



Influential factors and barriers change along the invasion continuum of an alien plant

Ana Montero-Castaño · Marcelo A. Aizen ·
Pablo González-Moreno · Laura Cavallero ·
Montserrat Vilà · Carolina L. Morales

Received: 24 September 2022 / Accepted: 9 May 2023 / Published online: 12 June 2023
© The Author(s) 2023

Abstract Upon arrival to a new area, alien species have to overcome a series of biotic and abiotic barriers to survive, reproduce, and spread and thus, succeed along the invasion continuum. Failing to understand the role of the different sets of barriers and factors operating across the stages of the invasion continuum limit our ability to predict invasion dynamics, leading to misinformed management. Here, we explore how the European plant *Cytisus scoparius* overcomes the survival and reproductive barriers to establish along the roadsides of Nahuel Huapi National Park (Argentina). We evaluate the direct and indirect influence of climatic and landscape factors,

species traits and their interaction with patch cover, plant height, and pollinator visitation rates as proxies of population persistence, plant growth, and reproduction, respectively. *Cytisus scoparius* cover was positively associated with the length of water shores and urban cover, factors that may relate to the arrival of propagules, new introduction events, and high levels of disturbance. Plant height was positively associated with annual precipitation and mean temperature. Visitation rates positively related to shrubland cover and to a lesser extent to slope, two factors that may influence pollinator availability and long-distance detectability, respectively. However, factors positively affecting survival had no effect (in the case of height) or negative effect (in the case of cover) on visitation rates, probably due to the saturation of the pollinator

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10530-023-03087-3>.

A. Montero-Castaño (✉) · M. Vilà (✉)
Estación Biológica de Doñana (EBD-CSIC), Avda.
Américo Vespucio 26, 41092 Sevilla, Spain
e-mail: ana.montero.castano@gmail.com

M. Vilà
e-mail: montse.vila@ebd.csic.es

A. Montero-Castaño
School of Environmental Sciences, University of Guelph,
50 Stone Road East, Guelph, ON N1G 2W1, Canada

M. A. Aizen · C. L. Morales
Grupo de Ecología de La Polinización, Instituto de
Investigaciones en Biodiversidad y Medioambiente
(INIBIOMA), Universidad Nacional del Comahue-
CONICET, San Carlos de Bariloche, Río Negro, Argentina

P. González-Moreno
Department of Forest Engineering, Laboratory
of Dendrochronology, Silviculture and Global
Change-DendrodatLab-ERSAF, University of Córdoba,
Campus de Rabanales, Crta. IV, km. 396, 14071 Córdoba,
Spain

L. Cavallero
Centro Científico Tecnológico CONICET Córdoba,
X5000IND, Buenos Aires 1418, Córdoba, Argentina

M. Vilà
Department of Plant Biology and Ecology, Universidad de
Sevilla, Sevilla, Spain

pool within large flowering patches. Despite the strong environmental gradients, climatic variables did not seem to influence the cover nor the visitation rates of *C. scoparius*. The microhabitat provided by roadsides seemed to buffer the climatic variability acting at larger spatial scales. This study shows how the relevance of different barriers across the invasion process can vary due to the characteristics of the species and of the spatial context. Actions directed towards the most limiting barriers and limiting factors could be an efficient way to manage invasions and reduce their impacts. In our system, actions aimed at reducing propagule arrival, soil disturbance and availability of pollinators could limit the survival and reproductive success of *C. scoparius*.

Resumen Con su llegada a una nueva área, las especies exóticas deben superar una serie de barreras bióticas y abióticas para sobrevivir, reproducirse y expandirse y, por tanto, avanzar a lo largo del proceso de invasión. La falta de conocimiento acerca de las barreras y factores más influyentes en las distintas etapas de este proceso limita la capacidad de predecir las dinámicas de invasión y su gestión. Aquí exploramos cómo la planta europea *Cytisus scoparius* supera barreras para su supervivencia y reproducción y así establecerse en los bordes de carreteras del Parque Nacional Nahuel Huapi (Argentina). Evaluamos la influencia directa e indirecta de factores climáticos y del paisaje, de las características intrínsecas de la especie, y de su interacción con la cobertura, altura y tasa de visitas de *C. scoparius* como representantes de su persistencia poblacional, crecimiento y reproducción, respectivamente. La cobertura de *C. scoparius* resultó estar positivamente relacionada con la longitud de los cursos de agua y con la cobertura urbana, factores que pueden favorecer la llegada de propágulos, nuevos eventos de introducción y altos grados de perturbación. La altura se relacionó positivamente con la precipitación y la temperatura media anuales. La tasa de visitas resultó estar positivamente relacionada con la cobertura de matorral y en menor medida con la pendiente del terreno, factores que pueden estar influenciando, respectivamente, una mayor disponibilidad de polinizadores y la detección a larga distancia. Sin embargo, los factores que afectaron de forma positiva a la supervivencia tuvieron un efecto indirecto nulo (en el caso de la altura) o negativo (en el caso de la cobertura) sobre la tasa de visitas, probablemente

debido a la saturación de las comunidades de polinizadores en los parches de floración más grandes. Finalmente, y a pesar de los marcados gradientes ambientales, las variables climáticas parecen no afectar la cobertura ni la tasa de visitas en *C. scoparius*. Las condiciones microclimáticas en los bordes de carretera parecen amortiguar las condiciones climáticas que actúan a mayores escalas espaciales. Este estudio muestra cómo la importancia relativa de las distintas barreras a lo largo de los procesos de invasión cambia dependiendo de las características de las especies y del contexto espacial. Medidas enfocadas en las barreras y factores limitantes que influyen en la invasión podrían mejorar su gestión y reducir sus impactos. En nuestro sistema de estudio, acciones dirigidas a reducir la llegada de propágulos, la perturbación del suelo y la disponibilidad de polinizadores podrían limitar la supervivencia y éxito reproductivo de *C. scoparius*.

Keywords Establishment · Landscape scale · Linear infrastructures · Non-native species · Pollination · Reproduction · Scotch broom · Survival · Structural equation models

Introduction

Biological invasions are dynamic, non-equilibrium processes characterised by an increase in local abundance and geographical extent of alien species (Richardson et al. 2000). According to the conceptual framework proposed by Blackburn et al. (2011), alien species need to overcome different abiotic and biotic barriers (Richardson et al. 2000; Pyšek et al. 2004; Richardson and Pyšek 2006, 2012; Divíšek et al. 2018) to be able to arrive, survive, reproduce and spread in a new region, that is, to progress along the introduction-invasion continuum (hereafter, “the continuum”).

Depending on the characteristics of the alien species, the new area, and introduction events, the underlying mechanisms and factors influencing the success of alien species differ along the continuum (Václavík and Meentemeyer 2012), while a given factor can also have different direct or indirect effects. Moreover, the invading species can affect their own performance along the continuum through positive and negative feedbacks by altering their recipient environments (Vilà et al. 2011).

Understanding the transition of alien species along the continuum can contribute to the detection of the most limiting sets of barriers and factors influencing invasion, and thus, guide management decision-making (Richardson and Pyšek 2012). Such a dynamic approach can be especially interesting in the case of alien species associated with disturbed areas such as infrastructure networks. These usually linear infrastructures can act as corridors facilitating the arrival and spread of aliens into new areas (Dar et al. 2015; Asth et al. 2021). Therefore, exploring the barriers and factors mediating the establishment of the alien species, rather than for instance their arrival or spread, can be more informative and can provide new insights about their invasion success and potential management.

The establishment of an alien species in its new area requires the overcoming of survival and reproductive barriers. Overcoming survival barriers depends on the conditions that allow for the species population persistence and vegetative growth, the former depending on environmental factors but also on the characteristics of the introduction event (e.g. propagule pressure) (Blackburn et al. 2011). Overcoming reproductive barriers and the corresponding influential factors, highly depends on the reproductive system of the alien species (Montero-Castaño and Traveset 2020).

Here, we study the establishment of the European *Cytisus scoparius* (Scotch broom), a pollinator-dependent alien plant (Stokes et al. 2006) invading roadsides in southern South America along wide environmental gradients (Potter et al. 2009). Specifically, we test a series of hypotheses regarding its performance overcoming (1) survival and (2) reproductive barriers. Regarding (1) its survival, we expect *C. scoparius* patch cover to be positively associated with urban cover and length of river-or lake-shores, which are expected to provide suitable environmental conditions and disturbance regimes, while acting as sources of propagules and introduction events. We also expect the cover and the height to be positively associated with annual precipitation and annual mean temperature. Precipitation and temperature gradients in the study area fall within the lowest part of the wide annual precipitation (500 to >3000 mm)

and temperature ranges (optimal temperature during the growing season ranging from 18 to 23 °C) where *C. scoparius* is found in its native distribution area in Europe (Potter et al. 2009). Therefore, increasing precipitation and temperature in the study area are expected to relate positively with the two dimensions of population survival, persistence and growth (*C. scoparius* cover and height, respectively).

Regarding (2) its reproduction, we expect pollinator visitation rates to *C. scoparius* to be positively associated with the cover of open and mid-successional habitats, to annual mean temperature and mean slope of the terrain. Open and mid-successional habitats host diverse and abundant pollinator communities (Steffan-Dewenter and Tschardt 2002; Steffan-Dewenter and Westphal 2008; Wu et al. 2019). Increasing temperatures usually benefit foraging capacities of pollinators. While terrain slope could favour the attraction to *C. scoparius* patches because steep patches might be better detected visually by pollinators at long distances. On the contrary, we expect pollinator visitation rates to be negatively associated with patches with individuals of *C. scoparius* with reddish flowers and to patch height and cover. Most insect pollinators are able to discriminate colours in the ultraviolet to the yellow-orange spectrum (Kevan and Baker 1983) and are differently attracted to them (Bradshaw and Schemske 2003; Nuttman et al. 2006; Papiorek et al. 2016). *Cytisus scoparius* yellow flowers have an ultraviolet pattern invisible to the human eye that is more attractive to pollinators than the UV pattern of reddish flowers (Gavini and Farji-Brener 2015; Vidal and Farji-Brener 2020). Patch height and cover determine the floral abundance. In the study area, *C. scoparius* usually forms large monospecific stands with massive flower blooms (Cavallero et al. 2018). Therefore, at such high floral densities, we expected to find a negative relationship of both patch cover and height with visitation rate due to saturation of the pollinator pool. Consequently, we also expect the climatic variables annual precipitation and annual mean temperature, as well as urban cover and length of water shores, influencing patch growth to be indirect- and negatively associated to pollinator visitation rate.

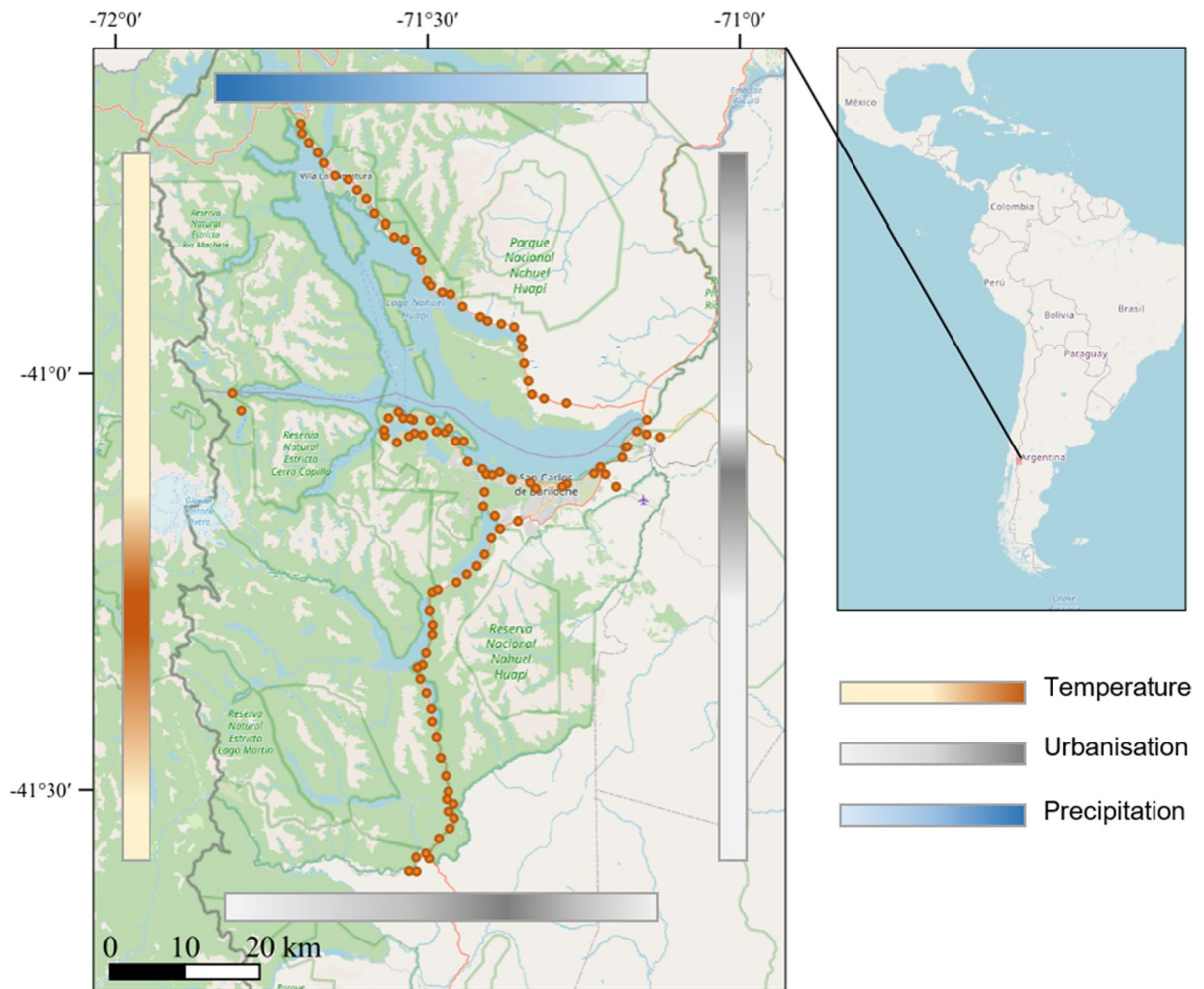


Fig. 1 Location and sampling design along national and provincial roads showing the environmental gradients of the study area. Temperature, urbanisation, and precipitation gradients are represented by colour bars (orange, grey and blue, respectively) where darker colours represent approximately higher

values of the corresponding variable. Dots show the 108 study patches, which were located along these roadsides by stopping every 2 km and selecting the closest patch of *C. scoparius* with at least 10 flowering individuals

Material and methods

Study system

The study was conducted in Nahuel Huapi National Park, in NW Patagonia, Argentina ($41^{\circ} 06' S$ – $41^{\circ} 36' S$, Fig. 1). The National Park covers strong environmental gradients along short distances. In the ca. $60 \times 120 \text{ km}^2$ covered in this study, the altitudinal gradient of the Andes ranges from 500 m above sea level at the bottom of glacial valleys, to 3500 m at the top of glacier-covered mountains. The rain

shadow caused by the Andean range creates a strong west–east precipitation gradient where annual precipitation drops from $>4000 \text{ mm}$ at the temperate Valdivian rainforest at the foothills, to $<500 \text{ mm}$ at the Patagonian steppe. Finally, an urbanisation gradient with several small to medium size cities lies within the matrix of natural habitats protected by the National Park.

This amplitude of environmental gradients determines a wide variety of habitats and associated vegetation, including alien plants, which represent 25% of the vascular Flora of the Park (Ezcurra and Brion

2005). Among them, *Cytisus scoparius* (L.) Link, (Scotch broom) is one of the most widespread invasive plant species, also reaching the highest local abundances (Cavallero et al. 2018). This perennial legume shrub is native from Europe and has become invasive in many temperate regions worldwide (Bossard and Rejmanek 1994; Downey et al. 2000; Sheppard et al. 2002; Suzuki 2003; Simpson et al. 2005; Potter et al. 2009; Cordero et al. 2016). In invaded regions, this species spreads along roadsides, water shores and disturbed areas where it forms dense stands (Fig. 2a, b), excluding native plants and altering community structure (Bossard and Rejmanek 1994; Wearne and Morgan 2004). Scotch broom was introduced in the region in the twentieth century—probably as an ornamental plant—and since 2021 is listed as a major “Invasive Alien Species” in Argentina (Boletín Oficial de la República Argentina 2021).

Cytisus scoparius lacks vegetative propagation; thus, population persistence, growth and spread depend entirely on seed production (Parker 1997,

2000). At reproductive maturity (3–5 years), each plant can produce several thousands of papilionate flowers that bloom during ca. 4–8 weeks in spring (Parker 2000; Stout 2000). Flowers are nectarless but rich in pollen and are mainly yellow, although some individuals produce reddish flowers (Fig. 2c, d) (Gavini and Farji-Brener 2015). Insect visitors must be large enough to push the keel down and split the petals, releasing the style and anthers, which then spring up to contact the back of the pollinator in an explosive motion. In this area, *Bombus dahlbomii*, *Apis mellifera* and more recently, the invasive *Bombus terrestris*, have been reported as effective pollinators of this alien plant (Morales and Aizen 2002; Aizen et al. 2008; Gavini and Farji-Brener 2015). Once a flower is “tripped”, it does not return to its original configuration (Parker 1997) and can be distinguished from virgin unvisited flowers (Fig. 2c, d). Thus, the proportion of tripped flowers is a reliable estimator of pollinators visitation rate at the plant and patch levels (Cavallero et al. 2018), allowing rapid estimations

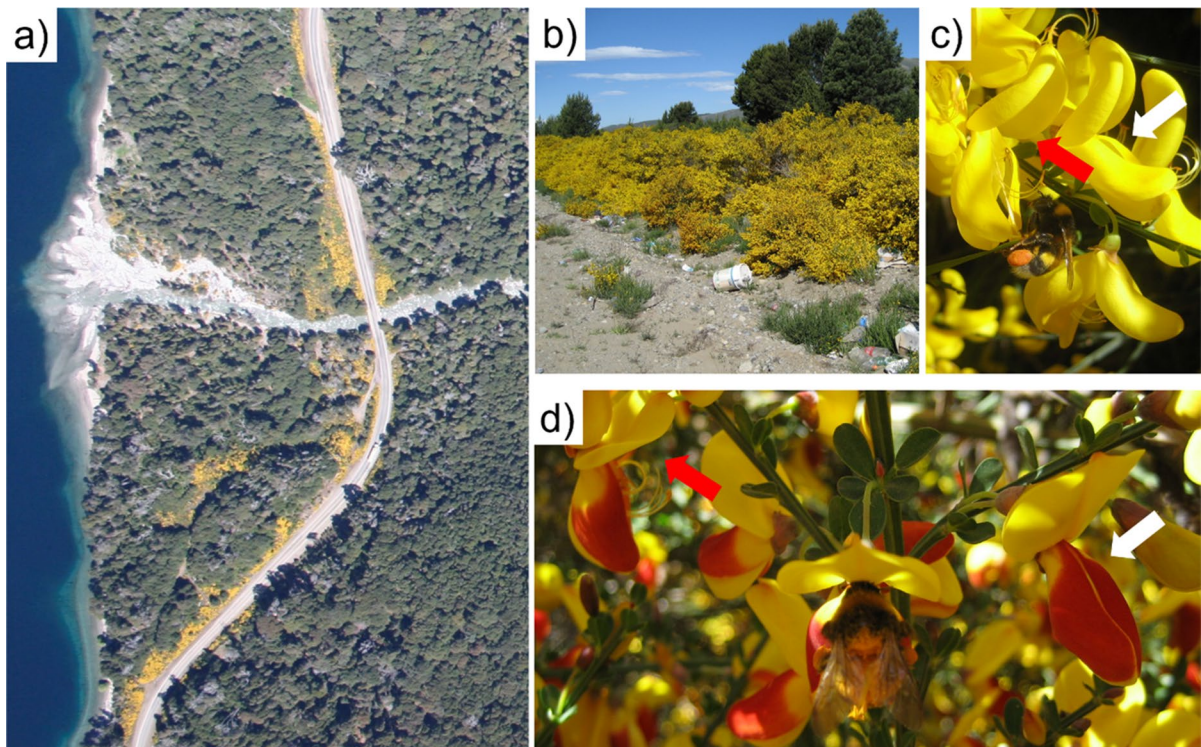


Fig. 2 *Cytisus scoparius* invading **a** roadsides and **b** disturbed areas in the study area in Nahuel Huapi National Park (Argentina). Examples of individuals with **c** yellow and **d** reddish

flowers being visited by invasive *Bombus terrestris*. Tripped and untripped flowers are pointed with red and white arrows, respectively

of visitation rates for large sample sizes. Moreover, the proportion of tripped flowers is closely related to fruit and seed production, as reproduction in *C. scoparius* is severely limited by visitation frequency, which in turn reflects pollinator availability (Cavallero et al. 2018). In the study area, while untripped flowers set no fruit, 36% of tripped flowers set fruits, and fruit set is significantly and positively related to seed output (Cavallero et al. 2018). In species lacking vegetative reproduction, seed output is only the first step for overcoming reproductive barriers. Other posterior barriers such as seed predation and seedling mortality, must be overcome as well. However, in the case of *C. scoparius*, as seed production is massive and seedling mortality is negligible (Sheppard et al. 2002), very high seed predation rates would be needed to significantly reduce its reproductive success (Paynter et al. 2010). Thus, because of strong pollinator dependence and severe pollination limitation, we consider the proportion of tripped flowers as an appropriate proxy of reproductive success.

Field sampling design

To embrace the widest environmental gradients of the study area while avoiding their covariation, we established three transects that run along different major national and provincial roads in different directions (RN 40, RP 237, RP 77 and RP 82). Overall, we covered an annual mean precipitation gradient ranging from 797 to 1785 mm; an annual mean temperature gradient ranging from 6.8 to 9.7 °C, corresponding to a ca. 500 m altitudinal gradient (Fig. 1); and an urbanisation gradient covering natural areas and the cities of Villa La Angostura, Dina Huapi and San Carlos de Bariloche and their surroundings. Along these roadsides, we selected a total of 108 patches of *C. scoparius*. Every 2 km at a randomly selected side of the road, we located the closest patch lying on the roadside (i.e., 0–2 m from the border, depending on the conditions of the roadside) of *C. scoparius* with at least 10 flowering individuals. Mean (\pm SE) distance between consecutive patches was 1.79 ± 0.04 km (Fig. 1). Field sampling took place during the 2010 flowering peak, from October 15 to December 13. To avoid any phenological bias, we sampled patches at a similar blooming stage, when individual plants had most of their flowers open (i.e., there were <10% pre-anthesis flower buds and no well-developed fruits).

Variables

We measured in situ or calculated from aerial photos or digital thematic maps the set of patch, landscape and climatic variables that we expected to explain the success of *C. scoparius* in overcoming survival and reproductive barriers (see Fig. 3).

- a. *Variables measured in situ.* For each study patch, we estimated visitation rate, height and flower colour. First, in 10 randomly selected *C. scoparius* individual plants we counted the proportion of tripped flowers over the total number of open flowers in three randomly selected branches of ca. 30 cm. We then pooled together the per branch and per individual flower counts and estimated the visitation rate per patch as a proxy of *C. scoparius* success overcoming reproductive barriers. Visitation rate estimated this way positively influences fruit set and seed output in this species (Cavallero et al. 2018), and therefore is a good proxy of the overall reproductive success. Second, we measured the height (m) of each of the 10 individuals to estimate the average patch as a proxy of growth, one of the dimensions of population survival (Blackburn et al. 2011). Third, we recorded patch colour as a categorical variable with two levels: yellow (i.e.; all individuals in the study patch had yellow flowers) and bicolour (i.e., there were individuals in the study patch with reddish flowers; there were no patches with only reddish flowers).
- b. *Patch cover calculated from aerial photographs.* We built a Cover Map from aerial colour photos taken during *C. scoparius* blooming peak in 2010 to estimate *C. scoparius* cover. We took advantage of the mass blooming and bright-yellow flowering display of *C. scoparius*, which form patches that can be easily distinguished from other associated vegetation or background structures from a long distance (see Cavallero et al. 2018). Aerial photographs were taken in two cloud-free days (22 and 25 November 2010) near noon (11:00–13:15) to minimise shadow effects. Aerial photographs were georeferenced using ArcGIS 9.2 and the Esri World Imagery basemap, and then combined into image mosaics. The software ENVI 4.4 was used for the automated identification of *C. scoparius* patches.

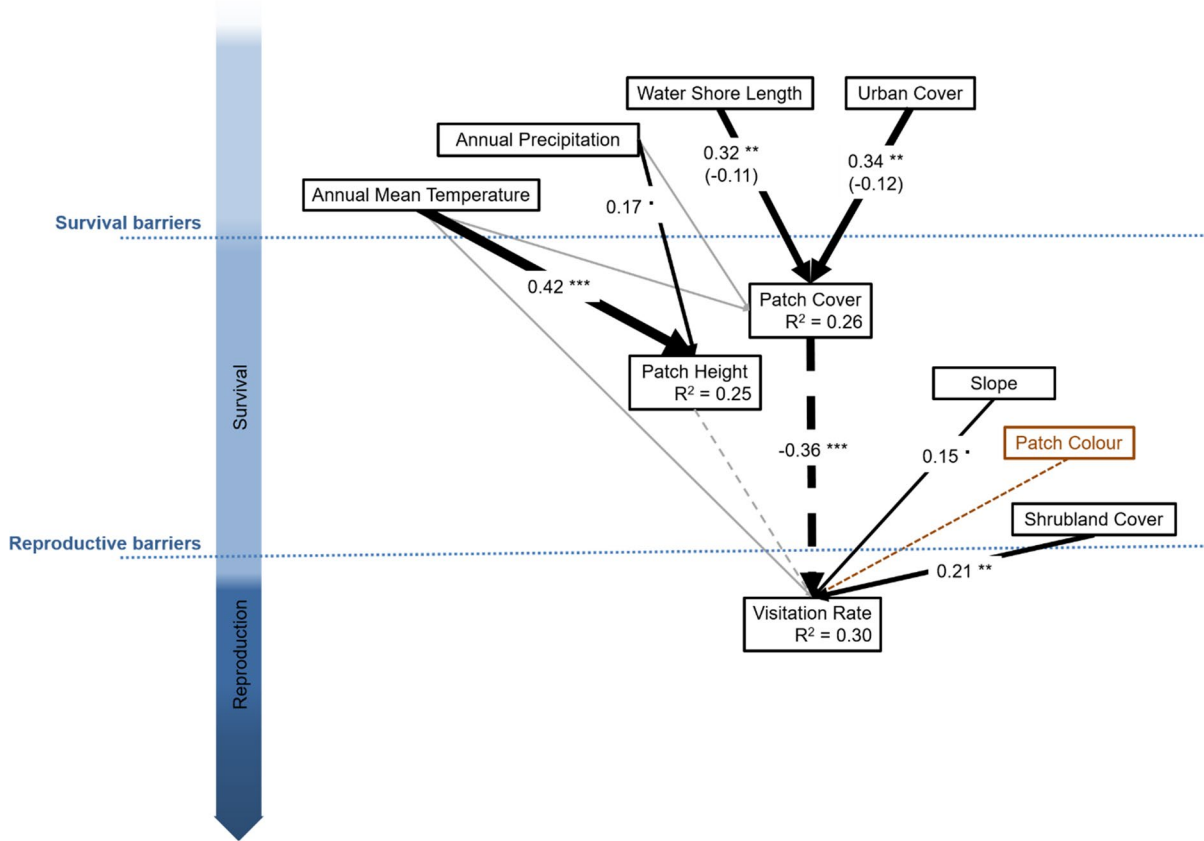


Fig. 3 Causal model proposed (grey, black and brown cells and arrows) and optimised (grey and black cells and arrows) through a backward stepwise process based on the AIC. The key barriers (blue dotted lines) for the establishment of alien species according to Blackburn et al. (2011), Pyšek et al. (2004) and Richardson et al. (2000) are shown. One-headed arrows depict significant (p -value < 0.05) causal relationships. Positive, negative and non-significant effects are represented by solid, dashed and grey lines, respectively. Numbers over

the arrows represent the standardised path coefficients and p -values (* p -value: $0.05 < p < 0.06$, ** p -value: $0.01 < p < 0.001$, *** p -value: < 0.001). Arrow widths are proportional to the magnitude of these path coefficients. Values in parentheses are the strength of indirect effects on visitation rate of urban cover and annual mean temperature via patch cover. For each partial model (see Eqs. 1–3) the R^2 is given under the corresponding response variable. Fisher’s C goodness-of-fit test and the AIC of the optimised model are given in the text

Patch cover was quantified as the percentage of cover of *C. scoparius* in an area of 100 m radius from the centroid of the study patch where in situ variables were measured (see above). The selection of this radius was a compromise between an area large enough to maximise the variability of *C. scoparius* cover, and an area where a representative in situ sampling of the previously mentioned variables were feasible. In the study area, *C. scoparius* patches are usually large, thus, a smaller sampling radius would have implied

most of the patches having covers close to 100%, impeding a proper exploration of *C. scoparius* cover as a response variable. On the other hand, sampling a larger radius in the field would have required sampling more than 10 individuals per site in order to properly represent the patch, which was not feasible due to logistic limitations. Patch cover, together with patch height, was used as a proxy of *C. scoparius* success in overcoming survival barriers.

Table 1 Predictor variables included in the proposed causal model (Fig. 3) and the processes they are expected to influence

| Variable | Process they influence | Source | Reference | Radii (m) | Mean \pm SE (min, max) |
|--|--|---|---|--------------------------|-----------------------------------|
| Urban cover (%) | Propagule arrival and disturbance | Land cover Map of Nahuel Huapi N.P. ^{*1} | Gowda et al. (2014) | 100, 250, 500, 750, 1000 | 14.64 \pm 2.10 (0, 89.20) |
| Water shore length (m) | Propagule arrival and disturbance | Water streams shapefile | Instituto Geográfico Nacional de la República Argentina | 100, 250, 500, 750, 1000 | 1806.76 \pm 106.74 (0, 4938.16) |
| Annual precipitation (mm) | Plant growth Pollinator foraging activity | WorldClim | Fick and Hijmans (2017) | 0 | 1129.11 \pm 17.67 (797, 1785) |
| Annual mean temperature ($^{\circ}$ C*10) | Plant growth Pollinator foraging activity | WorldClim | Fick and Hijmans (2017) | 0 | 83.12 \pm 0.50 (68, 97) |
| Shrubland cover (%) | Abundance pollinators | Land cover Map of Nahuel Huapi N.P. | Gowda et al. (2014) | 100, 250, 500, 750, 1000 | 31.12 \pm 3.17 (0, 100) |
| Slope ($^{\circ}$) | Attractiveness floral rewards | Digital elevation model | http://asterweb.jpl.nasa.gov/gdem.asp | 100, 250, 500, 750, 1000 | 11.20 \pm 0.84 (0, 44.59) |
| Patch cover (%) | Attractiveness floral rewards | Aerial photo | n.a | 100 | 1.48 \pm 0.18 (0.01, 10.04) |
| Patch height (m) | Attractiveness floral rewards | in situ | n.a | 100 | 1.72 \pm 0.04 (1.03, 2.80) |
| Patch colour (yellow or reddish) | Attractiveness floral rewards | in situ | n.a | 100 | n.a |
| Visitation rate (tripped/open flowers) | | in situ | n.a | 100 | 0.47 \pm 0.03 (0.08, 0.98) |

The variables patch cover and height were also included in the model as proxies of *C. scoparius* population growth and persistence, respectively, representing the population success in overcoming survival barriers. Visitation rate was included only as a proxy of *C. scoparius* success in overcoming reproductive barriers. The sources and references for each variable are provided together with the radii at which the variables were calculated: 0 (i.e., the value of the variable in the centroid of the patch), 100, 250, 500, 750 and 1000 m. The mean \pm SE and ranges of variation of each variable included in the model are also given. For those variables calculated at several radii, the values at the 750 m consensus radius are the ones given

^{*1}Updated based on Google Earth 2011

n.a.: not applicable

c. Variables calculated from digital thematic maps.

The rest of the variables in Fig. 3 (urban cover, annual precipitation, annual mean temperature, shrubland cover and mean slope) were obtained from digital thematic maps with ArcGIS 9.2. To calculate urban cover (%), we used the Land cover Map based on 2003 Landsat 30 m resolution images (Table 1). Because in the study region urbanisation is among the most expanding land uses, we updated the land cover map by manually digitising new urban areas based on 2011 Google maps images. The length of river

or lakeshore in the surrounding landscape of study patches was calculated from the shapefile of Water streams (Table 1). Annual precipitation and annual mean temperature were obtained for the centroid of the study patches from the WorldClim dataset (Table 1). Shrubland cover was calculated from the Land cover Map of Nahuel Huapi National Park by pooling together all the different open and mid-successional covers distinguished in the map. Specifically, the classes named (in Spanish) *alto andino*, *matorral*, *estepa y pradera*, *pastizal húmedo*, *pastizal antropizado*,

lenga achaparrada and *vacíos*, were included as shrubland cover. Finally, we calculated the mean slope in the surrounding area of study patches from the Digital Elevation Model (Table 1).

When possible, depending on the spatial resolution of the digital maps, we calculated these variables at five radii distances (100, 250, 500, 750 and 1000 m) from each patch centroid. For example, the Land Cover Map of Nahuel Huapi National Park has a 30×30 m resolution. Therefore, shrubland cover was calculated at those five radii distances. However, the resolution of the WorldClim map is ~1 km², allowing the calculation of one value of annual mean temperature and annual precipitation for the centroid of each patch (Table 1). For those variables calculated at different radii, we selected a consensus radius of 750 m. This radius represented a compromise between maximising significant relationships based on simple regressions, while preventing the covariation among explicative variables at larger spatial scales (see the section *Piecewise Structural Equation Modelling* below and Supplementary Material). Though the spatial scale of influence of the climatic variables considered here (annual precipitation and annual mean temperature) could be expected to be larger than the 750 m radius, due to their marked elevation and environmental gradients in the study area, we expect these variables to be influential even at the spatial extent of this study.

Piecewise structural equation modelling

To test our hypotheses, we built a causal model with the predicted relationships shown in Fig. 3 and conducted a piecewise structural equation model (SEM) with the *piecewiseSEM* R package (Lefcheck 2016). When needed, we transformed all the predictive and response variables to achieve multivariate normality (see Table S1) and standardised them by subtracting their respective mean and dividing by the standard deviation to make their effects (i.e. coefficients) comparable (Shipley 2000). A full piecewise SEM is decomposed into linear partial models that are analysed individually and allow the incorporation of corrections for potential data structure owing to

hierarchical sampling, phylogenetic or spatial correlations (Lefcheck 2016). Our SEM was decomposed in the three linear partial models shown in Eqs. 1–3:

$$\text{patch cover} \sim \text{urban cover} + \text{water shore length} \\ + \text{annual mean temp.} + \text{annual precip.} \quad (1)$$

$$\text{patch height} \sim \text{annual mean temp.} + \text{annual precip.} \quad (2)$$

$$\text{visitation rate} \sim \text{patch cover} + \text{patch height} + \text{slope} \\ + \text{annual mean temp.} + \text{shrubland cover} + \text{patch colour} \quad (3)$$

Due to our regular sampling along roads, we could expect certain spatial autocorrelation in our observations. We explored the potential spatial correlation for the three linear partial models in which our SEM was decomposed (Eqs. 1–3) by calculating Moran's Index for the residuals. Patch cover and visitation rate showed spatial autocorrelation that fitted an exponential and a Gaussian shaped model, respectively (Supplementary Material). Therefore, we included a correlation term in these partial models using the function *gls* from the *nlme* package (Pinheiro et al. 2021).

To be able to test the largest number of our hypotheses, we selected a final optimised model through a backward stepwise process based on the AIC statistic, choosing the model with the lowest AIC and the largest number of variables included with a difference of $\Delta\text{AIC} > 3$ (Shipley 2013; Supplementary Material). To assess model fit, we considered the results of the d-separation test for all the pathways not included in the SEM (i.e., pairs of variables not connected by an arrow) (Supplementary Material). These results are summarised in a Fisher's C test. Significant results in this test suggest possible path additions, whereas non-significant Fisher's C test indicates that the pattern predicted by the SEM agrees with that observed and, therefore, the model cannot be rejected. In addition to the path coefficients estimated by the SEM, we calculated the strength of the indirect effects in the SEM (Table 2). All analyses were conducted in R 3.6.2 (R Core Team 2020).

Table 2 Standardised coefficients, SE, and *p*-values of each path in the model (direct effects) and strength of indirect effects

| Effect | Response | Predictor | Coefficient | SE | <i>p</i> -value |
|----------|-----------------|------------------------------------|---------------|--------------|------------------|
| Direct | Patch cover | Urban cover (750 m radius) | 0.335 | 0.112 | 0.004 |
| | | Water shore length (750 m radius) | 0.317 | 0.100 | 0.002 |
| | | Annual mean temperature (centroid) | 0.145 | 0.124 | 0.245 |
| | | Annual precipitation (centroid) | -0.143 | 0.152 | 0.350 |
| | Patch height | Annual mean temperature (centroid) | 0.422 | 0.088 | <0.001 |
| | | Annual precipitation (centroid) | 0.171 | 0.088 | 0.054 |
| | Visitation rate | Slope (750 m radius) | 0.151 | 0.079 | 0.060 |
| | | Patch cover (100 m radius) | -0.358 | 0.060 | <0.001 |
| | | Patch height (100 m radius) | -0.054 | 0.061 | 0.375 |
| | | Annual mean temperature (centroid) | 0.021 | 0.097 | 0.826 |
| | | Shrubland cover (750 m radius) | 0.212 | 0.080 | 0.009 |
| | | Mediated by | Strength | | |
| Indirect | Visitation rate | Urban cover (750 m radius) | Patch cover | -0.120 | |
| | | Water shore length (750 m radius) | Patch cover | -0.114 | |

Numbers in bold represent significant effects (i.e., *p*-value \leq 0.05)

Results

Response variables showed considerable variation. The cover of *C. scoparius* within a 100 m radius along the 108 study patches ranged from 0.01 to 10.04%, with an average cover (mean \pm SE) of $1.48 \pm 0.18\%$. The average patch height was 1.72 ± 0.04 , ranging from 1.03 to 2.80. After counting an average of 214.50 ± 10.67 flowers in each patch, the estimated average visitation rate (i.e.; proportion of tripped flowers per total number of open flowers) was 0.47 ± 0.03 , ranging from 0.08 to 0.98 (see Table 1 for the average values and variation ranges of the rest of variables in the model).

After a stepwise backward optimisation process of the model, the variable patch colour (and its predicted effect on visitation rate) was removed from the final SEM (Fig. 3). The final optimised model provided a good fit to the data according to the d-separation test of the independence claims chi-square test (Table S4.1) and the Fisher's C test (Fisher's $C = 14.22$, $df = 20$, p -value = 0.82).

Regarding factors influencing survival and reproduction, we found strong evidence that patch cover was positively influenced by urban cover and water shore length, but not by annual mean temperature or annual precipitation. However, we found strong

evidence that both climatic variables positively affected patch height (Table 2). In addition, we found very strong evidence of a negative effect of patch cover on visitation rate, and strong evidence of a positive effect of shrubland cover on the same response variable, while the evidence of a positive effect of slope was rather weak. Contrary to our predictions, annual mean temperature had no effect on pollination visitation rate (Table 2; Fig. 3).

Regarding indirect effects, urban cover and water shore length had a negative effect on visitation rate, mediated through their positive effect on patch cover. Contrary to our hypotheses, we did not find evidence of an effect of patch height on visitation rates. Therefore, there is no evidence that the climatic variables had an indirect effect on visitation rate through patch height (Table 2; Fig. 3).

Overall, visitation rate is the response variable better explained by the SEM ($R^2 = 0.30$) followed by patch cover ($R^2 = 0.26$) and patch height ($R^2 = 0.25$).

Discussion

Our study has provided insights about the most determinant factors influencing the invasion of *C. scoparius* in Nahuel National Park and the potential

underlying mechanisms. Factors explaining the cover and height of *C. scoparius*, as proxies of its survival, were associated to propagule arrival and disturbance, and to the suitability of temperature and water availability conditions for plant growth, respectively. Meanwhile, factors explaining pollinator visitation rates, as a proxy of its reproductive success, were associated with the availability and foraging behaviour of pollinators. In addition, one of the most striking results is that, despite the strong environmental gradients in the study area, climatic variables did not seem to influence the cover of *C. scoparius* in roadsides. Finally, we found evidence of negative feedbacks along the invasion continuum; in particular, that the increased population persistence and growth can negatively influence the reproduction of the invasive species.

Factors influencing *Cytisus scoparius* survival

Cytisus scoparius cover was positively related to the length of water shores and the cover of urban areas. Rivers and lakes can naturally contribute to the disturbance regimes in their surrounding areas (Décamps et al. 1995) and seed dispersal by water (Pyšek and Prach 1993). Many terrestrial invasive species benefit from water courses which disperse their propagules and increase dispersal distance downstream (Boedeltje et al. 2003; Catford and Jansson 2014), even if species are primarily dispersed by other mechanisms (Säumel and Kowarik 2010). Water dispersion can also favour seed germination if for instance, seedlings are sensitive to dry conditions (Funkenberg et al. 2012). *Cytisus scoparius* seeds have a dormancy caused by a water-impermeable seed coat (Bossard 1993). Whether *C. scoparius* seeds dispersed by water also have higher chances to germinate than dry dispersed ones remains to be explored. In any case, in riparian and lacustrine systems like those found in the study area, water courses can play an important role as sources of alien propagules (Pyšek and Prach 1993). Besides, water courses contribute to the availability of water resources, indispensable for plant growth. Urban areas also imply high disturbance levels. Besides, seeds and plants of this invasive species are sold in gardening shops and used in local gardens as fences in the area (Rovere et al. 2013; Akasaka et al. 2015), converting urban areas as sources of propagules as for other ornamental alien plant species worldwide (van Kleunen et al. 2018). Finally,

water courses and urban areas are also intrinsically disturbed habitat types (Décamps et al. 1995) which create space and nutrient conditions favourable for seedling establishment (Gassó et al. 2009). In particular, germination rates of *C. scoparius* are positively associated with soil disturbances such as soil turn over and vegetation removal (Bossard 1993).

We did not find any evidence that climatic conditions affect the cover of *C. scoparius*. Although climate is a major driver of species distribution in general (Woodward 1987) and temperature and precipitation are probably the most relevant climatic variables affecting plant invasions at large scales (Pino et al. 2005), it is likely (though it could not be tested here) that such climatic conditions are buffered in the roadsides where our sampling was conducted. Roads, artificial infrastructures and other modified areas provide a series of conditions at the local scale such as bare and nutrient-rich soils, lack of natural vegetation, high light availability and altered drainage (Parendes and Jones 2000; Christen and Matlack 2006), which to some extent may buffer factors operating at larger spatial scales. This hierarchical pattern allows the presence of alien species in areas that otherwise would not meet the environmental requirements for their survival (Pauchard and Alaback 2004). Besides, these linear infrastructures can act as stepping stones where aliens are able to survive and disperse towards more suitable areas (e.g. Dar et al. 2015; González-Moreno et al. 2013; Ibáñez et al. 2009). According to experimental data, *C. scoparius* has a lowest temperature occurrence threshold at 8.5 °C (Potter et al. 2009). That would make part of our study area unsuitable for this species as the annual mean temperature ranges from 6.8 to 9.7 °C. However, we found *C. scoparius* along roadsides throughout the entire temperature gradient, supporting the hypothesis that road habitats are a favourable microhabitat for this species despite limiting climatic conditions. Therefore, our results suggest that factors related with propagule arrival and disturbance levels, like water shore length and urban cover, positively influence the performance of *C. scoparius* in overcoming survival barriers.

Factors directly and indirectly influencing *Cytisus scoparius* reproduction

Pollinator visitation rates, as expected, were positively related to shrubland cover. Open and

mid-successional habitats usually host richer and more abundant pollinator communities because they offer more nesting and feeding resources to most pollinator species than late-successional habitats (Steffan-Dewenter and Tscharrntke 2002; Steffan-Dewenter and Westphal 2008). In addition, open habitats are often part of agricultural landscapes where managed pollinators are introduced for crop pollination (Velthuis and Doorn 2006), thus these areas might be especially important in our study system because managed honeybees and invasive bumblebees were the main pollinators observed visiting *C. scoparius* flowers (personal observation). Also as expected, visitation rates were positively related to slope, though this relationship was weak, which agrees with our hypothesis of higher visibility of *C. scoparius* patches growing on slopes than on flat terrains. Patches growing in terrains with certain slopes might be more easily detected by pollinators at long distances.

Annual mean temperature did not seem to affect visitation rates. This might be partially explained by the fact that the main pollinator species observed visiting *C. scoparius* flowers was the bumblebee *Bombus terrestris* (personal observation). Bumblebees have lower temperature thresholds for flight activity due to their thermoregulation capacity (Heinrich 1975). However, a more plausible explanation is that this broad scale variable (i.e., 1 km resolution) might not capture variation in microclimatic conditions that affect bee foraging behaviour (Corbet et al. 1993). Conversely, we found that other factors in the model with a direct and positive influence on cover, had a negative indirect effect on visitation rate.

Patch cover negatively influenced visitation rate and a similar trend, though not significant, was observed for patch height (Fig. 3). Both factors explain floral offer and were expected to negatively influence visitation rate to *C. scoparius* patches through density dependent effects. Rathcke (1983) proposed a model of density-dependent visitation rate that predicts contrasting effects on per-flower pollinator visits at low (facilitation) and at high (competition) flower densities because the local pool of pollinators becomes saturated. In this study, we only found evidence of the competitive part of the model, which can have two non-mutually exclusive explanations. First, *C. scoparius* floral offer is always massive, even in small patches (see Fig. 2b), as one single individual can produce thousands of flowers (Parker

1997). Second, only a handful of pollinator species present in the study area are able to trip *C. scoparius* flowers (Cavallero et al. 2018; Vidal and Farji-Brener 2020). The saturation effect was previously observed in this study system (Cavallero et al. 2018) and could slow down the transitioning of *C. scoparius* along the invasion continuum by limiting its reproduction. Interestingly, the magnitude and significance of this (negative) saturation effect are higher than any of the factors explored with a positive effect on visitation rate (Table 2). Therefore, potential management decisions should also take into account the relative importance of significant factors.

Our results suggest that factors related to pollinator availability (like shrubland cover), and plant detectability (like slope) have a positive influence, while factors related to competition for pollinator visits (like patch cover) have a negative and stronger influence on the performance of this alien plant overcoming reproductive barriers. Finally, factors positively influencing the performance in overcoming survival barriers can have at the same time a negative indirect influence in overcoming reproductive barriers.

Concluding remarks

Exploring the performance of alien species along different stages of the invasion continuum can be much more informative than approaches which implicitly or explicitly assume that species are in equilibrium—i.e., that they have already successfully overcome all the barriers. Management decisions would benefit from such a dynamical approach, especially in the case of alien species with specialised reproductive or dispersal systems, and for alien species spreading along linear infrastructures.

In the case of *C. scoparius*, with negligible rates of seed mortality and high germination rates (close to 90%, Sheppard et al. 2002), control measures focused on post-fertilisation mortality seem unfeasible, while measures to reduce seed production could be more effective (Potter et al. 2009). In the case of entomophilous invasive species, like our study species, for which pollination interactions can favour certain invasion processes, effective eradication, control or prevention measures could be based on disrupting or avoiding such interactions (Montero-Castaño and Traveset 2020). In fact, there is evidence that seed production in *C. scoparius* is limited by pollinator

availability (Cavallero et al. 2018) and that population growth rate in this invasive plant is strongly influenced by seed production (Parker 1997). In the study area *C. scoparius* is mainly visited by another European invader, *B. terrestris* (Cavallero et al. 2018; Vidal and Farji-Brener 2020, and personal observations). In this case, a decrease in both the abundance of this bumblebee species after a volcano eruption in the area and in *C. scoparius* visitation rate was observed (Morales et al. 2014). Therefore, the control of the invasive bumblebee, for instance through implementation of removal programs (Nagamitsu and Yamagishi 2010), could also limit the invasion of *C. scoparius* in this region with the extra benefit of limiting the negative impacts of this bumblebee on the native flora and pollinator communities (Aizen et al. 2019; Gavini et al. 2022). Yet, habitat characteristics should be also taken into account as rapid restoration of roadsides and river banks with disturbance-thriving native species could hinder the propagation of this species along these corridors. Finally, banning the sale of this species in local nurseries as well as education campaigns could contribute to decreasing propagule arrival and further spread.

Acknowledgements We thank Agustín Sáez, Cristina Tur, Amaya Gallagher, Manuel de Paz, Malena Sabatini, Vanina R. Chalcoff and Cecilia for their help with fieldwork. María Jesús Serrano built the *Cytisus scoparius* cover map. We thank David Aragonés (LAST-EBD) and Juan Gowda (Ecotono Lab) for their valuable contribution and advice on GIS and remote sensing analyses.

Author contributions AMC, CLM and MAA conceived the study and designed the field sampling, with the collaboration of the rest of co-authors, who decisively contributed to theoretical and methodological aspects. Data collection in the field was conducted by AMC. Analyses were performed by AMC and PGM. All authors contributed to the writing and discussion of the results. All authors read and approved the final manuscript.

Funding Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature. This study was funded by the Spanish Ministry of Science and Innovation project REDESIN (CGL 2007-61165-BOS), by the EU 7FP project STEP (244090-STEP-CP-FP) and by the Argentinean National Scientific and Technical Research Council (CONICET) through the project “Ecological and evolutionary determinants of pollination efficiency at population, species and community levels in the flora of Nahuel Huapi National Park”. AMC was supported by a JAE-Predoc fellowship and by a Short Term Scientific Mission of the Alien Challenge COST Action (TD1209).

Data availability The datasets generated during and/or analysed during the current study are available in the GitHub repository, https://github.com/anamontcast/dataset_Montero-Castano_et_al_Biological_Invasions_2023/tree/main.

Declarations

Competing interests The authors have not disclosed any competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article’s Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Aizen MA, Morales CL, Morales JM (2008) Invasive mutualists erode native pollination webs. *PLOS Biol* 6:0396–0403. <https://doi.org/10.1371/journal.pbio.0060031>
- Aizen MA, Smith-Ramírez C, Morales CL et al (2019) Coordinated species importation policies are needed to reduce serious invasions globally: the case of alien bumblebees in South America. *J Appl Ecol* 56:100–106. <https://doi.org/10.1111/1365-2664.13121>
- Akasaka M, Osawa T, Ikegami M (2015) The role of roads and urban area in occurrence of an ornamental invasive weed: a case of *Rudbeckia laciniata* L. *Urban Ecosyst* 18:1021–1030. <https://doi.org/10.1007/s11252-015-0466-4>
- Asth MDS, Rodrigues RG, Zenni RD (2021) Canals as invasion pathways in tropical dry forest and the need for monitoring and management. *J Appl Ecol* 58:2004–2014. <https://doi.org/10.1111/1365-2664.13950>
- Blackburn TM, Pyšek P, Bacher S et al (2011) A proposed unified framework for biological invasions. *Trends Ecol Evol* 26:333–339. <https://doi.org/10.1016/j.tree.2011.03.023>
- Boedeltje G, Bakker JP, Bekker RM et al (2003) Plant dispersal in a lowland stream in relation to occurrence and three specific life-history traits of the species in the species pool. *J Ecol* 91:855–866. <https://doi.org/10.1046/j.1365-2745.2003.00820.x>
- Bossard CC (1993) Seed germination in the exotic shrub *Cytisus scoparius* (Scotch broom) in California. *Madroño* 40:47–61
- Bossard CC, Rejmanek M (1994) Herbivory, growth, seed production, and resprouting of an exotic invasive shrub *Cytisus scoparius*. *Biol Conserv* 67:193–200. [https://doi.org/10.1016/0006-3207\(94\)90609-2](https://doi.org/10.1016/0006-3207(94)90609-2)

- Bradshaw HDJ, Schemske DW (2003) Allele substitution at a flower colour locus produces a pollinator shift in monkey-flowers. *Nature* 426:176–178
- Catford JA, Jansson R (2014) Drowned, buried and carried away: effects of plant traits on the distribution of native and alien species in riparian ecosystems. *New Phytol* 204:19–36. <https://doi.org/10.1111/nph.12951>
- Cavallero L, Morales CL, Montero-Castaño A et al (2018) Scale-dependent effects of conspecific flower availability on pollination quantity and quality in an invasive shrub. *Oecologia* 188:501–513. <https://doi.org/10.1007/s00442-018-4239-7>
- Christen D, Matlack G (2006) The role of roadsides in plant invasions: a demographic approach. *Conserv Biol* 20:385–391. <https://doi.org/10.1111/j.1523-1739.2006.00315.x>
- Corbet SA, Fussell M, Ake R et al (1993) Temperature and the pollinating activity of social bees. *Ecol Entomol* 18:17–30. <https://doi.org/10.1111/j.1365-2311.1993.tb01075.x>
- Cordero RL, Torchelsen FP, Overbeck GE, Anand M (2016) *Cytisus scoparius* (Fam. Fabaceae) in southern Brazil—first step of an invasion process? *An Da Acad Bras Ciências* 88:149–154. <https://doi.org/10.1590/0001-3765201620140532>
- Dar PA, Reshi ZA, Shah MA (2015) Roads act as corridors for the spread of alien plant species in the mountainous regions: a case study of Kashmir Valley, India. *Trop Ecol* 56:183–190
- Décamps H, Planty-Tabacchi AM, Tabacchi E (1995) Changes in the hydrological regime and invasions by plant species along riparian systems of the Adour River, France. *Regul Rivers Res Manag* 11:23–33. <https://doi.org/10.1002/rrr.3450110104>
- Divíšek J, Chytrý M, Beckage B et al (2018) Similarity of introduced plant species to native ones facilitates naturalization, but differences enhance invasion success. *Nat Commun* 9:1–10. <https://doi.org/10.1038/s41467-018-06995-4>
- Downey PO, Brown JMB, Smith JMB (2000) Demography of the invasive shrub Scotch broom (*Cytisus scoparius*) at Barrington Tops, New South Wales: insights for management. *Austral Ecol* 25:477–485. <https://doi.org/10.1046/j.1442-9993.2000.01083.x>
- Ezcurra C, Brion C (2005) Plantas del Nahuel Huapi. Catálogo de la flora vascular del Parque Nacional Nahuel Huapi Argentina. Universidad Nacional del Comahue y Red Latinoamericana de Botánica, San Carlos de Bariloche
- Fick SE, Hijmans RJ (2017) Worldclim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int J Climatol* 37:4302–4315
- Funkenberg T, Roderus D, Buhk C (2012) Effects of climatic factors on *Fallopia japonica* s.l. seedling establishment: evidence from laboratory experiments. *Plant Species Biol* 27:218–225. <https://doi.org/10.1111/j.1442-1984.2011.00349.x>
- Gassó N, Sol D, Pino J et al (2009) Exploring species attributes and site characteristics to assess plant invasions in Spain. *Divers Distrib* 15:50–58. <https://doi.org/10.1111/j.1472-4642.2008.00501.x>
- Gavini SS, Farji-Brener A (2015) La importancia del color: Morfos florales, tasas de visita y éxito reproductivo en el arbusto *Sarothamnus scoparius*. *Ecol Austral* 25:204–211. <https://doi.org/10.25260/ea.15.25.3.0.82>
- Gavini SS, Moreno E, Zamorano-Menay F et al (2022) Bumblebee floral neighbors promote nectar robbing in a hummingbird-pollinated plant species in Patagonia. *Arthropod-Plant Interact* 16:183–190. <https://doi.org/10.1007/s11829-022-09895-z>
- González-Moreno P, Pino J, Gassó N, Vilà M (2013) Landscape context modulates alien plant invasion in Mediterranean forest edges. *Biol Invasions* 15:547–557. <https://doi.org/10.1007/s10530-012-0306-x>
- Heinrich B (1975) Thermoregulation in bumblebees—II. Energetics of warm-up and free flight. *J Comp Physiol* 96:155–166. <https://doi.org/10.1007/BF00706595>
- Ibáñez I, Silander JA, Allen JM et al (2009) Identifying hot-spots for plant invasions and forecasting focal points of further spread. *J Appl Ecol* 46:1219–1228. <https://doi.org/10.1111/j.1365-2664.2009.01736.x>
- Kevan PG, Baker HG (1983) Insects as flower visitors and pollinators. *Annu Rev Entomol* 28:407–453. <https://doi.org/10.1146/annurev.en.28.010183.002203>
- Lefcheck JS (2016) piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods Ecol Evol* 7:573–579. <https://doi.org/10.1111/2041-210X.12512>
- Montero-Castaño A, Traveset A (2020) Pollination interactions promoting plant invasions. In: Traveset A, Richardson DM (eds) *Plant invasions: the role of biotic interactions*. CABI, Wallingford, pp 67–89
- Morales CL, Aizen MA (2002) Does invasion of exotic plants promote invasion of exotic flower visitors? A case study from the temperate forests of the southern Andes. *Biol Invasions* 4:87–100
- Morales CL, Sáez JA, Arbetman MP et al (2014) Detrimental effects of volcanic ash deposition on bee fauna and plant-pollinator interactions. *Ecol Austral* 24:42–50
- Nagamitsu T, Yamagishi H (2010) Competitive effects of the exotic *Bombus terrestris* on native bumble bees revealed by a field removal experiment. *Popul Ecol* 52:123–136. <https://doi.org/10.1007/s10144-009-0151-7>
- Nuttman CV, Semida FM, Zalut S, Willmer PG (2006) Visual cues and foraging choices: bee visits to floral colour phases in *Alkanna orientalis* (Boraginaceae). *Biol J Linn Soc* 87:427–435. <https://doi.org/10.1111/j.1095-8312.2006.00582.x>
- Papiorek S, Junker RR, Alves-dos-Santos I et al (2016) Bees, birds and yellow flowers: pollinator-dependent convergent evolution of UV patterns. *Plant Biol* 18:46–55. <https://doi.org/10.1111/plb.12322>
- Parendes LA, Jones JA (2000) Role of light availability and dispersal in exotic plant invasion along roads and streams in the H. J. Andrews Experimental Forest. *Oregon Conserv Biol* 14:64–75
- Parker IM (1997) Pollinator limitation of *Cytisus scoparius* (Scotch Broom), an invasive exotic shrub. *Ecology* 78:1457–1470
- Parker IM (2000) Invasion dynamics of *Cytisus scoparius*: a matrix model approach. *Ecol Appl* 10:726–743. [https://doi.org/10.1890/1051-0761\(2000\)010\[0726:IDOCSA\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0726:IDOCSA]2.0.CO;2)
- Pauchard A, Alaback PB (2004) Influences of evaluation, land use and landscape context on patterns of alien plant invasions along roadsides in protected areas of

- south-central Chile. *Conserv Biol* 18:238–248. <https://doi.org/10.1111/j.1523-1739.2004.00300.x>
- Paynter Q, Main A, Gourlay AH et al (2010) Disruption of an exotic mutualism can improve management of an invasive plant: varroa mite, honeybees and biological control of Scotch broom *Cytisus scoparius* in New Zealand. *J Appl Ecol* 47(2):309–317. <https://doi.org/10.1111/j.1365-2664.2010.01784.x>
- Pino J, Font X, Carbó J et al (2005) Large-scale correlates of alien plant invasion in Catalonia (NE of Spain). *Biol Conserv* 122:339–350. <https://doi.org/10.1016/j.biocon.2004.08.006>
- Potter KJB, Kriticos DJ, Watt MS, Leriche A (2009) The current and future potential distribution of *Cytisus scoparius*: a weed of pastoral systems, natural ecosystems and plantation forestry. *Weed Res* 49:271–282. <https://doi.org/10.1111/j.1365-3180.2009.00697.x>
- Pyšek P, Prach K (1993) Plant invasions and the role of riparian habitats: a comparison of four species alien to central Europe. *J Biogeogr* 20:413–420
- Pyšek P, Richardson DM, Rejmánek M et al (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon* 53:131–143
- Richardson DM, Pyšek P (2006) Progress in physical geography plant invasions: merging the concepts of species invasiveness and community invasibility. *Prog Phys Geogr* 30:409–431. <https://doi.org/10.1191/0309133306pp490pr>
- Richardson DM, Pyšek P (2012) Naturalization of introduced plants: ecological drivers of biogeographical patterns. *New Phytol* 196:383–396. <https://doi.org/10.1111/j.1469-8137.2012.04292.x>
- Richardson DM, Ek PPYS, Rejmánek M et al (2000) Naturalization and invasion of alien plants: concepts and definitions. *Divers Distrib* 6:93–107
- Rovere AE, Molares S, Ladio AH (2013) Plantas utilizadas en cercos vivos de ciudades patagónicas: Aportes de la etnobotánica para la conservación. *Ecol Austral* 23:165–173
- Säumel I, Kowarik I (2010) Urban rivers as dispersal corridors for primarily wind-dispersed invasive tree species. *Landsc Urban Plan* 94:244–249. <https://doi.org/10.1016/j.landurbplan.2009.10.009>
- Sheppard AW, Hodge P, Paynter Q, Rees M (2002) Factors affecting invasion and persistence of broom *Cytisus scoparius* in Australia. *J Appl Ecol* 39:721–734
- Shipley B (2013) The AIC model selection method applied to path analytic models compared using a d-separation test. *Ecology* 94:560–564. <https://doi.org/10.1890/12-0976.1>
- Simpson SR, Gross CL, Silberbauer LX (2005) Broom and honeybees in Australia: an alien liaison. *Plant Biol* 7:541–548. <https://doi.org/10.1055/s-2005-865855>
- Steffan-Dewenter I, Tschamtk T (2002) Insect communities and biotic interactions on fragmented calcareous grasslands—a mini review. *Biol Conserv* 104:275–284
- Steffan-Dewenter I, Westphal C (2008) The interplay of pollinator diversity, pollination services and landscape change. *J Appl Ecol* 45:737–741. <https://doi.org/10.1111/j.1365-2664.2008.01483.x>
- Stokes KE, Buckley YM, Sheppard AW (2006) A modelling approach to estimate the effect of exotic pollinators on exotic weed population dynamics: bumblebees and broom in Australia. *Divers Distrib* 12:593–600. <https://doi.org/10.1111/j.1366-9516.2006.00239.x>
- Stout JC (2000) Does size matter? Bumblebee behaviour and the pollination of *Cytisus scoparius* L. (Fabaceae). *Apidologie* 31:129–139. <https://doi.org/10.1051/apido:2000111>
- Suzuki N (2003) Significance of flower exploding pollination on the reproduction of the Scotch broom, *Cytisus scoparius* (Leguminosae). *Ecol Res* 18:523–532
- Václavík T, Meentemeyer RK (2012) Equilibrium or not? Modelling potential distribution of invasive species in different stages of invasion. *Divers Distrib* 18:73–83. <https://doi.org/10.1111/j.1472-4642.2011.00854.x>
- van Kleunen M, Essl F, Pergl J et al (2018) The changing role of ornamental horticulture in alien plant invasions. *Biol Rev* 93:1421–1437. <https://doi.org/10.1111/brv.12402>
- Velthuis HW, Van DA (2006) A century of advances in bumblebee domestication and the economic and environmental aspects of its commercialization for pollination. *Apidologie* 37:421–451
- Vidal VB, Farji-Brener A (2020) Lo esencial es invisible a los ojos (humanos): patrones UV explican la mayor tasa de visita de los polinizadores a las flores amarillas del arbusto *Cytisus scoparius*. *Ecol Austral* 30:012–018. <https://doi.org/10.25260/ea.20.30.1.0.911>
- Vilà M, Espinar JL, Hejda M et al (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol Lett* 14:702–708. <https://doi.org/10.1111/j.1461-0248.2011.01628.x>
- Wearne LJ, Morgan JW (2004) Community-level changes in Australian subalpine vegetation following invasion by the non-native shrub *Cytisus scoparius*. *J Veg Sci* 15:595–604. <https://doi.org/10.1111/j.1654-1103.2004.tb02301.x>
- Woodward FI (1987) Climate and plant distribution. Cambridge University Press, Cambridge
- Wu P, Axmacher JC, Li X et al (2019) Contrasting effects of natural shrubland and plantation forests on bee assemblages at neighboring apple orchards in Beijing, China. *Biol Conserv* 237:456–462
- Boletín Oficial de la República Argentina (2021) Resolución 109/2021
- Gowda J, Kitzberger T, Mermoz M, Edwards P, Suárez M, Cavallero L, Blackhall M, Rapoport E, Ladio A (2014) Comunidades vegetales y ecosistemas terrestres. In: Informe final. Delegación Regional Patagonia Norte.
- Pinheiro J, Bates D, DebRoy S, et al (2021) nlme: Linear and nonlinear mixed effects models
- R Core Team (2020) R: A language and environment for statistical computing
- Rathcke B (1983) Competition and facilitation among plants for pollination. In: Real L (ed) *Pollination biology*, pp 305–329
- Shipley B (2000) Cause and correlation in biology. In: *A user's guide to path analysis, structural equations and causal inference*. Cambridge University Press, Cambridge