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RESEARCH

Drivers of compositional turnover of the non-native urban flora in the Western Cape, South Africa

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Abstract

Interest in understanding the drivers of biological invasions in urban centres is increasing globally. Previous research focused primarily on the drivers of non-native species richness in urban centres (i.e. why some cities harbour more species than others) and there has been much less focus on compositional turnover (i.e. why different cities harbour different species). Exploring compositional turnover between urban centres can differentiate drivers and barriers of non-native species at different stages along the introduction-naturalisation-invasion continuum and help to inform effective management strategies. This paper explores the drivers of compositional turnover of wild-growing non-native plants across urban centres of the Western Cape province in South Africa, ranging from the city of Cape Town (821 km^2) to the small town of Bot River (1.7 km^2). We assess the role of temperature, precipitation, urbanisation intensity, urban area, travel time, year of establishment, and population density in mediating richness-independent species turnover between a range of urban centres. Multi-site generalised dissimilarity modelling (MSGDM) of zeta diversity (number of shared species among multiple urban centres), and variance partitioning are applied to analyse inventories compiled from cleaned iNaturalist occurrence records. The importance of environmental conditions increased toward the later stages of the invasion continuum while variables related to introductions decreased. The study concludes that, despite the major changes to habitats caused by urbanisation and anthropogenic activities, climate is the primary driver of turnover of urban non-native plant species within the Western Cape. Management initiatives in the Western Cape should be guided by regional biogeographic context, with strategies adapted to local species pools and climatic constraints rather than relying on uniform, across-city approaches.

Keywords Biological invasions · Citizen science · iNaturalist · Multi-site generalised dissimilarity modelling · Plant invasions · Species turnover · Urban ecology · Zeta diversity

Introduction

Biological invasion is the process whereby non-native species are introduced through human activities to novel ranges where they need to negotiate several barriers to advance along an introduction-naturalisation-invasion continuum (Richardson et al. 2000; Blackburn et al. 2011) (henceforth 'the invasion continuum'). The field of invasion science has traditionally focused on natural and semi-natural ecosystems (Gaertner et al. 2017), but urban ecosystems are receiving increasing attention because of the central role of urban centres in the introduction, establishment and spread of many non-native species (Salomon Cavin and Kull 2017). Invasive non-native species (those that have progressed far along the invasion continuum) are often associated with various socio-economic and environmental impacts in urban areas but can

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simultaneously provide some benefits (Potgieter et al. 2017, 2020; Roy et al. 2024). This paper assesses non-native 'wild-growing' (non-cultivated) plant species, i.e. those that have overcome one of the initial barriers in the invasion continuum and escaped from cultivation. For brevity, henceforth we refer to these as 'non-native' species or plants.

Urban centres are often the first point of introduction of non-native plants into novel regions through the ornamental horticulture industry and other pathways (Padayachee et al. 2017; Potgieter and Cadotte 2020). Once plant species are introduced, urban centres can further serve as hubs for rapid regional dispersal. For example, Botella et al. (2022) highlighted the spread of the invasive non-native plant *Coleus barbatus* throughout the Western Cape, South Africa, following its introduction as an ornamental species and rapid subsequent spread through human-mediated long-distance dispersal. Urban centres are also important for launching or sustaining biological invasions into surrounding natural and agricultural areas (Alston and Richardson 2006; McLean et al. 2017). Many non-native species, however, remain concentrated in highly urbanised areas where novel habitats and frequent disturbances favour their persistence and limit competition from native species (Cadotte et al. 2017). For example, intense urbanisation can create unique habitats such as 'hardscapes', a novel anthropogenic habitat in the form of asphalt and paved surfaces resembling deserts, which filters for a non-random subset of species (Frazee et al. 2019).

Potgieter et al. (2024) outlined four main axes that drive non-native species diversity and spread in urban habitats. (1) Connectivity, such as distances between habitats, which can control the rate of movement of propagules between and within urban centres; (2) Physical properties, often anthropogenically induced, which can determine the habitats available and stresses experienced by species; (3) Cultural and socio-economic history, such as wealth, age of the urban centre, and demographics of the inhabitants, which influences patterns of cultivation and suitable habitats for non-native species; and (4) Biogeography and climate, the abiotic conditions of an area such as temperature and precipitation, which affects non-native species diversity and spread, despite some of these being overridden by urbanisation. While some of these drivers of urban plant invasions have been explored, most studies have focused on target species and alpha diversity metrics such as species richness. Much less attention has been given to examining how these drivers influence non-native species differentially and thus contribute to their turnover across a region, i.e. beta diversity (Potgieter et al. 2024).

Species turnover represents a separate diversity component from species richness. Turnover can be partitioned into two distinct parts: species addition and species replacement (Baselga 2010). Species addition reflects differences in species richness between sites which can lead to nested species lists. Consequently, the same processes that drive species richness also mediate species addition (Baselga 2010, 2012). Species replacement is richness independent and reflects solely differences in species composition, where species at one site are replaced by different species at another site. Considering richness alone therefore overlooks ecologically meaningful processes which act at different stages along the invasion continuum to drive changes in species composition, such as dispersal limitation and niche differentiation without necessarily changing richness (Latombe et al. 2019; Pyšek et al. 2020). By revealing the processes that drive the differential exchange and establishment of non-native species within and between urban centres, patterns of compositional turnover can inform targeted management actions across invasion stages (Potgieter et al. 2022). For example, long-term control, containment and impact mitigation can be supported by applying predictive models to identify environmentally similar areas for biological invasions.

Traditional measures of turnover typically utilise pairwise dissimilarity indices (beta diversity); these measures capture predominately turnover resulting from the gain and loss of rare, localised species between sites and are poorly suited for capturing turnover components of more widespread species that are likely to be more advanced along the invasion continuum (Latombe et al. 2017). Consequently, the drivers and assembly processes behind these species at more advanced invasion stages, in contrast to those of species at earlier invasion stages, are largely unknown. To capture the full spectrum of compositional turnover, the concept of zeta diversity (Hui and McGeoch 2014; details provided in the Methods section) can help in identifying the factors that drive species turnover between relatively narrow-ranged species (likely to be present at the early stages of the invasion continuum) and widespread species (present at advanced stages of invasion). At the early stages, anthropogenic factors such as introduction pathways and propagule pressure play important roles in determining the composition of non-native plant species (Williamson 2006; Donaldson et al. 2014; Pyšek et al. 2020). Habitats into which species are introduced do not necessarily coincide with their preferred habitat (Robeck et al. 2024). At the later stages of the invasion continuum, species have likely already overcome some barriers to dispersal and have dispersed or been disseminated to more suitable habitats (Hui et al. 2014). Factors affecting species introductions (or habitat accessibility) are thus likely to play a stronger role at the early stages of the invasion continuum, whereas habitat suitability is more likely to play a stronger role at the later stages of the invasion continuum.

The Western Cape province of South Africa has a long history of non-native plant species introductions and invasions (Macdonald and Richardson 1986; van Wilgen et al.

2020). The region is well known for its exceptionally high diversity of native plant species (Cowling et al. 1997) and is potentially vulnerable to increasing additional plant invasions in the future (Paganeli et al. 2025). The Western Cape (and indeed all of South Africa) has a long and complex history of urban development. Colonisation by the Dutch and later the British, and subsequent apartheid policies, have to a large extent shaped urbanisation in the region and the composition of plant species in these urban centres (Shackleton and Gwedla 2021). Gildenhuys et al. (2025) constructed non-native plant inventories for a number of urban centres throughout the Western Cape using carefully cleaned iNaturalist records. This dataset provides an opportunity to explore the drivers of compositional turnover of non-native urban flora across a highly diverse, and biogeographically and historically complex region. A better understanding of these drivers can inform better management of biological invasions in the province and help mitigate some of the associated negative impacts on environments and people (Roy et al. 2024).

This study investigates the drivers of inter-urban non-native floral turnover in the Western Cape province of South Africa. It explores the effects of (1) climate, including temperature and precipitation; (2) physical properties, including urban area and urbanisation intensity; (3) socio-economic properties, including population density and year of establishment (of the urban centre); and (4) connectivity between urban centres, estimated as the average travel time on roads between urban centres. We hypothesised that the relative importance of different drivers would vary along the gradient from narrow-ranged to widespread species captured by increasing orders of zeta diversity. Specifically, we predicted that temperature, precipitation, urbanisation intensity, and urban area (variables associated with habitat suitability) would become increasingly important at higher orders of zeta diversity, which are dominated by widespread species. We also predicted that population density, year of urban establishment, and travel time (variables linked to anthropogenic species introductions) would decline in importance as drivers of turnover at higher orders of zeta diversity, as they primarily influence narrow-ranged species mostly representing earlier stages of non-native species along the invasion continuum.

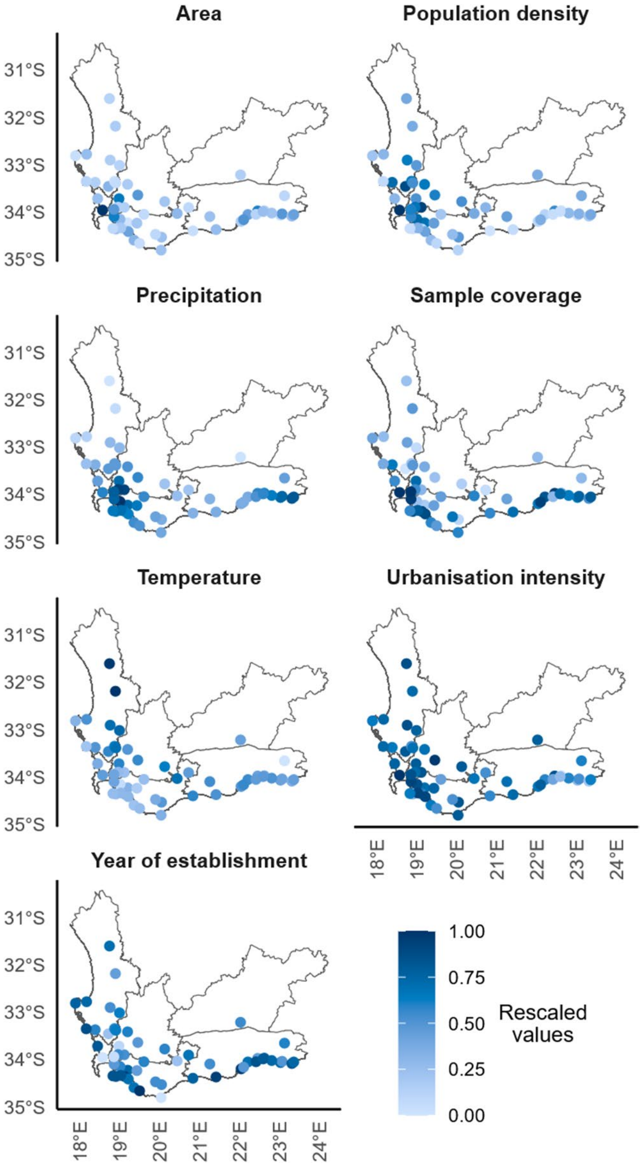

Fig. 1 Urban centres in the Western Cape province, South Africa. Dots indicate centroid locations of centres included in this study (for visualisation only; no urban centres actually overlap). The internal divisions of the province indicate the district municipality boundaries. The colour gradient indicates the rescaled values for each variable (rescaled between 0 and 1) in each urban centre

Methods

Study area and history

This study area covers the Western Cape, a province of South Africa at the southwestern tip of Africa, approximately 129,000 km^2 in size (Fig. 1). The region is known for its mild Mediterranean-type climate with hot dry summers and cool rainy winters. According to the Köppen-Geiger climate classification scheme (extracted for the urban centres using the kgc package in R; Bryant et al. 2017), local climates range between mediterranean (Cs) in the far southwest, warm temperate (Cf) in the southeast, and semi-arid (BS) climate zones in the centre and towards the interior of the province. A large part of the Cape Floristic Region (CFR), one of the world's most unique and biodiverse floristic regions (Linder 2003; Born et al. 2007), falls within the Western Cape. The CFR is particularly well known for the high turnover of native vascular plant species which is thought to be driven (in part) by the high environmental heterogeneity in the region (Cowling et al. 1997). The region has had a long and complex history of urbanisation, and introduction and invasion of non-native species.

Although small numbers of Indigenous Peoples have inhabited the region for millennia, the first permanent urbanisation occurred with the colonisation by Europeans in the mid-17th century. Although the rate of urbanisation was slow at first, it increased over time and the establishment of new towns in the province peaked in the late 19th and early 20th centuries (Floyd 1960; Fransen 2006). Many of these early settlements were established for regional governance or as religious centres. The establishment of new towns continued into the mid and late 20th century. Under apartheid, and particularly following the Group Areas Act of 1950, several settlements and townships were established to accommodate the forced relocation of 'non-white' communities (Mabin 1992). Simultaneously, many coastal holiday towns were developed, reflecting the growing culture of seaside leisure among predominantly 'white' communities residing in inland urban centres.

Gildenhuys et al. (2025) constructed polygons for 100 urban centres in the Western Cape. The polygons closely follow the 'built-up' feature class in the South African National Land Cover dataset (more details in Gildenhuys et al. 2025; Appendix 1). These ranged in size from 821 km^2 (Cape Town) to 1.7 km^2 (Bot River). Exact polygons are available at https://zenodo.org/records/15210704.

iNaturalist occurrence records

We used the curated dataset derived by Gildenhuys et al. (2025) from iNaturalist. The 'semi-Automated Non-Native Inventory Compilation' (sANNIC) workflow was used to derive the dataset for the non-native flora in urban centres of the Western Cape from iNaturalist. Urban centres were delineated by Gildenhuys et al. (2025) following the built-up layer of the National Land Cover dataset (https://www.dffe.gov.za/egis). Species were identified as native or non-native by matching and cross-referencing taxonomic names with the World Checklist of Vascular Plants (WCVP) and their recorded native distributions. Observations were thoroughly curated and reviewed to maximise data quality. Species were identified to the best possible taxonomic resolution using all available taxonomic resources. Problematic taxa, which could not be consistently identified to species level from iNaturalist images, were identified and collapsed to a higher taxonomic level. Taxa collapsed to genus level included *Alocasia*, *Amaranthus*, *Avena*, *Brugmansia*, *Eucalyptus*, *Fraxinus*, *Gamochaeta*, *Hedera*, *Narcissus*, *Neltuma*, *Pinus*, *Sagina*, *Salsola*, *Sambucus* and *Vitis*. All taxa within the subfamily Bambusoideae and the section Oenothera of the genus *Oenothera* were also collapsed (see Gildenhuys et al. 2025). All records were tagged as wild-growing or cultivated where appropriate using secondary information such as visible signs of cultivation in the image, geographic location of the observation, and consultation with original observers (for details of the protocols followed, see Richardson and Potgieter 2024). Only wild-growing (i.e. non-cultivated) observations were included in the dataset. A thorough description of the sANNIC workflow application is available in Gildenhuys et al. (2025) and all observation data, urban shapefiles and R scripts used in the workflow are available at https://doi.org/10.5281/zenodo.15210704. All analyses were conducted in R version 4.5.1 (R Core Team 2025).

Selecting urban centres based on completeness assessments

Sample completeness of each urban centre can be calculated using sample completeness profiles based on Hill numbers ($q = 0$–2) (Chao et al. 2020). The sample completeness value where $q = 0$ is more sensitive to the influence of rare species and represents the completeness for species richness. With increasing q in Hill numbers the measure becomes increasingly sensitive to the influence of abundant species, with $q = 1$ and $q = 2$ representing completeness for Shannon and Simpson diversity respectively (Chao et al. 2020). The shape of the profile (completeness as a function of q) can be used to assess overall sample completeness. A rising profile with sample completeness close to 1 with small confidence intervals indicates a well sampled area; see Chao et al. (2020) and Gildenhuys et al. (2025) for more discussion. Sample completeness profiles were computed for each urban centre using the *iNEXT.4steps* package in R (Chao et al. 2020). Of the original 100 urban centres assessed by Gildenhuys et al. (2025), urban centres for which the profile was decreasing, interpreted as an unreliable sample completeness estimate, were removed from the dataset. Thus, 54 urban centres were retained for analysis (Fig. 1). Considering the remaining uneven sampling effort between urban centres, *sample coverage* (sample completeness measure, $q = 1$) was computed for each urban centre and included as a control variable in all models to account for the effect of sampling effort.

Usage of environmental variables

Total annual precipitation and *mean annual temperature* were obtained from WorldClim version 2.1 (at 1 km resolution) using the *geodata* package in R (Hijmans et al. 2024;

https://www.worldclim.org/). Since the urban centre polygons intersected multiple tiles from this dataset, values were averaged across all tiles intersected by the spatial extent of each urban centre. Average annual temperature across all months and total annual precipitation were calculated for each urban centre. *Urban area* was calculated as the log of the area of the polygons used to delineate the urban centres using the *sf* package (Pebesma 2018). The built-up surface of each urban centre was extracted from the Global Human Settlement Layer (GHSL-S) for 2025 at 3 arcsecond resolution, including both residential and non-residential surface area (Pesaresi et al. 2024). The mean of the highest quartile was used as an estimate of *urbanisation intensity*. This dataset is available from: https://human-settlement.emergency.copernicus.eu/. The human population size for each urban centre was extracted from the worldpop dataset (Bondarenko et al. 2020). Population counts were summed for each urban centre but were strongly correlated with urban area and were therefore divided by urban area to derive *population density*.

Year of establishment was determined for each urban centre by consulting diverse secondary historical sources. We estimated the year of establishment based on the following criteria: (1) the earliest official recognition of the area as a village or town (this includes the reported year of 'founding' or 'establishment'); (2) the earliest record of town planning or allotment for the purpose of urban development (as opposed to agricultural development) and (3) the earliest non-agricultural infrastructure, e.g., including railway stations, churches, fortifications and hotels. The sources used for each urban centre were recorded as well as a short motivation or reasoning for the chosen year based on the criteria mentioned. As available information on some urban centres was deficient, the level of confidence of each source was also recorded. The dates provided are approximate indicators of establishment and the onset of high-density human activity and built infrastructure, in line with the ecological definition of urban centres (Pickett et al. 2001).

Travel time between urban centres was obtained using travel time estimations extracted using the Google Maps distance matrix Application Programming Interface (API) via the *gmapsdistance* package in R (Melo and Zarruk 2025). We estimated the fastest travel time (in seconds) between the centroid coordinates of each urban centre using the optimistic traffic model and a departure time set as 5 May 2025 at 18h00 local time (to avoid confounding effects of peak traffic times). Since the resulting matrix was not symmetrical, one-way travel times between urban centre pairs were averaged. Travel time represents the connectivity between urban centres in the form of human-mediated, accidental or intentional dispersal (Wilson et al. 2009; Faulkner et al. 2024). Travel time reflects the effective 'cost' of difficulty for propagules to move between specific site pairs, as human-mediated dispersal is the primary mode of dispersal of non-native species at the spatial scale considered in this study.

We considered seven predictors: mean annual *temperature* and *precipitation*, the natural logarithm of the *urban area*, the mean of the highest quartile of built-up cover (as a measure of *urbanisation intensity*), *year of establishment*, *population density*, and average *travel time*. *Estimated sample coverage* ($q=1$) was included as a control variable for sampling effort in all models. The rescaled values of all variables at each urban centre are visualised in Fig. 1.

Zeta diversity and multi-site generalised dissimilarity modelling

The concept of zeta diversity was developed to unify incidence-based species turnover measures (Hui and McGeoch 2014). It is defined as the number of species shared by any given number of sites, with normalised values extending typical Jaccard, Sorensen and Simpson metrics across zeta orders. Zeta diversity captures the entire incidence information on species turnover, rather than traditional pairwise (beta diversity) measures. Zeta diversity is defined following orders, where the order represents the number of sites compared. For example, zeta order-1 is the number of species present at a single site; this is equivalent to alpha diversity metrics such as species richness (not the scope of this research). Zeta order-2 is defined as the number of species shared by two sites and is equivalent to traditional pairwise beta diversity measures. Zeta order-3 is the number of species shared by three sites and does not have any equivalent alpha or beta diversity metrics. This is true for all higher orders of zeta. Note that the number of species shared by three sites is necessarily a subset of all species shared by at least two sites as any species shared by three sites is also shared by at least two sites.

As the order of zeta increases, the value of zeta (number of shared species) typically decreases (known as zeta decline), systematically filtering out species shared only by a small number of sites (McGeoch et al. 2019). Average values of zeta of orders 1 to 7 were calculated across all urban centres considered (Table 1). Higher orders than seven were not considered as the average value of zeta becomes negligibly small. Zeta diversity, therefore, allows for the differentiation of components representing predominately narrow-ranged versus widespread species, as narrow-ranged species are more likely to contribute to compositional turnover at low orders of zeta than at higher orders of zeta (Latombe et al. 2018b; Basel et al. 2024). As an extension of Generalised Dissimilarity Modelling (GDM) (Ferrier et al. 2007), Multi-Site Generalised Dissimilarity Modelling (MSGDM) was

Table 1 Average zeta value (number of shared species observed among n number of sites) and standard deviation (SD) for the zeta orders $n = 1–7$. Note that the high SD values indicate high heterogeneity among sites. Some sites share high numbers of species while others share almost none

Order of zeta	Zeta value	SD
1	94.9	126.0
2	20.9	33.2
3	7.0	12.3
4	2.9	5.4
5	1.3	2.7
6	0.7	1.4
7	0.4	0.9

developed to utilise zeta diversity (Latombe et al. 2017), with order-1 and order-2 zeta metrics equivalent to the traditional alpha and pairwise beta diversity measures.

We conducted MSGDMs to assess the drivers of species turnover of non-native urban plants across the Western Cape. MSGDMs model the geographic distance (represented by travel time) and environmental dissimilarities between site combinations against their compositional turnover (zeta values). All seven predictors (candidate drivers) were included in the MSGDMs as only moderate to weak correlation between predictors were detected (the highest correlation coefficient detected was 0.62). Models were fitted using I-spline regressions with a quasibinomial family and logit link function for zeta diversity orders 2 (equivalent to pairwise beta turnover), 3, 4, and 5. The variance explained dropped rapidly after zeta order 5 since very few species occurred in more than five urban centres (see Table 1). Models with zeta orders above five were therefore excluded from analysis.

As compositional turnover could reflect nested species assemblages between sites, we used the Simpson-normalised form of zeta diversity to remove the effect of differences in species richness and thus capture true (richness-independent) species turnover (Baselga 2010); this Simpson-normalised form divides raw zeta diversity by the minimum number of species in the compared site combination. I-spline regressions assume that compositional turnover increases with increasing differences in environmental variables and increasing travel distance between sites, i.e. isolation by resistance (also known as, environmental filtering) and distance decay of similarity. The models were fitted with 3000 random samples of site combinations. We used the *zetadiv* package in R (Latombe et al. 2018a) to fit all models.

To determine variable importance for all variables considered, variance partitioning was conducted. For each variable, a full MSGDM (with all predictors included) and a reduced MSGDM (with the focal predictor removed) were fitted with the same 1000 random samples of site combinations, this was done for each order of zeta and repeated ten times with each using a different random seed for samples of site combinations to estimate the standard error of variable importance. The variable importance for each variable was calculated as the difference between the variance explained by the full model and the reduced model ($V_{full} – V_{reduced}$).

Results

MSGDM and zeta diversity

Average observed zeta values across all sites (urban centres) declined rapidly from 94.9 estimated for zeta order 1 (equivalent to species richness per urban centre) to 1.3 for zeta order 5 (average number of species shared by five randomly selected urban centres). High standard deviations estimated for all orders indicate high heterogeneity with some sites sharing a large number of species and some sharing very few species. All MSGDMs explained a substantial amount of variance ($p < 0.001$). The proportion of variance explained for Simpson-equivalent zeta diversity of orders 2, 3, 4 and 5 was 0.230, 0.326, 0.310 and 0.288, respectively. Precipitation was a significant predictor of turnover in all models but only for urban centres in relatively arid parts of the Western Cape, as can be seen by the non-linear response curve in Figs. 2 and 3. Precipitation had no effect in the more mesic parts of the province. This could reflect the differentiation between semi-arid and more mesic climates. Once precipitation exceeds the threshold separating semi-arid from non-arid climates, further increases have little effect on differentiating species establishment. Temperature was also a significant predictor of turnover in all models with

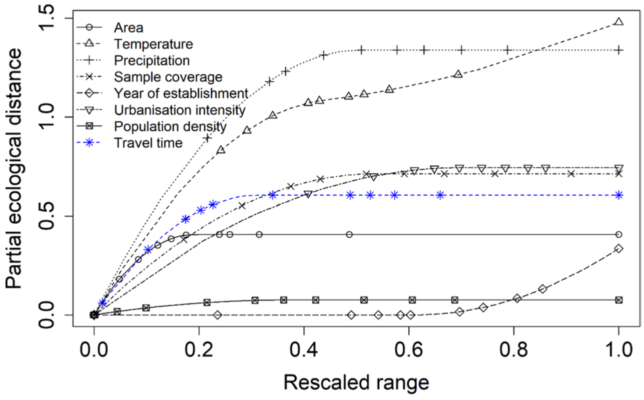

Fig. 2 I-spline regressions for all environmental variables of zeta 2. The right-most height of each curve represents the overall importance of the predictor variable in the model. The slope of each curve along the rescaled range represents the differential importance of the variable at different ranges of the predictor variable

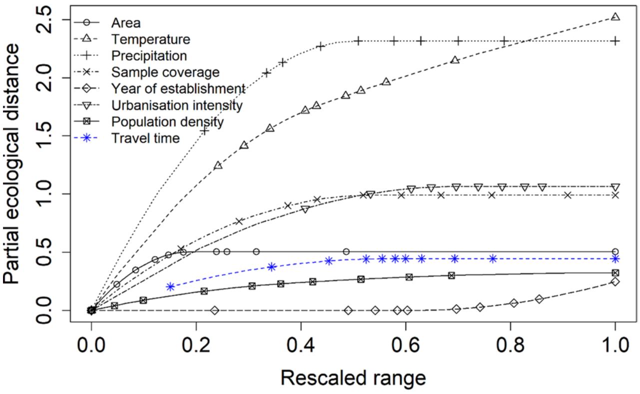

Fig. 3 I-spline regressions for all environmental variables of zeta 5. The right-most height of each curve represents the overall importance of the predictor variable in the model. The slope of each curve along the rescaled range represents the differential importance of the variable at different ranges of the predictor variable

the strongest effects in relatively cool climates, although it remained influential in relatively warmer climates (Figs. 2 and 3).

Urbanisation intensity was overall a significant predictor in all models particularly in areas with relatively low and intermediate levels of urbanisation, but the effect was lower at high levels of urbanisation intensity (Figs. 2 and 3). Urban area has a significant effect in all models but only for small urban centres. Travel time between urban centres was a significant predictor only at zeta order 2. In other models, travel time had a small, non-significant effect. The effect of travel time was also non-linear, with the strongest effect for centres in relatively close proximity. This could reflect a distance-decay pattern of species dispersal between urban centres. Species are most likely to be transported between urban centres that occur close together; as the travel distance increases the probability of transport becomes disproportionately less likely.

Year of establishment was a relatively weak but statistically significant predictor in all models except for zeta order 5 where it was narrowly non-significant ($p = 0.058$). The effect was strongly non-linear and only significant for urban centres established relatively recently (Figs. 2 and 3). This could reflect a lag phase whereby differential species establishment has not occurred yet in relatively recently established areas; it could also reflect recent changes in planting patterns and thus species introductions. Population density was the weakest predictor variable and was only narrowly statistically significant in one model (zeta order 4).

Estimated sample coverage was a statistically significant control variable in all models. The effect of sample coverage was strongest at poorly sampled areas but plateaued towards the intermediate and higher ranges. This is likely because insufficient sampling of urban centres results in many species being overlooked, thereby biasing estimates of compositional turnover. However, as sample coverage increased, a relatively smaller proportion of species were missed, having less influence on estimates of turnover compared to other predictors.

Variance partitioning

From the variance partitioning, variable importance was greatest for the climatic variables, temperature and precipitation, followed by physical properties, urban area and urbanisation intensity, then travel time, population density and year of establishment (Fig. 4). Overlap of the standard error bars was used to differentiate variance explained between the different variables. Variable importance shifted across zeta orders in distinct ways. Precipitation and temperature both peaked at intermediate orders, with precipitation increasing from zeta 2 to zeta 3 before declining towards zeta 5, and temperature rising from zeta 2 to zeta 4 before tapering slightly at zeta 5. Urbanisation intensity showed a modest rise from zeta 2 to zeta 3 but remained stable thereafter, while urban area showed no change across zeta orders. In contrast, travel time declined from zeta 2 to zeta 4 before increasing slightly again at zeta 5. Year of establishment was most influential at zeta 2 and steadily declined in importance with increasing zeta order, whereas population density, although the least important overall, showed a slight upward trend across the gradient.

Discussion

Key findings of the study

This study explored the drivers of urban non-native plant compositional turnover across the Western Cape, South Africa. All variables considered explained significant amounts of variance in at least one of the models. Temperature, precipitation and urbanisation intensity were consistently the top predictors (Figs. 1 and 2). However, the ranking of the bottom four predictors changed for the different orders of zeta. For zeta order 2, they were: travel time, area, year of establishment and population density. For zeta order 5 in contrast, they were: area, travel time, population density and year of establishment. This is indicative of the different factors of compositional turnover at the early and late stages of invasion.

We found partial support for our hypotheses, with an expected increase in variable importance (Fig. 4) for widespread species observed for temperature, precipitation and urbanisation intensity (reflecting habitat suitability), and an expected decrease in variable importance

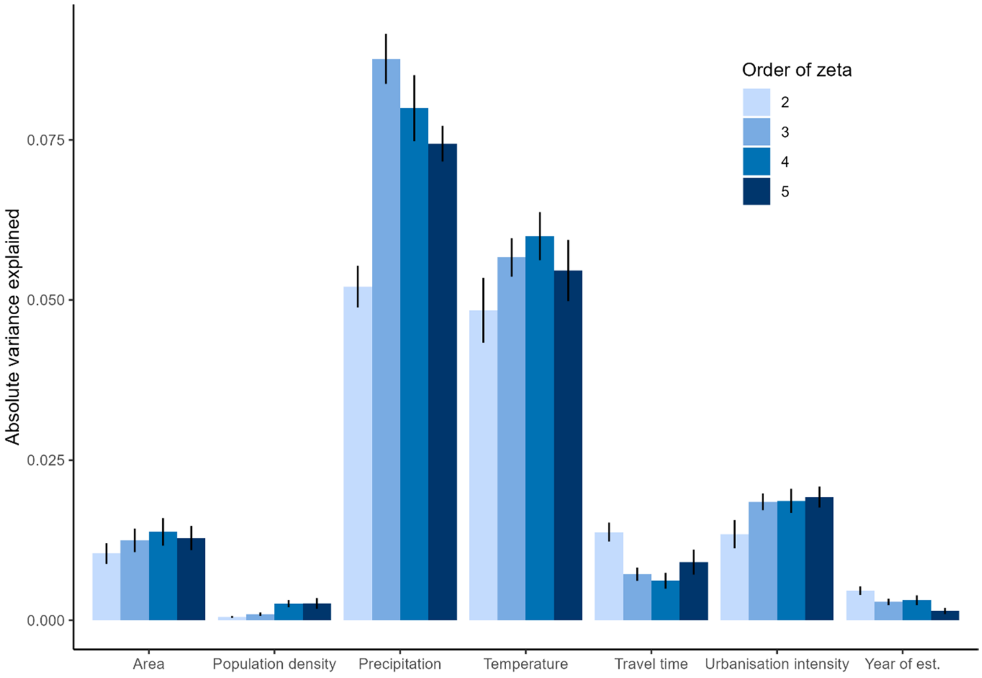

Fig. 4 Variance explained by each predictor variable included in the multi-site generalised dissimilarity models (MSGDMs). We fit a full model with all predictors included and a reduced model with one predictor removed using the same data. Variance explained was then calculated as the difference between the full and reduced models (V_{full} - $V_{reduced}$). This was repeated ten times, with different random subsets of the data, for each predictor variable and each order of zeta (zeta 2–5) to calculate standard errors. Vertical lines indicate standard errors

from narrow-ranged to widespread species observed for travel time and year of establishment (reflecting anthropogenic species introductions). However, we did not observe an increase in variable importance of urban area, nor did we observe a decrease in importance for population density with an increase in order of zeta, as was hypothesised. This potentially calls for a reassessment of how these drivers affect species compositions. Further discussion on each driver follows below.

Effects of biogeography and climate

Overall, temperature and precipitation were the most important variables driving compositional turnover (Figs. 2, 3 and 4). This aligns with findings from previous studies on non-native plant species turnover in South Africa which found that climate was generally an important driver of non-native plant compositions, though the relative importance of climatic variables varied (Hugo et al. 2012; Rouget et al. 2015; de Beer et al. 2023). These same studies found a close association between non-native species compositions and biomes defined on the basis of native species compositions. This may mirror the effects that climate has on native plant diversity, the so-called 'Goldilocks hypothesis' which posits that non-native species assemblages are driven by the same abiotic variables that drive native species assemblages (Rouget et al. 2015; Latombe et al. 2018b). The highly heterogeneous climatic conditions that result in strong environmental gradients of the CFR are a major driver of native species diversity and turnover (Cowling et al. 1997), and the same drivers seem to drive a high turnover of non-native species, even in highly modified urban areas. Alternatively, these patterns could be explained by the 'Biome decides hypothesis' which postulates that the composition of non-native flora is mediated by the biotic effects of native flora and fauna (Rouget et al. 2015; Latombe et al. 2018b). We did not account for potential biotic interactions involving native species and therefore cannot disentangle the relative support for the two proposed hypotheses. However, the effects of native species on the composition and turnover of non-native species are likely to be greatly reduced due to the effects of urbanisation (Cadotte et al. 2017).

The effect of precipitation was strongly non-linear; it was significant in explaining turnover for urban centres in more arid parts of the province but had no effect in relatively mesic parts. This may reflect a differentiation between arid and mesic conditions along the east-west gradient in the province (Cowling et al. 1997). Hugo et al. (2012) found a strong differentiation between arid and mesic climates on the non-native plant compositions in Southern Africa. Potential management implications include the need for region-specific management plans (e.g. for semi-arid parts of the province) as the barriers to naturalisation and invasion are likely different. For example, Milton et al. (2007) revealed the importance of nucleation and dispersal by birds in the establishment of fleshy-fruited species in a semi-arid savanna from adjacent urban areas. Temperature was also non-linear, the strongest effect occurring in relatively cool regions, although the non-linear effect was not as prominent as precipitation.

Influence of physical properties

The physical properties we examined were urbanisation intensity and urban area (Figs. 2 and 3). Urbanisation intensity is a well-established driver of non-native species distributions and diversity (Potgieter et al. 2024). However, the effects of urbanisation intensity have mostly been discussed in the context of species richness rather than turnover. Urbanisation intensity is a source of disturbance to natural habitats and is primarily associated with novel habitat conditions that are created by intense anthropogenic activities. Non-native species may be differentially associated with higher or lower urbanisation intensities thus explaining turnover of non-native species between urban centres experiencing different levels of urbanisation intensity. As we used the Simpson-equivalent zeta diversity, which controls for differences in species richness among site combinations (Baselga 2010; Latombe 2018b), the notable effect of urbanisation intensity on true turnover (species replacement) suggests that increasing urbanisation does not solely lead to an addition of novel habitats but also to losses of existing habitats, thereby driving shifts in habitat composition. This is generally in line with previous studies assessing species compositions across urban areas (Lososová et al. 2011; Williams et al. 2015).

In all models, the effect of urbanisation intensity was non-linear, the strongest effect occurring at low to medium urbanisation intensities. This accords with the finding of de Beer et al. (2023) who reported a strong non-linear effect of road density (often associated with urbanisation) on non-native woody species turnover across South Africa. At high urbanisation, non-native plant assemblages are dominated by urban specialist species but at lower urbanisation intensities a greater variety of habitats may be available. The importance of urbanisation intensity was higher for widespread species than for narrow-ranged species, as hypothesised. This suggests that urbanisation acts primarily as a driver of opportunistic habitats for species at later invasion stages rather than as a filter of species introduction.

The effect of urban area could be explained by the theory of island biogeography (MacArthur and Wilson 1967). However, the effect of area in island biogeography of both native and non-native species is usually discussed in the context of species richness (Aronson et al. 2014; Blackburn et al. 2016; Latombe et al. 2019). In this case study, urban area was a significant driver of richness-independent turnover, indicating that variation in species composition was not driven by differences in species richness or nestedness. This is supported by the use of Simpson normalisation, which specifically captures true species turnover between sites. The observed correlation between area and turnover is similar to the finding of Latombe et al. (2018b) who found that the non-native plant turnover between nature reserves in Czechia was related to the area of study sites. Though area is a strong predictor of species richness, the reason for its effect on richness-independent turnover is not well understood. Larger urban areas have greater environmental heterogeneity, promoting different species compositions compared to smaller more homogenous urban areas (Gao et al. 2023). Alternatively, patterns of species introduction could vary, with larger urban areas experiencing greater propagule pressure and thus a higher likelihood of receiving newly introduced species (Blackburn et al. 2016). However, while greater heterogeneity may explain nestedness-related turnover, it does not explain replacement-related turnover. Furthermore, if species introductions were the primary driver, we would expect area to explain different proportions of variance across zeta orders – a pattern not evident in our results (Fig. 4).

A clue to the effect of urban area on richness-independent turnover may lie in the non-linear effect of urban area, which was a significant predictor of turnover only among small urban centres and showed no detectable effect in medium or large ones (Figs. 2 and 3). The effect of urban area may reflect stochastic processes operating in small urban centres but less so in larger ones. Small centres may, by chance, experience different environmental conditions that drive species composition, whereas large centres, because of their greater internal heterogeneity are more environmentally similar to one another and show less turnover driven by such chance effects. In other words, due to their internal heterogeneity, large urban centres tend to be less dissimilar in composition. As far as we are aware, this pattern has not been extensively explored in the literature, and more work is needed to understand it.

Significance of travel time

Travel time between urban centres was an important driver of compositional turnover, particularly for narrow-ranged non-native species (Fig. 4). This highlights the non-equilibrium nature of invasion, where narrow-ranged species at early stages of the invasion continuum are limited by barriers to dispersal (Pyšek et al. 2020). The primary mode of dispersal at the spatial scale of this study is likely the transport (accidentally or purposefully) of propagules by humans. Widespread species, those further along the invasion continuum, have already overcome some dispersal barriers; travel time is thus a weak predictor of their presence. The non-linear relationship observed for travel time could be due to the non-linear dispersal kernel of propagule pressure over distance (i.e. a steep decline in propagule numbers close to the source and a more gradual decline further away). Our findings are consistent with those of de Beer et al. (2023), who studied invasions across South Africa, and showed that the importance of distance decreased with order of zeta (implying that connectivity and dispersal barriers were more important to narrow ranged species' compositions). Their study, however, considered a much larger spatial scale (all nine provinces of South Africa) and distance may have been more closely related to covariates not considered in their analysis.

Travel time or geographic distance may be poor proxies for species dispersal over long distances where human-mediated accidental long-distance dispersal is more important (Wilson et al. 2009). Though our use of travel time does provide a more nuanced estimation of connectivity as opposed to Euclidean distance, it may not capture all dimensions of the interconnectivity of urban centres. Future work should consider alternative measures of connectivity such as actual traffic volume, and propagule movement as well as the presence of ports, airports, botanical gardens, or other institutions that may affect species introductions. Network-based measures such as edge betweenness and centrality within the transport network could also improve our understanding of species introductions.

Significance of establishment year and population density

Year of establishment was a significant, though relatively weak, driver of turnover at low orders of zeta (Fig. 4). The effect was only clear for relatively recently established urban centres, i.e. established from the 1950s onwards. Urban non-native species assemblages are driven by historic and on-going plantings and these patterns change over time (Potgieter and Cadotte 2020; Richardson and Potgieter 2024). It is likely that with the relatively recent onset of globalisation there was a change in the species assemblages planted in urban centres. For example, within the genus *Quercus* (oaks), *Q. robur* was historically the most widely planted species in the Western Cape, however, this species has increasingly been replaced by other more disease-resistant species in the same genus (Gildenhuys et al. 2024). This shift may also reflect more recent advances in environmental awareness and could be influenced by the implementation of NEM: BA (National Environmental Management: Biodiversity Act 10 of 2004) regulations in South Africa. In newly established urban centres, at least for trees, more native species and fewer invasive species are being planted. Shackleton and Gwedla (2021) show that older urban areas in South Africa have a higher proportion of cultivated non-native trees as well as a higher abundance of cultivated trees overall.

Population density has widely been used in urban ecology as a measure of human activity but could also reflect some other socio-economic patterns (Potgieter et al. 2024). However, we did not find strong evidence for the importance of population density in driving compositional turnover, which is unexpected given its frequent emphasis in urban studies, typically in relation to alpha diversity. The gradients of population density between urban centres in the Western Cape might not be strong enough to detect an effect. Population density may be a more useful predictor between urban and rural sites rather than between urban centres.

Study limitations

This study examined the turnover of non-native plant species between urban centres at a regional scale but did not consider within-urban area effects. Specifically, observations are not necessarily randomly distributed across urban centres; this means that the environmental variables that are averaged across urban centres may not adequately explain the true environmental pressures experienced by the observed assemblages. There are also some potential biases present in the data due to the opportunistic nature of collection of iNaturalist records. Though uneven sampling effort was addressed using data coarsening and sample completeness estimations, and taxonomic biases were addressed through careful curation of the dataset (see Gildenhuys et al. 2025 for more details), it was not feasible to account for all potential biases such as seasonal or temporal biases, or motivational biases of the observers. While these biases can add additional noise to the data, we do not believe that they would have significantly changed the outcomes of the modelling. Nonetheless, more work is needed to examine the drivers of non-native species turnover within urban centres and how these are influenced by potential biases from data sources such as iNaturalist.

We intentionally controlled for the potential confounding effect of species richness by using only Simpson-equivalent zeta diversity to quantify turnover arising from species replacement between urban centres. It would nevertheless be informative to examine how these factors also contribute to variation in observed non-native species richness among urban centres, although such variation is expected to primarily reflect the effects of urban area, time of urban establishment and sample coverage. If total compositional turnover (including both species addition due to differences in richness and species replacement) were of interest, Sørensen-equivalent zeta diversity could be applied, where species richness would be tentatively considered as an additional factor, but this is beyond the scope of the study. We did not consider the biotic effect of native species due to a lack of well curated data for native species for the area of interest. However, if data were available, turnover of native species (or any community) could be included as a predictor within the MSGDM framework; as discussed previously, we suspect this would not play a strong role in structuring the non-native urban assemblages.

Conclusions

The drivers of non-native plant species turnover between urban centres are multifaceted. Urban centres can differ markedly in the habitats available and opportunities for establishment, survival and proliferation of non-native plant species. We found climatic variables to be most influential in explaining species turnover across urban centres in the Western Cape province. This is likely due to the same strong environmental gradients which have driven high native species turnover in the region. Our results reinforce the idea that biogeographical regions may require different approaches and priorities for management, and that this applies even in urban contexts. We also found that various anthropogenic factors affected species compositions in both the early and late stages of the invasion continuum. In particular, the effect of travel time highlights the dynamic nature of invasion at the early stages and that many non-native species are likely to continue expanding their ranges.

The non-linear effects of all variables highlight the importance of context-dependence. For example, if arid areas were removed from our study, precipitation would likely have had no effect, whereas it is currently one of the strongest predictor variables when considering the whole set of urban centres. Future studies should carefully consider the ranges of predictor variables in the study area as the drivers of non-native compositional turnover may vary depending on the range of variables considered. Though urban biological invasion management can be informed by the identified drivers, continuous monitoring and rapid response remain important management strategies to curb the impacts of these non-native plant species.

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Data availability All occurrence records used in the analysis can be found at:https://doi.org/10.5281/zenodo.15210704. Environmental variables and R scripts used in the analysis are included in the supplementary material.

Declarations

Competing interests The authors do not have any financial or non-financial interests to declare that may have influenced this work.

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