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BIODIVERSITY-PRODUCTIVITY RELATIONSHIP IN URBAN VASCULAR FLORA: A COMPARISON BETWEEN WILD EDIBLE AND NON-EDIBLE PLANTS

RELACIÓN BIODIVERSIDAD-PRODUCTIVIDAD EN LA FLORA VASCULAR URBANA: UNA COMPARACIÓN ENTRE PLANTAS SILVESTRES COMESTIBLES Y NO COMESTIBLES

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Abstract

Background: Wild edible plants are species that are not cultivated but can be consumed as food. These plants may exhibit the highest taxonomic and phylogenetic diversity within urban floras, since they have a longer history of use associated with humans than non-edible plants. Also, because biodiversity is strongly associated with biomass, edible plants plant might show higher productivity (biomass per site) than non-edible plants.

Questions: Is taxonomic and phylogenetic diversity of wild edible plants higher than non-edibles within urban areas? Is the alpha-biodiversity of wild edible plants positively related to biomass productivity in urban areas?

Study sites and years of study: Cities of the coastal Mediterranean-type ecosystem, central Chile, 2015 and 2016.

Methods: We characterized the taxonomic and phylogenetic diversity of urban flora differentiating wild edible and non-edible plants. Then, we assessed whether alpha-diversity of assemblages is related to their biomass productivity.

Results: Both taxonomic and phylogenetic diversity were higher for edibles than non-edible plants. For edible plants, biomass was positively related to species richness and negatively with the mean phylogenetic diversity (MPD, a measure of evolutionary relationship among plants within an assemblage).

Conclusions: Species richness is a suitable proxy to estimate wild edible plant diversity and their biomass in cities surpassing other proxies, such as phylogenetic diversity. Negative effect of MPD on biomass suggests that only a subgroup of related plants, possibly highly adapted to urban conditions, contribute to edible plant production. The distinction between wild edible and non-edible plants offers a better understanding of the assembly rules and biodiversity-biomass relationship within urban floras.

Keywords: assembly mechanism, community ecology, phylogenetic diversity, urban flora, wild edible plants.

Resumen

Antecedentes: Las plantas silvestres comestibles son especies no cultivadas que pueden utilizarse como alimento. Estas pueden exhibir una mayor diversidad taxonómica y filogenética dentro de las floras urbanas, debido a un historial de uso más largo asociado con los humanos que las plantas no-comestibles. Debido a la relación biodiversidad-biomasa, las plantas comestibles pueden mostrar una mayor productividad que las no-comestibles.

Preguntas: ¿Es la diversidad taxonómica y filogenética de las plantas silvestres comestibles mayor que la de las no-comestibles en áreas urbanas? ¿La alfa-biodiversidad de las plantas comestibles está relacionada positivamente con la productividad de biomasa en áreas urbanas?

Sitios de estudio y años: Ciudades del ecosistema mediterráneo costero, Chile central, 2015 y 2016.

Métodos: Caracterizamos la diversidad taxonómica y filogenética de la flora urbana diferenciando plantas silvestres comestibles y no-comestibles, evaluando si la alfa-diversidad de los ensambles está relacionada con su productividad.

Resultados: La diversidad taxonómica y filogenética fue mayor para las plantas comestibles que las no-comestibles. Para las comestibles, la biomasa se relacionó positivamente con la riqueza de especies y negativamente con la diversidad filogenética media (MPD).

Conclusiones: La riqueza de especies es un proxy adecuado para estimar la diversidad de plantas silvestres comestibles y su biomasa en las ciudades. El efecto negativo de MPD sobre la biomasa sugiere que solo un subgrupo de plantas relacionadas contribuye a la producción de plantas comestibles. La distinción entre plantas silvestres comestibles y no-comestibles ofrece una mejor comprensión de las reglas de ensamblaje y la relación biodiversidad-biomasa en la flora urbana.

Palabras clave: mecanismos de ensamblaje, ecología de comunidades, diversidad filogenética, flora urbana, plantas silvestres comestibles.

Urban areas are considered novel anthroposystems with distinctive species composition (Hobbs *et al*. 2006, Kowarik 2011) mainly due to the arrival of alien species (Mack & Lonsdale 2001), native species loss (Hahs *et al*. 2009) and stressful abiotic conditions (Bolund & Hunhammar 1999). Flora in urban areas has been widely characterized worldwide showing a high proportion of alien species, as described in cities of Europe (between 19 - 40 %, Ricotta *et al*. 2012a, Lososová *et al*. 2016, 2018), North America (19 - 58 %, Clemants & Moore 2003, Knapp *et al*. 2012), Asia (43 - 77 %, Zhao *et al.* 2010, Nagendra & Gopal 2011, Wang *et al.* 2011) and South America (83 - 96 %, Gartner *et al.* 2015, Figueroa *et al.* 2016, Fischer *et al.* 2016). Historical records of urban species allow us to trace their native origin and arrival time in the new ranges (Ricotta *et al.* 2012a, Lososová *et al.* 2016, 2018), which raise urban floras as suitable models for the understanding of community assembly mechanisms and vegetation succession dynamics (Corlett *et al.* 2002, Termote *et al.* 2012).

Wild edible plants are an important component of urban floras (Díaz-Betancourt *et al.* 1999). Wild edible plants are defined as species that grow spontaneously in self-sufficient populations in natural or disturbed ecosystems and can exist independently of direct human action (Heywood 1999, Cordero *et al*. 2020). These species have been considered as a potential contributor to human diets (Guil-Guerrero *et al.* 1998, Guil-Guerrero 2001, Penafiel *et al.* 2011, Romojaro *et al.* 2013, Turan *et al.* 2003). Will edible plants consider native and naturalized species (including weeds and ruderal plants), as well as domesticated species that scape cultivation and can grow without human interaction (Cordero *et al*. 2020). Generally wild edible plants in urban areas are alien species (Díaz-Betancourt *et al.* 1999, Ladio & Rapoport 2002, Tardío 2010, Turner *et al.* 2011) that show tolerance to the stressful conditions imposed by urban environments. Indeed, wild edible plants shows short life cycles, wind-pollinated flowers, genetic self-compatibility, and higher specific leaf area, which allow them to occur in urban areas (*e.g*., Lososová *et al.* 2006, Knapp *et al.* 2008, 2012). The study of urban flora differentiating wild edible plants from non-edibles may provide information on assembly rules (the mechanisms that explain species co-occurrence) especially when we consider that wild edible plants were dispersed by humans and they were closely linked to human use (Corlett *et al.* 2002, Termote *et al.* 2012, Rangel-Landa *et al.* 2017).

The positive relationship between plant biodiversity and biomass production has been widely recognized in several communities (Cadotte 2013, Sandau *et al.* 2017). However, whether some clades contribute meaningfully to community biodiversity in urban flora is an unexplored topic that could be filled by identifying the phylogenetic properties of plant assemblages. In this sense, it is expected that phylogenetic diverse assemblages, such as non-edible plants, host a greater plant biomass than edible plants, since in the last group the environmental filters have operated by selecting a group of traits that give adaptive value, reducing phylogenetic diversity of edible plants (Knapp *et al.* 2012, Cadotte 2013). This hypothesis has been scarcely tested especially in Latin American cities which have a younger history than European ones and could impact plant diversity patterns (Ricotta *et al.* 2012a, 2012b).

A key factor determining plant distribution and their diversity are climatic conditions, operating both from local (MacKey *et al.* 2012) to global levels (Seddon *et al.* 2016). For example, temperature might act as a filter for plant species in cities (which are considered as heat islands) modifying flora composition (Kendal *et al*. 2018). In this sense, a conclusive characterization of plant biodiversity requires to assess the effects of climatic variables among localities. In addition, whether climatic conditions drive biodiversity (*e.g*., low precipitation reduces plant diversity), these variables indirectly may drive plant biomass of edible plants. In this study we characterized the taxonomic and phylogenetic diversity of urban flora differentiating wild edible plants from non-edibles in urban areas of central Chile, a biodiversity hotspot characterized by Mediterranean-type climate (Myers *et al.* 2000). We consider as non-edible those plant species that have not being reported as edible, regardless of whether they are used for other purposes such as fodder, medicine, or fuel. Second, we assessed whether α-diversity (both taxonomic and phylogenetic) is related with productivity (plant biomass). We hypothesize that wild edible plants may exhibit the highest taxonomic and phylogenetic diversity within urban floras, since they have a longer history of use associated with humans than non-edible plants. Furthermore, because biodiversity is strongly associated with biomass, edible plants plant might show higher productivity (biomass per site) than non-edible plants. The positive biodiversity-biomass relationship has been widely described (Cadotte 2013) and it is feasible for urban flora. Overall, our study aims to characterize the taxonomic and phylogenetic α-diversity of urban flora differencing wild edible plants from non-edibles.

Materials and methods

Study area and sampling. The study was conducted in the northern portion of the Chilean Winter Rainfall-Valdivian Forest hotspot (Myers *et al.* 2000), which is characterized by a Mediterranean-type climate. We studied urban areas within and around the Valparaíso metropolitan area (Figure 1), which has a population of 1,539,852 inhabitants. This is the third most populated city in Chile, with a density of 93.9 inhabitants·km^2 (INE 2007). In this region, rains show marked seasonality, with a peak between May and September (373 mm·year^{-1}) and a dry period from October to April (Di Castri & Hajek 1976, Luebert & Pliscoff 2006). Annual mean temperature is around 13.5 °C (Valparaíso), with the lowest in July (11.4 °C) and the highest in January-February (18.5 °C) (Luebert & Pliscoff 2006). This region has been historically disturbed by different anthropogenic impacts such as land cover change and fires (Armesto *et al.* 2010). These factors have favored a greater proportion of alien plants compared with native plants in this ecoregion (Fuentes *et al.* 2013).

During the austral spring of 2015 and summer of 2016 (from September 2015 to January 2016) we performed a stratified sampling in urban areas within 500 × 500 m plots (n = 74). Within each plot, we randomly settled 1 × 1 m quadrats distributed where plants occurred, mainly covering parks, vacant lots, and sidewalks. We used 500 × 500 m plots to sample the same number of quadrats per site making our results comparable. This sampling approach allow us data gathering where sampling was feasible because the main surface of cities are pavement areas and private properties that limited a fully random sampling scheme. In total, 277 quadrats were distributed in 74 plots. Our approach might bias results, *e.g.*, overestimating indices of taxonomic diversity such as Shannon-Wiener, when the number of samples is small (Peet 1974), although rarefaction methods were used to avoid this situation (see below). Within each quadrat, we counted the number of plant individuals for each species. All recorded specimens were taxo-

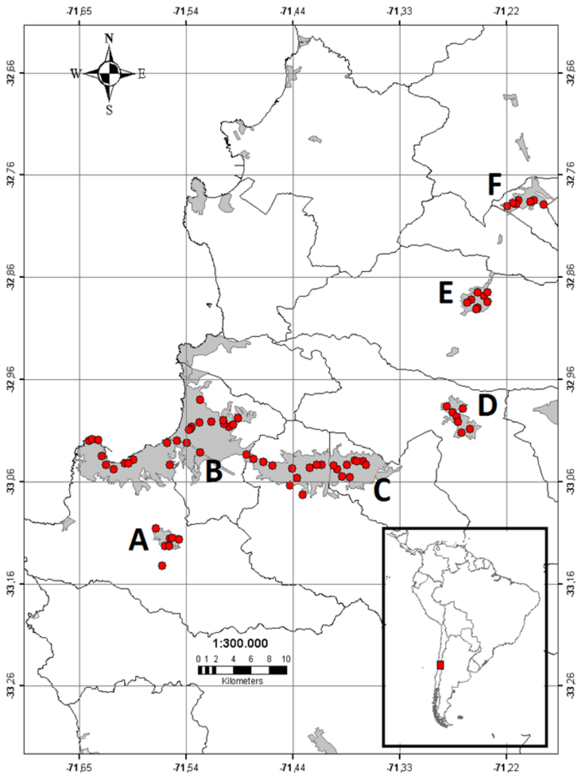

Figure 1. Locations of sampled plots (red dots) in the Valparaíso region. Urban areas are represented by grey polygons and the name of cities by letters. (A) Placilla, (B) Valparaíso-Viña del Mar conurbation, (C) Quilpué-Villa Alemana conurbation, (D) Limache, (E) Quillota and, (F) La Calera.

nomically identified and subsequently categorized according to their edibility following the databases PFAF Plants for a Future (2015), SEPASAL (2016) and GRIN (2015). These databases contain around 7,000, 2,745 and 1,603 records of edible plants, respectively. Because these databases are geographically biased, being the flora of South America underrepresented, we also reviewed bibliography allusive to the edible uses of the Chilean flora to complement the available records (Supplementary Material 1).

We settled plots, from north to south, in the following urban areas: La Calera (n = 6/33, numbers are the 500 × 500 m plots and 1 × 1 m quadrats surveyed), Quillota (n = 9/37), Limache (n = 7/32), Valparaíso-Viña del Mar conurbation (n = 25/70, hereafter called Valparaíso), Quilpué-Villa Alemana conurbation (n = 20/70, hereafter called Quilpué) and Placilla-Curauma conurbation (n = 7/35, hereafter called Placilla) (Figure 1; Table S1).

Taxonomic diversity. We estimated the taxonomic ∝-diversity for each using plant species richness and Shannon-Wiener index. These estimators were calculated from rarefaction curves using 999 randomizations and sampling without replacement using the R package iNEXT (Hsieh *et al.* 2016). To obtain comparable observations among sites, we extrapolated curves up to 60 samples and sites were considered statistically different when 95% confidence intervals of curves did not overlap for 40 samples (RAR_{40}) (Gotelli & Colwell 2001). These analyses were performed independently for wild edible plants and non-edibles.

Phylogenetic diversity. We estimated the phylo-α-diversity of edible and non-edible plants independently, which describe the shared phylogenetic history of species within urban areas. Among the myriad of indexes used to estimate the phylo-α-diversity, we choose Faith's index (Faith 1992), the mean phylogenetic distance (MPD) and the mean nearest taxon distance (MNTD) (Webb 2000). These indexes are by far, the most common metrics used in the phylogenetic diversity studies (Swenson 2009, Miller *et al.* 2017) and represent two of three dimensions of evolutionary history: the phylogenetic richness and the species divergence (Tucker *et al.* 2016). Specifically, Faith's index (Faith 1992) measures the cumulative phylogenetic distance from the tips to the roots of a phylogenetic tree containing all species within a local assemblage (here, a 500 × 500 m plot). Faith's index has shown low type I error rates and high power to detect phylogenetic clustering (Miller *et al.* 2017). The mean phylogenetic distance (MPD) is the average phylogenetic distance among all species pairs within a local assemblage and it is used to characterize phylogenetic relatedness among taxa and to detect phylogenetic overdispersion (unevenness). Finally, the mean nearest taxon distance (MNTD) is the mean distance of each taxon to the nearest terminal node and is a measure of "terminal" (*e.g.*, species, genera) phylogenetic diversity (Webb 2000).

Previous to the estimation of phylogenetic diversity indexes, we built a cladogram that included all recorded species using PHYLOMATIC v.3 (Webb & Donoghue 2005; www.phylodiversity.net/phylomatic). PHYLOMATIC generates a tree that usually contains polytomies at the family and genus level. We obtained a tree with 92 % of the internal nodes resolved and the remaining nodes showed polytomies (nodes with more than two daughter branches). Although the use of incomplete phylogenetic trees could impact estimation of phylogenetic diversity indexes (Swenson 2009), the level of polytomies in our phylogenetic tree allowed us a robust estimation of metrics, since it is far from a maximum of 60 % of polytomies recommended (Davies *et al.* 2012). The obtained phylogeny was based on the tree version proposed by Zanne *et al.* (2014), which is the largest time-calibrated phylogeny of plants available to the date. This tree was used to estimate all phylogenetic diversity indexes described in this study. Phylogenetic diversity indexes were estimated using the R package *picante* (Kembel *et al*. 2014).

Plant biomass and relationship to diversity. A representative individual was collected per 1 × 1 m quadrat for each species, which was taken to the laboratory, dehydrated for 48 h at 60 °C and weighed. These individuals were considered as representatives of each species since they belonged to the same cohort and did not exhibit considerable variation in their sizes. Weights of representative individuals were used as estimators of the productivity of each species multiplying the weight of the representative individual by the number of individuals of each species within each 1 × 1 m quadrat. Based on this dataset we compared biomass (i) between edible and non-edible plant species, and (ii) among sites. Statistical differences between status (edible vs non-edibles) *x* sites were assessed using a generalized linear model (*glm*, Zuur *et al.* 2009) with gamma distribution, which is used for continuous and positive data, such as biomass (Zuur *et al*. 2009).

We also assessed the relation between α-diversity (both taxonomic and phylogenetic) and climatic variables on the biomass of edible plants using generalized linear models (*glm*). We excluded non-edible plants, since the absence of this kind of plants in several samples made it unfeasible to obtain reliable estimators. As α-diversity descriptors (independent variables) we used species richness, Faith's index, MPD and MNTD. In addition, since climatic variables are a key factor determining diversity, we included the annual mean temperature and annual precipitation in the analyses. These were obtained from WorldClim (Hijmans *et al*. 2005) and extracted for each plot using DivaGis 7.5 (www.diva-gis.org). To determine the variables that were included in our models, we performed an exhaustive search using the regression subset selection (Lumley & Scott 2017), then, we built three *glm* models using the suggested variables. Models were ranked according to the Akaike information criterion obtained.

Results

Taxonomic diversity. A total of 77 angiosperm species (57 wild edible plants and 20 non-edibles) were recorded at the studied urban sites. Most of the species were alien: 98 % of wild edible plants and 100 % non-edibles. *Solanum maglia* (Solanaceae) was the only native edible plant recorded. The edible species were distributed in 20 families and 43 genera; non-edible plants species comprised 11 families and 17 genera (Table S2). The families that contained the greatest richness of wild edible plants were Asteraceae (17 species; 30 % of the species), Brassicaceae (5 species; 9 %), Fabaceae (5 species; 9 %), Malvaceae (4 species; 7 %) and Polygonaceae (4 species; 7 %). The families with the greatest richness of non-edible plants were Poaceae (8 species; 40 % of non-edibles) and Fabaceae (3 species; 15 %).

All the studied sites showed a similar proportion of edible plants (0.74 ± 0.02, mean ± SE, range: 0.63 - 0.79) and non-edibles (0.26 ± 0.02, range: 0.21 - 0.36). The rarefaction curves showed that both richness (S) and Shannon's index (H'), were greater for wild edible plants (S_{RAR40} = 48 species ± 2; H'_{RAR40} = 3.4 ± 0.1; mean ± SE) than non-edible plants (S_{RAR40} = 16 species ± 1; H'_{RAR40} = 1.1 ± 0.1) (Table 1; Figure S1). We evidenced a greatest diversity for the edibles using the criterion that 95% confidence intervals did not overlap between studied groups (Table 1; Figure S1). Amon sites, La Calera showed the greatest taxonomic diversity of edible plants, while Quillota showed the greatest biodiversity of non-edible plants (Table 1; Figure S1).

Table 1. Taxonomic richness (S) and diversity (Shannon's index, H) of wild edible and non-edible plants in urban areas from central Chile (mean ± SE).

		Observed richness (relative proportion in parenthesis)		Estimated richness (S_{RAR40})		Estimated diversity (H_{RAR40})	
Urban areas	**Number of plots**	**Edibles**	**Non-edibles**	**Edibles**	**Non-edibles**	**Edibles**	**Non-edibles**
La Calera	6	26 (0.79)	7 (0.21)	49 ± 13	19 ± 7	3.7 ± 0.7	1.4 ± 0.4
Quillota	9	21 (0.63)	12 (0.36)	28 ± 8	21 ± 7	2.2 ± 0.3	1.9 ± 0.4
Limache	7	24 (0.77)	7 (0.23)	33 ± 7	8 ± 3	2.9 ± 0.4	0.9 ± 0.3
Quilpué	20	31 (0.74)	11 (0.26)	38 ± 4	12 ± 2	2.6 ± 0.2	0.9 ± 0.1
Valparaíso	25	29 (0.74)	10 (0.26)	32 ± 2	11 ± 4	2.4 ± 0.2	0.9 ± 0.1
Placilla	7	33 (0.77)	10 (0.23)	36 ± 12	14 ± 5	3.6 ± 0.4	1.2 ± 0.3
Total	74	57	20	48 ± 2	16 ± 1	3.4 ± 0.1	1.1 ± 0.1

Estimated values were obtained from rarefaction curves for 40 samples per locality (RAR_{40}); number of plots refers to the number of 500 × 500 m in each site.

Phylogenetic diversity. Wild edible plants showed a higher phylogenetic diversity (Faith's index, MPD, and MNTD) than non-edibles in all the studied sites (Table 2). Among sites, we did not detect statistical differences in phylo-α-diversity, except for MNTD for wild edible plants: Quilpué showed the lowest value of MNTD and Valparaíso the highest (Table 2).

Table 2. Phylo-α-diversity estimators of the edible and non-edible plants using three different indexes: Faith's index, the mean phylogenetic distance (MPD), and the mean nearest taxon distance (MNTD).

	Faith's index		**MPD**		**MNTD**	
Urban areas	**Edibles**	**Non-edibles**	**Edibles**	**Non-edibles**	**Edibles**	**Non-edibles**
La Calera	333 ± 64	80 ± 2	56 ± 12	4 ± 2	70 ± 14^{ab}	16 ± 3
Limache	357 ± 99	176 ± 19	60 ± 11	37 ± 18	75 ± 12^{ab}	45 ± 20
Quillota	291 ± 49	202 ± 69	53 ± 12	43 ± 20	79 ± 13^{ab}	63 ± 24
Quilpué	292 ± 41	123 ± 14	41 ± 7	28 ± 8	65 ± 8^{a}	39 ± 12
Placilla	457 ± 90	187 ± 35	52 ± 11	37 ± 10	65 ± 13^{ab}	66 ± 26
Valparaíso	257 ± 25	123 ± 9	51 ± 7	23 ± 7	101 ± 6^{b}	100 ± 18
Total	309 ± 21	145 ± 13	50 ± 4	30 ± 5	79 ± 4	62 ± 9
Kruskal-Wallis χ^2	4.256^{ns}	8.811^{ns}	2.408^{ns}	4.378^{ns}	12.525*	7.225^{ns}

All values are expressed in millions of years (Myr). Different letters indicate significant differences among the sites for each index. * $P < 0.05$; ns: non-statistical effects.

Plant biomass. Biomass was greater for edible (147.5 g ± 31.6, mean ± SE; N = 57 species) than non-edible plants (62.7 g ± 29.5, N = 20 species; Figure 2), with statistical differences between contrasted groups (*glm*: d.f. = 1, deviance =1175, $P < 0.001$) but neither among sites (d.f. = 5, deviance = 1028, $P = 0.227$) nor interaction between factors

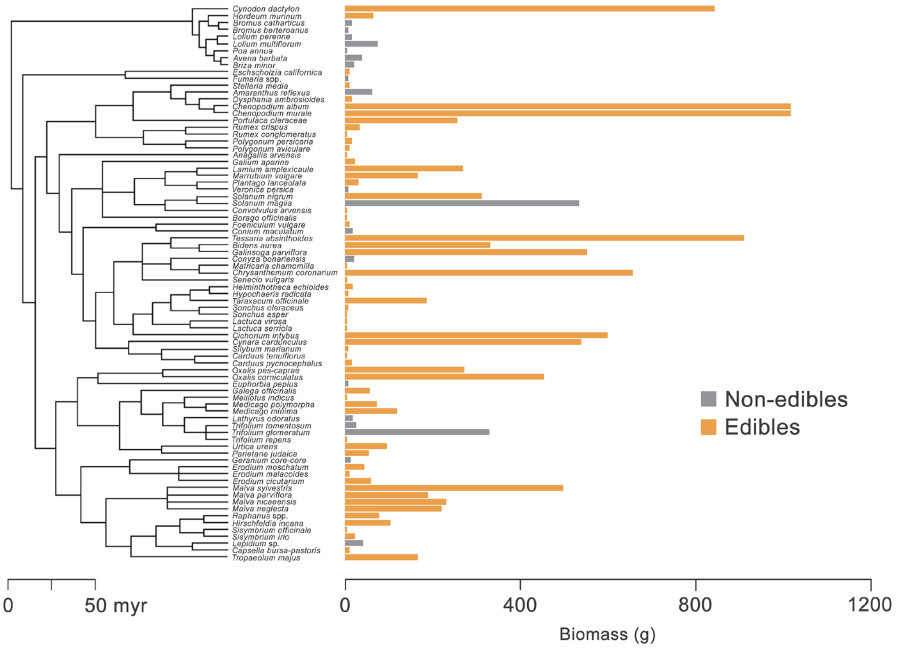

Figure 2. Phylogenetic relationships and biomass of edible and non-edible plants studied in the urban flora of the coastal Mediterranean-type ecosystem, central Chile.

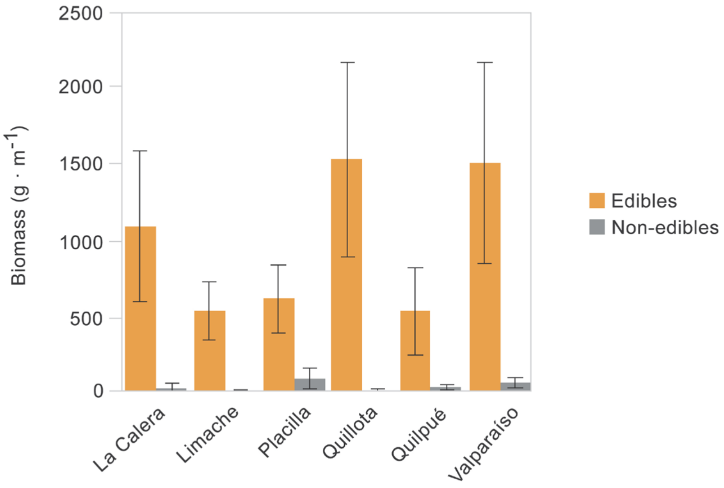

Figure 3. Plant biomass by urban site differentiating wild edible plants and non-edibles. Bars and errors are the mean and SE.

(d.f. = 5, deviance = 995, *P* = 0.458; Figure 3). The edible species with the greatest biomass (criteria: > 400 g per 1 × 1 m quadrat) were *Chenopodium album* L. (Amaranthaceae, 1,013 g ± 137, mean ± se, N = 52 quadrat where the plant occurred), *Cichorium intybus* L. (Asteraceae, 851 g ± 185, N = 38), *Cynodon dactylon* (L.) Pers. (Poaceae, 839 g, N = 1), *Chrysanthemum coronarium* L. (Asteraceae, 655 g ± 205, N = 10), *Galinsoga parviflora* Cav. (Asteraceae, 550 g, N = 1), and *Solanum maglia* Schltdl. (Solanaceae, 532 g, N = 1). The only non-edible plant with production greater than 500 g was *Conium maculatum* L. (Apiaceae, 537 g ± 44, N = 37).

The best model that explained biomass variability of edible plants was related to the taxonomic diversity and climatic variables, but not phylogenetic diversity (Table 3). Indeed, variable selection ruled out PD and MNTD as potential descriptors of edible plant biomass. We detected a positive and significant effect of the plant richness on edible plants biomass (Table 4; Figure 4). In addition, a negative and significant relationship between the mean phylogenetic distance and edible plants biomass was observed (Table 4; Figure 4). In spite of the fact that climatic factors (temperature and annual rain) were included in the models (Table 3), they did not influence edible plant biomass (Table 4).

Table 3. Summarized results of selection of models explained the variation of edible plants biomass in relation to α-diversity descriptors and climatic variables. Models were ordered according to Akaike information criterion (AIC). *k* is the number of parameters.

Model	*k*	AIC	Residual deviance
S + PP + TEM	4	1218.7	51.9
PP + TEM	3	1224.8	57.4
MPD	2	1232.0	55.9
S + MPD	3	1233.3	55.5
S	2	1235.4	58.4

S: species richness; PP: mean annual precipitation; TEM: mean annual temperature; MPD: mean phylogenetic distance.

Discussion

Our results show a higher proportion (~ 75 %) of edible plant species in urban areas, demonstrating that this group is an important component of urban floras in central Chile. This pattern may reflect the results of the human-mediated

Table 4. Fixed effects estimates (± standard error) for generalized linear models of edible plant biomass response to plant richness, climatic variables, and phylogenetic diversity. Boldfaced estimates are statistically significant in each model.

	Models		
Explanatory variables	S + PP + TEM	PP + TEM	MPD
Intercept	$-3.9\cdot10^{-3} \pm 3.4\cdot10^{-3}$	$-5.5\cdot10^{-3} \pm 3.5\cdot10^{-3}$	$\mathbf{-7.4\cdot10^{-4}} \pm 1.1\cdot10^{-4}$***
S	$\mathbf{2.6\cdot10^{-3}} \pm 8.9\cdot10^{-3}$***	-	-
TEM	$-2.4\cdot10^{-4} \pm 1.9\cdot10^{-4}$	$-3.3\cdot10^{-4} \pm 2.0\cdot10^{-4}$	-
PP	$-2.3\cdot10^{-4} \pm 1.3\cdot10^{-6}$	$-2.7\cdot10^{-6} \pm 1.4\cdot10^{-6}$	-
MPD	-	-	$\mathbf{-4.7\cdot10^{-6}} \pm 1.6\cdot10^{-6}$***

S: species richness; PP: mean annual precipitation; TEM: mean annual temperature; MPD: mean phylogenetic distance. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

dispersal history on plants: people tend to select plants with food, medicinal or ornamental uses and disperse them within urban areas (Díaz-Betancourt *et al.* 1999, Rapoport *et al*. 2009). In general, a high proportion of medicinal and ornamental plants also can be categorized as edibles (Cordero *et al.* 2017). Thus, the selection and use of these plants may indirectly increase the frequency of wild edible plants in urban areas. In Chile, many plant species introduced in the past for food, medicinal, and ornamental purposes escaped from croplands, gardens, or parks, colonizing urban areas (Matthei 1995). Some of these plants were introduced in Chile during the 19th century in botanical gardens due to their different uses, from where they dispersed and became naturalized in the following decades (Gay 1845-1854). This situation could explain, least partially, the high proportion of wild edible plants in urban areas (Gartner *et al.* 2015).

Other potential explanation to the great proportion of edible plants in urban areas is the ability of alien weeds to adapt to harsh conditions (McKinney 2006). Almost all the recorded plants in urban areas were alien species (98.7 %). In addition, we observed that taxonomic-productivity relationship, a pattern widely described in several plant systems (Cadotte 2013), also occurs among edible plants of studied cities, but not in not edibles. Contrary to our expectations, we detected a negative relationship between phylogenetic diversity (specifically MPD) and biomass. The mean phylogenetic distance (MPD) is a measure of the basal evolutionary diversity, thus, depicts diversity of plant orders and families. The observed result suggests that less phylogenetic diverse assemblages, which contain species with

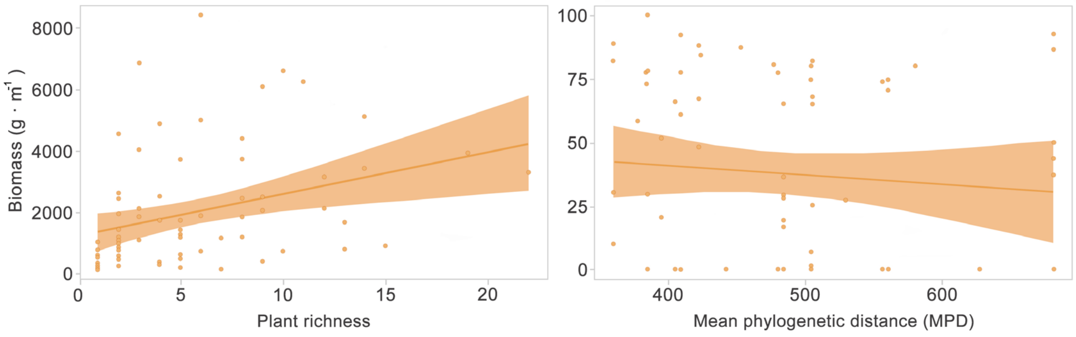

Figure 4. Relationship between plant richness (left panel) and the mean phylogenetic distance (right panel) on edible plant biomass. Continuous line is the result of a linear model and shaded area is the 95 % confidence interval for the slope.

similar ecological attributes (Cadotte *et al*. 2008), might host plants that are adapted to harsh conditions of cities (*e.g*., extreme temperatures) that acted as environmental filters selecting specific plant clades (Knapp *et al.* 2012, Cadotte 2013). Under this scenario, more similar assemblages show strategies that maximize the use of resources in harsh environments, hampering other potential negative effects of the ecological similarity (*e.g*., competition, Grime *et al*. 1973). Conversely, assemblages with a high phylogenetic diversity reduce plant productivity because only diverse singletons (specimens registered once) might occur in these sites, which marginally contribute to productivity.

Worldwide, the plant families that contain the greatest richness of wild edible plants are a subgroup of the richest families (*e.g*., Apiaceae, Asteraceae, Brassicaceae, Fabaceae, Poaceae, and Rosaceae; Kunkel 1984). We observed an overrepresentation of Asteraceae, Brassicaceae and Fabaceae families among the edible flora studied, which are also the richest families of the alien flora of Chile (Fuentes *et al.* 2013, Rodríguez *et al*. 2018). Conversely, Rosaceae was poorly represented in our dataset, as well as among alien plants in Chile where only nine species have been reported (Fuentes *et al.* 2013). This low number of Rosaceae species in Chile explain, at least partially, their underrepresentation in the edible flora, despite that some edible species are widely distributed out of urban areas, such as *Rosa rubiginosa* L. and *Rubus ulmifolius* Schott*.* In addition, although some Poaceae species were recorded (*Hordeum* sp. and *Lolium* sp., both genus with edible species), these specimens were not considered as edibles because individuals only in vegetative stage were observed making their identification unfeasible. Only 4 % and less than 1 % from a total of 30,176 individuals registered in our study belong to *Hordeum* and *Lolium*, respectively. Thus, it is likely that their exclusion as edibles did not affect our results.

To the best of our knowledge, this is a pioneer study in the ecology of urban flora since it is the first to characterize different biodiversity components of wild edible plants. However, this must not be considered as an ethnobotanical study. It is necessary design specific studies to elucidate whether wild edible plants that inhabit cities are recognized and potentially used by local people, considering that these areas are subject to greater threats to their biological and cultural diversity (Joos-Vandewalle 2015). The knowledge and use of edible plants in cities may be lost over time. In this sense, counting with an ecological approach to known urban flora will help people to promote the safe use of these wild resources, improving food security in urban contexts (Cordero *et al.* 2017) and, renewing the interest in the use of plants.

Most people are still unaware of the diversity of useful flora in cities, as well as their beneficial properties, which restricts the use of wild plants for food (Ladio 2005).

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Supplementary material

Supplemental data for this article can be accessed here: https://doi.org/10.17129/botsci.2892

Literature cited

Armesto JJ, Manuschevich D, Mora A, Smith-Ramirez C, Rozzi R, Abarzúa AM, Marquet PA. 2010. From the Holocene to the Anthropocene: a historical framework for land cover change in Southwestern South America in the past 15,000 years. *Land Use Policy* **27**: 148-160. DOI: https://doi.org/10.1016/j.landusepol.2009.07.006

Bolund P, Hunhammar S. 1999. Ecosystem services in urban areas. *Ecological Economics* **29**: 293-301. DOI: https://doi.org/10.1016/S0921-8009(99)00013-0

Cadotte MW. 2013. Experimental evidence that evolutionarily diverse assemblages result in higher productivity. *Proceedings of the National Academy of Sciences of the USA* **110**: 8996-9000. DOI: https://doi.org/10.1073/pnas.1301685110

Cadotte MW, Cardinale B, Oakley TH. 2008. Evolutionary history and the effect of biodiversity on plant productivity. *Proceedings of the National Academy of Sciences of the USA* **105**: 17012-17017. DOI: https://doi.org/10.1073/pnas.0805962105

Clemants SE, Moore G. 2003. Patterns of species diversity in eight north-eastern United States cites. *Urban Habitats* **1**: 4-16.

Cordero S, Abello L, Galvez F. 2017. *Plantas silvestres comestibles y medicinales de Chile y otras partes del mundo*. Chile: Concepción, Corporación Chilena de la Madera. ISBN:978-956-8398-10-1

Cordero S, Gálvez F, Arenas J, Rodríguez-Valenzuela E. 2020. Does access to natural environments explain differences in the use of wild plants between rural and urban populations? *Botanical Sciences* **99**: 104-123. DOI: https://doi.org/10.17129/botsci.2622

Corlett JL, Clegg MS, Keen CL, Grivetti LE. 2002. Mineral content of culinary and medicinal plants cultivated by Hmong refugees living in Sacramento, California. *International Journal of Food Sciences and Nutrition* **53**: 117-128. DOI: https://doi.org/10.1080/09637480220132139

Davies TJ, Kraft NJB, Salamin N, Wolkovich EM. 2012. Incompletely resolved phylogenetic trees inflate estimates of phylogenetic conservatism. *Ecology* **93**: 242-247. DOI: https://doi.org/10.1890/11-1360.1

Di Castri F, Hajek E. 1976. *Bioclimatología de Chile*. Santiago: Universidad Católica de Chile. ISBN: 9502908228.

Díaz-Betancourt M, Ghermandi L, Ladio A, López-Moreno IR, Raffaele E, Rapoport EH. 1999. Weeds as a source for human consumption. A comparison between tropical and temperate Latin American. *Revista de Biología Tropical* **47**: 329-338.

Faith DP. 1992. Conservation evaluation and phylogenetic diversity. *Biological Conservation* **61**: 1-10. DOI: https://doi.org/10.1016/0006-3207(92)91201-3

Figueroa JA, Teillier S, Guerrero-Leiva N, Ray-Bobadilla C, Rivano S, Saavedra D, Castro SA. 2016. Vascular flora in public spaces of Santiago, Chile. *Gayana Botanica* **73**: 85-103. DOI: https://doi.org/10.4067/S0717-66432016000100011

Fischer LK, Rodorff V, von der Lippe M, Kowarik I. 2016. Drivers of biodiversity patterns in parks of a growing South American megacity. *Urban Ecosystems* **19**: 1231-1249. DOI: https://doi.org/10.1007/s11252-016-0537-1

Fuentes N, Pauchard A, Sánchez P, Esquivel J, Marticorena A. 2013. A new comprehensive database of alien plant species in Chile based on herbarium records. *Biological Invasions* **15**: 847-858. DOI: https://doi.org/10.1007/s10530-012-0334-6

Gartner E, Rojas G, Castro SA. 2015. Compositional patterns of ruderal herbs in Santiago, Chile. *Gayana Botanica* **72**: 192-202. DOI: http://dx.doi.org/10.4067/S0717-66432015000200003

Gay C. 1845-1854. *Historia física y política de Chile. Botánica (Flora chilena).* 8 Volumes, 1 Atlas.Chile: Santiago, France: Paris.

Gotelli N, Colwell R. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* **4**: 379-391. DOI: https://doi.org/10.1046/j.1461-0248.2001.00230.x

Grime JP. 1973. Competitive exclusion in herbaceous vegetation. *Nature* **242**: 344-347. DOI: https://doi.org/10.1038/242344a0

GRIN [Germplasm resources information network]. 2015. USA: Agricultural Research Service. https://goo.gl/zvmy7y/ (accessed March 15, 2016).

Guil-Guerrero JL. 2001. Nutritional composition of *Plantago* species (*P. major* L., *P. lanceolata* L., and *P. media* L.). *Ecology of Food and Nutrition* **40**: 481-495. DOI: https://doi.org/10.1080/03670244.2001.9991663

Guil-Guerrero JL, Gimenez JJ, Torija ME. 1998. Mineral nutrient composition of edible wild plants. *Journal of Food Composition and Analysis* **11**: 322-328. DOI: https://doi.org/10.1006/jfca.1998.0594

Hahs AK, McDonnell MJ, McCarthy MA, Vesk PA, Corlett RT, Norton BA, Clemants SE, Duncan RP, Thompson K, Schwartz M, Williams NS. 2009. A global synthesis of plant extinction rates in urban areas. *Ecology Letters* **12**: 1165-1173. DOI: https://doi.org/10.1111/j.1461-0248.2009.01372.x

Heywood V. 1999. *Use and potential of wild plants in farm households*. Italy: FAO Farm Systems Management Series. ISBN: 978-9251041512

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**: 1965-1978. DOI: https://doi.org/10.1002/joc.1276

Hobbs RJ, Arico S, Aronson J, Baron JS, Bridgewater P, Cramer VA, Epstein PR, Ewel JJ, Klink CA, Lugo AE, Norton D, Ojima D, Richardson DM, Sanderson EW, Valladares F, Vilá M, Zamora R, Zobel M. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography* **15**: 1-17. DOI: https://doi.org/10.1111/j.1466-822X.2006.00212.x

Hsieh TC, Ma KK, Chao A. 2016. iNEXT: a R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution* **7**: 1451-1456. DOI: https://doi.org/10.1111/2041-210X.12613

INE [Instituto Nacional de Estadísticas]. 2007. *División político administrativa y censal - Región de Valparaíso. Chile*: Instituto Nacional de Estadísticas. https://goo.gl/Pxbfck/ (accessed December 20, 2016). Joos-Vandewalle S. 2015. *The effects of urbanisation on non-timber forest product dependencies*. MSc. Thesis. University of Cape Town.

Kembel S, Ackerly D, Blomberg S, Cornwell W, Cowan P, Helmus M, Morlon H, Webb C. 2014. *Package 'picante'*. https://goo.gl/1VHpQu (accessed December 1, 2016).

Kendal D, Dobbs C, Gallagher RV, Beaumont LJ, Baumann J, Williams NSG, Livesley SJ. 2018. A global comparison of the climatic niches of urban and native tree populations. *Global Ecology and Biogeography* **27**: 629-637. DOI: https://doi.org/10.1111/geb.12728

Knapp S, Dinsmore L, Fissore C, Hobbie SE, Jacobsdottir I, Kattge J, King JY, Klotz S, Macfadden J, Cavender-Bares J. 2012. Phylogenetic and functional characteristics of household yard floras and their changes along an urbanization gradient. *Ecology* **93**: S83-S98. DOI: https://doi.org/10.1890/11-0392.1

Knapp S, Kühn I, Schweiger O, Klotz S. 2008. Challenging urban species diversity: contrasting phylogenetic patterns across plant functional groups in Germany. *Ecology Letters* **11**: 1054-1064. DOI: https://doi.org/10.1111/j.1461-0248.2008.01217.x

Kowarik I. 2011. Novel urban ecosystems, biodiversity, and conservation. *Enviromental Pollution* **159**: 1974-1983. DOI: https://doi.org/10.1016/j.envpol.2011.02.022

Kunkel G. 1984. Plants for human consumption. Koenigstein: Koeltz Scientific Books. ISBN: 9783874292160

Ladio A. 2005. Malezas exóticas comestibles y medicinales utilizadas en poblaciones del noroeste patagónico: aspectos etnobotánicos y ecológicos. *Boletín Latinoamericano y del Caribe de Plantas Tropicales* **4**: 75-80.

Ladio A, Rapoport E. 2002. La variación estacional de las plantas silvestres comestibles en baldíos suburbanos de Bariloche, Parque Nacional Nahuel Huapi, Patagonia, Argentina. *Vida Silvestre Neotropical* **11**: 33-41.

Lososová Z, Chytrý M, Kühn I, Hájek O, Horáková V, Pyšek P, Tichý L. 2006. Patterns of plant traits in annual vegetation of man-made habitats in central Europe. *Perspectives in Plant Ecology* **8**: 69-81. DOI: https://doi.org/10.1016/j.ppees.2006.07.001

Lososová Z, Chytrý M, Danihelka J, Tichý L, Ricotta C. 2016. Biotic homogenization of urban floras by alien species: the role of species turnover and richness differences. *Journal of Vegetation Science* **27**: 452-459. DOI: https://doi.org/10.1111/jvs.12381

Lososová Z, Tichý L, Divíšek D, Ĉeplová N, Danihelka J, Dřevojan P, Fajmon K, Kalníková V, Kalusová V, Novák P, Řehořek V, Wirth T, Chytrý M. 2018. Projecting potential future shifts in species composition of European urban plant communities. *Diversity and Distributions* **24**: 765-775. DOI: https://doi.org/10.1111/ddi.12725

Luebert F, Pliscoff P. 2006. *Sinopsis bioclimática y vegetacional de Chile*. Santiago: Editorial Universitaria. ISBN: 9789561125759

Lumley T, Scott A. 2017. Fitting Regression Models to Survey Data. *Statistical Science* **32:** 265-278. DOI: https://doi.org/10.1214/16-STS605

Mack RN, Lonsdale WM. 2001. Humans as global plant dispersers: getting more than we bargained for: current introductions of species for aesthetic purposes present the largest single challenge for predicting which plant immigrants will become future pests. *Bioscience* **51**: 95-102. DOI: https://doi.org/10.1641/0006-3568(2001)051[0095:HAGPDG]2.0.CO;2

MacKey B, Berry S, Hugh S, Ferrier S, Harwood TD, Williams KJ. 2012. Ecosystem greenspots: identifying potential drought, fire, and climate-change micro-refuges. *Ecological Applications* **22**: 1852-1864. DOI: https://doi.org/10.1890/11-1479.1

Matthei O. 1995. *Manual de las malezas que crecen en Chile.* Chile, Santiago: Alfabeta Impresores. ISBN: 9789562722148.

McKinney ML. 2006. Urbanization as a major cause of biotic homogenization. *Biological Conservation* **127**: 247-260. DOI: https://doi.org/10.1016/j.biocon.2005.09.005

Miller ET, Farine DR, Trisos CH. 2017. Phylogenetic community structure metrics and null models: a review with new methods and software. *Ecography* **40**: 461-477. DOI: https://doi.org/10.1111/ecog.02070

Myers N, Mittermeier R, Mittermeier C, da Fonseca G, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**: 853-858. DOI: https://doi.org/10.1038/35002501

Nagendra H, Gopal D. 2011. Tree diversity, distribution, history and change in urban parks: studies in Bangalore, India. *Urban Ecosystems* **14**: 211-223. DOI: https://doi.org/10.1007/s11252-010-0148-1

Peet RK. 1974. The measurement of species diversity. *Annual Review of Ecology and Systematics* **5**: 285-307. DOI: https://doi.org/10.1146/annurev.es.05.110174.001441

PFAF [Plants for a future]. 2015. *Edible, medicinal and useful plants for a healthier world.* http://pfaf.org/ (accessed March 15, 2016).

Penafiel D, Lachat C, Espinel R, Van Damme P, Kolsteren P. 2011. A systematic review on the contributions of edible plant and animal biodiversity to human diets. *EcoHealth* **8**: 381-399. DOI: https://doi.org/10.1007/s10393-011-0700-3

Rangel-Landa S, Casas A, García-Frapolli E, Lira R. 2017. Sociocultural and ecological factors influencing management of edible and non-edible plants: the case of Ixcatlan, Mexico. *Journal of Ethnobiology and Ethnomedicine* **13**: 59. DOI: https://doi.org/10.1186/s13002-017-0185-4

Rapoport E, Marzocca A, & Drausal B. 2009. *Malezas comestibles del cono sur y otras partes del planeta*. Bariloche: Ediciones Instituto Nacional de Tecnología Agropecuaria. ISBN: 9789872505097.

Ricotta C, La Sorte FA, Pyšek P, Rapson G, Celesti-Grapow L, Thompson K. 2012a. Phyloecology of urban alien flora. *Journal of Ecology* **97**: 1243-1251. DOI: https://doi.org/10.1111/j.1365-2745.2009.01548.x

Ricotta C, La Sorte F, Pyšek P, Rapson G, Celesti-Grapow L, Thompson K. 2012b. Phylogenetic beta diversity of native and alien species in European urban floras. *Global Ecology and Biogeography* **21**: 751-759. DOI: https://doi.org/10.1111/j.1466-8238.2011.00715.x

Rodríguez R, Marticorena C, Alarcón D, Baeza C, Cavieres L, Finot VL, Fuentes N, Kiessling A, Mihoc M, Pauchard A, Ruíz E, Sanchez P, Marticorena A. 2018. Catálogo de las plantas vasculares de Chile. *Gayana Botánica* **75**: 1-430. DOI: https://dx.doi.org/10.4067/S0717-66432018000100001

Romojaro A, Botella M, Obón C, Pretel M. 2013. Nutritional and antioxidant properties of wild edible plants and their use as potential ingredients in the modern diet. *International Journal of Food Sciences and Nutrition* **64**: 944-952. DOI: https://doi.org/10.3109/09637486.2013.821695

Sandau N, Fabian Y, Bruggisser OT, Rohr RP, Naisbit RE, Kehrli P, Aebi A, Bersier L-F. 2017. The relative contributions of species richness and species composition to ecosystem functioning. *Oikos* **126**: 782-791. DOI: https://doi.org/10.1111/oik.03901

Seddon AWR, Marcias-Fauria M, Long PR, Benz D, Willis KJ. 2016. Sensitivity of global terrestrial ecosystems to climate variability. *Nature* **531**: 229-232. DOI: https://doi.org/10.1038/nature16986

SEPASAL [Survey of economic plants for arid and semiarid regions]. 2016. UK https://cgspace.cgiar.org/handle/10568/48722 (accessed March 15, 2016).

Swenson NG. 2009. Phylogenetic resolution and quatifying the phylogenetic diversity and dispersion of communities. *Public Library of Science* **4**: e4390. DOI: https://doi.org/10.1371/journal.pone.0004390

Tardío J. 2010. Spring is coming: the gathering and consumption of wild vegetables in Spain. *In*: Pardo de Santayana M, Pieroni A, Puri R, eds, *Ethnobotany in the New Europe: People, health and wild plant resources.* UK: Berghahn Press, pp. 211-238. DOI: https://doi.org/10.1080/00207233.2010.544068

Termote C, Meyi MB, Djailo BD, Huybregts L, Lachat C, Kolsteren P, Van Damme P. 2012. A biodiverse rich environment does not contribute to a better diet: a case study from DR Congo. *Public Library of Science* **7**: e30533. DOI: https://doi.org/10.1371/journal.pone.0030533

Tucker CM, Cadotte MW, Carvalho SB, Davies TJ., Ferrier S, Fritz SA, Grenyer R, Helmus MR, Jin LS, Mooers AO, Pavoine S, Purschke O, Redding DW, Rosauer DF, Winter M, Mazel F. 2016. A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biological Reviews* **92**: 698-715. DOI: https://doi.org/10.1111/brv.12252

Turan M, Kordali S, Zengin H, Dursun A, Sezen Y. 2003. Macro and Micro mineral content of some wild edible leaves consumed in eastern Anatolia. *Acta Agriculturae Scandinavica B-Soil & Plant Science* **53**: 129-137. DOI: https://doi.org/10.1080/090647103100095

Turner NJ, Łuczaj Ł, Migliorini P, Pieroni A, Dreon AL, Sacchetti L, Paoletti M. 2011. Edible and tended wild plants, traditional ecological knowledge and agroecology. *Critical Reviews in Plant Science* **30**: 198-225. DOI: https://doi.org/10.1080/07352689.2011.554492

Wang HF, López-Pujol LA, Mayerson JX, Qiu XK, Wang XK, Ouyang ZY. 2011. Biological invasions in rapidly urbanizing areas: a case study of Beijing, China. *Biodiversity and Conservation* **20**: 2483-2509. DOI: https://doi.org/10.1007/s10531-011-9999-x

Webb C, Donoghue M. 2005. Phylomatic: tree assembly for applied phylogenetics. *Molecular Ecology Resources* **5**: 181-183. DOI: https://doi.org/10.1111/j.1471-8286.2004.00829.x

Webb C. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *The American Naturalist* **156**: 145-155.

Zanne AE, Tank DC, Cornwell WK. 2014. Three keys to the radiation of angiosperms into freezing environments. *Nature* **506**: 89-92. DOI: https://doi.org/10.1038/nature12872

Zhao JJ, Ouyang ZY, Xu WH, Zheng H, Meng XS. 2010. Sampling adequacy estimation for plant species composition by accumulation curves-A case study of urban vegetation in Beijing, China. *Landscape and Urban Planning* **95**: 113-121. DOI: https://doi.org/10.1016/j.landurbplan.2009.12.008

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GA. 2009. *Mixed effects models and extensions in ecology with R*. NY: Springer Science+Business Media.

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