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Quantifying the contributions of native and non-native trees to a city's biodiversity and ecosystem services

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ABSTRACT

Urban trees are appreciated for their intrinsic value and their contributions to human well-being. Here, we analysed a database of 115′686 non-forest trees (1'025 species) to quantify the present contributions of native and non-native trees to biodiversity (taxonomic richness) in the metropolitan area of Geneva, Switzerland. Non-native trees made up 90 % of species and 40 % of individuals. A subset of these individuals with more detailed phenotypic information (N = 50'718 trees; 527 species) was used to quantify five regulating ecosystem services (micro-particle capture, carbon sequestration, water interception, microclimatic cooling, and support for pollinators), three cultural ecosystem services (natural heritage, recreational, and aesthetic value) and two disservices (allergies and biological invasiveness). Non-native and native trees generated roughly identical regulating services, on a per-tree basis, as these are linked primarily to tree morphology rather than to tree-origin. Non-native trees generated cultural ecosystem services that were greater than native trees, on a per-tree basis, with the exception of the notion of "natural heritage". For example, 79 % (163/207) of trees independently identified as "remarkable" by the canton of Geneva were non-native. Our results illustrate that non-native trees represent a significant source of biodiversity and ecosystem services both in absolute terms and on a per-tree basis. Given the empirical importance of non-native trees in many cities, and the likelihood that their importance will increase with future climate change, we suggest that non-native trees be considered in conservation assessments and strategic planning both for intrinsic reasons and for their contributions to human well-being.

1. Introduction

Trees have come to play a key-stone role in urban settings because of their multi-dimensional values. For instance, trees contribute to different dimensions of the concept "biodiversity" through the taxonomic diversity of the trees themselves, the other species they physically support, and through the species-interactions and ecological functions they facilitate (Kowarik, 2011). In addition, they represent a source of contributions to human well-being and landscape functions (e.g., Dobbs et al., 2011; Endreny et al., 2017; Kardan et al., 2015; McKinney et al., 2018). For example, they contribute to carbon sequestration (Price et al., 2017), intercept micro-pollutants that are detrimental to human health (McDonald et al., 2016; Nowak et al., 2014), provide shade and local cooling during summer months (Willis and Petrokofsky, 2017) and attenuate the urban heat-island effect (Pramova et al., 2012).

Trees also contribute to cultural ecosystem services such as human recreation, historical and cultural heritage (Dobbs et al., 2014; Hermes et al., 2018). Cultural services are typically appreciated in urban settings, where they can make up an estimated 81 % of a typical tree's total projected value (McPherson et al., 2011, 2016). Trees also generate disservices in the form of allergenic pollen, damage to infrastructure, the harm done by invasive species to local native biodiversity, amongst others (Dobbs et al., 2014; Eisenman et al., 2019; von Doehren and Haase, 2015). Studies that have attempted to monetise tree ecosystem services and disservices report a net present value of trees 5–6 times greater than the sum of their estimated direct costs (e.g., planting, management), indirect costs (e.g., allergies) and negative externalities (e.g., carbon emissions from management) when trees are allowed to grow to maturity (McPherson et al., 2007, 2016; Soares et al., 2011; Vogt et al., 2015).

Cities are highly modified environments to which some regional native tree species may be poorly adapted and where, conversely, non-na-

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tive species can occasionally thrive (Kowarik et al., 2013; Sjöman et al., 2016). Non-native species make up more than half of the species richness in some European, North American, and Australian cities (Clemants and Moore, 2003; Frank et al., 2006; Kowarik et al., 2013; Pyšek, 1998; Zerbe et al., 2003). A small fraction of non-native trees can become invasive and cause undesirable biological, social, or economic effects (Mack et al., 2000; Richardson and Rejmánek, 2011; Simberloff, 2013). On the other hand, non-native trees also contribute to species richness and human well-being through their ecosystem services (Kowarik, 2011; Riley et al., 2018; Schlaepfer, 2018b; Schlaepfer et al., 2011). Managers of trees recognise that many native tree species will likely face increasingly high mortality rates in urban environments if phenomena such as urban heat-island effects and climate change lead to warmer, drier environments (Aflaki et al., 2017; Aitken et al., 2008; Endreny et al., 2017; Estoque et al., 2017; Myint et al., 2013; Ren et al., 2013; Sun et al., 2017). As a result, a number of recent studies have called for the integration of non-native species into conservation strategic planning and urban forestry management plans (Bodnaruk et al., 2017; Conway et al., 2019; Dobbs et al., 2014; Kowarik, 2018; McKinney et al., 2018; Sjöman et al., 2016).

Several studies have quantified the fraction of species or individuals that are non-native (Frank et al., 2006; Kowarik et al., 2013; Sjöman et al., 2012) or quantified specific ecosystem services that are produced by individual non-native tree species in both urban (e.g., Dickie et al., 2014; Hurley and Emery, 2018; Kim, 2016; Riley et al., 2018) and rural settings (Lugo, 1997; Rodriguez, 2006). But lacking to date are comprehensive assessments of the relative contributions of non-native and native trees to both biodiversity and ecosystem services (although see Riley et al., 2018). Such studies would not only serve practical purposes (e.g. adaptation planning to climate change) but also nourish the broader debate regarding the role that should be attributed to the bulk of non-native species that are not invasive (Conway et al., 2019; Schwarz et al., 2017). Indeed, some scientists focus on the risks associated with non-native species, and suggest that they should be controlled and eradicated because their undesirable effects could emerge at a later date (e.g., Ricciardi and Simberloff, 2009; Simberloff, 2013). Others have highlighted that some non-native species make positive contributions that further societal and conservation objectives (e.g., Ewel et al., 1999; Fischer et al., 2009; Mascaro et al., 2012; Rodriguez, 2006; Schlaepfer et al., 2011; Severns and Warren, 2008). A science-based strategy to managing non-invasive non-native species will require a site-specific evaluation of the present positive and negative contributions, but also likely future positive and negative effects (Conway et al., 2019; Kowarik, 2011; Sádlo et al., 2017).

The canton of Geneva, Switzerland is used here as a case-study to quantify the contributions of native and non-native trees. Historically, residents of Geneva have been large importers of non-native trees for their botanical gardens or as decoration in large private properties (Beer et al., 2017). For example, a large number of conifers, cedars and sycamores were imported from North America and the Mediterranean basin in the 16th and 17th century for their aesthetic value, their resistance to diseases and perennial leaf-cover (Roguet, 1988). By 1834, the botanical garden in Geneva was host to more than 700 non-native tree species, primarily from the Americas and Asia (Aeschimann and Bocquet, 1982). In the 1980–1990 s, non-native species were viewed more cautiously with the rise of the conservation movement. This period also marks the rise of pro-native values. The canton of Geneva's law seeking to preserve and restore biodiversity (*Loi sur la Biodiversité*, 2012) remains focused on native species, as do numerous urban planning documents in other countries (Chalker-Scott, 2015; Chan et al., 2014; Conway et al., 2019; Dobbs et al., 2014).

To contribute to the discussion on the role of non-native trees in urban planning, we sought to quantify the current contributions of individual, non-forest trees (≥ 2 m tall) to both biodiversity and ecosystem services in a metropolitan environment. Specifically, we ask: What percentage of trees and tree species in the Canton of Geneva is non-native? What percentage of ecosystems services flows from native and non-native trees? What are the risks and opportunities associated with each group of species? Finally, we discuss these results in the broader debate that asks to what extent non-native species should be considered as part of the biotic environment our societies wish to value and preserve for present and future generations.

2. Methods

Our study area is the terrestrial portion of the canton of Geneva (area: 242 km^2 excluding rivers and lake, 495'249 residents in 2017, mean human density: 1800/km^2). The canton of Geneva maintains a database of individual (non-forest) trees (*Inventaire cantonal des arbres*; ICA) for scientific and management purposes. In 2018, the ICA database contained 237'461 individual live trees, which represent half of the estimated 412'000 individual, non-forest, trees within the canton (Schlaepfer et al., 2018). The database includes both spontaneous and planted trees but does not distinguish between these two categories. For this study, we first extracted all records of live trees in the ICA database with a species-level identifier and GPS coordinates (hereafter, the "Species-ID" dataset) to describe biodiversity. We then extracted a subset of records that contained further auxiliary information (diameter of trunk at breast height, crown diameter and soil type; hereafter the "Species & Morphology" dataset) necessary to quantify regulating ecosystem services. Cultural ecosystem services and disservices were also quantified with the "Species & Morphology" dataset for purposes of comparison with regulating ecosystem services.

The ICA database includes information on Tree Origin and Leaf Phenology. The variable Tree Origin has three possible states: Native; Archeophyte or Neophyte. Archeophytes are defined in ICA as species having been introduced to Switzerland prior to the year 1492. Unless specified, Archeophytes and Neophytes were grouped under the label "non-native". Origin for species within the database that were not part of the federal InfoFlora database (www.infoflora.ch) were attributed to the Neophyte category, after verification by a botanical expert (co-author P.M.). The variable Leaf Phenology has two possible states depending on whether leaves drop in the winter (Deciduous) or not (Perennial). The full ICA database is available upon request.

2.1. Indicators for biodiversity and ecosystem services

Species richness and the number of individuals are used as indicators for biodiversity. Indicators for tree ecosystem services and disservices were drawn from CICES (Haines-Young and Potschin, 2018), Dobbs et al. (2014) and completed with customised indicators through a participatory process involving 27 stake-holders (academics, NGO, state, and practitioners) with an interest in urban trees (GE-21, 2016; Schlaepfer et al., 2018). Tree crown area, leaf-area, and soil type are key determinants of regulating services. Crown area and leaf-area were estimated using species-specific allometric equations within i-Tree based on species-name, total height (m), canopy health, and diameter at breast height (DBH). Importantly, i-Tree is populated primarily with allometric equations for North-American tree species. Allometric growth equations for European tree species are generated within the i-Tree database by the average equation of the closest taxonomic level (species, genus, family) found, and then adjusted to match local climatic conditions. Micro-pollutant cleansing, carbon-sequestration, and storm water interception services were estimated for each tree using the i-Tree Eco software based on tree morphology inputs (i-Tree, no date). Tree crown surface area is used as a proxy for the regulating service micro-climatic cooling.

Tree species with floral resources (nectar and pollen) support pollinator taxa, and thus, indirectly, the regulating service of crop pollination. We consulted three sources (Darricau, 2018; Feltin and Hummel, 2016; Van Daele, 2011) that quantify nectar and pollen resources of French tree species that did not explicitly exclude non-native species, although one (Van Daele, 2011) excluded invasive species. Tree species were described as a pollinator support species (in a binary manner), if the species had high or very high in floral resources (scores 4–5 for pollen or nectar, on a scale of 1–5) or if they provide any floral resources in the spring or fall.

Several indicators of cultural ecosystem services were defined. We include the cultural ecosystem service "Natural Heritage" (Dobbs et al., 2014) to acknowledge the contribution of native species towards the relational – and possibly symbolic – values of Identity and Sense of Place (Chan et al., 2016) amongst certain stake-holders (Gbedomon et al., 2020). It is important to include such an indicator and limit its definition to native species to capture the belief-position by some conservation biologists that non-native species do not make up part of "biodiversity" that society seeks to protect (Schlaepfer, 2018a). We calculated natural heritage with and without archeophytes to account for the possibility that trees that have been present in the canton of Geneva since 1492 could be considered "belonging to" the region by some stakeholders.

Recreational ecosystem services (Hermes et al., 2018) were estimated using the percentage of tree species and individuals found in parks and planted on street sidewalks. This was done to include only trees located in public spaces where they can be enjoyed by the public. The geolocality of all trees was projected, and then filtered using GIS layer of all parks and green spaces provided by the Canton and of all streets. Both GIS layers were accessed via the Canton's web-portal (https://ge.ch/sitg/).

Other cultural services included a bundle of services that we termed "Landscape/Historic/Aesthetic", which was quantified using various indicators based on the number of species and individuals designated as "remarkable" or as a "horticultural variety". These classifications were established prior to, and independently of, our study. For example, the canton of Geneva maintains a list of trees considered "remarkable", which are characterized by their large size, association with historic events, position in the landscape, and aesthetic aspects (Beer et al., 2017; Canton of Geneva, 2018). The number of remarkable individuals was curtailed between 1976 (n = 1292) and 2018 (n = 207) in an effort to make the list more exclusive, and we included both lists in our analysis.

Horticultural varieties reflect artificial selection by breeders, generally to highlight morphological characteristics considered unusual, useful, or beautiful. Horticultural varieties are defined in the International Code of Nomenclature for Cultivated Plants (Art. 28 Notes 2, 4, and 5). For example, *Gleditsia triacanthos* 'Inermis' is a cultivar of the Honey or Thorny locust. The cultivar was selected for the absence of the typical spines in the parental lineage. As a result, the cultivar is frequently used in parks and playgrounds. Other cultivars capture unique phenologies (e.g., the copper Beech, *Fagus sylvatica* 'Purpurea'). We therefore use the number of varieties and number of species with multiple varieties as indicators of aesthetics.

Tree species that generate significant disservices were identified through independent and authoritative sources. Tree species were scored as "allergenic" only when described by the national Swiss Allergy Center (www.pollenundallergie.ch) as "strongly" or "very strongly allergenic". Invasive trees can locally displace native biodiversity and induce rapid aesthetic changes to the landscape, both of which can reduce the value of the Natural Heritage cultural ecosystem service for certain groups of stakeholders. Invasiveness was scored in a binary manner, and invasive tree species were identified using a classification established by the Swiss Federal Office for the Environment (InfoFlora, 2014; Wittenberg, 2006). Raw data on individual trees and species-specific characteristics are available in the Supplementary Materials.

2.2. Summary statistics

We report all biodiversity indicators and ecosystem services by tree origin and by leaf phenotype. Summary statistics about the location of native and native trees in the Species & Morphology dataset are provided by land-use (5 categories); ownership (public or private); and urban gradient (urban or suburban). The urban perimeter was defined by county sub-divisions in which at least a third of the area was covered by large buildings (>400m^2); the urban area had 453'444 inhabitants in 79 km^2 (density: 5'740 inhab/km^2) and the suburban area had 53'160 in 163 km^2 (326 inhab/km^2). We report the 50th (median), 10th, and 90th percentiles for each ecosystem service and disservice, per-tree, to facilitate comparisons with other cities. The total contribution of each service is obtained by multiplying the median value by the total number of trees in a given category. We chose not to monetise ecosystem services because of high uncertainty and over-riding influence of assumptions, particularly when estimating the value of cultural ecosystem services. No indicator was excluded *a posteriori*.

3. Results

The ICA database contained 241'591 records of live, non-forest trees. 115'686 trees were identified to one of 1025 species (Table 1). Non-native trees made up 90 % of tree species (916 neophytes and 8 archaeophytes) and 40 % of individuals (37′780 neophytes and 8′683 archaeophytes). The ten most common native and non-native tree species (Table 2) represent, respectively, 34 % and 22 %, of all individuals in the Species-ID dataset. 197 non-native tree species (and 0 native species) had 5 or fewer individuals in the "Species-ID" dataset; we suspect that these are mostly non-reproducing species that were introduced into private or botanical gardens.

Table 1
Number of records of live trees in the ICA dataset, in the "Species-ID" sub-dataset composed of trees identified to species, and the "Species-Morphology" sub-dataset composed of tree records with auxiliary morphological information (tree diameter, crown diameter and soil type at base of tree, and geographical coordinates), by Species Origin.

Dataset	Purpose	Individuals			Species		
		Native	Non-Native	Total	Native	Non-Native	Total
ICA	Multi-purpose database of live individual trees in Canton of Geneva, Switzerland	–	–	237'461	–	–	–
Species-ID	Describe abundance and species richness	69'223	46'463	115'686	101	924	1'025
Species & Morphology	Quantify ecosystem services	30'546	20'172	50'718	68	459	527

Table 2
Ten most abundant trees identified to species, by origin (native or non-native) and leaf-type (D = deciduous, P = persistent), in the ICA database ("Species-ID" dataset; 115'686 individuals, 1025 species) of the Canton of Geneva, Switzerland 2018.

Origin	Rank	Scientific name	English name	Individuals	Leaf-type
Native	*1*	*Quercus robur*	Common oak	10395	D
	2	*Carpinus betulus*	Common hornbeam	8719	D
	3	*Fraxinus excelsior*	Common ash	5300	D
	4	*Acer platanoides*	Norway maple	4919	D
	5	*Acer campestre*	Field maple	4857	D
	6	*Acer pseudoplatanus*	Sycamore	4356	D
	7	*Prunus avium*	Wild cherry	4046	D
	8	*Taxus baccata*	Common yew	3817	P
	9	*Pinus sylvestris*	Scots pine	3542	P
	10	*Betula pendula*	Silver birch	2439	D
Non-native	*1*	*Aesculus hippocastanum*	Horse chestnut	3431	D
	2	*Pinus nigra*	Black pine	3423	P
	3	*Malus domestica*	Apple	3182	D
	4	*Juglans regia*	Common walnut	3178	D
	5	*Prunus domestica*	Plum	2712	D
	6	*Robinia pseudoacacia* [a]	Black locust	2316	D
	7	*Platanus x acerifolia*	Hybrid plane	2011	D
	8	*Pyrus communis*	Common pear	1793	D
	9	*Platanus x hispanica*	London plane	1266	D
	10	*Acer saccharinum*	Silver maple	911	D

[a] On national black-list of invasive species.

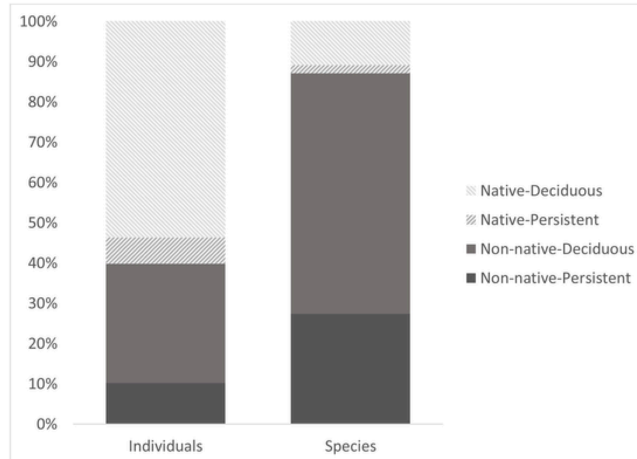

Fig. 1. Relative composition of non-forest individual trees (Species-ID & Morphology dataset; n = 50'718) and tree-species (n = 527) for which ecosystem services were quantified, by origin (native or non-native) and leaf-phenology (deciduous or persistent), Canton of Geneva, 2018.

A subset of the records in the Species-ID dataset (50'718 trees belonging to 527 species) had sufficient auxiliary information to quantify the chosen ecosystem service indicators (Table 1). In this "Species & Morphology" dataset, 99.5 % of trees were 2 m or taller and had a diameter at breast height of 3 cm or wider. Non-native trees made up 87 % of species (n = 459) and 40 % of individuals (n = 20'172) (Fig. 1). Trees in the Species & Morphology dataset came primarily from the urban part of the canton, but with relatively good geographical coverage of the entire canton (Fig. 2) and from a variety of different land-uses (Table 3). Land-uses associated with cultural ecosystem services (cemeteries, parks, green areas, residential areas), and public spaces in general, were particularly species rich (per area) and had a high proportion of non-native individuals and species (Table 3). Trees on public domain are over-represented within the Species & Morphology dataset relative to available surfaces, probably because access to these trees is easier than on private property.

Overall, median trunk diameter at breast height, which serves as a proxy for size, tree crown diameter, and canopy cover were all virtually identical between non-native and native trees (Table 4). There were, however, important differences in trunk diameter when comparing native trees with persistent leaves (median 32 cm) to non-native trees with persistent leaves (median 46 cm) (Table 4).

Regulating services are driven primarily by tree morphology (canopy cover and leaf-surface area) over the course of a year. As a result, larger trees with persistent leaves generally provided greater regulating ecosystem services than smaller or deciduous trees on a per-tree basis (Table 5). On a per-tree basis, the typical (median) native trees provides regulating services that were 3–4 % greater than non-native trees, with the exception of pollination services, where non-native species made up a similar fraction of species that support pollination, but native trees constituted a majority of pollinator-friendly individuals (Table 5).

Native trees provided 98.5–100 % of the cultural ecosystem service Natural Heritage, depending on whether archaeophtyes are considered non-native or not (Table 6). In both parks and streets, non-native trees represented about half of all individuals and roughly three-quarters of species, reflecting the fractions of non-native trees in our overall sample. In the "Landscape/Historic/Aesthetic" bundle of cultural ecosystem services, most remarkable trees were non-native (Table 6). For example, 207 individual trees were identified as "remarkable" in 2017 (Beer et al., 2017; Canton of Geneva, 2018), of which 163 (79 %) were non-native. Remarkable trees were represented by 62 species, 43 (69 %) of which were non-native (Fig. 3).

Disservices were remarkable for their extreme results, with the disservice of allergens emanating from native trees, whereas the disservice of "threat to biodiversity loss" attributed solely to non-native species. Four species of trees (*Alnus glutinosa, Betula pendula, Corylus avellana, Fraxinus excelsior*) are considered strongly or very strongly allergenic, all of which are native (

Table 7). A total of 3'253 individuals belong to these four allergenic species, representing 6.4 % of the 50'718 trees and 0.7 % of the 527 analysed species. Six species of tree or woody shrubs are currently considered invasive (national black-list) in Switzerland (*Ailanthus altissima, Buddleja davidii, Prunus laurocerasus, Prunus serotina, Rhus typhina, Robinia pseudoacacia)* all of which are found in the Geneva region (Table 7). A total of 1'232 individuals belonged to these six species, representing 2.4 % of the 50′718 trees and 1.1 % of the analysed species.

4. Discussion

The primary take-home message of this work is that non-native trees represent an important contribution to both biodiversity and ecosystem services in the metropolitan area and canton of Geneva. The

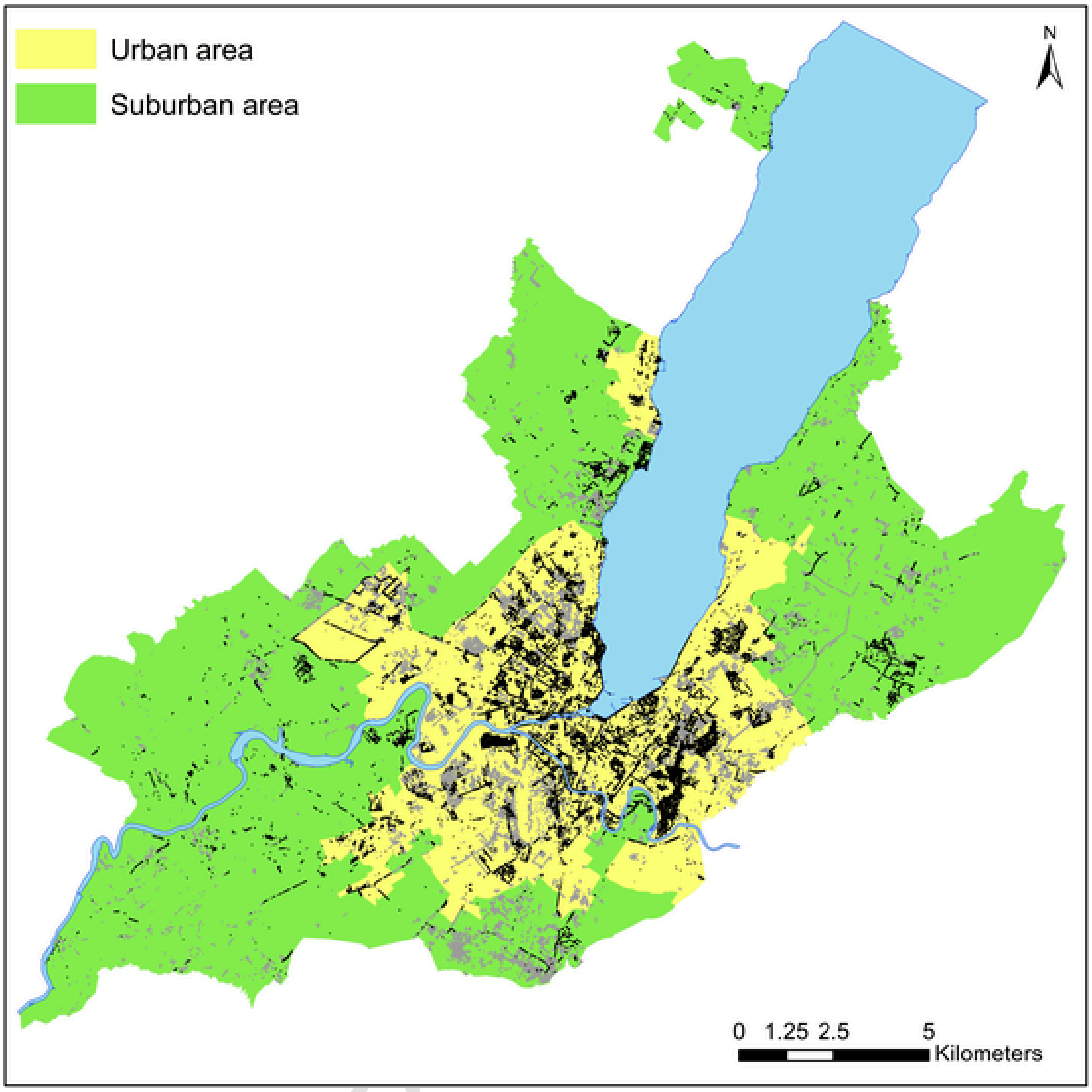

Fig. 2. Geographical location of trees in "Species & Morphology"" database (black points, n = 50'718) and the additional trees only within "Species – ID" database (grey points, n = 64'968) within the canton of Geneva, by urban gradient.

Table 3
Number (percentage) of native and non-native trees from the Species&Morphology dataset (n = 50'718), by land-use, land-ownership, and built (urban) environment, relative to available areas in the Canton of Geneva (lake and river surfaces excluded).

Categorization	Sub-categories	Surface (km^2) (%)	Count of Individuals			Count of Species		
			Native	Non-Native	Total	Native	Non-Native	Total
Land-cover	Residential	61.6 (25.4)	12'679	9'322	22'001	56	221	277
	Parks and urban green areas	39.4 (16.2)	8'505	6'304	14'808	62	377	439
	Agricultural	125.5 (51.7)	7'936	3'227	11'163	47	113	160
	Industrial	15.5 (6.4)	1'057	414	1'471	32	57	89
	Cemeteries	0.6 (0.3)	369	906	1'275	27	107	134
Land-ownership	Public	65.8 (27.2)	19'608	13'676	33'282	66	430	496
	Private	176.6 (72.8)	10'937	6'497	17'436	57	208	265
Urban gradient	Urban	78.0 (32.2)	23'016	16'569	39'585	67	450	517
	Suburban	164.4 (67.8)	7'530	3'603	11'133	48	132	180

total number of tree species in the region has increased from 101 native species prior to the year 1500 to roughly 1000 species in 2018 (an as a result of an additional 8 archaeophytes and 916 non-native species, of which only a fraction are probably self-sustaining) primarily as a result of historical efforts to import non-native tree species. Today, non-native trees are found in all types of environments (Fig. 2, Table

Table 4
Phenotyptic description of native and non-native trees (median, 10th-90th percentiles; "Species-ID&Morphology" dataset), and fraction non-native (NN) to total (non-native + native).

	Native			Non-Native			Fraction NN
Origin/Phenotype	All native	Persistant	Deciduous	All non-native	Persistant	Deciduous	
Sample size (individuals)	30'545	3'331	27'214	20'173	5'153	15'020	0.34
Tree trunk dbh (cm)	32 (12–83)	32 (13–60)	32 (12–86)	34 (12–80)	46 (15–115)	31 (11–70)	0.51
Canopy cover (m^2)	38.5 (7–154)	28.3 (7–78.5)	38.5 (7–177)	38.5 (7–154)	38.5 (7–177)	38.5 (7–133)	0.50
Leaf-surface area (m^2)	233 (33–669)	181 (35–510)	242 (33–693)	211 (24–731)	254 (28–1095)	197 (22–669)	0.46

Table 5
Regulating ecosystem service values (median, 10th-90th percentiles; "Species & Morphology" dataset) provided per tree by native and non-native trees in Geneva and fraction non-native (NN) to total (non-native + native).

	Native			Non-Native			Fraction NN
Origin/Phenotype	All native	Persistant	Deciduous	All non-native	Persistant	Deciduous	
Sample size (n individuals)	30'545	3'331	27'214	20'173	5'153	15'020	0.40
Air-cleansing regulation, per tree							
Micro-pollution – O_3(g/yr per tree)	126 (17–408)	292 (57–1037)	113 (15–349)	121 (14–655)	428 (58–2180)	87 (10.8–311)	0.49
Micro-pollution – NO_2(g/yr per tree)	33 (4.5–108)	77 (15–274)	30 (4–92)	32 (3.7–173)	113 (15.3–576)	23 (3–82)	0.49
Micro-pollution – PM_{10}(g/yr per tree)	87 (14–266)	116 (26–299)	84 (13–256)	86 (11–329)	158.8 (19–683)	70 (9–229)	0.49
Micro-pollution – CO(g/yr per tree)	3.1 (0.4–9.9)	7 (1.4–25)	2.7 (0.4–8.4)	2.9 (0–16)	10.3 (1–53)	2 (0.3–7.5)	0.48
C-sequestration (kg C/yr), per tree	10 (2.5–38.5)	5.9 (1.5–18.8)	10.7 (2.8–41)	9.7 (2.3–32)	8.40 (2–28)	10.8 (3–35)	0.49
Micro-climatic cooling (m^2), per tree	38.5 (7–154)	28.3 (7–78.5)	38.5 (7–176)	38.5 (7–154)	38.5 (7–176)	38.5 (7–133)	0.50
Water interception (m^3/year), per tree	0.97 (0.15–2.90)	1.3 (0.25–3.65)	0.94 (0.15–2.70)	1 (0.10–3.80)	1.8 (0.2–7.90)	0.77 (0.08–2.60)	0.51
Support of Pollinators (number of species)	36	3	33	35	4	28	0.49
Support of Pollinators (number of individuals)	12'265	883	11'382	7'159	618	6'541	0.37

3) and their contributions to biodiversity and ecosystem services are roughly proportional to their species richness and relative abundance, respectively. Although this conclusion may sound self-evident, one important implication is that biodiversity indicators that exclude non-native species such as the Singapore Index for urban biodiversity (Chan et al., 2014) are likely to be deeply flawed in cities where non-native trees make up a large fraction of species and individuals (Riley et al., 2018; Schlaepfer, 2018a).

A second important take-home message is that our analysis suggests that for most regulating services (capture of carbon, capture of micro-pollutants; interception of heavy rainfall) native and non-native trees are roughly equivalent on a per-tree basis. Indeed, the magnitude of most regulating services is driven primarily by tree morphology such as surface of canopy cover, surface of leaf-area, and duration of leaves over the year (Chalker-Scott, 2015), which, in turn, depends in part on species-specific morphology, but also how well-adapted a tree is to its local environment. We acknowledge that this conclusion could change marginally once allometric equations specific to local species are integrated into the i-Tree software but there is no theoretical reason to believe that one group of tree species will "perform" better than another in this category of services. In our study, the individual trees that produced the greatest regulating service were large, non-native perennially-leafed trees (Table 4; Fig. 3). These results reinforce the point that non-native species provide useful regulating ecosystem services on par with, and sometimes much greater than, native species.

Thirdly, non-native species provide more ecosystem services than native trees for some cultural ecosystem services. We were particularly surprised to observe that indicators used to capture the cultural ecosystem services such as Geneva's "remarkable" trees were dominated by non-native species. We had initially assumed that the canton's database of remarkable tree - a source of considerable local pride and fanfare (Beer et al., 2017; Jim, 2005) - would showcase native trees that "belong" to the region. That non-native species and individuals should dominate this list (as well as the earlier edition from 1976) suggests that non-native trees can have desirable cultural characteristics that trump the notion of nativeness (Gerstenberg and Hofmann, 2016; Sommer, 1997).

Are there potential drawbacks to non-native species that were not considered in this study? Local biologists often assume that the native trees will harbour more insects, epiphytic plants and birds than non-native trees, but we found no data from Geneva to test this assumption. Available evidence in the literature is mixed and does not provide strong support for this hypothesis (Chalker-Scott, 2015). For example, one recent study in South Africa found more birds and bird species on native street trees than on non-native trees, but the opposite pattern was found for mistletoes (Shackleton, 2016). Understanding the role of non-native trees in supporting animals and plants from different trophic levels in urban environments remains a major gap in knowledge (Chalker-Scott, 2015).

One could also fear that such a large number of non-native species and individuals could lead to the local extirpation of native species. Some non-native tree species (e.g., *Robinia pseudoacacia*) can become locally abundant in rural areas, where they tend to invade grasslands and result in the local extirpation of native dry grassland species (Cier-

Table 6
Cultural ecosystem services provided by native and non-native (NN) trees in Geneva, and fraction non-native (NN) to total (non-native + native).

		Native			Non-Native			Fraction NN
Ecosystem Services	Indicator	All native	Persistant	Deciduous	All non-native	Persistant	Deciduous	
Sample size (individuals)		30’545	3’331	27’214	20’173	5’153	15’020	0.40
Sample size (species)		68	11	57	459	144	315	0.87
Natural heritage	Percent nativeness of species	100	100	100	0 (1.5 including archaeophytes)	0 (0.5 including archaeophytes)	0 (1.9 including archaeophytes)	< 0.02
Recreational	Number of individuals found in parks	7’299	1’089	6’210	6’379	2’306	4’073	0.47
	Number of species found in parks	61	10	51	394	130	264	0.87
	Number of individuals found on streets	1’325	29	1’296	1’053	58	995	0.44
	Number of species found on streets	28	4	24	64	15	49	0.70
Landscape/Historic/Aesthetic								
	Number of remarkable trees 1976 – individuals	583	77	506	709	410	299	0.55
	Number of remarkable trees 1976 –species	30	7	23	95	42	53	0.76
	Number of remarkable trees 2018 – individuals	44	7	37	163	128	35	0.79
	Number of remarkable trees 2018 – species	19	3	16	43	23	20	0.69
	Number of horticultural varieties	105	23	82	248	71	177	0.70
	Number of species with min. 1 variety	27	5	22	78	31	47	0.74
	Individuals belonging to a variety	1582	65	1517	2400	679	1721	0.60

Fig. 3. An example of a non-native tree (Himalayan cedar, *Cedrus deodara*) designated as a remarkable tree (cultural ecosystem service) by the Canton of Geneva. Photo by Manuel Faustino, reprinted with permission.

Table 7
Disservices generated by native and non-native (NN) trees in Geneva, and fraction non-native (NN) to total (non-native + native).

			Native			Non-Native		Fraction NN
Ecosystem Disservices	Indicator	All native	Persistant	Deciduous	All non-native	Persistant	Deciduous	
Sample size (individuals)		30'545	3'331	27'214	20'173	5'153	15'020	0.34
Sample size (species)		68	11	57	459	144	315	0.87
Potential Health impacts	Allergenic (individuals)	3253	0	3253	0	0	0	0.00
	Allergenic (species)	4	0	4	0	0	0	0.00
Potential Native Biodiversity loss and reduced Sense of Place	Invasive (individuals)	0	0	0	8087	0	8087	1.00
	Invasive (species)	0	0	0	6	0	6	1.00

jacks et al., 2013; Vítková et al., 2017). But to our knowledge, not one species (of plant nor animal) has become locally extirpated due to these invasive non-native tree species in Geneva since the first survey of species was conducted in 1850. In addition, the six invasive tree species are relatively rare in the study area, with the exception of *Robinia* (Table 2). Thus, trees that have been classified as invasive and that are potentially problematic in natural settings may have fewer opportunities to do harm in urban settings (Sádlo et al., 2017). Finally, one might also fear that non-native species could become invasive and induce more costs in the future (financial or through negative externalities) than would native trees (Kowarik, 2011). This is a legitimate concern that we were unable to assess with existing information.

Are there potential advantages to non-native species not considered in this study? High species richness is generally viewed as desirable because it is assumed to confer a greater variety of services, redundancy in ecological functions that could provide resilience to future perturbations and bet-hedging against novel diseases (Ehrenfeld, 2010; Kremen and Merenlender, 2018; Liao et al., 2008; Mascaro et al., 2012; Sandifer et al., 2015; Sjöman et al., 2016, 2012; Vilà et al., 2011). City densification and climate change both will lead to warmer and possibly drier conditions for urban trees (Aflaki et al., 2017; Aitken et al., 2008; Endreny et al., 2017; Estoque et al., 2017; Myint et al., 2013; Ren et al., 2013; Roloff et al., 2009; Sun et al., 2017; Wilby and Perry, 2006). The majority of the most abundant non-native species in Geneva (Table 2) have native ranges from south-eastern Europe and could be pre-adapted to future climate, increasing the proportion of trees that are likely to survive and generate desirable ecosystem services.

5. Conclusions

Our primary goal in this study was to quantify the contributions of native and non-native trees to biodiversity and ecosystem services. Our goal was not to measure which category of tree was "better", especially since many non-native trees have undergone a vetting process (for aesthetics, low maintenance cost, robustness, etc.) before being imported and thus they likely do not represent a random sample of non-native trees. Our assessment provides further evidence that non-native tree increase regional species richness (Chalker-Scott, 2015; Kowarik et al., 2013; Sjöman et al., 2016; Zerbe et al., 2003), and that these trees provide valuable ecosystem services (Riley et al., 2018). Native tree species are more likely to cause allergies, which may induce greater economic costs (Eisenman et al., 2019). Finally, a fraction of non-native trees may help ensure that some trees survive future climate change. Thus, our assessment is that both local biodiversity and ecosystem services provided by trees in the metropolitan area of Geneva have likely improved thanks to non-native species.

Urban tree management integrates notions of economics, ecology, human values and climate science (Bodnaruk et al., 2017; Jenerette et al., 2016; Kowarik, 2011). Our results add to a growing set of examples illustrating that non-native trees make contributions to both local biodiversity and human well-being. As such they should be included in indicators that track biodiversity and the contributions of nature to people.

CRediT authorship contribution statement

Martin A. Schlaepfer: Conceptualization, Investigation, Writing - original draft, Writing - review & editing, Supervision, Project administration, Funding acquisition. **Benjamin P. Guinaudeau:** Conceptualization, Investigation, Formal analysis, Writing - original draft, Visualization. **Pascal Martin:** Investigation, Writing - review & editing. **Nicolas Wyler:** Investigation, Visualization, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest

The authors report no declarations of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ufug.2020.126861.

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