



# Roadsides and gardens facilitate the expansion of non-native clonal succulent plants to wetlands in the coastal fringe of the Atacama Desert

Moisés A. Aguilera<sup>\*</sup>, Víctor Pastén, Felipe Espinoza

Departamento de Ciencias, Facultad de Artes Liberales, Universidad Adolfo Ibáñez, Diagonal Las Torres, 2640 Peñalolén, Santiago, Chile

## ARTICLE INFO

### Keywords:

Coastal management  
Non-native species  
Roadsides  
Succulent plants  
Urban habitats  
Wetlands

## ABSTRACT

Urban habitats such as coastal road verges can host a wide range of non-native plant species, which can increase urban biodiversity but also have the potential to impact natural ecosystems. However, the mechanism through which these novel habitats facilitate alien species establishment/invasion in arid coastal systems is not well known. Here, we assessed the potential of roadsides and gardens to facilitate the spread of non-native clonal succulent species to coastal natural ecosystems. We surveyed urban habitats and rural wetlands located from 18°S to 23°S, in the coastal fringe of the Atacama Desert in northern Chile. Using generalized mixed linear models (GLMMs), we explored the effects of habitat extent and distance to urban sources as the main factors contributing to non-native species propagation. Non-native-to-native species spatial association were also examined. We found the occurrences of *Sesuvium portulacastrum* were higher in roadsides and gardens located from 18°S to 22°S, followed by *Malephora crocea*, *Carpobrotus edulis* and *Mesembryanthemum (Aptenia) × vascosilvae*. *S. portulacastrum*, followed by *C. edulis* and, to a lesser extent, *M. × vascosilvae*, were recorded in urban and rural crypto-wetlands. Increase in species occurrences with built habitat perimeter and a linear reduction by distance to urban sources were detected. Positive association of *S. portulacastrum* and *M. crocea* with the native *Heliotropium curassavicum* was recorded. These results highlight the importance of the coastal landscape composition (diversity and extent of habitat types) and configuration (distance from built to natural habitats) in the process of non-native plant species' expansion. Given many coastal ecosystems are already damaged by different human-derived impacts, planting non-native succulents in urban habitats should be carefully managed to balance the services/disservices they provide/provoke to urban and natural habitats.

## 1. Introduction

Urban habitats such as road verges can host a wide range of alien plant species (Forman and Alexander, 1998; Milton et al., 2015; Milton and Dean, 2010), but can provide important ecosystem services that contribute to urban biodiversity (Phillips et al., 2020; Weber et al., 2014). Especially roadsides are considered important built habitats for species invasions in arid zones (Milton and Dean, 2010) because different processes such as vehicle traffic, recipient plant community traits, and natural dispersal process, among others, may facilitate alien species spread into adjacent remnant habitats (Boscutti et al., 2022; Forman and Alexander, 1998; Haider et al.,

<sup>\*</sup> Corresponding author.

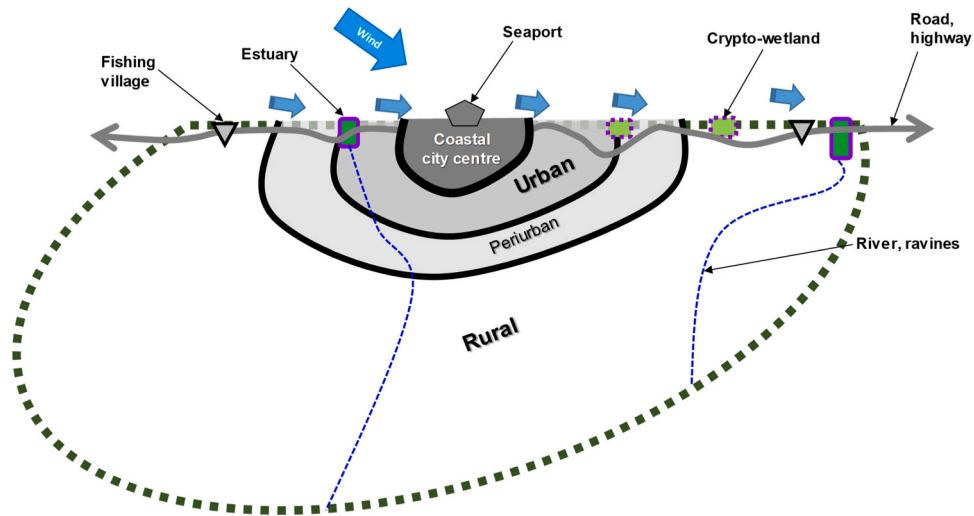
E-mail address: [moises.aguilera@uai.cl](mailto:moises.aguilera@uai.cl) (M.A. Aguilera).

<https://doi.org/10.1016/j.gecco.2023.e02637>

Received 22 May 2023; Received in revised form 8 September 2023; Accepted 13 September 2023

Available online 15 September 2023

2351-9894/© 2023 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).



**Fig. 1.** Schematic representation of the structural-functional configuration of the coastal urban-rural system considered. The intensity of the gray-shaded area corresponds to the gradient from the urban center to the periurban area, with a seaport located to the seaward and protruding from the city center. A green dotted line envelops the entire region or coastal landscape (e.g., at the scale of 100 km). Fishing villages (gray triangles) are located within the limits of the rural zone. Wetlands (green areas) can be present in both rural and urban zones. *Estuaries*: continuous line; *Crypto-wetlands*: dotted line. Blue arrows represent the predominant coastal winds (big arrow) and currents, and the ‘coastal drift’ (small arrows). Gray arrows are coastal roads or inter-city highways.

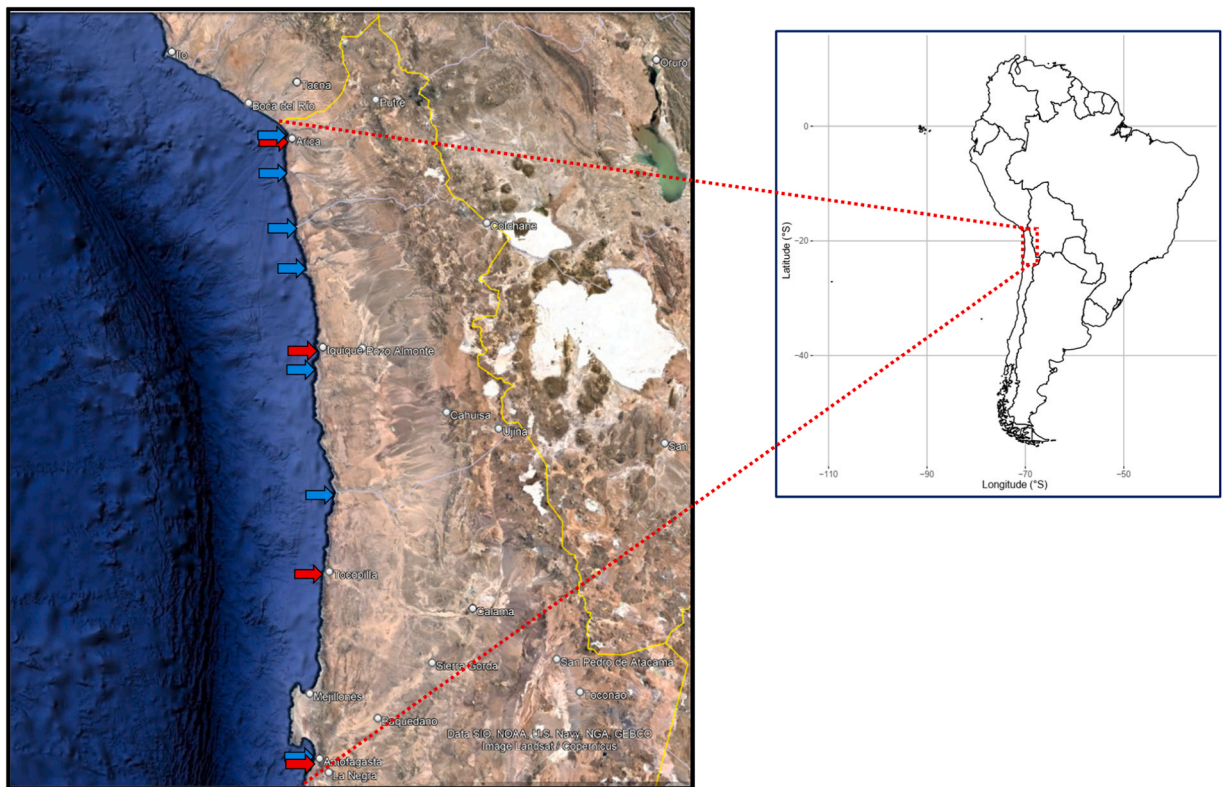
Adapted from the ‘flattened-sliced-indented donut’ urban model of Forman (2008).

2018; Lembrechts et al., 2017; McDougall, 2001; Pauchard et al., 2016; Turner et al., 2021; Von Der Lippe and Kowarik, 2007). Gardens are also considered important built habitats where supplemental watering, weeding, and fertilization are common and can have direct consequences on plant functional diversity within urban zones (Kendal et al., 2012; Padulles Cubino et al., 2021). Thus, it is expected that the plant invasion process can be mainly driven by the proportion or extent of urban built habitats (e.g., roadsides, gardens: Aikio et al., 2012; Guo et al., 2019; Štajerová et al., 2017) and also by the configuration of the entire landscape (e.g., habitat complexity: Boscutti et al., 2022; distance to urban sources: Aikio et al., 2012). However, the mechanism through which these novel habitats facilitate exotic species spread into coastal natural habitats, and in arid systems in particular, is not completely clear (Kalwij et al., 2008).

In coastal semi-arid zones, drought-tolerant plant species such as clonal succulents can provide important local services if selected for urban greening (e.g. Griffiths and Males, 2017). However, these species could expand rapidly to/from human-constructed habitats, especially if they are selected for revegetation in newly constructed road verges in coastal cities. This can be the case for many succulent plants of the family *Aizoaceae*, which have rapid propagation and establishment in a wide range of natural and human-created environments, even those with low levels of soil irrigation (e.g. *Carpobrotus* spp.; Campoy et al., 2018; Fenollosa et al., 2016; Roiloa, 2019). Some clonal succulent species are competitively dominant and may displace native plants when they propagate to natural habitats (e.g. *Carpobrotus edulis*, *Mesembryanthemum crystallinum*; D’Antonio and Mahall, 1991; Pyšek et al., 2004; Vivrette and Muller, 1977). Then, it is critical to manage urban green spaces that include the planting of non-native clonal succulent forms which could modify the local plant community composition (e.g. Pyšek et al., 2020; Simberloff et al., 2013).

The hyperarid Atacama Desert constitutes an important barrier for plant species dispersal from tropical to temperate latitudes because it is characterized by very limited rainfall and extreme temperatures (e.g. Latorre et al., 2005; Ossa et al., 2013). Notwithstanding, the development of human activities (e.g. mining) and urban infrastructure such as roads, railways, and walkways (Calderón-Seguel et al., 2021) are increasing the potential for species expansion through this extremely dry biome. Urban infrastructure expansion and land reclamation in this system, could transform small patches of remnant habitats (e.g. wetlands) into ‘novel’ (Hobbs et al., 2009) or ‘hybrid’ ecosystems (Kowarik, 2018). This may occur by means of invasive species dominance which drive a novel community composition (e.g. Schittko et al., 2020; Boscutti et al., 2020). Thus, there is a challenge related to the greening of impervious urban zones with non-native species (Gaertner et al., 2017; Milton et al., 2015; Phillips et al., 2020; Weber et al., 2014), and the conservation of the ‘wilderness’ of remnant ecosystems (Kowarik, 2018). Despite important recommendations have been made regarding the plantation of non-native species in urban areas, and their spread potential to natural habitats (Milton et al., 2015; Milton and Dean, 2010; Potgieter et al., 2022), less is known about the planting of non-clonal succulent species and their expansion potential into coastal ecosystems. Given it is expected a patchy distribution of natural ‘wet’ ecosystems along the coastal fringe in arid environments, urban areas may facilitate non-native species spread into natural habitats through a ‘stepping-stone’ model of range expansion (e.g., Leidner and Haddad, 2011; Saura et al., 2014).

At the coastal fringe of the Atacama Desert, many drought-tolerant plant species such as the non-native clonal succulents *Sesuvium portulacastrum* and *Carpobrotus edulis* have been planted/introduced on coastal roadsides and gardens in subtropical cities in northern Chile (~ 18–20°S). This scenario represents a challenge for the management of urban-built habitats in arid systems in general, and for



**Fig. 2.** Map of the study region located in the coastal fringe of the Atacama Desert in northern Chile (18–23°S). The red and blue arrows show the location of the study cities (with roadsides and gardens) and natural (rural, urban) wetlands (estuaries and crypto-wetlands), respectively. The yellow line shows the country limits (Image from Google Earth v.2022).

conservation of the still pristine or remnant coastal habitats (e.g., wetlands) in particular.

The presence of non-native clonal succulent species seems related to the extent of urban habitats where large road verges are irrigated and mowed (i.e., grasses) more frequently than smaller ones hosting a large plant cover. Given clonal succulent species may propagate via the transport of stolons or ramets (Fenollosa et al., 2016; Roiloa, 2019), urban zones may be a source of effective plant dispersion by the sea (Souza-Alonso et al., 2020).

Here, we investigated the occurrences and spatial patterns of abundance of non-native succulent species planted in coastal urban roadsides and gardens, and in natural rural habitats from 18°S to 23°S, in the coastal fringe of the Atacama Desert, in northern Chile. Despite the diverse habitat types present in this system, no specific management of urban infrastructure expansion related to natural remnants has been considered before (e.g. see Pinto et al., 2006).

The study system characterizes by well-defined city boundaries which commonly expand predominantly alongshore (Fig. 1). Natural habitats are represented by small estuaries and crypto-wetlands, which are located in rural areas or are within city boundaries (Fig. 1). There is no information, however, about which is the abundance of non-native species in different coastal built and natural habitats in this system, and about the facilitative or competitive potential among non-native and native species. In this context, we highlight three main questions; what is the effect of roadsides and gardens extent on non-native clonal succulent plant species abundance? Is there an expansion from urban to natural rural habitats and across latitudes? What is the degree of spatial overlap among non-native clonal succulent species and native plants in urban habitats?

We hypothesized that the extent of different urban habitat types (composition) and the distance from built to natural habitats (spatial configuration) in the coastal landscape (see Fig. 1), could drive the abundance of non-native succulent plant species at urban zones (persistence potential) and in natural habitats at rural zones (spread potential), respectively. In general, urban built habitats cover can be a key factor in increasing invasive species abundance (e.g., Boscutti et al., 2022; Guo et al., 2019). Thus, the presence of non-native succulent species is expected to increase with roadsides and gardens' perimeter within the boundaries of the urban zones (Fig. 1). Given coastal drift is persistent alongshore the study system by predominantly westerly winds (Aguilera et al., 2018), rural wetlands could be the recipient of different materials (organic, inorganic) drifted from urban sources including anthropogenic litter and alien species (see Thiel and Fraser, 2016; Thiel and Gutow, 2005 for reviews). Inter-city roads or highways intersect the natural urban and rural habitats (gray arrows in Fig. 1) and may serve as conduits for the spread of non-native species even beyond the limits of the city (e.g. Milton et al., 2015; Turner et al., 2021).

Given the high tolerance to dry and salty environments of *S. portulacastrum*, this species is promoted for revegetation in urban

settings at tropical latitudes (e.g. Meentemeyer et al., 2020) but can invade rapidly both natural and highly disturbed habitats (Lonard and Judd, 1997). Thus, there is expected a higher abundance or dominance of this species in roadsides and gardens, and in rural wetlands, with negative spatial association (e.g., by direct interference) with other non-native and/or native species at local scales (e.g., roadsides patches).

## 2. Material and methods

### 2.1. Description of urban and rural study sites

The study was conducted in four coastal cities, located in the coastal fringe of the Atacama Desert (i.e., from 18°S to 23°S) (Fig. 2). Five rural and one periurban estuary were included in the sampling together with two rural and seven urban crypto-wetlands present in the latitudinal range considered (Fig. 2). The four study coastal cities have different population (Arica, 18°S; ~ 250,000 inhab.; Iquique: 20°S; ~ 227,000 inhab.; Tocopilla: 22°S; ~ 25,000 inhab.; Antofagasta: 23°S; ~ 450,000 inhab.) (INE, 2019), and characterizes by host large private or state seaports (see Fig. 1). Arica, Iquique, and to a lesser extent Antofagasta, are important touristic cities which increase their local population during the holidays, with inter-city roads increasing the traffic during these seasons (SERNATUR, 2019). Most cities are increasing their investment in coastal infrastructures, with road verges, parks, gardens, and associated roads and walkways, being the most important ones (MOP, 2022). Rural, urban and periurban estuaries can increase considerably the water influx from rivers during the rainy season of the 'Andes Altiplano' (i.e. late spring-summer) (e.g. Sepúlveda et al., 2014). Crypto-wetlands correspond to upwelling waters of underground springs (called 'aguadas costeras') characterized by wet and salty soil that can create wet areas or small lagoons in the supralittoral fringe (i.e., above the high tide line).

### 2.2. Non-native clonal succulent plant occurrences/abundances across latitudes

We surveyed succulent plant species occurrences (presence/absence) in urban and natural habitats in four cities and corresponding rural areas from 18°S to 23°S, located in the coastal fringe of the Atacama Desert (Table S1 in Appendix A). In order to generate a standardized measure of frequency at each sampling locality, we recorded non-native succulent plant species presence/absence along 100 m long × 2 m wide strips (sampling plots) of roadsides, gardens, constructed dune mounds, and wetlands located within 500 m of the high tide line (i.e., including the coastal fringe; de Andrés et al., 2018). Preliminary surveys of roadsides width and length aided to set the sampling scale (Fig. S1 in Appendix A). Then, four or 7 'sites' distributed across the complete coastal boundaries of urban zones were considered for sampling the different habitat types (see Fig. S2). Sites were separated about 300 m in the urban and rural zones. At each site, and at the different habitat types, we deployed randomly 3 100 m long × 2 m wide plots, and at each plot, we recorded the presence/absence of the study plant species (see sampling details in Fig. S3 in Appendix A). Habitats were classified as 'built' (e.g., roadsides) or 'natural' (e.g., wetlands). At estuaries and crypto-wetlands (urban or rural), sampling plots were deployed on the verges of watercourses (Fig. S3), and due to the lower total area of some crypto-wetlands (e.g., ranging from 616 m<sup>2</sup> to 7047 m<sup>2</sup> approx.) only two sites or zones were considered for sampling in these habitats. Dune mounds (built habitat) were present in only one locality at 18°S, and also two zones were sampled in this habitat as indicated before.

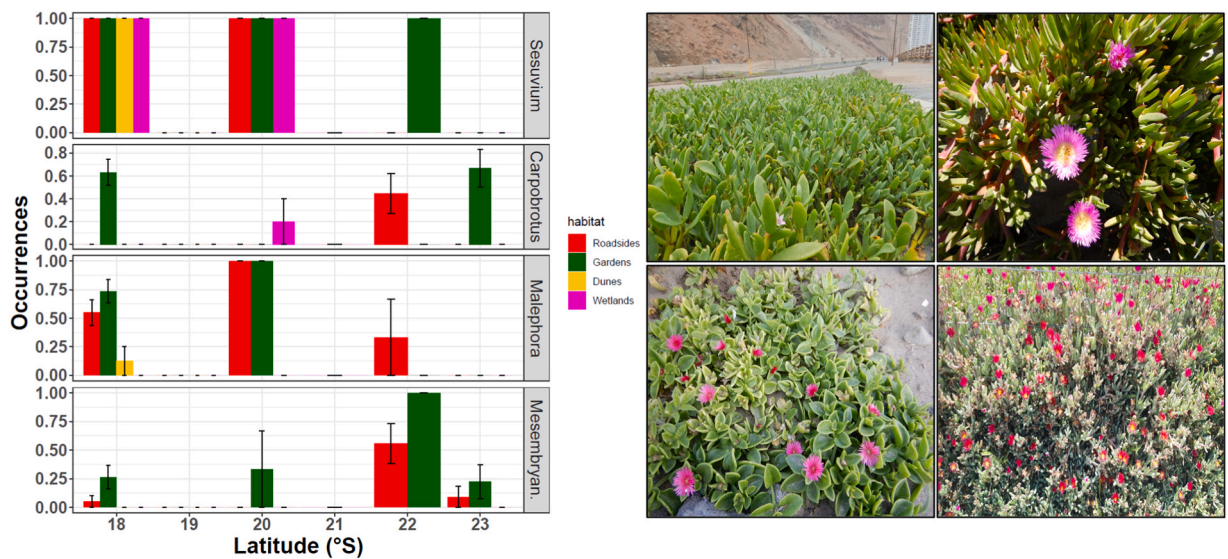
This specific sampling protocol also aided to examine the presence of native plant species, and to explore heterospecific plant associations in the different urban habitats sampled. Field measurements were made from September 2021 to January 2023.

Concurrently with our field samplings, we explored the potential effects of distance to urban 'sources' (roadsides, gardens) on non-native succulent plant species occurrences in the specific rural and urban wetland patches. To this end, we measured the Euclidian distance of each rural and urban wetland to the nearest recorded habitat patch of roadsides or gardens with presence of the study plant species (see above). We used tools of Google Earth Pro v.2022 for distance measurements.

At the different localities where *S. portulacastrum* was recorded, we measured the total area covered by this species in roadsides, gardens, wetlands, and dune mounds. In this sampling, we considered the complete coastal boundaries of the study cities and rural habitats. Commonly, *S. portulacastrum* formed mono-stands with no other plant species in the middle of the patches. Thus, after we identified the different patches of *S. portulacastrum*, we proceeded to estimate in situ the perimeter of each plant stand with the aid of a measuring tape. For this case, we assume that plant stands of *S. portulacastrum* had either a hexagonal or squared-rectangular shape (for irregular or regular patches, respectively), and we conducted six to four linear measurements per plant stand (Fig. S3 in Appendix A). With this information, and also the measurement of the distance from the sides to the center of the plant patch i.e., the apothem of the hexagonal shape, we calculated the plant patch area  $A$  as follows:  $A = p * ap / 2$ , where  $p$  is the perimeter of each plant stand and  $ap$  is the apothem. For plant patches with more rectangular or squared shapes (mainly at roadsides and gardens), the area was estimated as:  $A = l * w$ , where  $l$  is the side, and  $w$  corresponds to the width of each patch. Then, the proportion of area covered for *S. portulacastrum* at each habitat patch ( $i$ ), was then calculated based on the area of each specific habitat patch  $HA$ , in which the species was recorded i.e.,  $P_{Sesuvium(i)} = [(A)_{(i)} / (HA)_{(i)}]$ . This specific sampling was conducted from January 2022 to January 2023.

We also explored if the introduction/establishment of *S. portulacastrum* in natural and constructed habitats was recent (i.e., from 2015 to 2022) by visualizing the area covered by this species in constructed dune mounds located in urban areas at 18°S and in a rural crypto-wetland located at ~ 20°S. We used Google Earth Pro v.2022 for visualization and polygon construction for area estimations (habitat patch extent and plant cover), using images available from 2004 to 2022 (i.e., three dates per year). We were not able to conduct these analyses for roadsides or gardens given the low image resolution of plant species at the scale of these habitat types.

A recent taxonomic study indicates that only the species *Sesuvium sessile* and *S. americanus* were present in Chile at the subtropical locality of Arica (i.e., 18°S; Minué and Jocou, 2021). However, all specimens collected/sampled in this study corresponded to



**Fig. 3.** Left: Average ( $\pm$  SE) of non-native clonal succulent plant species occurrences (i.e., presence in  $100\text{ m} \times 2\text{ m}$  strips) recorded in urban and rural habitats in the coastal fringe of the Atacama Desert. Right: pictures depicting the different species; species order from top-left to bottom-left, clockwise: *Sesuvium portulacastrum*, *Carpobrotus edulis*, *Malephora crocea*, and *Mesembryanthemum*  $\times$  *vascosilvae*.

*S. portulacastrum* based on main taxonomic traits (e.g., flower pedicel  $> 3\text{ mm}$ ; Taylor, 1993, Minué and Jocou, 2021, Sukhorukov et al., 2021).

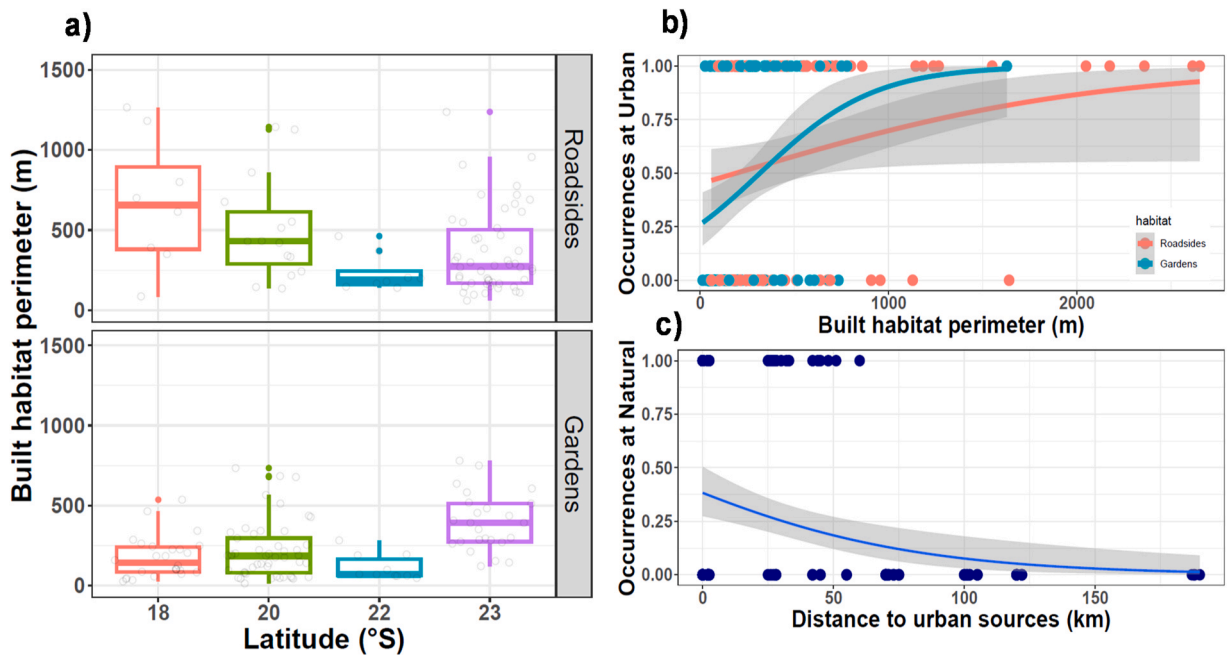
### 2.3. Coastal roadsides and gardens extent

We estimated the perimeter of all roadsides and gardens located within 500 m of the high tide line in the different study cities considered. First, we identify the different roadsides and gardens located at the different study sites. Ground-level imagery from Google Street View allowed a preliminary visualization of paved roads, verges, and gardens (Phillips et al., 2021). Field visits to the different localities aided in the identification and delimitation of the different roadsides and coastal gardens' strips. Measurement of roadsides and gardens perimeters were made by polygon construction with the aid of the software Google Earth Pro v.2022. We considered urban roadsides (see Fig. S2) as all those vegetated soil strips or verges, managed or not, located immediately at neighboring sides or center of road lanes (Forman and Alexander, 1998; Milton et al., 2015; Phillips et al., 2021). Only coastal gardens with public access (e.g., parks, squares, etc.) were considered in the analyzes (Fig. S2).

### 2.4. Statistical analyses

Differences in non-native clonal succulent plant species presence/absence at different latitudes, and effects of distances from urban sources and roadsides and gardens perimeter on plant occurrences were assessed by means of Generalized Linear Mixed Models (GLMM). In these analyzes, we considered plant species identity and 'habitat type' categories (built, natural), 'distance to urban sources', and 'habitat perimeter' as the fixed factors, respectively. We included 'latitude' as random factor in all models using a Binomial distribution (with logit link function) (Zuur et al., 2009). In particular, random effects in this case helped to take into account latitude-specific associations and also take into account potential lack of independence among samples from a same site/latitude (Venables and Ripley, 2002). Differences in the *S. portulacastrum* area covered in different habitat patches (i.e., proportion of habitat covered) were assessed using a quasi-Binomial GLM which also allowed to take into account overdispersion of our data sets (Zuur et al., 2009). Given *S. portulacastrum* was only present in 3 urban zones and 2 wetlands, no effect of latitude was considered in this case. Analyses were performed with the 'glmer' and 'glm' function in the 'lme4' library in R (R Development Core Team, 2021).

Spatial association (local-scale) of the different non-native succulent plant species, and with native species i.e., *Heliotropium curassavicum*, recorded at urban and natural habitats, were assessed with Kendall's tau correlation (Legendre, 2005). This method, based on ordinal association, helped to examine whether plant species were correlated over space at different habitats like roadsides and gardens. In order to increase the power of the test, we pooled the data (i.e., presence/absence) recorded in roadsides and gardens at all the studied localities for analysis (Gotelli and Ellison, 2004).



**Fig. 4.** (a) Boxplots of roadsides and gardens perimeter (m) present across different latitudes (i.e., reference latitude; °S), present in urban zones in the coastal fringe of the Atacama Desert (i.e., 500 m from the high tide line). Generalized Linear Mixed Model (GLMM; 'latitude' as random factor) relationships of (b) non-native succulent plant occurrences with roadsides (red) and gardens (light green) extent, and (c) occurrences in natural estuaries and crypto-wetlands with distance to urban areas. In (a) the black line in each box represents the median, and the boxes define the hinge (25, 75 % quartiles, the line is 1.5 times the hinge). Points outside the interval (outliers) are represented as dots. Envelopes in (b) and (c) correspond to the confidence intervals (95 % CI).

**Table 1**

Summary of Generalized Linear Mixed Model (GLMM) analyses on the effects of perimeter (m) of built urban habitats (roadsides and gardens) and of distance (km) to 'urban sources' of natural habitats (i.e., crypto-wetlands and estuaries), on non-native succulent species occurrences (presence/absence). 'Latitude' was considered the random factor in each model. Marginal (*fixed effect alone*), and conditional (*both fixed and random factor effects*) R-squared are presented. Significant ( $\alpha = 0.05$ ) P-values are indicated in bold.

Occurrences at urban habitats						Occurrences at natural habitats				
Predictors	Ratios	Error	CI	z	p	Ratios	Error	CI	z	p
(Intercept)	0.66	0.40	0.20–2.14	-0.70	0.484	0.75	0.60	0.16–3.61	-0.36	0.718
Habitat [Roadsides]	1.78	0.76	0.77–4.12	1.35	0.176					
Perimeter (m)	1.00	0.00	1.00–1.00	2.39	<b>0.017</b>					
Distance (km)						0.96	0.02	0.93–1.00	-2.10	<b>0.036</b>
<b>Random Effects</b>										
$\sigma^2$	3.29					3.29				
$\tau_{00}$	1.99 <sub>lat</sub>					1.49 <sub>lat</sub>				
ICC	0.38					0.31				
N	7 <sub>lat</sub>					7 <sub>lat</sub>				
Observations	199					148				
Marginal R <sup>2</sup> /Conditional R <sup>2</sup>	0.08/0.43					0.40/0.59				

### 3. Results

#### 3.1. Non-native clonal succulent species occurrences in urban and rural natural habitats

Four non-native clonal succulent species were frequently planted for the greening of coastal roadsides and gardens from 18°S to 23°S, in northern Chile: *Sesuvium portulacastrum*, *Carpobrotus edulis*, *Malephora crocea*, and the hybrid nothospecies *Mesembryanthemum (Aptenia) × vascosilvae*. We found variable occurrences (i.e., presences at 100 m × 2 m strips) of the four non-native succulent species with large occurrences at the roadsides, gardens, and to a lesser extent urban and rural wetland surveyed across the range considered (Fig. 3). Thus, significant differences in contribution to species occurrences in the linear model for natural and built habitat categories were recorded (Table S2 in Appendix A). In particular, *S. portulacastrum* had larger averaged (across latitudes) occurrences at most habitats surveyed from 18°S to 22°S, including one rural estuary and a crypto-wetland (Fig. 3), followed by *M. crocea* which was also

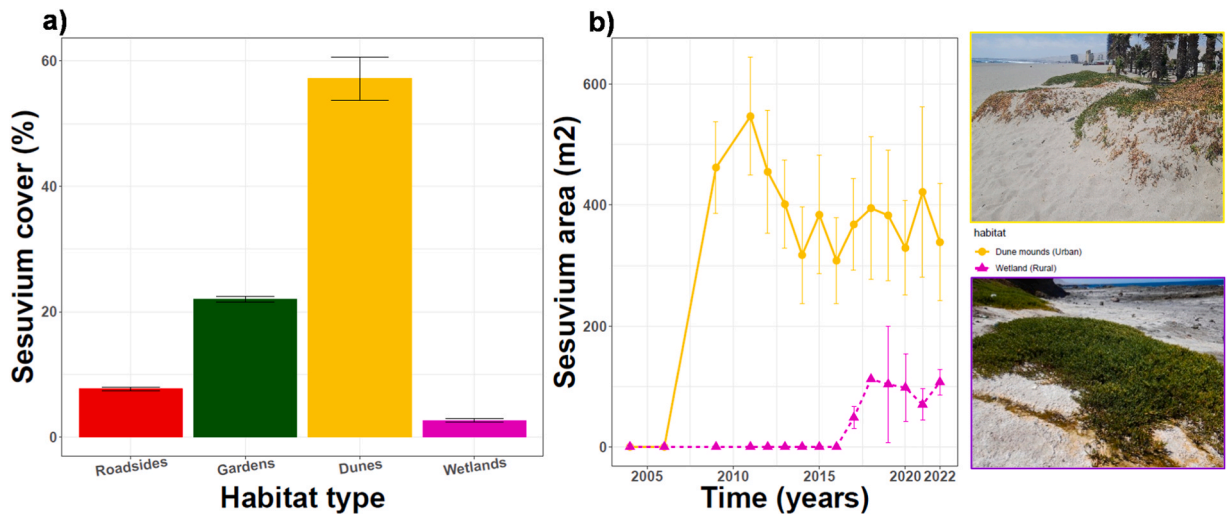


Fig. 5. (a) *Sesuvium portulacastrum* averaged percentage cover ( $\pm$  SE) estimated in the field at different urban and natural habitats from 18°S to 23°S alongshore the coastal fringe of the Atacama Desert, and (b) averaged ( $\pm$  SE) plant cover (i.e., total area) estimated via satellite images with Google Earth Pro v.2022, in constructed dune mounds (urban;  $\sim$  18°S, yellow line) and in a crypto-wetland (rural; at 20°S, magenta line).

frequent at roadsides and gardens. The presence of *M. x vascosilvae* was larger in gardens and roadsides but only at 22°S (Fig. 3), and lower occurrences were also recorded for *C. edulis* at most study sites surveyed but with an important presence in coastal gardens at 18°S and 23°S (Fig. 3). Thus, the last two species contributed less to the linear model compared with the formers, with a significant effect of 'latitude' ('random factor') on the model performance (i.e., high 'Conditional'  $R^2$ ; Table S2).

### 3.2. Effects of coastal roadsides and gardens perimeter and habitat distance patterns on plant occurrences

In total, we surveyed 36.9 km and 13.8 km of urban vegetated roadsides and gardens, respectively, at the four study latitudes (Fig. 4a). In particular, the median value of roadsides perimeter was larger at 18°S (800 m) and lower at 22°S (88 m) (Fig. 4a). At 23°S, median values of coastal gardens perimeter were larger than the other ones (i.e., 392 m) (Fig. 4a).

The occurrences of non-native succulent species increased significantly with the perimeter of roadsides and gardens (Fig. 4b, Table 1), but no differences in the contribution to this pattern by any of these habitats were recorded in the model (Table 1). Also, we found that occurrences of non-native clonal succulent plant species in rural estuaries and crypto-wetlands had a significant reduction with distance to urban zones in which the species were recorded (Fig. 4c, Table 1). A significant effect of 'latitude' ('random factor') on the models' performance was also recorded (i.e., high 'Conditional'  $R^2$ ; Table 1).

### 3.3. Spatial association of non-native succulent plant species at urban settings

We found non-native clonal succulent species association at roadsides and gardens was variable. Significant and positive spatial association at roadsides and gardens was detected for *S. portulacastrum* with *M. crocea* (Kendall's tau = + 0.55,  $P < 0.0001$ ), and despite a negative association was observed with *C. edulis*, this pattern was not significant (tau = - 0.066;  $P = 0.549$ ). Instead, the last species had a positive and significant association with *M. x vascosilvae* at gardens (tau = + 0.312;  $P = 0.005$ ). *Mesembryanthemum x vascosilvae* had also a positive and significant association with *M. crocea* at the same built habitat (tau = + 0.221;  $P = 0.043$ ).

The species *Heliotropium curassavicum* (Boraginaceae) was the only native species recorded at roadsides and gardens at the different latitudes considered. This species was not planted and had a very patchy distribution across the studied range (mean occurrences: Roadsides =  $0.523 \pm 0.076$ ; Gardens =  $0.333 \pm 0.079$ ; 'Crypto-wetlands' (urban):  $0.50 \pm 0.151$ ). It was detected a positive and significant association of *S. portulacastrum* and *M. crocea* with the native species at roadsides and gardens (*S. portulacastrum*-*H. curassavicum*: Kendall's tau = + 0.278;  $P = 0.009$ ; *M. crocea*-*H. curassavicum*: tau = + 0.215;  $P = 0.045$ ). Also, *C. edulis* had a positive association with *H. curassavicum* but this pattern was not significant (tau = + 0.007;  $P = 0.948$ ). On the other side, *M. x vascosilvae* had a negative but non-significant association with the native species (tau = - 0.064;  $P = 0.549$ ).

### 3.4. *S. portulacastrum* cover and temporal patterns in urban and natural habitats

A significantly higher proportional area covered by *S. portulacastrum* on constructed (urban) dune mounds was found compared with roadsides, gardens, and rural wetlands (Fig. 5a, Table S3 in Appendix A). Thus, non-significant differences in the contribution to *S. portulacastrum* cover were detected for wetlands, gardens, or roadsides (Table S3). We detected that *S. portulacastrum* established in

the constructed dune mounds (at  $\sim 18^\circ\text{S}$ ) in 2009, while in a rural crypto-wetland located at  $\sim 20^\circ\text{S}$  (i.e., 25 km from an urban source) this species established in 2017 (Fig. 5b). In January 2023, *S. portulacastrum* covered about 812 m<sup>2</sup> in the rural crypto-wetland and was on average 14.54 m ( $\pm 3.56$  m) from the high tide mark in the supralittoral zone.

#### 4. Discussion

We found the occurrences of non-native succulent species were variable at the different natural and built habitat surveyed across the coastal range considered. Higher dominance of *Sesuvium portulacastrum* was recorded in urban roadsides and constructed urban dune mounds, but also in a rural crypto-wetland adjacent to an urban center. The latitudinal expansion of this species seems recent, related to the planting in expanding/upgraded coastal infrastructures like roadsides and gardens in the different coastal cities considered. In the same line, *Carpobrotus edulis* and the cultivar *Mesembryanthemum*  $\times$  *vascosilvae* (a hybrid of *M. cordifolium*  $\times$  *M. haeckelianum*) (Smith et al., 2020) were recorded in rural and urban crypto-wetlands, respectively, although at much lower extent compared with *S. portulacastrum*.

Our study showed that the coastal landscape configuration (distance patterns from urban to natural habitats) and composition (habitat types and extent) seems critical to predicting invasive plant species' persistence and propagation in the study system (Fig. 1). These large-scale factors have been previously recognized as the main drivers of invasive species expansion in other systems (e.g., Urban-agricultural: Boscutti et al., 2022; Dune fields: Malavasi et al., 2014). Thus, our results suggest an effective expansion of non-native clonal succulent species from urban habitats, and support the evidence that constructed urban habitats can serve as potential conduits for the dispersal of non-native species to natural ecosystems (e.g., McDougall et al., 2018; Milton and Dean, 2010; Pauchard et al., 2016; Turner et al., 2021). Thus, the expansion of non-native succulent species alongshore the coastal fringe of the Atacama Desert represents a challenge for the greening of coastal cities and the conservation of remnant habitats.

##### 4.1. Greening of roadsides and gardens with non-native clonal succulent species

In general, cultivated species in gardens or roadsides are selected based on their specific traits (e.g., resistance to drought), or esthetic value (e.g., flower showiness) (Kendal et al., 2012; Cavender-Bares et al., 2020; Phillips et al., 2020).

All non-native clonal succulent species recorded in our study were planted for ornamental purposes and were frequent at roadsides and gardens except *C. edulis*. This pattern contrasts with the large coverage recorded for this invasive species in urban coastal dune fields in the semi-arid coast of north-central Chile ( $\sim 29^\circ\text{S}$ ) (Aguilera et al., 2022). In particular, among the different non-native succulent species recorded, *S. portulacastrum* is gaining success in coastal urban habitats at subtropical latitudes, and its high recovery potential (Spiller et al., 2016) and tolerance to drought and salty conditions (Meetam et al., 2020) make it potentially very persistent in arid environments. Together with *M. crocea*, *S. portulacastrum* was highly frequent at roadsides and gardens (i.e., commonly from 5 % to 20 % of the area of the entire habitat) from  $18^\circ\text{S}$  to  $22^\circ\text{S}$ , and their absence in the coastal fringe at  $\sim 23^\circ\text{S}$  may be related solely to that urban management plans that do not still consider the planting of these species for coastal landscaping. Thus, coastal greening plans of local authorities could be critical to driving the overrepresentation of non-native species in urban zones (Niinemets and Peñuelas, 2008). Further management strategies are required in this context to advice the inclusion/control of non-native clonal succulent species in coastal urban areas.

Despite most non-native clonal succulent plants studied being resistant to drought or salty conditions of the coast (Lonard and Judd, 1997; Roiloa, 2019), they might be most likely to persist in harsh environments like roadsides when their recipient habitat is frequently managed as many forbs and grasses do (e.g., Forman et al., 2003). In our study, large roadsides tended to be more frequently irrigated and mowed than smaller ones and we found larger occurrences of non-native succulents on them. This suggests that in coastal arid zones, large-size habitats with frequent irrigation can successfully sustain non-native local populations facilitating their 'naturalization' and further expansion (Pyšek et al., 2004; Štajerová et al., 2017).

##### 4.2. Urban zones as a source for non-native clonal succulent plant expansion to rural habitats

Human-mediated dispersion by planting for ornamental purposes is common in different plant species worldwide and is increasing in arid and semi-arid systems (Bradley et al., 2012). Our results suggest occurrences of non-native clonal succulent plant species in coastal rural natural habitats decrease with distance to urban sources. The high abundances of *S. portulacastrum*, and to a lesser extent *C. edulis*, in a rural crypto-wetland located at  $\sim 20^\circ\text{S}$  suggest an effective expansion from urban habitats. It is not clear how *S. portulacastrum* or *C. edulis* were established in this crypto-wetland which is located nearby urban sources i.e.,  $\sim 25$  km. Did these species spread to this habitat naturally from nearby urban areas, or were they directly planted there? This opens questions about 'naturalization' and the mechanisms, or 'conduits', of expansion of these species from urban areas through the arid matrix (Gaertner et al., 2017). Different hypotheses could be considered in this context based on the urban-rural shorescape structure of our study system (see Fig. 1). First, stolons and/or ramets of these non-native clonal succulent species might well have been transported from nearby coastal cities by currents (e.g., *C. edulis*; Souza-Alonso et al., 2020), similar to long-distance transport documented for many coastal organisms (Thiel and Fraser, 2016; Thiel and Gutow, 2005), with the potential to maintain photosynthetic ability and to develop adventitious roots (Souza-Alonso et al., 2020). Indeed, given its buoyancy and resistance to immersion in seawater, it is expected *C. edulis*, as well as other clonal succulent plant species, can be transported for long distances away from sources (i.e.,  $\sim 250$  km; Souza-Alonso et al., 2020). We recorded that *S. portulacastrum* was established recently (i.e., 2017) in the rural crypto-wetland, but established early (i.e., 2004) in constructed dune mounds further north at  $18^\circ\text{S}$ . In this context, an important



**Table 2**

Main actions for management of urban roadsides and gardens to control non-native species expansion, and conservation of remnant habitats biodiversity (e.g., wetlands).

Main focus	Specific actions; management or conservation measures
Management	1) -The creation of mono-stands with non-native clonal succulent species in roadsides and gardens should be discouraged. If planting non-native succulent species is considered necessary, only small patches of these plants should be considered (e.g., 10 % or less of roadsides extent) to allow native species (e.g., <i>Heliotropium curassavicum</i> ) to establish.
Management/ Conservation	2) -Coastal urban habitats should include a suite of native species with high tolerance to drought and salty conditions as, for example, <i>H. curassavicum</i> and <i>Nolana</i> spp., which can also provide ornamental services (e.g. showy flowers, pollinator attraction) (Riedeman et al., 2016) and could improve urban biodiversity and city 'wilderness' (Kowarik, 2018). -Patches of native and non-native plants could be planted interspersed to reduce species dominance.
Management	3) -Control the disposal of plants or organic wastes when upgrading city roadsides or gardens, reducing their potential to enter to the sea.
Management/ Conservation	4) -Urban greening plans (e.g., city roadsides and gardens) could be shared with local citizens (Weber et al., 2014), to improve environmental education about the hazards of planting non-native species for remnant habitats (e.g., wetlands, dunes). Thus, a more balanced, and controlled, incorporation of these non-native succulent species should be considered.
Conservation/ Management	5) -The inclusion of non-native species could be completely discouraged when focal urban habitats are neighbors to remnant habitats (e.g. Milton et al., 2015).
Conservation	6) -Special attention should be paid to urban and rural crypto-wetlands, which are 'coastal shelters' for the conservation of the native biodiversity in arid systems like the Atacama Desert (e.g. Pizarro-Araya et al., 2022), and can be also 'recipient' of non-native species expansion (this study) and are under strong pressure from neighbor urban activities (e.g. road traffic; Forman and Alexander, 1998).

tsunami hit the region in 2014 associated with an 8.1 Mw earthquake (Ruiz et al., 2014) which could have aided in the transportation of different materials, including litter and organisms, from urban zones (Carlton et al., 2017). This process could be reinforced when stolons or ramets of plants are removed from roadsides and gardens and thrown directly into the sea or accumulated close to beaches (Author's personal observations). Secondly, the rural crypto-wetland is located close to a fishing village and a coastal inter-city road, and camping activities are common there during the summer. Thus, *S. portulacastrum* and *C. edulis* could have been brought from urban areas and planted directly in this wetland. However, these complementary hypotheses need further examination.

#### 4.3. Spatial associations in urban habitats

It is expected that plant interspecific competition (e.g., by light, moisture, and nutrients) can be important mechanism of species abundances and persistence even in managed urban habitats (e.g. Kowarik, 2008; Williams et al., 2015). We recorded positive spatial association for *S. portulacastrum* with *M. crocea*, and for *C. edulis* with *M. × vascosilvae* at roadsides and gardens and likely this spatial patterns could be facilitated by the frequent management or disturbance of these habitats (Knapp et al., 2009). It is not clear, however, if facilitation among non-native clonal succulent plant species could occur in these built habitats which could have important consequences for their 'invasibility' potential (Cavieres, 2021). Positive spatial association was detected for the native plant *Heliotropium curassavicum* with the non-native clonal succulent species on roadsides and gardens, except with *M. × vascosilvae*. In this context, direct or indirect (e.g. allelopathy) competition with non-native species could be inferred by their similar habitat use, absence of consumer species, and patchy soil moisture of the built habitats (e.g., Ferenc et al., 2021; Vilà and D'Antonio, 1998; Vilà and Weiner, 2004). However, it has been reported that 'common' native plants could persist and even expand in the presence of non-native species depending also on the timing of their establishment (Ferenc et al., 2021; Zhang and van Kleunen, 2019). Given *H. curassavicum* is considered a common 'weed' with both sexual and vegetative reproduction (Hegazy, 1994), and most plants likely established after the planting of non-native succulent species in the roadsides and gardens we surveyed, this may suggest it could be highly tolerant to the presence of non-native clonal succulent plants. Further experiments, however, are required to test this hypothesis which could be relevant to propose specific management actions and conservation of the native biodiversity in urban zones.

#### 4.4. Conclusions and implications for conservation and management

Our study showed that urban greening with non-native succulent plants is facilitating its propagation alongshore the Atacama Desert. This allows us to hypothesize that, for example, *S. portulacastrum* latitudinal expansion will continue to the south, even from the subtropical to temperate systems. Although the planting of *S. portulacastrum* is recent and may contribute positively to urban biodiversity (e.g. see Kowarik, 2011 for discussion in this context), experimental studies are needed to determine its impacts on native flora and the potential for native herbivores to control the established populations (Rodríguez et al., 2022; Spiller et al., 2016).

Regarding the ornamental services and disservices or impacts that non-native clonal succulent plant species can have in urban and rural settings, specific management plans could be proposed in order to reduce species propagation to still pristine natural coastal ecosystems in arid environments (Gaertner et al., 2017; Milton et al., 2015; Potgieter et al., 2022) (see Table 2).

Despite more research is needed especially related to dispersal mechanisms and competitive-facilitative potential of non-native and native species in this system, different integrative measures need to be implemented based on control of non-native species planted in urban habitats and protection/conservation of the natural ecosystems present in urban and rural zones (see Table 2 for details). These measures are critical to improve the cities' wilderness, halt the loss of native biodiversity, and then build more balanced urban green spaces and sustainable cities.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data Availability

Data will be made available on request.

## Acknowledgements

The study was financed by FONDECYT Grant # 1210146 to MAA. We thank Constanza A. Aguilera and Cristina Díaz for assistance during the surveys. Two anonymous reviewers made important comments to improve this contribution.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e02637](https://doi.org/10.1016/j.gecco.2023.e02637).

## References

- Aguilera, M.A., Jaime, A., Aburto, Bravo, L., Broitman, B.R., García, R.A., Gaymer, C.F., Gelcich, S., López, B.A., Montecino, V., Pauchard, A., Rutllant, J.A., Sáez, C.A., Valdivia, N., Thiel, M., 2018. Chile: environmental status and future perspectives. In: Sheppard, C. (Ed.), *World Seas: An Environmental Evaluation: Volume I: Europe, The Americas and West Africa*, 2 edition. Academic Press, pp. 673–702 (August 24, 2018).
- Aguilera, M.A., Pacheco, S., Manzur, T., 2022. Human-derived effects and failure in management drive coastal urban foredune degradation and novel vegetation structure. *J. Environ. Manag.* 311 <https://doi.org/10.1016/j.jenvman.2022.114843>.
- Aikio, S., Duncan, R.P., Hulme, P.E., 2012. The vulnerability of habitats to plant invasion: disentangling the roles of propagule pressure, time and sampling effort. *Glob. Ecol. Biogeogr.* 21, 778–786. <https://doi.org/10.1111/j.1466-8238.2011.00711.x>.
- Boscutti, F., Pellegrini, E., Casolo, V., de Nobili, M., Buccheri, M., Alberti, G., 2020. Cascading effects from plant to soil elucidate how the invasive *Amorpha fruticosa* L. impacts dry grasslands. *J. Veg. Sci.* 31 (4), 667–677.
- Boscutti, F., Lami, F., Pellegrini, E., Buccheri, M., Busato, F., Martini, F., Sibella, R., Sigura, M., Marini, L., 2022. Urban sprawl facilitates invasions of exotic plants across multiple spatial scales. *Biol. Invasions* 24, 1497–1510. <https://doi.org/10.1007/s10530-022-02733-6>.
- Bradley, B.A., Blumenthal, D.M., Early, R., Grosholz, E.D., Lawler, J.J., Miller, L.P., Sorte, C.J.B., D'Antonio, C.M., Diez, J.M., Dukes, J.S., Ibanez, I., Olden, J.D., 2012. Global change, global trade, and the next wave of plant invasions. *Front. Ecol. Environ.* 10, 20–28. <https://doi.org/10.1890/110145>.
- Calderón-Seguel, M., Prieto, M., Meseguer-Ruiz, O., Viñales, F., Hidalgo, P., Esper, E., 2021. Mining, urban growth, and agrarian changes in the atacama desert: the case of the Calama Oasis in northern Chile. *Land* 10, 1–21. <https://doi.org/10.3390/land10111262>.
- Campoy, J.G., Acosta, A.T.R., Affre, L., Barreiro, R., Brundu, G., Buisson, E., González, L., Lema, M., Novoa, A., Retuerto, R., Roiloa, S.R., Fagúndez, J., 2018. Monographs of invasive plants in Europe: *Carpobrotus*. *Bot. Lett.* 165, 440–475. <https://doi.org/10.1080/23818107.2018.1487884>.
- Carlton, J.T., Chapman, J.W., Geller, J.B., Miller, J.A., Carlton, D.A., McCuller, M.I., Treneman, N.C., Steves, B.P., Ruiz, G.M., 2017. Tsunami-driven rafting: transoceanic species dispersal and implications for marine biogeography. *Science* (80-) 357, 1402–1406. <https://doi.org/10.1126/science.aao1498>.
- Cavender-Bares, J., Padullés Cubino, J., Pearse, W.D., Hobbie, S.E., Lange, A.J., Knapp, S., Nelson, K.C., 2020. Horticultural availability and homeowner preferences drive plant diversity and composition in urban yards. *Ecol. Appl.* 30, 1–16. <https://doi.org/10.1002/eap.2082>.
- Cavieres, L.A., 2021. Facilitation and the invasibility of plant communities. *J. Ecol.* 109 (5), 2019–2028.
- D'Antonio, C.M., Mahall, B.E., 1991. Root profiles and competition between the invasive exotic perennial, *Carpobrotus edulis* and two native shrub species in California coastal scrub. *Am. J. Bot.* 78, 885–894. <https://doi.org/10.2307/2445167>.
- de Andrés, M., Barragán, J.M., Scherer, M., 2018. Urban centres and coastal zone definition: which area should we manage? *Land Use Policy* 71, 121–128. <https://doi.org/10.1016/j.landusepol.2017.11.038>.
- Fenollosa, E., Roach, D.A., Munné-Bosch, S., 2016. Death and plasticity in clones influence invasion success. *Trends Plant Sci.* 21, 551–553. <https://doi.org/10.1016/j.tplants.2016.05.002>.
- Ferenc, V., Merkert, C., Zilles, F., Sheppard, C.S., 2021. Native and alien species suffer from late arrival, while negative effects of multiple alien species on natives vary. *Oecologia* 197, 271–281. <https://doi.org/10.1007/s00442-021-05017-3>.
- Forman, R.T.T., 2008. *Urban Regions Ecology and Planning Beyond the City*. Cambridge University Press, New York.
- Forman, R.T.T., Alexander, L.E., 1998. Roads and their major ecological effects. *Annu. Rev. Ecol. Syst.* 29, 207–231.
- Forman, R.T.T., Sperling, D., Bissonette, J.A., Clevenger, A.P., Cutshall, C.D., Dale, V.H., Fahrig, L., France, R., Goldman, C.R., Heanue, K., Jones, J.A., Swanson, F.J., Turrentine, T., Winter, T.C., 2003. *Road Ecology: Science and Solutions*. Island Press. <https://doi.org/10.5860/choice.40-6438>.
- Gaertner, M., Wilson, J.R.U., Cadotte, M.W., MacIvor, J.S., Zenni, R.D., Richardson, D.M., 2017. Non-native species in urban environments: patterns, processes, impacts and challenges. *Biol. Invasions* 19, 3461–3469. <https://doi.org/10.1007/s10530-017-1598-7>.
- Gotelli, N.J., Ellison, A.M., 2004. *A Primer of Ecological Statistics*. Sinauer Associates, Sunderland.
- Griffiths, H., Males, J., 2017. Succulent plants. *Curr. Biol.* 27, R890–R896. <https://doi.org/10.1016/j.cub.2017.03.021>.
- Guo, W.Y., van Kleunen, M., Pierce, S., Dawson, W., Essl, F., Krefth, H., Maurel, N., Pergl, J., Seebens, H., Weigelt, P., Pyšek, P., 2019. Domestic gardens play a dominant role in selecting alien species with adaptive strategies that facilitate naturalization. *Glob. Ecol. Biogeogr.* 28, 628–639. <https://doi.org/10.1111/geb.12882>.
- Haider, S., Kueffer, C., Bruehlheide, H., Seipel, T., Alexander, J.M., Rew, L.J., Arévalo, J.R., Cavieres, L.A., McDougall, K.L., Milbau, A., Naylor, B.J., Speziale, K., Pauchard, A., 2018. Mountain roads and non-native species modify elevational patterns of plant diversity. *Glob. Ecol. Biogeogr.* 27, 667–678. <https://doi.org/10.1111/geb.12727>.
- Hegazy, A., 1994. Trade-off between sexual and vegetative reproduction of the weedy *Heliotropium curassavicum*. *J. Arid Environ.* 27, 209–220.
- Hobbs, R.J., Higgs, E., Harris, J.A., 2009. Novel ecosystems: implications for conservation and restoration. *Trends Ecol. Evol.* 24, 599–605. <https://doi.org/10.1016/j.tree.2009.05.012>.
- INE, 2019. Censos de población y vivienda. Instituto Nacional de Estadísticas. (<https://www.ine.cl/estadisticas/sociales/censos-de>).
- Kalwij, J.M., Milton, S.J., McGeoch, M.A., 2008. Road verges as invasion corridors? A spatial hierarchical test in an arid ecosystem. *Landsc. Ecol.* 23, 439–451. <https://doi.org/10.1007/s10980-008-9201-3>.

- Kendal, D., Williams, K.J., Williams, N.S., 2012. Plant traits link people's plant preferences to the composition of their gardens. *Landsc. Urban Plan.* 105 (1–2), 34–42.
- Knapp, S., Kühn, I., Bakker, J.P., Kleyer, M., Klotz, S., Ozinga, W.A., Poschlod, P., Thompson, K., Thuiller, W., Römermann, C., 2009. How species traits and affinity to urban land use control large-scale species frequency. *Divers. Distrib.* 15, 533–546. <https://doi.org/10.1111/j.1472-4642.2009.00561.x>.
- Kowarik, I., 2008. On the role of alien species in urban flora and vegetation. *Urban Ecol.: Int. Perspect. Interact. Hum. Nat.* 321–338.
- Kowarik, I., 2011. Novel urban ecosystems, biodiversity, and conservation. *Environ. Pollut.* 159, 1974–1983. <https://doi.org/10.1016/j.envpol.2011.02.022>.
- Kowarik, I., 2018. Urban wilderness: supply, demand, and access. *Urban For. Urban Green.* 29, 336–347. <https://doi.org/10.1016/j.ufug.2017.05.017>.
- Latorre, C., Betancourt, J., Rech, J.A., Quade, J., Holmgren, C., Placzek, C., Maldonado, A., Vuille, M., Rylander, K., 2005. Late quaternary history of the Atacama Desert. In: Smith, M., Hesse, P. (Eds.), *Archaeology and Environmental History of the Southern Deserts*. Natural Museum of Australia, p. 422.
- Legendre, P., 2005. Species associations: the Kendall coefficient of concordance revisited. *J. Agric. Biol. Environ. Stat.* 10, 226–245. <https://doi.org/10.1198/108571105X46642>.
- Leidner, A.K., Haddad, N.M., 2011. Combining measures of dispersal to identify conservation strategies in fragmented landscapes. *Conserv. Biol.* 25, 1022–1031. <https://doi.org/10.1111/j.1523-1739.2011.01720.x>.
- Lembrechts, J.J., Alexander, J.M., Cavieres, L.A., Haider, S., Lenoir, J., Kueffer, C., McDougall, K., Naylor, B.J., Nuñez, M.A., Pauchard, A., Rew, L.J., Nijs, I., Milbau, A., 2017. Mountain roads shift native and non-native plant species' ranges. *Ecography (Cop.)* 40, 353–364. <https://doi.org/10.1111/ecog.02200>.
- Lonard, R.I., Judd, F.W., 1997. The biological flora of coastal dunes and wetlands. *Sesuvium portulacastrum* (L.). *J. Coast. Res.* 13, 96–104.
- Malavasi, M., Carboni, M., Cutini, M., Carranza, M.L., Acosta, A.T.R., 2014. Landscape fragmentation, land-use legacy and propagule pressure promote plant invasion on coastal dunes: a patch-based approach. *Landsc. Ecol.* 29, 1541–1550. <https://doi.org/10.1007/s10980-014-0074-3>.
- McDougall, K.L., 2001. Colonization by alpine native plants of a stabilized road verge on the Bogong High Plains, Victoria. *Ecol. Manag. Restor.* 2, 47–52. <https://doi.org/10.1046/j.1442-8903.2001.00068.x>.
- McDougall, K.L., Lembrechts, J., Rew, L.J., Haider, S., Cavieres, L.A., Kueffer, C., Milbau, A., Naylor, B.J., Nuñez, M.A., Pauchard, A., Seipel, T., Speziale, K.L., Wright, G.T., Alexander, J.M., 2018. Running off the road: roadside non-native plants invading mountain vegetation. *Biol. Invasions* 20, 3461–3473. <https://doi.org/10.1007/s10530-018-1787-z>.
- Meetam, M., Sripintusorn, N., Songnuan, W., Siriwattanakul, U., Pichakum, A., 2020. Assessment of physiological parameters to determine drought tolerance of plants for extensive green roof architecture in tropical areas. *Urban For. Urban Green.* 56, 126874. <https://doi.org/10.1016/j.ufug.2020.126874>.
- Milton, S.J., Dean, W.R.J., 2010. Plant invasions in arid areas: special problems and solutions: a South African perspective. *Biol. Invasions* 3935–3948. <https://doi.org/10.1007/s10530-010-9820-x>.
- Milton, S.J., Dean, W.R.J., Sielecki, L.E., Ree, R.Van Der, 2015. The function and management of roadside vegetation. In: *Handbook of Road Ecology*. Wiley & Sons, Ltd.
- Minué, C.R., Jocou, A.I., 2021. The genus *Sesuvium* (Aizoaceae, Sesuvioideae) in the Southern Cone. *Hacquetia* 20, 33–48. <https://doi.org/10.2478/hacq-2021-0006>.
- Niinemetts, Ü., Peñuelas, J., 2008. Gardening and urban landscaping: significant players in global change. *Trends Plant Sci.* 13, 60–65. <https://doi.org/10.1016/j.tplants.2007.11.009>.
- Ossa, P.G., Pérez, F., Armesto, J.J., 2013. Phylogeography of two closely related species of nolana from the coastal atacama desert of chile: post-glacial population expansions in response to climate fluctuations. *J. Biogeogr.* 40, 2191–2203. <https://doi.org/10.1111/jbi.12152>.
- Padulles Cubino, J., Borowy, D., Knapp, S., Lososová, Z., Ricotta, C., Siebert, S., Swan, C., 2021. Contrasting impacts of cultivated exotics on the functional diversity of domestic gardens in three regions with different aridity. *Ecosystems* 24 (4), 875–890.
- Pauchard, A., Milbau, A., Albiñ, A., Alexander, J., Burgess, T., Daehler, C., Englund, G., Essl, F., Evengård, B., Greenwood, G.B., Haider, S., Lenoir, J., McDougall, K., Muths, E., Nuñez, M.A., Olofsson, J., Pellissier, L., Rabitsch, W., Rew, L.J., Robertson, M., Sanders, N., Kueffer, C., 2016. Non-native and native organisms moving into high elevation and high latitude ecosystems in an era of climate change: new challenges for ecology and conservation. *Biol. Invasions* 18, 345–353. <https://doi.org/10.1007/s10530-015-1025-x>.
- Phillips, B.B., Bullock, J.M., Osborne, J.L., Gaston, K.J., 2020. Ecosystem service provision by road verges. *J. Appl. Ecol.* 57, 488–501. <https://doi.org/10.1111/1365-2664.13556>.
- Phillips, B.B., Bullock, J.M., Osborne, J.L., Gaston, K.J., 2021. Spatial extent of road pollution: a national analysis. *Sci. Total Environ.* 773, 145589. <https://doi.org/10.1016/j.scitotenv.2021.145589>.
- Pinto, R., Barría, I., Marquet, P.A., 2006. Geographical distribution of *Tillandsia lomas* in the Atacama Desert, northern Chile. *J. Arid Environ.* 65, 543–552. <https://doi.org/10.1016/j.jaridenv.2005.08.015>.
- Pizarro-Araya, J., Alfaro, F.M., Gómez, F.A., Villablanca, R., 2022. Arthropod fauna of the urban coastal wetland of Aguada La Chimba (Antofagasta Region, Chile): a wetland in an arid matrix. *Anthr. Coasts* 5. <https://doi.org/10.1007/s44218-022-00009-z>.
- Potgieter, L.J., Aronson, M.F.J., Brandt, A.J., Cook, C.N., Gaertner, M., Mandrak, N.E., Richardson, D.M., Shrestha, N., Cadotte, M.W., 2022. Prioritization and thresholds for managing biological invasions in urban ecosystems. *Urban Ecosyst.* 25, 253–271. <https://doi.org/10.1007/s11252-021-01144-0>.
- Pyšek, P., Chocholoušková, Z., Pyšek, A., Jarošík, V., Chytrý, M., Tichý, L., 2004. Trends in species diversity and composition of urban vegetation over three decades. *J. Veg. Sci.* 15, 781–788. <https://doi.org/10.1111/j.1654-1103.2004.tb02321.x>.
- Pyšek, P., Hulme, P.E., Simberloff, D., Bacher, S., Blackburn, T.M., Carlton, J.T., Dawson, W., Essl, F., Foxcroft, L.C., Genovesi, P., Jeschke, J.M., Kühn, I., Liebhold, A., Mandrak, N.E., Meyerson, L.A., Pauchard, A., Pergl, J., Roy, H.E., Seebens, H., van Kleunen, M., Vilà, M., Wingfield, M.J., Richardson, D.M., 2020. Scientists' warning on invasive alien species. *Biol. Rev.* 95, 1511–1534. <https://doi.org/10.1111/bvr.12627>.
- R Development Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Vienna.
- Riedeman, P., Aldunate, G., Tellier, S., 2016. *Flora Nativa de Valor Ornamental de Chile. Chagual, Zona Norte*.
- Rodríguez, J., Novoa, A., Sotes, G., Pauchard, A., González, L., 2022. Variation in defensive traits against herbivores of native and invasive populations of *Carpobrotus edulis*. *Biol. Invasions*. <https://doi.org/10.1007/s10530-022-02970-9>.
- Roiola, S.R., 2019. Clonal traits and plant invasiveness: the case of *Carpobrotus* N.E.Br. (Aizoaceae). *Perspect. Plant Ecol. Evol. Syst.* 40, 125479. <https://doi.org/10.1016/j.ppees.2019.125479>.
- Ruiz, S., Metois, M., Fuenzalida, A., Ruiz, J., Leyton, F., Grandin, R., Vigny, C., Madariaga, R., Campos, J., 2014. Intense foreshocks and a slow slip event preceded the 2014 Iquique Mw8.1 earthquake. *Science (80-)* 1165, 1165–1169. <https://doi.org/10.1126/science.1256074>.
- Saura, S., Bodin, Ö., Fortin, M.J., 2014. EDITOR'S CHOICE: stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. *J. Appl. Ecol.* 51, 171–182. <https://doi.org/10.1111/1365-2664.12179>.
- Schittko, C., Bernard-Verdier, M., Heger, T., Buchholz, S., Kowarik, I., von der Lippe, M., Seitz, B., Joshi, J., Jeschke, J.M., 2020. A multidimensional framework for measuring biotic novelty: how novel is a community? *Glob. Change Biol.* 26, 4401–4417. <https://doi.org/10.1111/gcb.15140>.
- Sepúlveda, S.A., Rebolledo, S., McPhee, J., Lara, M., Cartes, M., Rubio, E., Silva, D., Correia, N., Vásquez, J.P., 2014. Catastrophic, rainfall-induced debris flows in Andean villages of Tarapacá, Atacama Desert, northern Chile. *Landslides* 11, 481–491. <https://doi.org/10.1007/s10346-014-0480-2>.
- SERNATUR, 2019. Servicio Nacional de Turismo. (<https://www.sernatur.cl/#>).
- Simberloff, D., Martin, J.L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E., Vilà, M., 2013. Impacts of biological invasions: what's what and the way forward. *Trends Ecol. Evol.* 28, 58–66. <https://doi.org/10.1016/j.tree.2012.07.013>.
- Smith, G.F., Laguna, E., Verloove, F., Ferrer-Gallego, P., 2020. *Aptenia* × *vascosilvae* (*A. cordifolia* × *A. haeckeliana*) (Aizoaceae), the new nothospecies from which the horticulturally popular cultivar *Aptenia* 'Red Apple' was derived. *Phytotaxa* 441 (2), 221–224.
- Souza-Alonso, P., Lechuga-Lago, Y., Guisande-Collazo, A., Pereiro Rodríguez, D., Rosón Porto, G., González Rodríguez, L., 2020. Drifting away. Seawater survival and stochastic transport of the invasive *Carpobrotus edulis*. *Sci. Total Environ.* 712, 135518. <https://doi.org/10.1016/j.scitotenv.2019.135518>.
- Spiller, D.A., Schoener, T.W., Piovia-Scott, J., 2016. Predators suppress herbivore outbreaks and enhance plant recovery following hurricanes. *Ecology* 97, 2540–2546. <https://doi.org/10.1002/ecy.1523>.

- Štajerová, K., Šmilauer, P., Brůna, J., Pyšek, P., 2017. Distribution of invasive plants in urban environment is strongly spatially structured. *Landsc. Ecol.* 32, 681–692. <https://doi.org/10.1007/s10980-016-0480-9>.
- Sukhorukov, A.P., Sennikov, A.N., Nilova, M.V., Kushunina, M., Belyaeva, I.V., Zaika, M.A., Hanáček, P., 2021. A new endemic species of *Sesuvium* (Aizoaceae: Sesuvioideae) from the Caribbean Basin, with further notes on the genus composition in the West Indies. *Kew Bull.* <https://doi.org/10.1007/s12225-021-09985-w>.
- Taylor, C., 1993. *Sesuvium portulacastrum* and *Mesembryanthemum nodiflorum* new records for the flora of Chile. *Gayana - Bot.* 49, 11–15.
- Thiel, M., Fraser, C., 2016. The role of floating plants in dispersal of biota across habitats and ecosystems. *Mar. Macrophytes Found. Species* 76–94. <https://doi.org/10.4324/9781315370781-5>.
- Thiel, M., Gutow, L., 2005. The ecology of rafting in the marine environment. II. The rafting organisms and community. *Oceanogr. Mar. Biol.* 43, 279–418. <https://doi.org/10.1201/9781420037449.ch7>.
- Turner, S.C., Esler, K.J., Kalwij, J.M., 2021. Road verges facilitate exotic species' expansion into undisturbed natural montane grasslands. *Appl. Veg. Sci.* 24, 1–9. <https://doi.org/10.1111/avsc.12615>.
- Venables, W.N., Ripley, B.D., 2002. Random and mixed effects. In: *Modern Applied Statistics with S*. Springer, New York, pp. 271–300.
- Vilà, M., D'Antonio, C.M., 1998. Hybrid vigor for clonal growth in *Carpobrotus* (Aizoaceae) in coastal California. *Ecol. Appl.* 8, 1196–1205. <https://doi.org/10.2307/2640972>.
- Vilà, M., Weiner, J., 2004. Are invasive plant species better competitors than native plant species? – evidence from pair-wise experiments. *Oikos* 105, 229–238. <https://doi.org/10.1111/j.0030-1299.2004.12682.x>.
- Vivrette, N.J., Muller, C.H., 1977. Mechanism of invasion and dominance of coastal grassland by *Mesembryanthemum crystallinum* author (s): Nancy J. Vivrette and Cornelius H. Ecol. Monogr. 47, 301–318.
- Von Der Lippe, M., Kowarik, I., 2007. Long-distance dispersal of plants by vehicles as a driver of plant invasions. *Conserv. Biol.* 21, 986–996. <https://doi.org/10.1111/j.1523-1739.2007.00722.x>.
- Weber, F., Kowarik, I., Säumel, I., 2014. A walk on the wild side: perceptions of roadside vegetation beyond trees. *Urban For. Urban Green.* 2, 205–212. <https://doi.org/10.1016/j.ppees.2014.10.002>.
- Williams, N.S.G., Hahs, A.K., Vesk, P.A., 2015. Urbanisation, plant traits and the composition of urban floras. *Perspect. Plant Ecol. Evol. Syst.* 17, 78–86. <https://doi.org/10.1016/j.ppees.2014.10.002>.
- Zhang, Z., van Kleunen, M., 2019. Common alien plants are more competitive than rare natives but not than common natives. *Ecol. Lett.* 22, 1378–1386. <https://doi.org/10.1111/ele.13320>.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects Models and Extension in Ecology With R*, 2nd ed. Springer, New York.