007). The aim of this work was to contribute to the growing body of knowledge of patterns in urban ecology, filling the gap of information actually existing on the South American continent (chapter 2 and 3), assessing the drivers for taxonomic (chapter 2) and functional diversity (chapter 3). Moreover and to the best of my knowledge, I develop the first quantitative functional diversity analyses on urban floras in Latin America (chapter 3), using linear models and ordination techniques. The novelty of this work is based on the analysis of specific anthropogenic and environmental factors to disentangle their role in the patterns of species richness and functional diversity. The results of this thesis highlight the relevance of anthropogenic factors such as the positive effect of habitat and socioeconomic status as drivers of species richness (chapter 2) and variation in resource-use traits and thus in the persistence strategies of plants (chapter 3). Additionally, my results hint towards a strong relevance of bottom-up processes, from householders to the top stakeholders in shaping the diversity in this urban area given the relevance of socioeconomic status as a driving factor of change in species richness and traits associated with the conservative strategy.

Specifically, in chapter 2 I showed that a medium-sized city in Latin America does not follow the pattern of a high proportion of native plant species richness described for cities of the temperate Northern hemisphere. Rather, I found an opposite trend for temperate Latin America, where urban areas harbour a high proportion of exotic species (>80%), far surpassing the amount of native species (~20%) that can be found. Also, I showed how this pattern is not random, as it has a strong negative association with the socioeconomic status of the neighbourhood and the habitat type in which plants grow, linking human factors as drivers of spontaneous species richness beyond the effect of the environment, as reported in other cities worldwide.

Chapter 3 is, according to my literature revision, the first work in Latin America that analyse quantitative traits in the context of urban areas and give insight on the drivers of the functional composition of wild plant communities in lawns of residential areas. I evaluated the drivers of spontaneous plants persistence and performance traits (plant height, leaf dry matter content-LDMC, and specific leaf area-SLA) to understand the functional plant composition patterns and strategies in the city. I found that in general mean trait values (CWM) converge to similar values across the neighbourhoods of the city and show lower values for dissimilarity (Rao's index Q, named as FD_Q in this thesis). In particular, plant functional strategies for persistence shift differentially, with diverse anthropogenic and environmental mix of drivers modulating the variation in trait values. Thus, an acquisitive strategy (Westoby, 1998) of rapid growth and short leaf lifespan is mainly driven by the concentration of N in the soil, whereas a conservative strategy that promotes the efficient resource use responds positive and strongly to socioeconomic status, and while plant height has a complex interrelation of environmental and anthropogenic factors.

1.1 Taxonomic and functional diversity composition in public lawn areas

For the urban area of Valdivia, I found a high amount of vascular species exotic to Chile and South America (chapter 2). This finding contrast with the general global pattern described by Aronson et al. (2014), where the majority of plant species in urban areas are native to the area of the city, although data on plant species richness for the Neotropical biogeographic realm (Central and South America) was not available for that study. Therefore, chapter 2 provides valuable information about wet-temperate ecosystems in the Southern hemisphere, in line with trends found in other studies in this hemisphere. In general, there is evidence that urban areas belong to the most invasible areas given the altered environmental and disturbance regimes that may allow exotic species persistence and the

heterogeneity of habitats that they harbour (Richardson and Pyšek, 2006). In Valdivia, more than 80% of the species found in neighbourhoods are of exotic origin (chapter 2). The few studies that have covered this topic in Chile found for the mega-city of Santiago de Chile ("*Gran Santiago*" > 6 millions of inhabitants) more than 80% of exotic grassland species in urban parks (95% in Fischer et al. 2016), streets and sidewalks (81% in Gärtner et al., 2015), and 85% of exotic woody and herbs species in public green areas (Figueroa et al., 2016). Although Santiago is located ~840km north in a temperate dry Mediterranean climate zone and has a larger area compared Valdivia (~870 km² vs. ~20km²), both cities share a high proportion of exotic plant species, suggesting that either both cities share specific urban micro-climatic conditions (hot and dry urban environment) that are favourable for exotic species and are independent of their biogeographic locations, or that they have a similar history of colonization and trade that cause the pattern.

The phytogeographic origin of the exotic plant species found in Chile links the plant compositional pattern with the historic development of the region. Fischer et al. (2016) and Gärtner et al. (2015) found that most of the spontaneous herbs species in urban parks of Santiago de Chile were originally from Europe (79% and 81.1% respectively). The similar proportions of European plant species were found in New Zealand (Horne et al., 2005), and in this thesis, more than 80% of the exotic species have a European origin (chapter 2). In the oceanic part of the Southern hemisphere, the grassland-like environment of Australia and New Zealand have a range between 40 to ~85% of exotic species. In contrast, studies in the North-West Province of South Africa showed a higher amount of native species, in line with the pattern described for North America, Asia, Europe and north-Africa (Cilliers et al., 2000; 2004). Steward et al. (2009) compared values of exotic species for the Southern hemisphere and note that South Africa has a higher proportion of native annual and biennial species compared with the rest of the areas in the same hemisphere, explaining the higher proportion of native species in their urban areas. In a review of plant invasions and ecosystem invasibility, Richardson and Pyšek (2006) explained the high proportion of European species in the American continent as a result of invasibility because of the lack of adaptation of native flora to grassland disturbance conditions. In general, the high proportion of European grassland species in urban lawns is related to the historical development of pastures in Europe and west Asia for livestock, where these species evolved and adapted to the disturbance regimes through thousands of years. Later, grasslands were used for aesthetical appeal and adopted in the gardening designs in Europe, and the idea of lawns spread around the world (Ignatieva and Stewart, 2009), covering between 70-75% of the surface of the green areas in cities

(Ignatieva et al., 2015). As Steward et al. (2009) pointed out, temperate territories in the Southern hemisphere lack both, the presence of a relevant percentage of native annual and biennial grassland species and the frame time to adapt and develop an ecosystem with native grassland species. Thus, after the colonisation of the Americas, the propagule pressure that human activities exerted increased the establishment success of exotic European species in the new territories. In the particular case of South America, annual and/or biennial grasses arrived after the European colonisation, which is relatively recent (~500years). Summing up this evidence, it is strongly suggested that the temperate Southern hemisphere has an opposite trend in the proportion of exotic plant species compared to the temperate Northern hemisphere because of historic and environmental factors. More research in other cities of Latin America, Africa and Oceania could reinforce the North/South hemisphere pattern of exotic species proportion in cities.

At a finer scale, the land use changes impacted negatively in the maintenance of native species, as it is in the case of Valdivia. Several areas of the city were formerly wetlands that were transformed to develop and establish neighbourhoods (Skewes et al., 2012), changing the environmental factors from wet to dry as well as the disturbance regimes. Under these new conditions, originally present native species were not able to recolonize the areas, thus there was space for pre-adapted exotic species to establish and persist under the altered environmental conditions of the new neighbourhoods. Those species that persist in the city lawns belong to three plant families: *Poaceae*, *Asteraceae*, and *Fabaceae*. These families globally dominate lawns in other cities of the world (Stewart et al., 2009). Also, the top most common species found in Valdivia (Chapter 2) are in agreement with global patterns, with well-dispersed species of forbs and grasses as *Trifolium repens*, *Lolium sp.*, *Plantago lanceolata*, *Leontodon saxatilis*, and *Hypochaeris radicata*. Of these species, *Plantago lanceolata* is present in 93% of the cities worldwide (Aronson et al., 2014). The success of these species globally can be related to four factors: they found a suitable climate (climate matching); have advantages in reproduction and dispersal related with specific traits; they established early with enough time to adapt and persist in the new territories (residence time); and they were introduced in large quantities, *i.e.* having high propagule pressure (Richardson and Pyšek, 2012). Specifically for urban environments, these naturalized exotic species (*i.e.* species that are able to reproduce and sustain a population, and have a limited distribution (*sensu* Richardson and Pyšek, 2012), have a set of characteristic traits that allow them to success in environmental conditions making them superior to native species, especially when the landscape has been extremely transformed. A suite of traits for species that thrive in an urban environment has been

suggested (the so-called urbanites). Knapp et al. (2008) describe a typical urban species as an annual or biennial plant with the capacity to cope with dry environments (either avoiding it by their short lifespan or tolerating it via scleromorphic leaves), easily dispersed, with large leaves (and thus high SLA). However, this is a generalisation, because at the finer scale the heterogeneity of urban habitats may promote species with different strategies given the human stewardship, disturbance regime, soil characteristics, as chapter 3 discusses in deep.

In chapter 3 I showed a homogeneous composition of mean traits (CWM) across the neighbourhoods with different anthropogenic factors. Additionally, I found a general pattern of low and homogeneous values for functional diversity, showing that the urban plant community in Valdivia is functionally poor. First, this pattern suggests a dominant effect of environmental factors (compared to anthropogenic ones) filtering and affecting the community composition on the persistence and performance traits. Therefore, leaf traits and plant height had similar patterns across the public green areas of the city. Second, the high proportion of exotic species across all socioeconomic statuses (SES) and habitat types analysed (chapter 2) could explain the similarities in functional diversity values. The exotic plants could drive the CWM values of public green areas at city level leading to similar values across the different gradients. Further analyses of beta (β) diversity (the species turnover across space) of the different habitat types and socioeconomic statuses could clarify if there is, in fact, a homogenization effect on the communities due to the presence of generalist exotic species promoting a similar response across the city. In a global analysis, La Sorte et al. (2014) found that although cities retain some particular assemblies of native and exotic species according to their geographical regions, the joint presence of European species in many cities tends to homogenise them. This pattern could be similar at the city scale, for cities with a high amount of exotic species, like Valdivia. In particular, Fisher et al. (2016) found homogenization for grassland species of urban parks in Santiago de Chile and suggested a series of mechanism to explain it. These include dispersal limitation, lack of adaptation of native species to urban grassland or a higher competitive capacity of the exotic species that dominate the urban grasslands across the parks in Santiago de Chile, following the factors of success of naturalised species described by Richardson and Pyšek (2012).

The assessment of the amount of trait diversity, combining the three traits together in functional indices FD_Q and functional evenness (FEve) revealed a low variation of functional diversity, and reflect the uneven resource availability in the space (Mason et al., 2011). Palma et al. (2016) suggested a series of mechanism to explain functional trait changes under urbanisation. Specifically, there are two

mechanisms that could explain low functional diversity values (Figure 1). First, the non-random habitat transformation mediated by humans lead to altered environmental conditions that affect the original plant community. Some of the original species are lost and some of them persist. Under this new conditions, new species with the capacity to cope with the new conditions arrive and replace the species locally extinct, sharing the space with the persistent plant species and leading to a narrow functional diversity for the community (low variation in the values of functional diversity). Second, the new assembly of species might be the result of habitat filtering (Keddy, 1992) processes given new environmental conditions in urban areas that prevent the presence of the original flora and replace it with exotic species with extreme traits that made them able to survive. This filtering will produce a shift in the functional diversity towards new extreme values of functional traits, which may have low values and variation. Especially in the case of extreme habitat changes, like the transition from wetlands to dry areas that occur at least in some areas of the city of Valdivia, habitat filtering is the most likely explanation. However, both mechanisms can occur in different zones of the city at the local scale. To confirm either of these explanations, it would be necessary to compare our results with historical records and assess the temporal change in community composition.

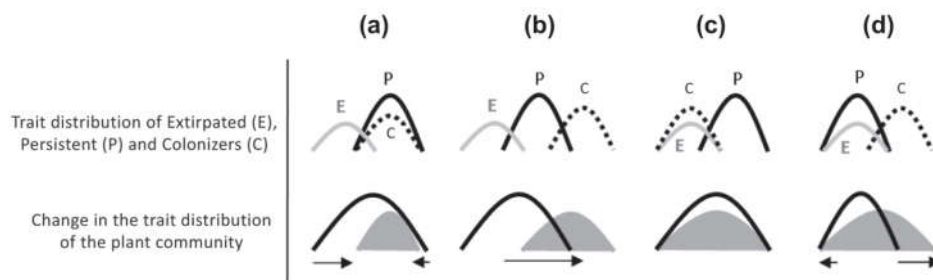


Figure 1: Scenarios to explain functional composition changes in urban areas. Urban floras are a mix of extirpated species (E), persistent species (P), and exotic colonisers (C) through a temporal analysis of urban flora (actual assembly versus historical records). The different assemblies of species will produce recognisable patterns of functional composition change. Scenario (a) shows a narrow functional composition in with colonisers share the niche with persistent species. Scenario (b) shows a shift in the niche as colonisers had extreme trait values due to habitat filtering of species. Scenario (c) shows no variation in functional composition as the colonisers replace the extirpated species by niche overlap. Scenario (d) explains niche widening by exploitation of new resources. Extracted from Palma et al. (2016).

This general assessment with collated functional traits to calculate functional indices may hinder some specific trends, especially in cases of traits like LDMC and SLA that reflect opposite strategies

(Lefcheck et al., 2015). Therefore, it is recommended to develop single trait analysis complementary to disentangle the drivers of trait variation and specific trends, as this thesis did.

Finally, although species richness is the most widely used method to estimate diversity, the lack of information on the individuals that make up species richness difficult the understanding of the processes shaping these species assemblies (Ricotta et al., 2008). For that reason, the use of functional diversity metrics gives insights in the way in which species interact with the environment and explains ultimately patterns of species assemblies. However, information about taxonomic patterns of diversity is necessary because changes in species composition finally affect the functional composition and structure of a community, as ultimate drivers of functional diversity (Mouillot et al., 2011).

1.2 Influence of anthropogenic factors on the shaping of plant composition in taxonomic and functional diversity at fine-scale

I analysed the effect of different anthropogenic and environmental factors on taxonomic and functional diversity at the fine-scale, to assess and disentangle the main drivers of diversity variation and the relative strength of each factor acting on the diversity patterns of the urban community. Chapters 2 and 3 highlight the positive relationship of socioeconomic status with both, species richness and functional diversity (FD_Q). There is agreement on the influence of socioeconomic factors on species richness in urban areas. This pattern, in which socioeconomic stratification drives species richness have been described as the “luxury effect” for other cities and bioclimatic regions like Arizona, a dry area (Hope et al., 2003; Martin et al., 2004), tropical private gardens in Africa (Bigirimana et al., 2012), and across cities in temperate south-eastern Australia (Luck et al., 2009). In temperate Mediterranean South America (megacity of Santiago de Chile), De la Maza et al. (2002) found a positive relation between socioeconomic status of the neighbourhoods and the diversity of planted woody species as a result of socioeconomic stratification. However, the luxury effect is not only associated with economic factors, but rather a combination of factors like property value, access to green space, and economic capacity to buy plants for gardening, and economic factors alone have proved no relation with biodiversity (Aronson et al., 2017). In this doctoral thesis, socioeconomic status aggregate a series of characteristics of the housing, household, and head of the household, and confirms the positive relationship between diversity and socioeconomic factors for wild plants in a temperate wet city in South America, showing that the socioeconomic effect of humans on urban plant diversity is a global trend.

Following the floristic changes hypothesised by Williams et al. (2009, chapter 1, table 2 in this chapter) it is possible to compare at a finer scale the differences between low socioeconomic status and high socioeconomic status on the taxonomic and functional diversity of the spontaneous urban flora. Mechanisms that can explain the low species richness and high exotic species in the lower socioeconomic status observed in chapter 2 are: a) the habitat loss due to urbanization, which leads to species loss under the new conditions, and b) the creation of novel habitat types, as the lawns analysed in this study, because they allow the gain of mainly naturalised species. Both mechanisms will lead to a lower functional diversity because of the new environmental conditions (habitat filtering). The presence of urban stressors, like higher disturbance by trampling, will promote the colonisation of the low socioeconomic status with exotic species having similar traits, narrowing the trait values and thus the functional diversity. Finally, Williams et al. (2009) suggest that a higher fragmentation will produce species losses in the urban flora. Cities provide fragmented habitats, due to the mosaic of different land use types resulting in heterogeneous landscapes (Grimm et al., 2008). Also, the areas of low socioeconomic status had a higher density of houses per unit area (*personal observation*) compared to a house with large gardens in areas with higher socioeconomic status. Even though housing density was not directly evaluated in this work, a higher population density may lead to a higher fragmentation of neighbourhoods because there are more dwellers in each block that manage their lawns in different ways and impact other green areas heavily by trampling and leisure activities. Moreover, low socioeconomic areas display impoverished species richness highlighting that social inequities impact also biodiversity, which was described as “biological poverty”, a side effect of the urbanisation process (Turner et al., 2004). On the contrary, I found a positive relation with both, species richness and functional diversity (as FD_Q index) for the medium and high SES neighbourhoods. In this particular case, the high proportion of exotic and native plant species can be interpreted as a net gain of species, resulting from the creation of novel habitats and human facilitation by the gardening practices (weeding but also watering and mowing) that are usual in the high socioeconomic status. This observation agrees with Williams et al. (2009) expectations (Table 1). Related to this gain of species and variety of conditions, a broad range of functional traits values and thus functional diversity can be observed, leading to higher values of functional diversity in higher socioeconomic status. In particular, these neighbourhoods have a higher proportion of exotic species (escaped ornamentals, chapter 2) broadening the range of species richness. However, gardening practices as weeding will extirpate the undesirable species from the lawns in these neighbourhoods affecting the functional

diversity range as a narrowing effect on trait values by selection of several traits. Thus, we observed a narrow range of traits and thus functional diversity, as predicted in the framework of Williams et al. (2009) as a net effect, even though the species richness may be high (Williams et al., 2009). However, this thesis can't test properly shifts in functional diversity because the original flora of the habitat surveyed is unknown.

Table 1: Predictions of changes in floristic composition and functional traits associated with four urbanisation filters proposed by Williams et al. (2009), and the comparisons of those predictions with this thesis. Italics letters show the expected dominant response to each filter. Modified from Williams et al. (2009).

	<i>Floristic composition</i>		<i>Valdivia Floristic composition</i>	<i>Functional traits</i>	<i>Valdivia Functional traits</i>	
<i>1. Habitat transformation</i>						
Habitat loss	<i>Loss</i>	✓	<i>wetlands</i>	<i>Narrowing</i>	<i>suggested</i>	<i>wetlands</i>
Novel habitat creation	<i>Gain</i>	✓	<i>dry city</i>	<i>Broaden</i>	-	-
<i>2. Fragmentation</i>						
Extirpation	<i>Loss</i>	✓	<i>wetlands</i>	<i>Narrowing</i>	<i>suggested</i>	
Invasion	<i>Gain</i>	✓	<i>dry city</i>	<i>Narrowing</i>	✓	<i>driver of plant height</i>
<i>3. Urban environment</i>						
Stressor on natural habitat	<i>Loss</i>	✓	<i>decrease of species with higher disturbance</i>	<i>Narrowing</i>	x	<i>shift to high SLA and plant height</i>
Novel urban habitat	<i>Gain</i>	✓	<i>NV habitat</i>	<i>Shift</i>	✓	<i>shift to high SLA and plant height</i>
<i>4. Human preferences</i>						
Introductions	<i>Gain</i>	✓	<i>high SES</i>	<i>Shift</i>	<i>suggested</i>	<i>shift to high LDMC</i>
Eradications	<i>Loss</i>	✓	<i>low SES</i>	<i>Narrowing</i>	<i>suggested</i>	

Regarding the patterns of habitat type, lawns in road verges (NV) are the most species-rich of the three selected habitats, even considering squares (SQ, “plazas”) or urban parks, analysed by previous studies in the country (Fischer et al., 2016; Figueroa et al., 2016). This highlights the relevance of these neglected patches of green areas along streets as reservoirs (or refuges) of species and shows that their existence in neighbourhoods may improve the experience of nature in cities, valuing them instead of paved them with concrete. Lawns in road verges (NV) with a low level of disturbance will have a higher amount of species compared to the other habitat types analysed, probably due to the effect of propagule pressure related with human-facilitated seed dispersal (chapter 2). In chapter 3, I found that

given the habitat type and/or socioeconomic status, plant species shows different strategies to persist: conservative strategy (i.e. slow growth and higher leaf density) or acquisitive strategy (i.e. fast growth and resource use), stressing the importance of fine-scale differences found in a city. Specifically, higher SES promote a conservative strategy with higher values of LDMC, and habitat type NV showed an acquisitive strategy (i.e. fast growth and resource use) given the higher values of SLA and plant height in them. Also, in the case of habitat type, I show the differential importance of drivers across the city. Road verges (NV) showed a higher percent of Nitrogen compared to the other habitat types, and several studies have already shown the positive relation between nitrogen content and SLA in lawns and grasslands (chapter 3). This habitat type will encompass a high species diversity of wild plants and also may have an interesting role in ecosystem functioning, given their high values for SLA, a trait linked to Carbon cycling. Interestingly, plant height was explained by a complex mix of anthropogenic and environmental factors, but this result must be taken with caution given the unknown mowing regime that prevailed in each socioeconomic status/habitat type (Bertoncini et al., 2012).

1.3 Concluding remarks

This study addressed the diversity of wild vascular plants across lawn-like green areas in a socioeconomic gradient in the neighbourhoods of a medium-size city in temperate South America, covering two facets of diversity: taxonomic and functional.

Through chapters 2 and 3 I showed the relevance of bottom-up processes in the patterns of taxonomic and functional diversity at the fine scale of green spaces in neighbourhoods, affecting positively species richness, the proportion of exotic plant species in them, and driving the plant strategies to persist in the cities. Although environmental factors play a role in the functional diversity of certain traits (SLA, height), the relevance of human gradients and actions have strong consequences for biodiversity conservation in neighbourhoods, giving an opportunity to enhance both facets of diversity with coordinate actions that scale from the individual to the city. Also, this work shows that road verges are not species-poor habitat, but the contrary (chapter 2), and that they play a relevant role for plants that grow fast and decompose easily (chapter 3), with the correspondent effect that it can have in the decomposition rates (Laughlin et al., 2015) and the carbon cycle in cities. Aronson et al. (2017) highlighted the role of lawns as species rich green spaces that have a critical role in several ecosystem services (C and N sequestration, control erosion and reduce rainwater runoff, human well-being, and nature connection).

The existence of public green areas in cities provide opportunities to persist for the native flora and the fauna associated with them as they serve as stepping stones and corridors between larger green protected areas that are established in close by urban areas. Moreover, these areas could serve as a natural classroom to help the people to connect with the native resources and profit from the benefits and services that of green areas provide.

The actual knowledge of patterns of native and exotic species worldwide suggest strongly that the Southern hemisphere has remarkable high proportions of exotic plant species, contrary to the Northern hemisphere patterns. However, the studies available, including this one, are still restricted to temperate areas in both hemispheres. As cities are centres of species introductions (La Sorte et al., 2014), it is necessary to expand the geographical areas of research in urban ecology to disentangle patterns of exotics and native species worldwide, and to understand the effect of species introduction in the diversity patterns of cities close to hotspot areas (Seto et al., 2012).

Although public green areas in neighbourhoods of Valdivia and other temperate cities in South America show a high proportion of worldwide common species, their research and monitoring are relevant because common species are the dominant ones in these habitats, providing ecosystem functions. Understand which services are promoted or detriment by the presence of exotic species will help to better management decision. Also, we need to know the effects of the dominance of exotic plant species to other taxa and the chain effects that it may have in the food webs. Specifically for Valdivia, it is fundamental to actively maintain and promote the native flora in green areas, both public and private ones (like private gardens and urban parks). Further research in the role of barriers for conservation, like management practices and human perception of nature will help to develop more accurate strategies to promote biodiversity conservation in urban areas. In Chile, and presumably in other Latin American countries, we still have deep gaps of basic knowledge of native species. Research in urban areas may encourage the financial aid to research the role of native plants and animals in this context. However, we need to move forward the species richness paradigm of diversity to fully understand how changes in the abundances and trait values of common species will affect the ecosystem functioning (Abadie et al., 2011).

With the expected growth in human population and the rapid conversion of natural areas to urban areas, especially in the hotspot of biodiversity (Seto et al., 2012), urban areas are especially relevant to biodiversity conservation (Aronson et al., 2017). Understanding the drivers of diversity in cities may help to meet the strategic goals A, B, D, and E (Table 2), and part of the 20 targets of the Aichi

Biodiversity Targets (UN-CBD, 2011) proposed by the Convention on Biological Diversity of the United Nations (UN-CBD) by the year 2020. Specifically, urban areas represent a fertile territory to mainstreaming biodiversity across the society and government (strategic goal A), increasing the population and governmental awareness on the benefits of biodiversity and what causes of biodiversity (Targets 1 and 2), and concrete actions at the citizen and governmental level that can be taken to safeguard biodiversity (Targets 3 and 4). Strategic goal B (to reduce the pressure on biodiversity) can be addressed in urban areas specifically through Target 5, with the reduction of degradation and fragmentation in natural habitats via sustainable development strategies in urban areas, identifying invasive species pathways related to cities and urbanization (Target 9), and decreasing the pressure on natural remanent areas like wetlands (Target 10). Also overcoming the environmental poverty described for poor areas in cities could be a direct action to enhance the benefits of diversity to the population stated on the strategic goal D, restoring the ecosystem services that are degraded in cities and promoting ecosystem resilience (targets 14 and 15). Finally, urban areas are the kind of ecosystem that most of the population experience every day, in wich the implementation of the targets with participatory planning strategies and knowledge management (Target 17) could be easily achieved, tearing apart the myth of grey cities for green cities.

Table 2: Overview of the five strategic goals of the Aichi Biodiversity Targets (UN-CBD, 2011) proposed by the Convention on Biological Diversity of the United Nations (UN-CBD). Source: <https://www.cbd.int/sp/targets/>

Strategic Goal	Description
A	Address the underlying causes of biodiversity loss by mainstreaming biodiversity across government and society
B	Reduce the direct pressures on biodiversity and promote sustainable use
C	To improve the status of biodiversity by safeguarding ecosystems, species and genetic diversity
D	Enhance the benefits to all from biodiversity and ecosystem services
E	Enhance implementation through participatory planning, knowledge management and capacity building

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Chapter Six

Appendices



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2013 Research stay: “*Partitioning of functional diversity into alpha and beta components using a variance partitioning approach*”. Centre de Biologie pour la Gestion des Populations – CBGP. Montpellier-sur-Lez, France. Supervisor: Dr Christine Meynard. Charge de recherche CR2, INRA. (13th-21th July).

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Publications

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Gutiérrez, A.G., Aravena, J.C., Carmona, M., **Carrasco, N.**, Christie, D.A., Peña M.P., Pérez, C. & Armesto, J.J. 2009. *Structural heterogeneity and environmental attributes of old-growth temperate rainforests of northern Chiloé Island, Chile*. Forest Ecology and Management. Special Issue. Forest Ecology and Management 258 (2009) 376–388.

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Conference contributions of this thesis

- **N. Carrasco-Farias**, Annika Meyer, Kühn, I. *A snapshot of the city: Composition of spontaneous plant communities in urban green areas in Valdivia, Chile*. 43rd Annual Conference of the Ecological Society of Germany, Switzerland and Austria (GfÖ). Potsdam, Germany (9-13 September 2013).
- **N. Carrasco-Farias**, Kühn, I. *The rich get richer: socioeconomic status, taxonomic and functional composition in urban green areas of Valdivia, Chile*. 7th European Conference on Biological Invasions (NEOBIOITA). Pontevedra, Spain (12-14 September 2012).
- **N. Carrasco-Farias**, Kühn, I. *Composition of vascular plants community in public green areas of Valdivia, Chile*. 41st Annual Conference of the Ecological Society of Germany, Switzerland and Austria (GfÖ). Oldenburg, Germany (5-9 September 2011).

Research Experience

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- 2004 - 2006** **Research assistant.** CMEB. Centro para Estudios en Ecología e Investigaciones Avanzadas en Biodiversidad (P02-051-F ICM). Grupo de Bosques. Supervisor: Dr Juan Armesto.
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Erklärung über den persönlichen anteil an den Publikationen

Chapter 2: Socio-economic status drives wild plant diversity in urban public green areas of a South American city (Valdivia, Chile)

Natalia Carrasco-Farias, Christine N. Meynard, Ingo Kowarik, Stefan Klotz, Isabell Hensen, Ingolf Kühn.

Research design: Carrasco-Farias, N. (85%), Kühn, I (15%).

Data collection: Carrasco-Farias, N. (100%)

Data Analysis: Carrasco-Farias, N. (80%), Meynard, C. (5%), Kühn, I (15%)

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Halle (Saale), den 11/05/2017

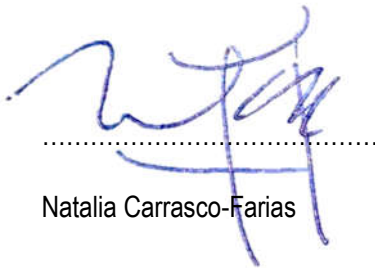
Unterschrift:.....

Natalia Carrasco-Farias

Eigenständigkeitserklärung

Hiermit erkläre ich, dass ich die vorliegende Arbeit mit dem Titel “ *Fine-scale effects of anthropogenic and environmental factors on diversity patterns of spontaneous vascular plants in a medium-sized city in South America (Chile)*“ selbstständig und ohne fremde Hilfe verfasst habe. Es wurden von mir keine anderen als die angegebenen Hilfsmittel und Quellen benutzt. Die in den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen wurden von mir als solche kenntlich gemacht. Diese Arbeit wurde weder an einer Fakultät der Martin-Luther-Universität noch an einer anderen wissenschaftlichen Einrichtung zur Erlangung eines Doktorgrades eingereicht. Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Halle/Saale, den 11/05/2017



Natalia Carrasco-Farias

