The role of the urban landscape on species with contrasting dispersal ability: insights from greening plans for Barcelona

Article

Accepted Version

Melero, Y. ORCID: https://orcid.org/0000-0002-4337-1448, Stefanescu, C., Palmer, S. C. F., Travis, J. M. J. and Pino, J. (2020) The role of the urban landscape on species with contrasting dispersal ability: insights from greening plans for Barcelona. Landscape and Urban Planning, 195. 103707. ISSN 0169-2046 doi: https://doi.org/10.1016/j.landurbplan.2019.103707 Available at https://centaur.reading.ac.uk/89756/

Published version at: http://dx.doi.org/10.1016/j.landurbplan.2019.103707
To link to this article DOI: http://dx.doi.org/10.1016/j.landurbplan.2019.103707

Publisher: Elsevier

The role of the urban landscape on species with contrasting dispersal ability: insights from greening plans for Barcelona

Highlights

Species colonisation of urban gardens depends on their dispersal and local landscape characteristics.

Successful colonisation mostly depends on the proximity to source populations.

Garden carrying capacity and local garden density have a secondary impact on colonisation.

Conserving natural areas in urban environments is key for urban biodiversity.

Urban planners should first increase garden carrying capacity and then garden cover.

The role of the urban landscape on species with contrasting dispersal ability: insights from greening plans for Barcelona

Yolanda MELERO[1,2*], Constantí STEFANESCU[1, 3], Stephen C.F. PALMER[4], Justin M.J. TRAVIS[4] and Joan PINO[1, 5]

[1]CREAF, Cerdanyola del Vallés 08193, Spain

[2]School of Biological Sciences, University of Reading, Harborne Building,Reading, Berkshire RG6 6AS, UK

[3]Natural History Museum of Granollers, Granollers, Barcelona, Spain

[4]Institute of Biological and Environmental Sciences, University of Aberdeen, Zoology Building, Tillydrone Avenue, Aberdeen, UK

[5]Universitat Autònoma Barcelona, Cerdanyola del Vallés 08193, Spain

[*]Correspondence author. E-mail: y.melero@creaf.uab.cat, Postal address: CREAF, Cerdanyola del Vallés 08193 Spain, Phone: +34 935814677

Constantí Stefanescu: canliro@gmail.com; Stephen C.F. Palmer: s.palmer@abdn.ac.uk; Justin M.J. Travis: justin.travis@abdn.ac.uk; Joan Pino: joan.pino@uab.cat

Declaration of Interest

There are no actual or potential conflicts of interest to declare for any author.

Acknowledgements

We thank BCNEcologia for providing information about the Barcelona City Hall Plan and the volunteers within the CBMS. YM was supported by a Beatriu de Pinos-B postdoctoral grant (2013 BP-B 00168, AGAUR) and by the Barcelona City Council. The CBMS is funded by the Departament de Territori i Sostenibilitat (Generalitat de Catalunya). The uBMS is funded by Fundación Biodiversitat (Ministerio para la Transición Ecológica). We thank the two revieers and the editor for their useful comments that improved the manuscript.

Abstract

With the expansion of urban areas, promoting urban biodiversity is now a priority. Many municipalities are implementing greening strategies to improve and increase green space within city boundaries. The effectiveness of these strategies, while rarely assessed, likely depends on the landscape and on relevant species intrinsic traits such as dispersal ability. Using a spatially explicit individual-based model, we evaluated the effect of the urban landscape on the projected distribution of three butterfly species with contrasting dispersal abilities, and assessed the effectiveness of the Barcelona greening strategy as a case study. Species distribution (in terms of patch occupancy) and effectiveness (in terms of population size and number of occupied gardens) were analysed using generalised linear models. The percentage of (semi)natural source area around each urban green space (garden hereafter) was the most important variable for the distribution of all three types of species, followed by the percentage of neighbouring gardens and by the garden carrying capacity, although the effect of neighbouring gardens was negative in the early phase of colonisation. The planned Barcelona greening strategy increased the number of gardens occupied by high and medium, but not by low dispersive species. Increasing the carrying capacity of the gardens improved colonisation for all three species types. While the best strategies can be context dependent, our results indicated that increasing garden area might be more effective in the long term but it can be overridden by garden capacity in the short term, especially if there are constraints to increasing garden area.

1. Introduction

Urbanisation is one of the main threats biodiversity is currently facing (McKinney, 2002; Shochat et al., 2010). Cities are expected to more than triple their area and house from currently ca. two billion people to ca. 6.5 billion people by 2050 (Mcdonnell & Macgregor-fors, 2016; Seto, Güneralp, & Hutyra, 2012). Paradoxically, as cities continue to expand, they might play an increasing role in the conservation of biodiversity if they become more suitable for a larger number of species and even the refuge of some of the most endangered

(Desrochers, Kerr, & Currie, 2011; Secretariat of the Convention on Biological Diversity, 2012). As such, cities are working towards better adapted management to design sustainable urban environments that favour biodiversity, in aligment with novel biodiversity strategies such as the "2050 vision" that the European Union adopted in May 2011, aiming to halt the loss of biodiversity and the degradation of ecosystem services in Europe in the coming years (http://biodiversity.europa.eu/policy) (European Comission, 2011; Ramalho & Hobbs, 2012; Sandström, 2008).

In most of cities, the deployment of green urban infrastructure is mainly focused on the improvement of the existing green spaces and on the creation of new ones (e.g. Paris, Rome, Barcelona in Europe, and of many cities worldwide; Barcelona City Council, 2013; Capotorti et al., 2017; Mairie de Paris, 2014). These greening strategies may increase the number of potential suitable habitat patches for different species and improve the structural connectivity of the landscape. Yet, there is still a lack of realistic evaluations of their actual effectiveness at favouring biodiversity.

Biodiversity in cities is strongly dependent on the urban landscape context (Lepczyk et al., 2017; Oliveira, Lion, & Cardoso, 2018; Prevedello & Vieira, 2010). In contrast to (semi-)natural areas, urban landscapes are typically dominated by a landscape matrix of unsuitable habitat and physical barriers (built-up and paved spaces), interspersed with suitable but isolated habitat patches frequently of small size and influenced by edge effects from the surrounding built matrix (Braaker, Ghazoul, Obrist, & Moretti, 2014; Lizée, Manel, Mauffrey, Tatoni, & Deschamps-Cottin, 2011; Verbeylen, De Bruyn, Adriaensen, & Matthysen, 2003; Zalucki, Parry, & Zalucki, 2016; Zeller, Mcgarigal, & Whiteley, 2012). In consequence, patch size, quality, and spatial distribution, but also matrix permeability, impact on the distribution and abundance of urban populations of many organisms (Beninde, Veith, & Hochkirch, 2015; Goddard, Dougill, & Benton, 2010; Lepczyk et al., 2017). In fact, recent empirical studies have evidenced a negative effect of the configuration (e.g. aggregation and shape) of the built matrix on species richness and abundance (Lizée et al., 2011; Watson, Whittaker, & Freudenberger, 2005; Weller & Ganzhorn, 2004). However, greening strategies of many urban cities aimed at promoting their biodiversity are still far from considering the role of the urban landscape composition and configuration on the species distributions and abundance (Boulton, Dedekorkut-Howes, & Byrne, 2018).

Moreover, it is largely known that the effectiveness of these strategies might depend on species' life-history traits. Particularly relevant seems the role of species dispersal, as indicated by recent empirical studies that show that species composition in urban landscapes is strongly biased towards a few highly dispersive species (Di Mauro, Dietz, & Rockwood, 2007; Olivier, Schmucki, Fontaine, Villemey, & Archaux, 2016; Villard & Metzger, 2014). However, to our knowledge, the role of dispersal under contrasting greening strategies has not been evaluated, probably because of limited availability of empirical data and methodological constraints.

To help managers to assess and prioritise alternative greening strategies we need more realistic models of species' distribution and abundance that account for the urban landscape composition and configuration as well as for the specific traits of the modelled species. Because empirical data are frequently limited, these models mostly consist of simulated projections based on predictions of the species' responses to management scenarios. Spatially explicit population models have become a proven useful tool to project realistic scenarios and to assess and prioritise alternative management strategies (Aben et al., 2016; Fordham et al., 2014; Pearson et al., 2014). Among these models, the stochastic movement simulator (SMS; see Appendix A1 for details) has the advantage in estimating functional connectivity of taking into account the matrix surrounding the patches by simulating individual dispersal trajectories based on the cost of movement across a landscape grid (Palmer, Coulon, & Travis, 2011). This gives more realistic predictions and assessments than least cost path analyses or landscape connectivity (Coulon et al., 2015; Kindlmann & Burel, 2008).

Butterflies are good study models (Brückmann, Krauss, & Steffan-Dewenter, 2010) because they exhibit different dispersal abilities and related functional traits (Eskildsen et al., 2015; Hanski, Saastomoinen, & Ovaskainen, 2006; Melero, Stefanescu, & Pino, 2016).

Therefore, modelling the responses of butterfly populations to urban management can contribute to general predictions applicable to a wide range of organisms (e.g. insects and other short-lived species). Moreover, empirical data on butterfly species are widely available in the literature.

In this study, we aimed to evaluate the effect of the urban landscape composition on the potential colonisation of urban green spaces (gardens hereafter) by three butterfly species having contrasting dispersal abilities. Specifically, we compared the effect and relative importance of the percentage of natural area and of the percentage of other gardens around each suitable patch (matrix-level), as well as the patch carrying capacity (i.e. the maximum number of individuals a patch can hold in relation of its size and habitat suitability; patch-level), on the patch occupancy probability by each butterfly species. We hypothesised that percentage of natural area was the main factor increasing the colonisation of urban gardens, followed by the carrying capacity and the percentage of other gardens in the surroundings. Because species with high dispersal ability are less limited by the availability of suitable habitat (Olivier, Schmucki, Fontaine, Villemey, & Archaux, 2016), we expected the positive effect of these factors to be higher for species with limited dispersal ability. To test these hypotheses, we projected simulated populations of the species over time in the current urban landscape of Barcelona, and analysed the species projected distributions in relation to the three mentioned variables.

We also projected simulated populations of the species on a set of alternative landscape scenarios corresponding to the greening strategies proposed by the City Council under the Green Infrastructure and Biodiversity Plan 2012-2020 (Barcelona City Council, 2013). Strategies consisted of the improvement and addition of gardens within the city (Fig. A1). The effectiveness of these strategies was evaluated as per their effect at increasing the total population size and of the number of occupied gardens by the model three butterfly species. As such we hypothesised that the addition of gardens would be more efficient for species with limited dispersal ability due to their dependency to close patches (Olivier, Schmucki, Fontaine, Villemey, & Archaux, 2016), while the improvement of habitat quality to especially favour highly dispersive species.

2. Methods

2.1. Study area

Our study was focused on the municipality of Barcelona city and its immediate conurbation (Fig 1). We included the southern portion of the Collserola Natural Park and the eastern natural part of the Llobregat River, providing the natural and initial source area for each modelled species (see modelling approach). The study area covered ~182 km^2, of which the natural area covered ~28%, the built matrix ~60%, and gardens ~12%. These gardens comprise public and private parks within the city, some of which include meadows, arable crops and forest. There were 25 large (>10 ha), 186 medium (>1 ha) and 1443 small gardens (> 0.4 ha, mostly private gardens).

2.2. Barcelona greening strategy

The Green Infrastructure and Biodiversity Plan of Barcelona City Council proposes two management scenarios aiming to increase the network of urban gardens so as to improve biodiversity in the city, in aligment with the European Biodiversity Strategy (http://biodiversity.europa.eu/policy; European Comission 2011). The first management scenario consists of the creation of ~150 small/medium gardens (mean size = 2ha) by the end of 2019, which adds 0.36 km^2 (0.3%) of green area to the present in the city. The second builds on the first scenario, with 8 additional large gardens (mean size = 10 ha) by 2030, representing an extra 0.6% of green area with a total increase of 0.9% compared to the present situation (1.2 km^2; Fig A1). Concurrently, it also intends to enhance the habitat quality of the existing and planned gardens by improving the vegetation composition, e.g. by the substitution of ornamental non-native vegetation by native vegetation suitable for a variety of butterfly species.

2.3. Model species

From the pool of butterfly species occurring within the metropolitan area of Barcelona and the ca. 40 species detected in gardens within the city (Catalan Butterfly Monitoring Scheme, CBMS, www.catalanbms.org/; urban Butterfly Monitoring Scheme, ubms.creaf.cat), we selected three species as models representing low, medium, and high dispersal abilities: respectively the silver-studded blue, *Plebejus argus*, the meadow brown, *Maniola jurtina*, and the large white, *Pieris brassicae* (Essens et al., 2017). They also characterised three functional clusters based on species traits (Carnicer et al., 2013; Eskildsen et al., 2015). *P. argus* represents sedentary, monovoltine grassland specialists of small size (forewing: 9-16 mm), overwintering in the egg stage. *M. jurtina* represents moderately mobile, monovoltine grassland specialists of medium size (23-27 mm), overwintering as larvae. *P. brassicae* represents highly mobile, multivoltine larger generalists (22-32.5 mm), overwintering in the pupal stage. The three species are representative of the overall community in the study area (Melero et al., 2016; CBMS, uBMS). Comprehensive data on their dispersal parameters were collected from the literature (Table A1). Estimated abundances, population trends of each species and their specific habitat preferences for the study area were extracted from Melero et al. (2016) and from the CBMS, and used to set model parameters (Table A2).

2.4. Landscape composition

The landscape composition was obtained from the official Catalan land cover map at 2m resolution (MCSC, http://www.creaf.uab.es/mcsc/usa/index.htm), which provides 50 land cover categories updated in 2015. The map was converted into a grid of 20m resolution. Habitat per cell was reclassified to six categories: gardens, scrub-grasslands, forest, arable crops, woody crops and built. Suitable patches (i.e. able to hold a breeding population of each species) were defined in both the natural area and in the municipality (Goddard et al., 2010) as patches of minimum size 0.4 ha and enclosing at least 75% of suitable habitat types (Thomas & Hanski, 1997). Despite no available information of plant composition in patches, we assumed that they contain basic nutritional plants for both larval and adult stages of the studied butterflies (e.g. very common Brassicaceae like *Diplotaxis erucoides* for *P. brassicae* and Fabaceae like *Lotus corniculatus* for *P. argus*, as well as a diversity of common grasses than can be used by *M. jurtina*). The natural area was divided into patches of 0.4 ha, whilst maintaining suitable habitat types at 20m resolution, in order that initial source populations would be of similar size to those in the gardens (see modelling approach). All gardens above 0.4 ha situated in the municipality were considered as potential suitable patches (N = 306; total area ~1050 ha). Among these gardens, fifteen included small parts of grassland, meadows, arable crops and paved and unpaved spaces, for which the habitat types were retained for the purpose of determining the overall garden carrying capacity (see modelling approach).

2.5. Modelling approach

Population projections were implemented within the spatially-explicit individual-based modelling platform RangeShifter (Bocedi et al., 2014). We used RangeShifter v1.1, which incorporates an additional memory size (MemSize) parameter for SMS (Aben et al., 2014, 2016).

Population dynamics of each species were based on female-only and non-overlapping generations, growing according to its intrinsic population growth rate and limited by the habitat-dependent carrying capacity of the suitable patches. Dispersal was modelled for each individual as a three-stage process: emigration, transfer, and settlement. Transfer was modelled using the stochastic movement simulator (SMS; Palmer et al. 2011), which simulates discrete individual stepwise nearest-neighbour movements. Within the SMS, at each given step, the probability of an individual to move to a neighbouring cell depends on: the individuals' perceptual range and its degree of directional persistence; the probability of mortality per step based on the species' dispersal ability; and the relative movement cost values of the cells set inversely related to the species-specific habitat preferences (see full modelling details in Appendix A1-A3), i.e. the greater the cost of a neighbouring cell, the lower the probability of moving to it. Models started with initial populations restricted to the patches in the natural area, from which they grew and dispersed into and through the city, occupying new suitable patches over time, i.e. the gardens, which could also act as source of dispersers once a population of a species established. Restricting the initial population in this way was due to the unavailability of species information within the city, yet this restriction did not compromise our analyses, which are based on relative comparisons rather than on absolute predictions. Initial populations were set at their carrying capacity ($N_{P.\ argus}$ ~ 100k, $N_{M.\ jurtina}$ ~ 120k and $N_{P.\ brassicae}$ ~ 100k individuals). Each model was run for 20 years (based on butterflies population stabilisation time frames; Pollard, Rothery, & Yates, 1996) and 100 replicates. We also performed a sensitivity analysis for four parameters likely to be crucial for the simulation outputs: maximum emigration rate (D_0), directional persistence (DP), maximum mean fecundity (R_{max}) and step mortality (*sm*; see parameters details in Appendix A1-A3 and sensitivity analyses in Appendix A4).

The population projection of each species was performed firstly under the current landscape scenario of Barcelona city (scenario M0) to assess the effect of the urban landscape on their occupancies, and then to the greening scenarios proposed for 2019 (M1) and 2030 (M2) to assess the effectiveness of the Greening and Biodiversity Plan on the species occupancies and abundances. The effectiveness of increasing habitat quality was also evaluated by combining M0, M1 and M2 with landscapes scenarios enhancing by 1.5, two and three times the habitat quality of the gardens, simulated in the models as an increase of the garden species-specific carrying capacity (K_i) for each species independently (K_{baseline}, $K_{\mathrm{x}1.5}$, $K_{\mathrm{x}2}$ and K_{x3}; $N_{\mathrm{scenarios\ total}} = 12$ per species).

2.6. Statistical Analyses

Occupancy was described as the probability of each garden to be occupied by each species in a particular year (see time periods below). A garden was considered to be occupied if the mean occupancy probability over 100 replicates was >0.5. The percentage of occupied gardens and the predicted species distribution in the area were also derived from occupancy data.

To test the effect of the urban landscape on garden occupancy by each species over time and spatial scale, we fitted the predicted occupancies to the percentage of natural area, the percentage of area covered by gardens and the carrying capacity of the garden. The percentage of natural and of garden area were calculated within four buffer zones (100, 500, 1000 and 2000 m radius) around the garden. Buffer distances were chosen to cover potential butterfly dispersal ranges within the city (Baguette, & Schtickzelle, 2006; Kuussaari et al., 2014; Stevens, Turlure, & Baguette, 2009). A set of linear models combining one scale (i.e. buffer radius) with each of these landscape variables was fitted per species at each of four time periods (5, 10, 15 and 20 years). Separate analyses were performed to analyse occupancy for each species and year using generalised linear models (GLM) having a binomial error distribution for occupancy probability. The optimum scales per species and year were then identified using model selection based on lowest AIC. The relative importance of the variables was assessed in terms of variance explained; i.e. the proportion of the total variance explained by each variable in the model.

The performance of each greening scenario was evaluated by comparing the resulting projected abundance (i.e. the total number of individuals occupying the gardens) and the number of occupied gardens in the city by each butterfly species at year 20. The number of occupied gardens was calculated as the sum of all gardens with presence of the respective species. Comparisons were performed for the scenarios (M1 and M2) and per improved carrying capacity, all compared to the baseline scenario (M0). We used generalised linear models for both population size and number of gardens for each species separately, with Poisson error distributions. The best model was chosen based on the lowest AIC.

Analyses were performed in R 3.3.3 using package lme4 (Bates, Maechler, Bolker, & Walker, 2014).

3. Results

3.1. The effect of urban landscape on garden occupancy

As expected, the percentage of natural area around each garden was the most important variable for the occupancy of the gardens for all three species, achieving full occupancy in gardens surrounded by at least 70% of natural area. The effect of the percentage of natural area was especially important for the less dispersive species *P. argus* (35-37% relative importance in terms of variance explained), whose probability of occupancy increased ca. 1.5 times per unit increase of percentage of natural area for all analysed years, followed by *M. jurtina* especially at the start of the projections (33% relative importance at year five, decreasing to 11% at year 20) and with occupancies increasing from 1.15 to 1.07 per unit increase of percentage of natural area. The effect was lowest for *P. brassicae* (15% or lower relative importance) since it rapidly colonised the entire city (Table 1; Fig 2). The effect was consistently most apparent at the 2 km radius scale for all species, except for *P. brassicae* from year 15, when the 500 m radius was the optimum (Table 1 and Table 2).

The percentage of garden area was the next most important variable, but its effect was substantially lower than that of the natural areas, and decreased in importance over time for all three species (Table 1; Fig 2). The effect shifted from negative, i.e. reducing probability of occupancy, at the start of the projections to positive for *P. brassicae* and *P. argus* from year 15 or 20, but not for *M. jurtina*. The spatial range of its effect was small for *P. argus* (1 km to 100 m), while constant at 2 km for the other two species (Table 1, Table 2; Fig 2).

The carrying capacity (*K*) of the garden area was the variable with the lowest relative importance (0.7-0.04; Table 1) and effect (i.e. the estimated slope, the increase of occupancy probability per unit increase of *K*) for all species. However, it was also the variable with the widest range of values (0-1800), such that large *K* could lead to overall high occupancy probabilities (Fig 2). The effect *K* slightly decreased over time for *M. jurtina* and *P. brassicae*; which over time managed to achieve full occupancy of gardens at carrying capacity, unlike the low dispersive *P. argus* (Table 1; Fig 2).

3.2. Assessment of Barcelona greening strategy

The scenario consisting of increased garden area in the city, M1, increased the total population size in the gardens for the highly dispersive *P. brassicae* by the end of the simulations compared to the current landscape (M0), while M2 slightly increased the total population size of the three species (*P. argus* $N_{M0,\ K\mathrm{baseline}} \sim 1900$, $N_{M1,\ K\mathrm{baseline}} \sim 2000$, $N_{M2,\ K\mathrm{baseline}} \sim 2400$ individuals; *M. jurtina* $N_{M0,\ K\mathrm{baseline}} \sim 4200$, $N_{M1,\ K\mathrm{baseline}} \sim 4300$, $N_{M2,\ K\mathrm{baseline}} \sim 5100$; *P. brassicae* $N_{M0,\ K\mathrm{baseline}} \sim 12000$, $N_{M1\ \&\ M2\ K\mathrm{baseline}} \sim 14000$; Table 3a; Fig 3a-c). The increase was constant for all combinations of carrying capacities (interaction term dismissed in model selection, Table 4). Notwithstanding, carrying capacity had the stronger effect on the population size with relative importance > 76% for all species, and increases of ca. twice ($K_{x1.5}$) to 3.5 times (K_{x3}) in all scenarios (Table 3a; Fig 3a-c).

The positive effect of these scenarios was more noticeable on the number of occupied gardens, but differed between the species (Fig 3d-e). The most dispersive species, *P. brassicae*, occupied on average ~1.3 times more gardens in the scenarios M1 and M2 than in M0 (*P. brassicae*$_{M0} \sim 288$ gardens; $_{M1\ \&\ M2} \sim 365$). Projections for *M. jurtina* predicted similar values for M1 and M0 but 1.2 times more occupied gardens in M2 (*M. jurtina*$_{M0\ \&\ M1} \sim 185$; $_{M2} \sim 210$), while *P. argus* did not show any significant increase of the number of occupied gardens and its distribution was almost limited by the proximity to the natural areas (*P. argus*$_{M0,\ M1\ \&\ M2} \sim 50$) (Fig 3d-f, Fig A2-A4 and Table 3b). Differences were also evident in relation to the carrying capacities (interaction terms dismissed, Table 4). In fact, carrying capacity had a larger effect than the landscapes scenarios for *P. argus* with 1.3 and 1.5 more occupied gardens when K increased to K_{x2} and K_{x3} respectively. The effect of the carrying capacity was lower for *M. jurtina* and similar to that of the scenarios M1 and M2, with 1.4 more gardens when doubling or tripling to $K$for *M. jurtina*; while the effect was minimal for *P. brassicae,* which managed to colonise all gardens independently of K (Fig 3d-f, Table 3b).

4. Discussion

By simulating realistic population projections of three butterfly species in the city of Barcelona, we provided indications of the effect of the urban landscape on the presence of species with contrasting dispersal ability in the urban environment. Both matrix- and patch-level landscape characteristics impacted on the occupancy (i.e. the presence) of the species in the city. While their effect varied over time, space and species, the percentage of natural area around each garden (i.e. a proxy for their connectivity to natural areas) was consistently the most important landscape characteristic for all three species, especially for low dispersive species as hypothesised. The next most important variable was another matrix-level characteristic (i.e. the percentage of garden area), and by the carrying capacity of the garden (patch-level). The importance of these factors in the landscape highlights the influence of the urban landscape composition on the dynamics of populations and, therefore, on the effectiveness of the potential greening strategies. Contrary to our expectations, Barcelona management strategies were more effective when improving the habitat than when increasing green spaces especially for low dispersive species due to the low increase of green spaces. However, the effect of garden spaces was higher in the modelled simulations, indicating that increasing total garden area in the cities may be more efficient at improving biodiversity if done at sufficient (yet still unknown) levels.

The stronger effect and the higher relative importance of the percentage of natural area provide further evidence of the importance of semi- and natural areas external to the city acting as source areas for determining species occupancy in urban environments, especially at the start of the colonisation, as also reported in other studies for species richness of butterflies (e.g. Öckinger, Dannestam, & Smith, 2009; Lizée et al., 2011; Öckinger et al., 2012; Snep et al., 2006) and other organisms (e.g. birds; Melles, Glenn & Martin 2003; Croci *et al.* 2008). The importance of the natural area could be due to a rescue effect of natural areas that feed and maintain the local garden populations, especially at the start of the colonisation when few gardens act as source patches (Eriksson, Elías-Wolff, Mehlig, & Manica, 2014). Within this role of population source, maintaining (semi)natural areas around (and within) the city can therefore be crucial to achieve and maintain the urban biodiversity.

The impact of the percentage of natural area was twice-to-thirteen times higher in low dispersive species than in high dispersive species (from year 5 to 20); and half-to-six times higher in medium than high dispersive species (yet not correlated over time). This indicates the importance of dispersal ability as a key species trait in urbanised environments owing to its interaction with the urban matrix, and accounts for the contrasting patterns of wide distributions in the city of high dispersive species and restricted distributions in gardens close to the natural source areas of low dispersive species (Fig A2). The effect of the percentage of natural area also explains the observed bias of urban butterfly communities dominated by highly dispersive species in several studied cities (e.g. Lizée et al., 2011; Öckinger, Dannestam, & Smith, 2009). Thus, enhancing biodiversity in the city entails accounting for the matrix configuration and composition to increase the occurrence of those species most affected by the urban matrix, i.e. those with limited dispersal ability.

The percentage of garden area around each garden was the second most important landscape characteristic for determining species presence in the city. However, it had a negative effect on the species occupancy at the start of the projections, especially for low and medium dispersive species. Highly dispersive butterfly species could rapidly colonise and saturate (i.e. achieving the maximum population size) all gardens, since they are frequently associated with high growth rate, so that colonised gardens may rapidly become a new source of dispersers. Since fewer individuals manage to occupy the available gardens as dispersive ability of the species declines, fewer gardens achieve sufficient density to become potential source of dispersers of species with restricted dispersal ability. In these cases, close proximity to other gardens may not benefit occupancy since they do not provide dispersers; rather, the number of unsaturated gardens may reduce the probability of colonisation at the local level (i.e. individuals will be faced with a series of settlement choices (the gardens) potentially settling in different gardens and failing to establish new breeding populations through stochastic demographic effects). Reduced colonisation could delay the colonisation process of gardens by butterflies, especially by low dispersive species, due to potential colonisation credits (*sensu* Jackson & Sax, 2010). Yet, these processes are still not described for urban environments. Moreover, the negative effect of the gardens might also be due to the fact that these patches would act not as stepping-stones but as ecological traps or attractive sinks (i.e. a habitat patch with negative population growth) that is preferred rather than avoided (*sensu* Delibes et al. 2001), attracting individuals to settle in relatively low-quality habitats surrounded by an intensely urbanized matrix. The problem of urban suitable patches acting as ecological traps has been proposed as a fundamental question for biodiversity conservation and urban ecology (Lepczyk et al., 2017), yet demographic data are currently not available to support it. However, in our study system, and even for species with restricted dispersal, more gardens were colonised as the populations expanded resulting in more gardens becoming a source. Thus, the effect of the percentage of gardens in the matrix became positive over time; the exception for *M. jurtina* was likely due to the larger spatial scale compared to that of *P. argus* and its lower growth rate compared to the other species, such that the populations did not have time to grow, attain carrying capacity and produce dispersers, so as to switch from a negative to a positive effect of the garden percentage. These results are consistent with the fragmentation threshold hypothesis (Brudvig et al., 2016; Pardini, de Bueno, Gardner, Prado, & Metzger, 2010), according to which the strength of the positive effects of the patches depends on the population dynamics but also on the size and isolation of remaining patches.

The effect and relative importance of garden carrying capacity, a patch-level characteristic, was overridden by those factors related to the urban matrix. The relative importance of patch-level factors such as the carrying capacity over matrix-level factors is still under discussion, with some studies pointing to a higher relevance of patch-level effects (see Beninde et al., 2015). Yet, most studies consider species richness and abundances while overlooking key functional traits such as dispersal ability. The few empirical studies available accounting for this trait in the city also suggest a higher relevance of matrix-level characteristics (e.g. Lizée et al., 2011; Öckinger, Dannestam, & Smith, 2009; Snep et al., 2006). However, at high levels of carrying capacity (range 500-2500indv/ha) the effect of the carrying capacity could also be remarkable. Indeed, its positive effect increased over time - approximately four and twelve times in medium and high dispersive species (in parallel to the colonisation of the gardens) - while its effect was relatively constant for low dispersive due to its relative low success at garden colonisation.

The assessment of the Barcelona greening strategy exemplified the importance of the landscape effect on the effectiveness of management strategies, especially for improving the presence and abundance of low and medium dispersive species. Scenario M2 increased the species abundances of all three dispersal types by 1.2 times the baseline scenario M0 at the end of the simulations. Yet in terms of occupied gardens and the species distribution in the city, the effect of the scenarios (both M1 and M2) was only visible for the high (x1.3 times more occupied gardens) and medium (x1.2 times more occupied gardens) dispersive species. This result means that the increase of garden area with the expansion and addition of green spaces in the planned greening scenarios (resulting in 23.2% of total garden area in the city in M2) is not enough to benefit the presence within a time frame of two decades of those species currently lacking in the city, while it potentially could increase that of the already present species (i.e. high dispersive species). While the minimum green cover area in cities has not been identified, studies in natural environments suggest a threshold of 20–30% of suitable habitat to maintain sustainable populations (Hedblom & Söderström, 2010). This figure might easily be higher in urban environments, especially for low dispersive species (e.g. Drinnan, 2005), as suggested by our results. Strikingly however, increasing garden areas in dense cities such as Barcelona is a challenge due to the limitation of free built areas (Boulton et al., 2018).

Our results on occupancy probability indicated that carrying capacity was the variable with the lowest relative importance on the species occupancy, yet its effect was always positive. In concordance, the assessment of the greening strategies showed that its improvement (by either expanding garden size and/or habitat quality) was more effective than the addition of green spaces for all scenarios. This was also probably affected by the low increase of garden percentage in the strategies; in fact our occupancy predictions relate ~ 23% of total garden area in the city to predicted probabilities of occupancy ~0.2 and 0.6 for low and medium dispersive species. In fact, it was the only factor increasing the number of occupied gardens by low dispersive species; yet, the species distribution was still mostly focused on gardens connected to natural areas.

Increasing the percentage of natural areas could have higher and faster effectiveness than increasing the garden area and the carrying capacity. Indeed, its predicted effect as a matrix-level variable on the probability of occupancy was constantly positive and higher than the other variables for all three species. Therefore, while this is difficult to achieve, the conservation of natural areas should be a priority in urban planning, especially in cities under development.

5. Conclusions

Our study highlights the importance of accounting for the surrounding urban matrix in terms of coverage of natural areas and, less significantly, of garden areas for the presence of butterfly species, especially those with limited dispersal ability. These findings have implications for urban planning focused in enhancing biodiversity in cities. While the best strategies can be context dependent, our results indicated that natural areas are highly important as a source for urban biodiversity. We thus advocate conserving them and, if possible, increasing their coverage and the connectivity of the gardens to them. Yet, the possibility of increasing their coverage might be limited to cities that are still under development. Likewise, increasing garden area can also be effective; however, the minimum required area for being effective could be hard to achieve in dense built cities owing to spatial limitations preventing a minimum level of garden coverage to be achieved for the species of interest (low and medium dispersive). Besides, seeing a positive effect of the increase of garden coverage on these species also requires longer time than increasing natural areas cover and the garden carrying capacity. Therefore, to increase biodiversity in dense cities such as Barcelona, we recommend to conserve the (semi)natural areas and, in terms of urban planning, to focus first on increasing garden carrying capacity. This increase can be done by better adapting the composition of the garden vegetation to the requirements of the species of interest. Secondly, we propose to increase the coverage of garden areas in the city, as the carrying capacities of the existing gardens improved. This study also demonstrated the utility of landscape-scale models coupled with dynamic metapopulation models to assess the relative importance of the landscape on populations and the effectiveness of management strategies.

References

Aben, J., Bocedi, G., Palmer, S. C. F., Pellikka, P., Strubbe, D., Hallmann, C., … Matthysen, E. (2016). The importance of realistic dispersal models in planning for conservation: application of a novel modelling platform to evaluate management scenarios in an Afrotropical biodiversity hotspot. *Journal of Applied Ecology*, *53*, 1055–1065. https://doi.org/10.1111/1365-2664.12643

Aben, J., Strubbe, D., Adriaensen, F., Palmer, S. C. F., Travis, J. M. J., Lens, L., & Matthysen, E. (2014). Simple individual-based models effectively represent Afrotropical forest bird movement in complex landscapes. *Journal of Applied Ecology*, *51*(3), 693–702. https://doi.org/10.1111/1365-2664.12224

Baguette, M. & Schtickzelle, N. (2008). Negative relationship between dispersal distance and demography in butterfly metapopulations. *Ecology, 87*: 648-654. https://doi.org/10.1890/04-1631

Barcelona City Council. (2013). *Green and Biodiversity Plan Barcelona 2020*.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4 version 1.1-7. Retrieved from http://cran.r-project.org/package=lme4.

Beninde, J., Veith, M., & Hochkirch, A. (2015). Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. *Ecology Letters*, *18*(6), 581–592. https://doi.org/10.1111/ele.12427

Bocedi, G., Palmer, S. C. F., Pe'er, G., Heikkinen, R. K., Matsinos, Y. G., Watts, K., & Travis, J. M. J. (2014). RangeShifter: a platform for modelling spatial eco-evolutionary dynamics and species' responses to environmental changes. *Methods in Ecology and*

Evolution, *5*(4), 388–396. https://doi.org/10.1111/2041-210X.12162

Boulton, C., Dedekorkut-Howes, A., & Byrne, J. (2018). Factors shaping urban greenspace provision: A systematic review of the literature. *Landscape and Urban Planning*, *178*, 82–101. https://doi.org/10.1016/J.LANDURBPLAN.2018.05.029

Braaker, S., Ghazoul, J., Obrist, M. K., & Moretti, M. (2014). Habitat connectivity shapes urban arthropod communities: the key role of green roofs. *Ecology*, *95*(4), 1010–1021. https://doi.org/10.1890/13-0705.1

Brückmann, S. V., Krauss, J., & Steffan-Dewenter, I. (2010). Butterfly and plant specialists suffer from reduced connectivity in fragmented landscapes. *Journal of Applied Ecology*, *47*(4), 799–809. https://doi.org/10.1111/j.1365-2664.2010.01828.x

Brudvig, L. A., Leroux, S. J., Albert, C. H., Bruna, E. M., Davies, K. F., Ewers, R. M., … Resasco, J. (2016). Evaluating conceptual models of landscape change. *Ecography*, *40*, 74–84. https://doi.org/10.1111/ecog.02543

Capotorti, G., Alós Ortí, M. M., Copiz, R., Fusaro, L., Mollo, B., Salvatori, E., & Zavattero, L. (2017). Biodiversity and ecosystem services in urban green infrastructure planning: A case study from the metropolitan area of Rome (Italy). *Urban Forestry & Urban Greening*. https://doi.org/10.1016/J.UFUG.2017.12.014

Carnicer, J., Stefanescu, C., Vila, R., Dinca, V., Font, X., & Josep Peñuelas. (2013). A unified framework for diversity gradients: the adaptive trait continuum. *Global Ecology and Biogeography*, *22*, 6–18. https://doi.org/DOI: 10.1111/j.1466-8238.2012.00762.x

Coulon, A., Aben, J., Palmer, S. C. F., Stevens, V. M., Callens, T., Strubbe, D., … Travis, J. M. J. (2015). A stochastic movement simulator improves estimates of landscape connectivity. *Ecology*, *96*(8), 2203–2213. https://doi.org/10.1890/14-1690.1

Croci, S., Butet, A., Georges, A., Aguejdad, R., & Clergeau, P. (2008). Small urban woodlands as biodiversity conservation hot-spot: a multi-taxon approach. *Landscape Ecology*, *23*(10), 1171–1186. https://doi.org/10.1007/s10980-008-9257-0

Desrochers, R. E., Kerr, J. T., & Currie, D. J. (2011). How, and how much, natural cover loss increases species richness. *Global Ecology and Biogeography*, *20*(6), 857–867.

https://doi.org/10.1111/j.1466-8238.2011.00658.x

Di Mauro, D., Dietz, T., & Rockwood, L. (2007). Determining the effect of urbanization on generalist butterfly species diversity in butterfly gardens. *Urban Ecosystems*, *10*(4), 427–439. https://doi.org/10.1007/s11252-007-0039-2

Drinnan, I. N. (2005). The search for fragmentation thresholds in a Southern Sydney Suburb. *Biological Conservation*, *124*(3), 339–349. https://doi.org/10.1016/J.BIOCON.2005.01.040

Eriksson, A., Elías-Wolff, F., Mehlig, B., & Manica, A. (2014). The emergence of the rescue effect from explicit within- and between-patch dynamics in a metapopulation. *Proceedings. Biological Sciences*, *281*(1780), 20133127. https://doi.org/10.1098/rspb.2013.3127

Eskildsen, A., Carvalheiro, L. G., Kissling, W. D., Biesmeijer, J. C., Schweiger, O., & Høye, T. T. (2015). Ecological specialization matters: long-term trends in butterfly species richness and assemblage composition depend on multiple functional traits. *Diversity and Distributions*, *21*(7), 792–802. https://doi.org/10.1111/ddi.12340

Essens, T., Langevelde, F., Vos, R.A., Swaay, C.A.M. & WallisDeVries, M.F. (2017). Ecological determinants of butterfly vulnerability across the European continent. *Journal of Insect Conservation, 21*(3), 439-450. https:// 10.1007/s10841-017-9972-4

European Comission. (2011). EU Biodiversity Strategy to 2020 – towards implementation. Retrieved from http://ec.europa.eu/environment/nature/biodiversity/comm2006/2020.htm

Fordham, D. A., Shoemaker, K. T., Schumaker, N. H., Akçakaya, H. R., Clisby, N., & Brook, B. W. (2014). How interactions between animal movement and landscape processes modify local range dynamics and extinction risk. *Biology Letters*. https://doi.org/10.1098/rsbl.2014.0198

Goddard, M. A., Dougill, A. J., & Benton, T. G. (2010). Scaling up from gardens: biodiversity conservation in urban environments. *Trends in Ecology & Evolution*, *25*(2), 90–98. https://doi.org/10.1016/j.tree.2009.07.016

Grömping, U. (2006). Relative Importance for Linear Regression in R : The Package relaimpo. *Journal of Statistical Software*, *17*(1), 1–27. https://doi.org/10.18637/jss.v017.i01

Hanski, I., Saastomoinen, M., & Ovaskainen, O. (2006). Dispersal-related life-history trade-offs in a butterfly metapopulation. *Journal of Animal Ecology*, *75*(1), 91–100. https://doi.org/10.1111/j.1365-2656.2005.01024.x

Hedblom, M., & Söderström, B. (2010). Landscape effects on birds in urban woodlands: an analysis of 34 Swedish cities. *Journal of Biogeography*, *37*(7), 1302–1316. https://doi.org/10.1111/j.1365-2699.2010.02299.x

Jackson, S. T., & Sax, D. F. (2010, March 1). Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends in Ecology and Evolution*. Elsevier Current Trends. https://doi.org/10.1016/j.tree.2009.10.001

Kindlmann, P., & Burel, F. (2008). Connectivity measures: a review. *Landscape Ecology*, *23*(8), 879–890. https://doi.org/10.1007/s10980-008-9245-4

Kuussaari, M., Saarinen, M., Korpela, E., Pöyry, J. & Hyvönen, T. (2014). Higher mobility of butterflies than moths connected to habitat suitability and body size in a release experiment. *Ecology and Evolution, 4*(19), 3800-3811. https:// doi.wiley.com/10.1002/ece3.1187

Lepczyk, C. A., Aronson, M. F. J., Evans, K. L., Goddard, M. A., Lerman, S. B., & Macivor, J. S. (2017, September 1). Biodiversity in the City: Fundamental Questions for Understanding the Ecology of Urban Green Spaces for Biodiversity Conservation. *BioScience*. Oxford University Press. https://doi.org/10.1093/biosci/bix079

Lizée, M.-H., Manel, S., Mauffrey, J.-F., Tatoni, T., & Deschamps-Cottin, M. (2011). Matrix configuration and patch isolation influences override the species–area relationship for urban butterfly communities. *Landscape Ecology*, *27*(2), 159–169. https://doi.org/10.1007/s10980-011-9651-x

Mairie de Paris. (2014). *The Paris greening programme*. Paris.

Mcdonnell, M. J., & Macgregor-fors, I. (2016). The ecological future of cities. *Science (New*

York, N.Y.), *352*(6288), 936–938. https://doi.org/10.1126/science.aaf3630

McKinney, M. L. (2002). Urbanization, Biodiversity, and Conservation. *BioScience*, *52*(10), 883. https://doi.org/10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2

Melero, Y., Stefanescu, C., & Pino, J. (2016). General declines in Mediterranean butterflies over the last two decades are modulated by species traits. *Biological Conservation*, *201*. https://doi.org/10.1016/j.biocon.2016.07.029

Melles, S., Glenn, S., & Martin, K. (2003). Urban Bird Diversity and Landscape Complexity: Species–environment Associations Along a Multiscale Habitat Gradient. *Conservation Ecology*, *7*, 5.

Öckinger, E., Bergman, K.-O., Franzén, M., Kadlec, T., Krauss, J., Kuussaari, M., … Bommarco, R. (2012). The landscape matrix modifies the effect of habitat fragmentation in grassland butterflies. *Landscape Ecology*, *27*(1), 121–131. https://doi.org/10.1007/s10980-011-9686-z

Öckinger, E., Dannestam, Å., & Smith, H. G. (2009). The importance of fragmentation and habitat quality of urban grasslands for butterfly diversity. *Landscape and Urban Planning*, *93*(1), 31–37. https://doi.org/10.1016/j.landurbplan.2009.05.021

Oliveira, I. F., Lion, M. B., & Cardoso, M. Z. (2018). A plaza too far: High contrast in butterfly biodiversity patterns between plazas and an urban reserve in Brazil. *Landscape and Urban Planning*, *180*, 207–216. https://doi.org/10.1016/J.LANDURBPLAN.2018.09.002

Olivier, T., Schmucki, R., Fontaine, B., Villemey, A., & Archaux, F. (2016). Butterfly assemblages in residential gardens are driven by species' habitat preference and mobility. *Landscape Ecology*, *31*(4), 865–876. https://doi.org/10.1007/s10980-015-0299-9

Palmer, S. C. F., Coulon, A., & Travis, J. M. J. (2011). Introducing a "stochastic movement simulator" for estimating habitat connectivity. *Methods in Ecology and Evolution*, *2*(3), 258–268. https://doi.org/10.1111/j.2041-210X.2010.00073.x

Pardini, R., de Bueno, A. A., Gardner, T. A., Prado, P. I., & Metzger, J. P. (2010). Beyond the fragmentation threshold hypothesis: Regime shifts in biodiversity across fragmented landscapes. *PLoS ONE*, *5*(10), e13666. https://doi.org/10.1371/journal.pone.0013666

Pearson, R. G., Stanton, J. C., Shoemaker, K. T., Aiello-lammens, M. E., Ersts, P. J., Horning, N., … Akçakaya, H. R. (2014). Life history and spatial traits predict extinction risk due to climate change. *Nature Climate Change Change*, *4*(February), 217–221. https://doi.org/10.1038/NCLIMATE2113

Pollard, E., Rothery, P., & Yates, T. J. (1996). Annual growth rates in newly established populations of the butterfly Pararge aegeria. *Ecological Entomology*, *21*(4), 947–952. https://doi.org/10.1046/j.1365-2311.1996.00003.x

Prevedello, J. A., & Vieira, M. V. (2010). Does the type of matrix matter? A quantitative review of the evidence. *Biodiversity and Conservation*, *19*(5), 1205–1223. https://doi.org/10.1007/s10531-009-9750-z

Ramalho, C. E., & Hobbs, R. J. (2012). Time for a change: dynamic urban ecology. *Trends in Ecology & Evolution*, *27*(3), 179–188. https://doi.org/10.1016/j.tree.2011.10.008

Sandström, U. (2008). *Biodiversity and Green Infrastructure in Urban Landscapes*. Orebro University.

Secretariat of the Convention on Biological Diversity. (2012). *Cities and biodiversity outlook. A global assessment of the links between action and policy: Urbanization, biodiversity, and ecosystem services*. Montreal.

Seto, K. C., Güneralp, B., & Hutyra, L. R. (2012). Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(40), 16083–16088. https://doi.org/10.1073/pnas.1211658109

Shochat, E., Lerman, S. B., Anderies, J. M., Warren, P. S., Faeth, S. H., & Nilon, C. H. (2010). Invasion, competition, and biodiversity loss in urban ecosystems. *BioScience*, *60*(3), 199–208. https://doi.org/10.1525/bio.2010.60.3.6

Snep, R. P. H., Opdam, P. F. M., Baveco, J. M., WallisDeVries, M. F., Timmermans, W., Kwak, R. G. M., & Kuypers, V. (2006). How peri-urban areas can strengthen animal populations within cities: A modeling approach. *Biological Conservation*, *127*(3), 345–

355. https://doi.org/10.1016/j.biocon.2005.06.034

Stevens, V., Turlure, C. & Baguette, M. (2010). A meta-analysis of dispersal in butterflies. *Biological reviews of the Cambridge Philosophical Society, 85*(3), 625-642. https:// 10.1111/j.1469-185X.2009.00119.x

Thomas C.D. & Hanski, I. (1997). Butterfly Metapopulations. In: Metapopulation Biology Ecology, Genetics, and Evolution. Pp 359-386. https://doi.org/10.1016/B978-012323445-2/50020-1

Verbeylen, G., De Bruyn, L., Adriaensen, F., & Matthysen, E. (2003). Does matrix resistance influence Red squirrel (Sciurus vulgaris L. 1758) distribution in an urban landscape? *Landscape Ecology*, *18*(8), 791–805. https://doi.org/10.1023/B:LAND.0000014492.50765.05

Villard, M.-A., & Metzger, J. P. (2014). REVIEW: Beyond the fragmentation debate: a conceptual model to predict when habitat configuration really matters. *Journal of Applied Ecology*, *51*(2), 309–318. https://doi.org/10.1111/1365-2664.12190

Watson, J. E. M., Whittaker, R. J., & Freudenberger, D. (2005). Bird community responses to habitat fragmentation: how consistent are they across landscapes? *Journal of Biogeography*, *32*(8), 1353–1370. https://doi.org/10.1111/j.1365-2699.2005.01256.x

Weller, B., & Ganzhorn, J. U. (2004). Carabid beetle community composition, body size, and fluctuating asymmetry along an urban-rural gradient. *Basic and Applied Ecology*, *5*(2), 193–201. https://doi.org/10.1078/1439-1791-00220

Zalucki, M. P., Parry, H. R., & Zalucki, J. M. (2016). Movement and egg laying in Monarchs: To move or not to move, that is the equation. *Austral Ecology*, *41*(2), 154–167. https://doi.org/10.1111/aec.12285

Zeller, K. A., Mcgarigal, K., & Whiteley, A. R. (2012). Estimating landscape resistance to movement: a review. *Landscape Ecol*, *27*(27), 777–797. https://doi.org/10.1007/s10980-012-9737-0

Table 1. Model parameter estimates and relative importance (Imp %) for the occupancy probability of *Plebejus argus*, relation to the percentage of natural area (Natural %), the percentage of garden area (Garden %) and the carrying capac 10, (c) 15 and (d) 20. Model optimum spatial scales, identified by model selection based on lowest AIC value (Table 2

		Plebejus argus				*Maniola jurtina*				
		Scale	Estimate	SE	Imp (%)	Scale	Estimate	SE	Imp (%)	Scale
(a)	Natural %	2 km	0.14	0.018	35.16	2 km	0.13	0.017	32.59	2
	Garden %	1 km	-0.15	0.061	4.12	2 km	-0.26	0.057	8.54	2
	K		0.0021	0.00085	1.71		0.00074	0.00012	0.088	
(b)	Natural %	2 km	0.14	0.019	36.10	2 km	0.10	0.013	24.15	2
	Garden %	1 km	-0.11	0.045	2.74	2 km	-0.13	0.037	3.68	2
	K		0.0017	0.00074	1.26		0.00012	0.00010	0.0038	
(c)	Natural %	2 km	0.13	0.018	35.55	2 km	0.078	0.012	15.39	50
	Garden %	1 km	-0.088	0.039	2.01	2 km	-0.10	0.032	3.030	2
	K		0.0016	0.00074	0.91		0.0019	0.0017	0.75	
(d)	Natural %	2 km	0.14	0.018	37.52	2 km	0.069	0.012	11.03	
	Garden %	100 m	0.031	0.015	2.03	2 km	-0.016	0.011	0.86	
	K		0.00056	0.00051	0.09		0.0026	0.0023	0.078	

* All gardens were occupied by *P. brassicae* at year 20.

Table 2. Model selection based on lowest AIC for the occupancy probability of each species in relation to the (*N_percent_*), percentage of garden area (*G_percent_*), and garden carrying capacity (*K*) over time (5, 10, 15 scenario (M0) and setting the two first variables at different spatial scales (100 and 500 m, 1 and 2 km). Best number of parameters is three for all models.

		Year5		Year10		
Model Variables & scale	Model	AIC	ΔAIC	AIC	ΔAIC	AIC
N_percent_100, G_percent_100, Kgarden	1	-36.87	131.97	151.58	157.24	186.29
N_percent_100, G_percent_500, Kgarden	2	-40.90	127.93	150.87	156.52	188.66
N_percent_100, G_percent_1K, Kgarden	3	-44.97	123.86	145.40	151.06	183.20
N_percent_100, G_percent_2K, Kgarden	4	-51.85	116.98	136.96	142.61	173.78
N_percent_500, G_percent_100, Kgarden	5	-44.57	124.26	148.57	154.22	186.70
N_percent_500, G_percent_500, Kgarden	6	-50.11	118.72	146.16	151.81	187.78
N_percent_500, G_percent_1K, Kgarden	7	-55.93	112.90	138.57	144.22	179.90
N_percent_500, G_percent_2K, Kgarden	8	-63.23	105.60	129.62	135.27	169.76
N_percent_1K, G_percent_100, Kgarden	9	-114.59	54.24	72.00	77.66	112.11
N_percent_1K, G_percent_500, Kgarden	10	-117.64	51.20	72.80	78.45	116.26
N_percent_1K, G_percent_1K, Kgarden	11	-121.77	47.07	66.63	72.28	109.84
N_percent_1K, G_percent_2K, Kgarden	12	-129.31	39.53	57.12	62.77	99.24
N_percent_2K, G_percent_100, Kgarden	13	-161.17	7.66	-0.58	5.07	17.71
N_percent_2K, G_percent_500, Kgarden	14	-166.90	1.93	-2.45	3.20	20.63
N_percent_2K, G_percent_1K, Kgarden	15	**-168.83**	0.00	**-5.65**	0.00	**16.16**
N_percent_2K, G_percent_2K, Kgarden	16	-165.62	3.21	-3.58	2.07	16.93
N_percent_100, G_percent_100, Kgarden	1	288.54	171.48	308.10	163.66	313.00
N_percent_100, G_percent_500, Kgarden	2	281.32	164.26	302.29	157.84	312.05
N_percent_100, G_percent_1K, Kgarden	3	271.28	154.23	290.42	145.97	309.28
N_percent_100, G_percent_2K, Kgarden	4	251.14	134.08	265.41	120.96	292.93

N_percent_500, G_percent_100, Kgarden	5	295.14	178.08	318.06	173.61	322.79
N_percent_500, G_percent_500, Kgarden	6	284.48	167.42	308.39	163.94	319.87
N_percent_500, G_percent_1K, Kgarden	7	272.26	155.20	293.77	149.32	315.26
N_percent_500, G_percent_2K, Kgarden	8	251.65	134.60	268.10	123.66	297.13
N_percent_1K, G_percent_100, Kgarden	9	235.60	118.54	276.27	131.82	310.29
N_percent_1K, G_percent_500, Kgarden	10	226.83	109.77	268.15	123.71	308.01
N_percent_1K, G_percent_1K, Kgarden	11	214.78	97.72	253.50	109.05	303.70
N_percent_1K, G_percent_2K, Kgarden	12	191.99	74.93	226.11	81.67	285.98
N_percent_2K, G_percent_100, Kgarden	13	144.76	27.70	179.68	35.23	243.29
N_percent_2K, G_percent_500, Kgarden	14	130.87	13.81	167.65	23.20	240.77
N_percent_2K, G_percent_1K, Kgarden	15	122.27	5.21	155.17	10.73	238.37
N_percent_2K, G_percent_2K, Kgarden	16	**117.06**	0.00	**144.45**	0.00	**229.76**
N_percent_100, G_percent_100, Kgarden	1	323.07	65.71	210.04	3.17	-433.22
N_percent_100, G_percent_500, Kgarden	2	321.95	64.59	210.11	3.24	-433.59
N_percent_100, G_percent_1K, Kgarden	3	319.67	62.31	210.06	3.19	-436.19
N_percent_100, G_percent_2K, Kgarden	4	308.42	51.06	210.13	3.26	-438.78
N_percent_500, G_percent_100, Kgarden	5	332.05	74.69	215.24	8.37	-437.86
N_percent_500, G_percent_500, Kgarden	6	328.98	71.62	215.18	8.31	-437.81
N_percent_500, G_percent_1K, Kgarden	7	325.14	67.78	215.18	8.31	-439.61
N_percent_500, G_percent_2K, Kgarden	8	312.62	55.26	215.10	8.23	-434.86
N_percent_1K, G_percent_100, Kgarden	9	322.51	65.15	213.25	6.38	-430.67
N_percent_1K, G_percent_500, Kgarden	10	320.02	62.65	213.23	6.36	-430.58
N_percent_1K, G_percent_1K, Kgarden	11	316.45	59.09	213.23	6.35	-431.89
N_percent_1K, G_percent_2K, Kgarden	12	304.31	46.95	213.17	6.30	-434.10
N_percent_2K, G_percent_100, Kgarden	13	266.51	9.14	**206.87**	0.00	-430.80
N_percent_2K, G_percent_500, Kgarden	14	263.89	6.53	207.91	1.04	-430.73
N_percent_2K, G_percent_1K, Kgarden	15	262.13	4.77	207.99	1.11	-432.17
N_percent_2K, G_percent_2K, Kgarden	16	**257.36**	0.00	208.00	1.13	**-442.02**

Table 3. Model parameter estimates for the projected (a) population size and (b) number of occupied gardens at year 2

scenario (M0 set as intercept), and increases of carrying capacity of $K_{x1.5}$, K_{x2} and K_{x3} for *Plebejus argus*, *Maniola jurti*

		Plebejus argus				*Maniola jurtina*				
		Estimate	SE	p	Imp	Estimate	SE	p	Imp	Estima
(a)	M1	0.0011	0.00010	0.54	1.94	0.0023	0.00012	0.19	3.85	0.15
	M2	0.12	0.0016	<0.0001		0.17	0.0018	<0.0001		0.029
	$K_{x1.5}$	0.32	0.0012	<0.0001	76.22	0.28	0.0025	<0.0001	94.95	0.27
	K_{x2}	0.80	0.0022	<0.0001		0.67	0.0024	<0.0001		0.64
	K_{x3}	1.24	0.0020	<0.0001		1.05	0.0022	<0.0001		1.017
(b)	M1	0.045	0.0024	0.31	2.17	0.025	0.016	0.31	36.78	0.24
	M2	0.022	0.0015	0.62		0.12	0.024	<0.0001		0.25
	$K_{x1.5}$	0.095	0.0045	0.082	30.97	0.061	0.0030	0.035	25.80	0.0019
	K_{x2}	0.28	0.0055	<0.0001		0.10	0.0029	<0.0001		0.0012
	K_{x3}	0.28	0.0059	<0.0001		0.15	0.0028	<0.0001		0.0024

Table 4. Model selection based on lowest AIC for (a) the population size and (b) the number of occupied gar

the management scenario (M0, M1 and M2) and the increases of garden carrying capacity (*K*). Best models a

parameters is two for additive models and three for models with an interaction term.

	Model Variables	AIC	ΔAIC	Species
(a)	Scenario + K	6325646	0	P. argus
	Scenario * K	6326494	848	P. argus
	Scenario + K	23551	0	M. jurtina
	Scenario * K	23845	294	M. jurtina
	Scenario + K	268575	0	P. brassicae
	Scenario * K	268609	34	P. brassicae
(b)	Scenario + K	98.169	0	P. argus
	Scenario * K	109.99	11.821	P. argus
	Scenario + K	324.88	0	M. jurtina
	Scenario * K	336.88	12	M. jurtina
	Scenario + K	467.83	0	P. brassicae
	Scenario * K	479.82	11.99	P. brassicae

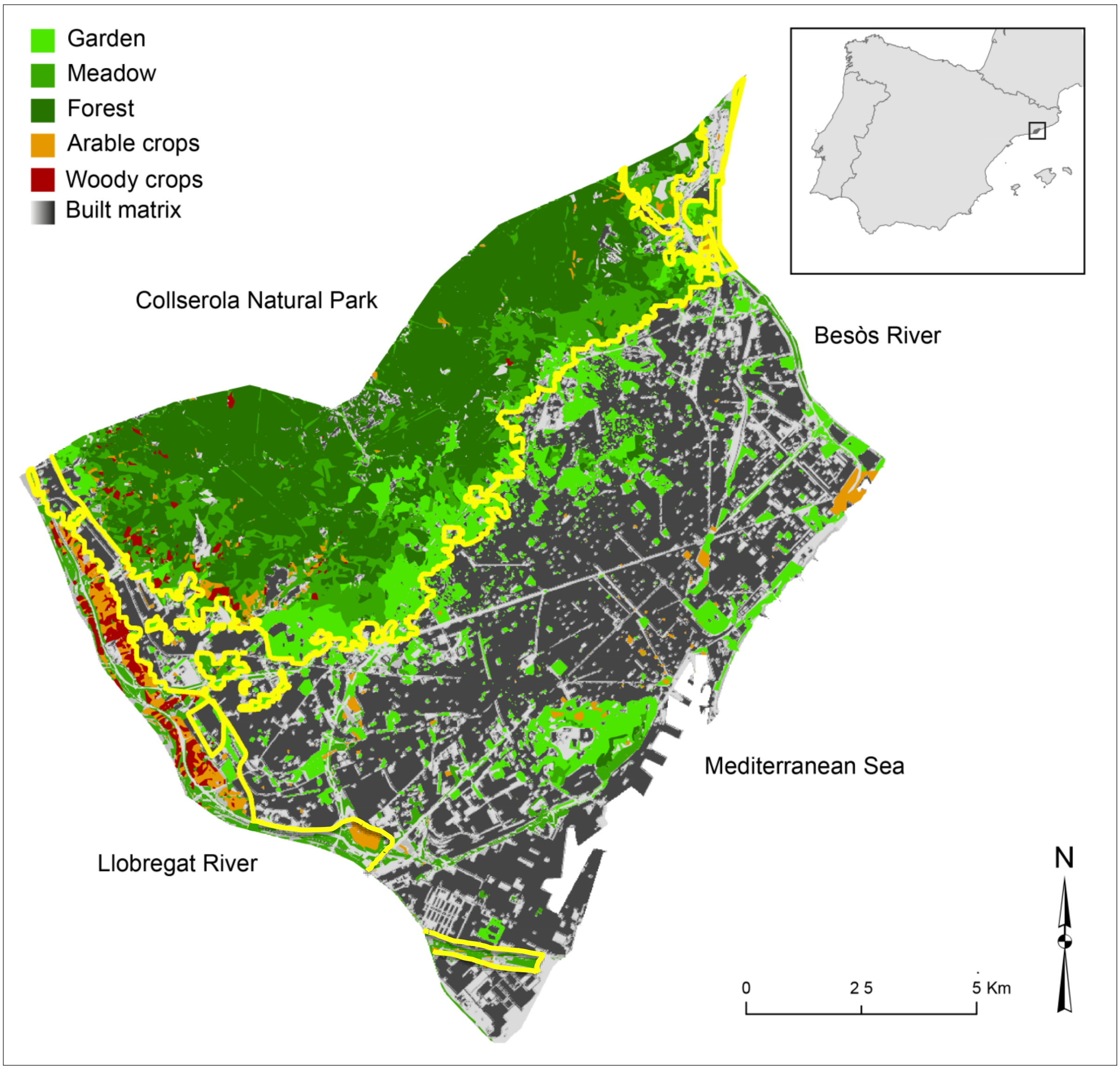


Fig. 1. Landscape composition of the study area, including the limit of the Catalan Coastal Range of the Natural Parks (the natural and initial source area) shown as a solid yellow line. Suitable habitat types are shown in colours (see legend). The grey-gradient relates to the built matrix with light grey for paved areas without buildings to dark grey for fully built-up areas.

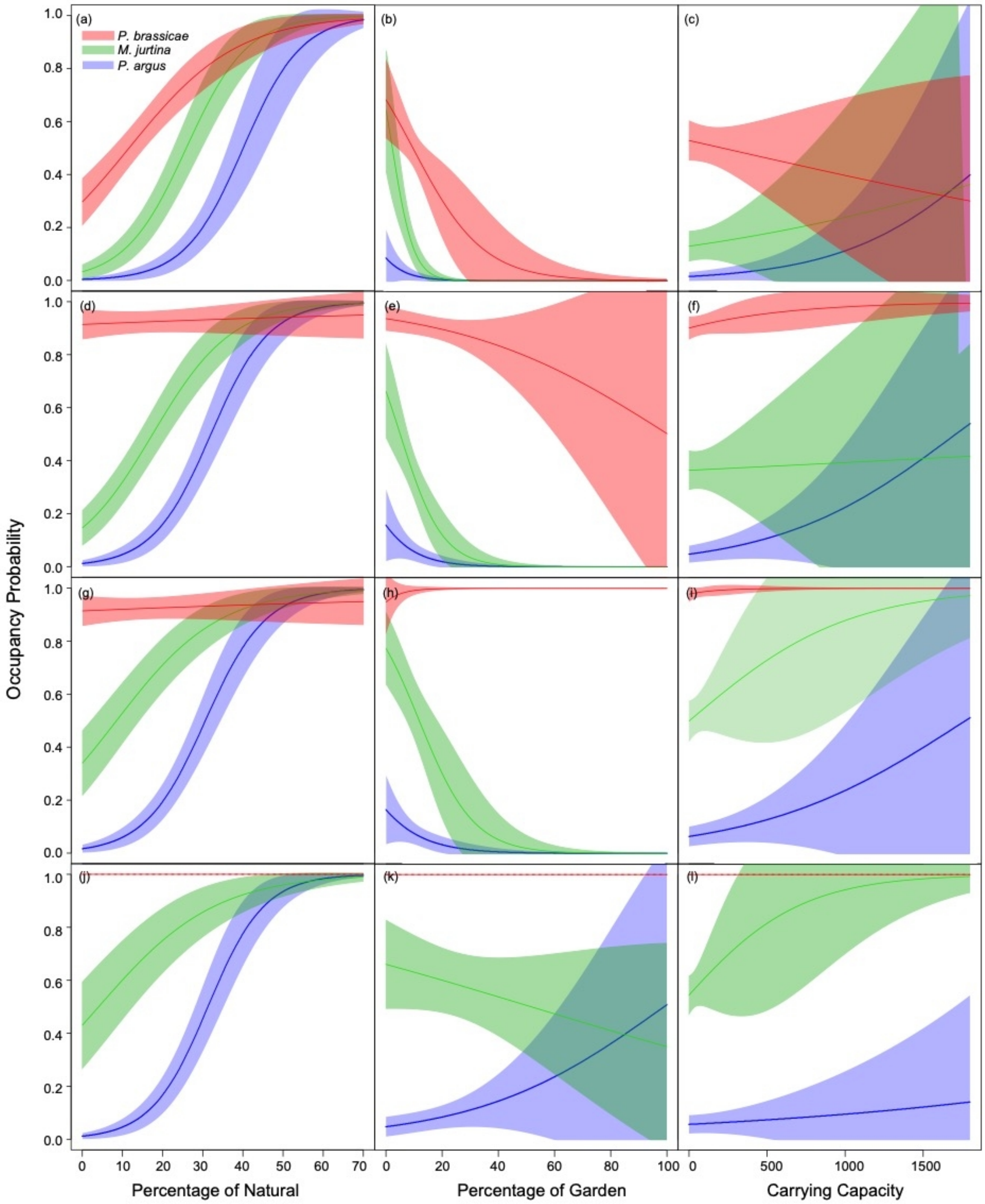


Fig. 2. Projected occupancy probability of gardens (average and 95% CI) at (a-c) 5 years, (d-f) 10 years, (g-i) 15 years and (k-l) 20 years for the three study species in relation to (a,d,g,j) the percentage of natural area, (b,e,h,k) the percentage of garden area and (c,f,i,l) the carrying capacity of the garden, each within the species-specific radius chosen through model-selection (see text and Table 1).

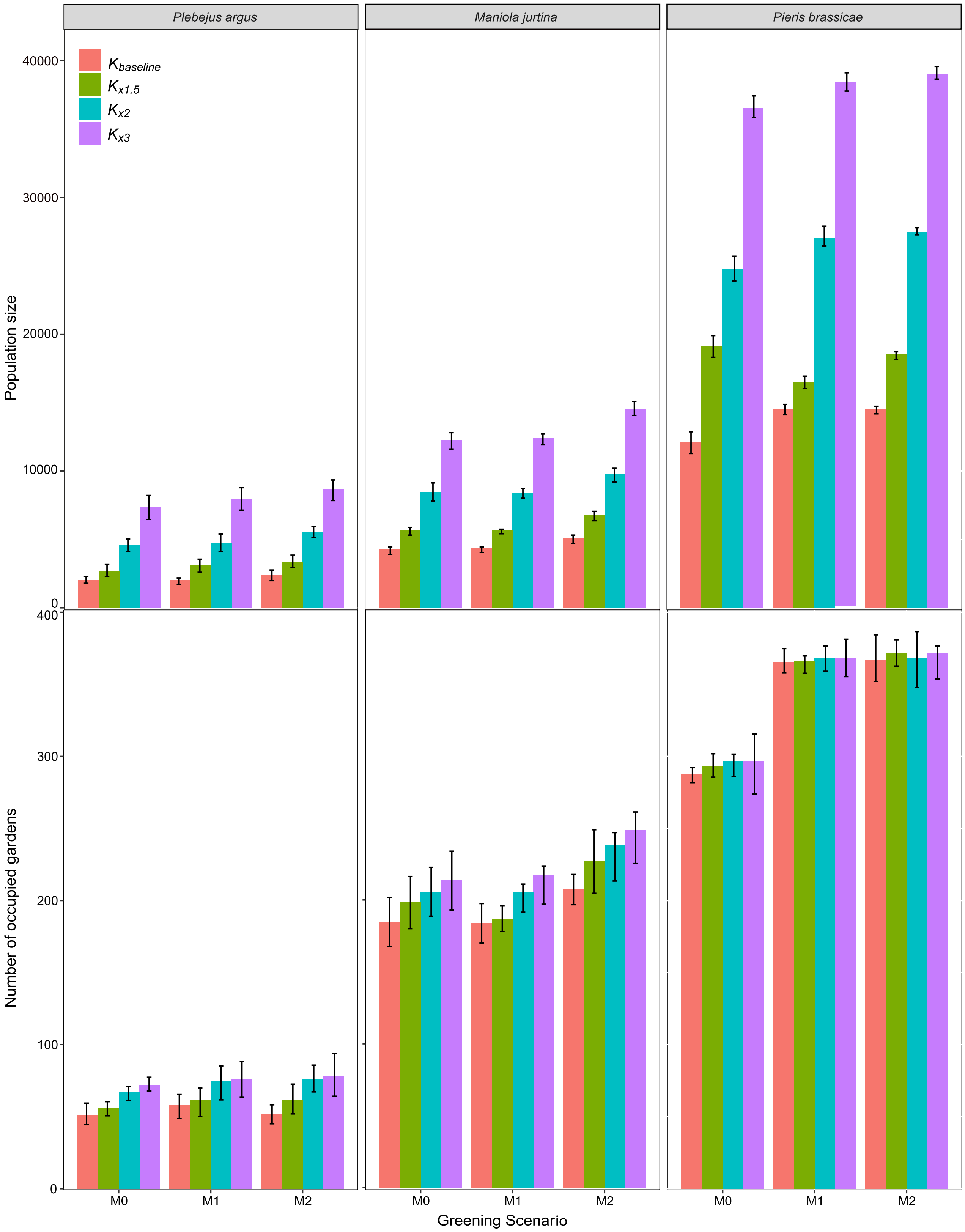


Fig. 3. Projected (a-c) Population size and (d-f) Number of occupied gardens and their 95% confident intervals (error bars) at year 20, for the three species in the current landscape (M0), the proposed greening scenarios (M1 and M2) and the combined increases of carrying capacity of the gardens ($K_{x1.5}$, K_{x2}, K_{x3}).

Supporting Information

Appendix A1. The Stochastic Movement Simulator

Appendix A2. Estimating the species intrinsic population growth rate

Appendix A3. Estimating species-specific step mortality

Appendix A4. Sensitivity Analysis

Figure A1. Landscape composition of M0, M1 and M2

Figure A2. Predicted distributions of *P. argus* in M0, M1 and M2.

Figure A3. Predicted distributions of *M. jurtina* in M0, M1 and M2.

Figure A4. Predicted distributions of *P. brassicae* in M0, M1 and M2.

Table A1. References for emigration probability

Table A2. Model parameters and related references

Acknowledgements

We thank BCNEcologia for providing information about the Barcelona City Hall Plan and the volunteers within the CBMS. YM was supported by a Beatriu de Pinos-B postdoctoral grant (2013 BP-B 00168, AGAUR) and by the Barcelona City Council. The CBMS is funded by the Departament de Territori i Sostenibilitat (Generalitat de Catalunya). The uBMS is funded by Fundación Biodiversitat (Ministerio para la Transición Ecológica). We thank the editor and two anonymous reviewers for their useful comments.

Appendix A1

The Stochastic Movement Simulator

The Stochastic Movement Simulator (SMS) is a spatially explicit movement model, which may be used to estimate functional connectivity by simulating individual dispersal trajectories. SMS can give more realistic predictions than, for example, least cost path (LCP) or landscape conductivity methods (Coulon et al., 2015; Kindlmann & Burel, 2008; e.g. Aben et al., 2016, 2014). The basis of SMS is similar to LCP, but it incorporates a limited perceptual range and removes any a priori destination, which relaxes the assumptions of individuals perceiving the entire landscape and being motivated by a known destination (Stevens *et al.* 2006; Poniatowski *et al.* 2016; Adriaensen *et al.* 2003). SMS has been shown to produce better population connectivity estimates than LCP (Coulon et al., 2015). As such, SMS can be used in spatially explicit population models by conservationists and urban planners to project population trends and to assess and prioritise potential strategies (e.g. Aben *et al.* 2016).

Modelling approach

We modelled the population dynamics of each species based on female-only and non-overlapping generations at the scale of individual patches, starting with initial populations restricted to the source area, from which they grew and dispersed through the area (including the city), occupying new suitable patches over time.

Populations of each species grew according to its intrinsic population growth rate (see Appendix A2), limited by the habitat-dependent carrying capacity of the suitable patches. For each patch, RangeShifter (RS) defines the patch carrying capacity (K_i) as the maximum number of breeding individuals that each habitat type could hold per hectare. The species-specific maximum mean fecundity, R_{max}, was estimated by simulating in RS the conditions at which it can be observed: no density dependence and environmental stochasticity in fecundity, and fitting to the observed values of each species' population growth rate in Catalonia (Melero, Stefanescu, & Pino, 2016). The species-specific habitat quality was obtained from a previous study on habitat suitability for 66 species among

19 gardens (Melero et al., 2016). The built matrix was set as unsuitable for all three species (Table A2).

Dispersal is modelled in RS as a three-stage process (emigration, transfer and settlement). Only adults dispersed, at most once before reproducing, and died immediately following reproduction. Emigration started from the patches in the source area, but once new garden patches were occupied, they also became a source of dispersers. For all patches, emigration was modelled as the density-dependent probability (*d*) that an individual leaves its natal patch:

$$d = \frac{D_0}{1 + e^{-\left(\frac{N_{i,t}}{K_i} - \beta\right)\alpha}}$$

where D_0 is the maximum emigration probability, β is the inflection point of the function while α determines the slope at the inflection point (e.g., Kun & Scheuring 2006; Heikkinen et al. 2014; Aben et al. 2016). $N_{i,t}$ represents the population size in patch *i* at time *t*, and K_i is the carrying capacity of the patch. Species-specific parameter estimates were obtained based on theoretical and empirical estimates in the literature for the studied species (Tables A1 and A2).

The movement of individuals that dispersed (transferred) through the landscape was modelled using SMS, which simulates discrete individual stepwise nearest-neighbour movements across the landscape grid. At each given step, individuals move to a neighbouring cell depending on relative cost values, which determine the probability of moving to a particular cell (i.e. the greater the cost of a neighbouring cell, the lower the probability of moving to it). The probability is also determined by the individuals' perceptual range (PR) and its degree of directional persistence (DP) (Palmer, Coulon & Travis 2011). Individuals were subject to a probability of mortality per step (step mortality, *sm*), which reflects the species' dispersal ability: if it is high then the species is a relatively poor disperser and *vice versa*. Species-specific *sm* values were estimated based on theoretical and empirical studies analysing species dispersal (i.e. long distance dispersal events; see Appendix A3). Variation between studies was reconciled following the approach of Heikkinen *et al*. (2014, 2015); i.e. using the mean distance of long movements to calculate the average *sm* (Appendix A3).

Each 20 m landscape cell was assigned a movement-cost value for SMS. For habitat types excluding the built area, costs were inversely related to the relative preference of the species (1 for the breeding habitats: grassland, meadows, arable crops and gardens, 5 for woody crops and forest; Melero et al., 2016). Values for the cells within the built area were calculated as the percentage of built cells at 2 m resolution within each 20 m resolution cell, from 2 (entirely paved spaces without buildings) to 100 for cells with 100% built coverage. We assumed that the cost surface was the same for the three species but dispersal patterns would differ owing to the species-specific per-step mortality (above). We assumed a PR of 60 m (three cells), MemSize of 3 cells (which controls the distance over which the current direction is determined) and DP of 5.0 for all species. These values were based on the literature (Table A1), which gave us a potential range for each parameter. We then plotted all parameters together varying their values as per their range until dispersal graph coincided with the expected for each species (see review in Stevens et al. 2006) and checked by experts in the subject. Dispersers moved through the built matrix until either finding a suitable non-natal habitat patch in which they settled, or dying due to the mortality risk *sm*.

Appendix A2: Estimating the species intrinsic population growth rate

For a non-structured population, R_{max} is the maximum average fecundity per female (in terms of the next generation of adults) when breeding at very low density (i.e. when density dependence is reduced to near zero) and under average environmental conditions. R_{max} is therefore rarely observed empirically, since in any established population, the effect of density dependence in fecundity would cause the observed number of offspring per female (R) to fall below R_{max}. Besides, since butterfly populations often respond quite strongly to weather conditions (Pollard, 1988), the observed R might be lower or higher than R_{max}.

However, RS can simulate the effect of annual variation of R_{max} in its optimal conditions by applying low density, no density dependence and environmental stochasticity in fecundity (and hence in the population growth rate). Therefore, to obtain the species R_{max}, we combined the results of the species abundance for 20 years (1994-2014) obtained from our previous analyses (Melero et al., 2016) on the long term Catalan Butterfly Monitoring Scheme (http://www.catalanbms.org/) with simulations in RS. First, we used the annual abundance data per species to calculate the annual growth rate for the 20 years as:

$$\lambda_t = \mathrm{N}_{t+1} / \mathrm{N}_{t}. \qquad \text{Eqn. S.1}$$

Because at low densities, annual growth rate (λ_t) relates directly to R_{max}, we extracted the observed minimum, maximum and average values ($r_{\text{obs-min}}$, $r_{\text{obs-max}}$ and $r_{\text{obs-mean}}$ respectively) from the obtained series of annual population growth rate (λ_t) (Table S1). We then set $r_{\text{obs-mean}}$ as the initial R_{max} value in the model parameters whilst $r_{\text{obs-min}}$ and $r_{\text{obs-max}}$ were used to set the range of variation allowed within the environmental stochasticity; the latter set as global in RS. We also estimated the mean annual temporal autocorrelation between the annual growth rates per species and added it into the model. Temporal autocorrelation was estimated using the autocorrelation function in R.

Once we had these parameters we ran a sequential series of simulations of increasing spatial complexity, starting with a single occupied patch of the landscape and increasing to n patches, until n

led to stability of R_{max} value (i.e., the value of the estimated R_{max} did not vary when adding more patches, n = 6-10). Patch sizes ranged from 1 to 6ha.

Each simulation followed the model described in the main text: female-only and non-overlapping generation population dynamics at the scale of individual patches, and habitat-dependent carrying capacity (*K*) of each species. However, we initialised each species at low density and set the habitat-dependent carrying capacities to a higher value (K*100) to avoid density dependence. For all species the built matrix was kept as unsuitable. Emigration was set as nil to emulate a closed population per patch, but population growth rates were obtained from the total metapopulation (all patches included). Each model was replicated 100 times for 20 years.

The species differed in the number of generations, with one for *P. argus* and *M. jurtina* but two or three for *P. brassicae*. However, this difference was already included when estimating R_{max} so that it reflected the annual maximum growth per year instead of per generation. Thus, we set the number of generations per year in the models in RS as one for the three species regardless of their true voltinism.

Table S1. Observed minimum ($r_{\text{obs-min}}$), maximum ($r_{\text{obs-max}}$) and mean ($r_{\text{obs-mean}}$) annual population growth rate from empirical data on the species abundances extracted from Melero, Stefanescu & Pino (2016), their temporal autocorrelation (*ac*) and estimated R_{max} by means of simulations in RS.

Species	$r_{\text{obs-min}}$	$r_{\text{obs-max}}$	$r_{\text{obs-mean}}$	*ac*	R_{max}
Plebejus argus	0.77	1.28	0.95	0.027	1.50 ± 0.06
Maniola jurtina	0.89	1.24	1.01	0.027	1.39 ± 0.05
Pieris brassicae	0.70	1.63	1.04	0.021	1.69 ± 0.04

Appendix A3: Estimating species-specific step mortality during transfer

Species-specific step mortality sm (i.e., the probability of dying per step) was calculated as the inverse of the distance travelled by the species during long distance dispersal events with distances expressed in the form of number of steps (i.e. number of 20 m resolution cells travelled):

$$sm = {}^{1}\!\Big/_{\frac{D}{20}} \qquad \text{Eqn. S2}$$

where D is the travelled distance (m) during long distance dispersal events by individuals of the species, calculated following Heikkinen *et al.* (2014, 2015) as the mean distance of reported long distance dispersal events (Table S2).

Table S2. Long distances range and mean (m) for the parameterisation of the species-specific step mortality and the source references number linked to Table A1 by their ID.

Species	D_{range}	D_{mean}	sm	Reference ID
Plebejus argus	500-1200	700	0.029	1-3
Maniola jurtina	1000-5000	3000	0.007	5, 10-11
Pieris brassicae	3000-10000	5000	0.004	12,15-19

Appendix A4: Sensitivity Analyses

We conducted a sensitivity analysis to evaluate the effects of varying four key parameters on the simulated population dynamics (Naujokaitis-Lewis et al., 2013): maximum emigration rate (D_0), directional persistence (DP), maximum fecundity (R_{max}) and step mortality (*sm*). To do so we set a lower and a higher value for each parameter (increased and decreased value by 5 %, respectively), and ran the models with these new values (Table S3). We then calculated the rate of change (%) of population size and number of occupied gardens results compared to the original models.

The parameter to which the model was most sensitive for all species was maximum fecundity (R_{max}), in concordance with previous studies (e.g. Heikkinen et al., 2014). Population size and number of occupied gardens increased with the increase of R_{max} (and decreased with its decrease) for all three species but stronger for the low dispersive *Plebejus argus*. However, their similar response assures the viability of comparision between models (Figs. S1-S3). Besides, all models (with original and varied values) included stochasticity in R_{max}. All other values had a percentage of change below 10 % for both *M. jutina* and *P. brassicae*

Table S3. Original, inflated and deflated values (by 5 %) of maximum emigration rate (D_0), directional persistence (DP), maximum fecundity (R_{max}) and step mortality (*sm*) for the sensitivity analysis.

	Plebejus argus			*Maniola jurtina*			*Pieris brassicae*		
Parameter	Original	Increased	Decreased	Original	Increased	Decreased	Original	Increased	Decreased
D_0	0.013	0.01365	0.01235	0.4	0.42	0.38	0.7	0.735	0.665
DP	5	5.25	4.75	5	5.25	4.75	5	5.25	4.75
R_{max}	1.50	1.575	1.425	1.39	1.4595	1.3205	1.69	1.7745	1.6055
sm	0.029	0.03045	0.02755	0.007	0.00735	0.00665	0.004	0.0042	0.0038

Figure S1. Percentage of change of Population size (left graphs) and Number of occupied gardens (right graphs) of the and decreased values of the parameters: maximum emigration rate (D_0), directional persistence (DP), maximum fecunc *Plebejus argus*. Change is shown for all garden carrying capacity (see legend).

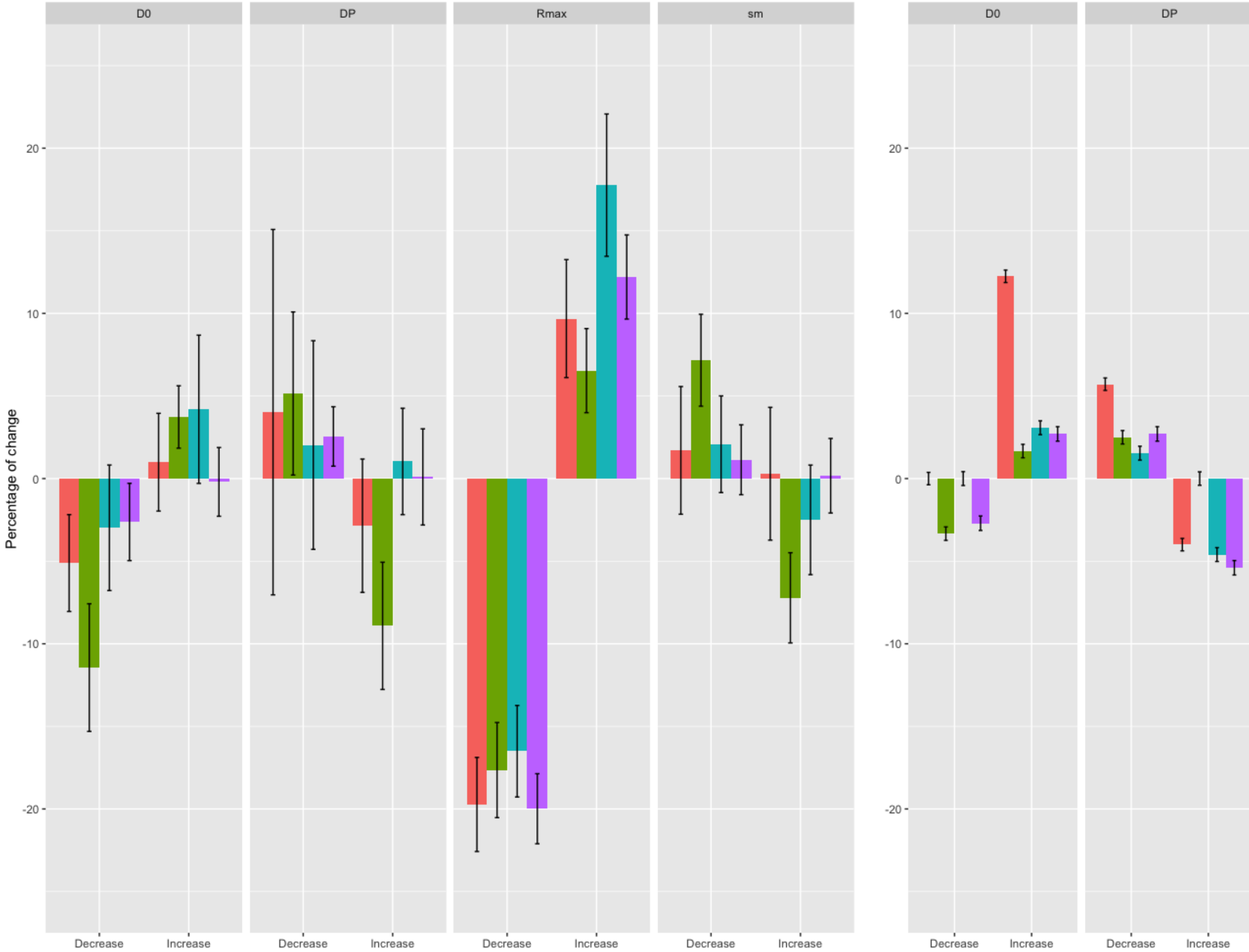


Figure S2. Percentage of change of Population size (left graphs) and Number of occupied gardens (right graphs) of th
and decreased values of the parameters: maximum emigration rate (D_0), directional persistence (DP), maximum fecunc
Maniola jurtina. Change is shown for all garden carrying capacity (see legend).

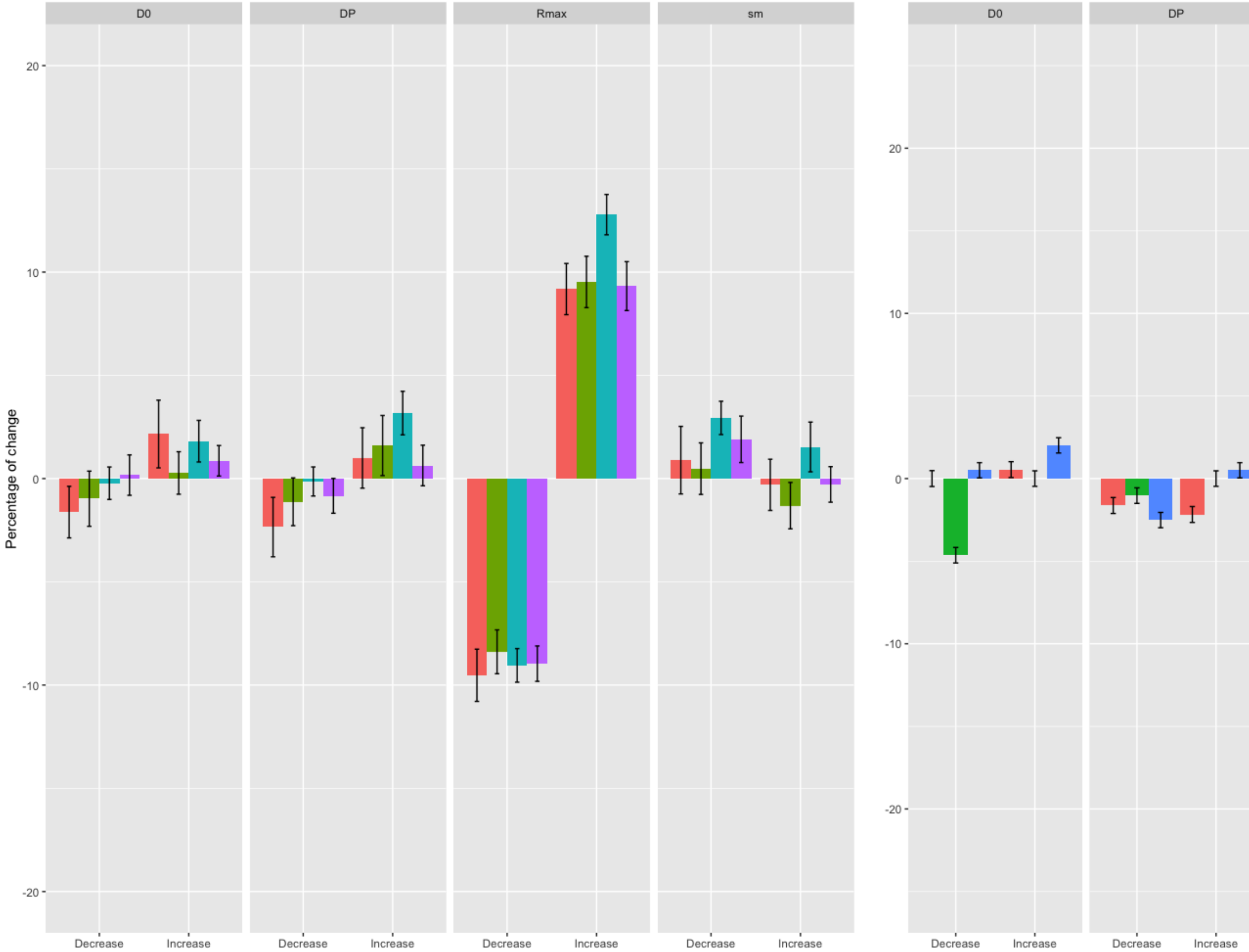
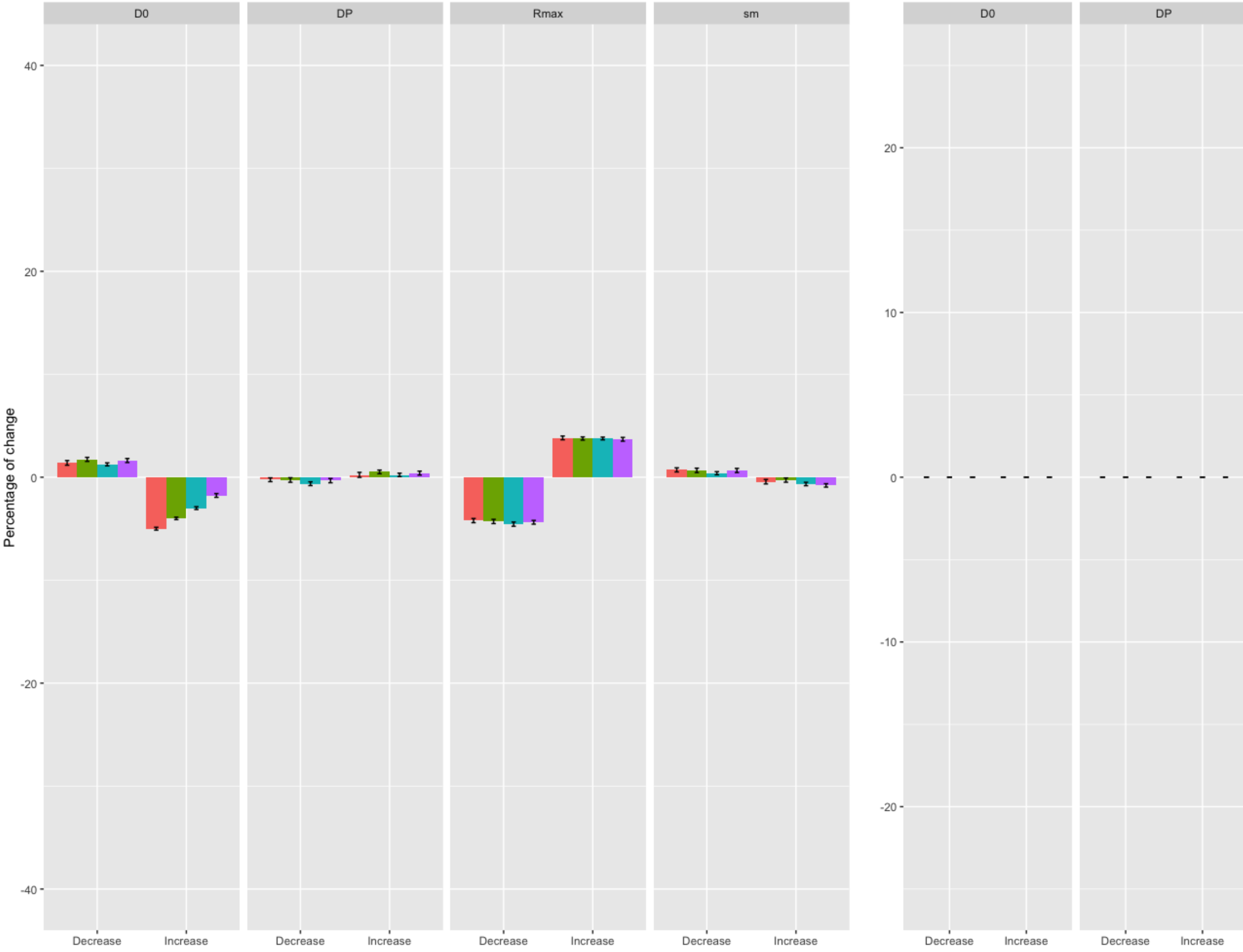


Figure S3. Percentage of change of Population size (left graphs) and Number of occupied gardens (right graphs) of the and decreased values of the parameters: maximum emigration rate (D_0), directional persistence (DP), maximum fecunc *Pieris brassicae*. Change is shown for all garden carrying capacity (see legend).



References

Aben, J., Bocedi, G., Palmer, S. C. F., Pellikka, P., Strubbe, D., Hallmann, C., … Matthysen, E. (2016). The importance of realistic dispersal models in planning for conservation: application of a novel modelling platform to evaluate management scenarios in an Afrotropical biodiversity hotspot. *Journal of Applied Ecology*, *53*, 1055–1065. https://doi.org/10.1111/1365-2664.12643

Adriaensen, F., Chardon, J. P., De Blust, G., Swinnen, E., Villalba, S., … Matthysen, E. (2003). The application of 'least-cost' modelling as a functional landscape model. *Landscape and Urban Planning*, *64*, 233–247. https://doi.org/10.1016/S0169-2046(02)00242-6

Coulon, A., Aben, J., Palmer, S. C. F., Stevens, V. M., Callens, T., Strubbe, D., … Travis, J. M. J. (2015). A stochastic movement simulator improves estimates of landscape connectivity. *Ecology*, *96* (8), 2203–2213. https://doi.org/10.1890/14-1690.1

Heikkinen, R. K., Bocedi, G., Kuussaari, M., Heliölä, J., Leikola, N., Pöyry, J., & Travis, J. M. J. (2014). Impacts of land cover data selection and trait parameterisation on dynamic modelling of species' range expansion. *PloS One*, *9* (9), e108436. https://doi.org/10.1371/journal.pone.0108436

Heikkinen, R. K., Pöyry, J., Virkkala, R., Bocedi, G., Kuussaari, M., Schweiger, O., … Travis, J. M. J. (2015). Modelling potential success of conservation translocations of a specialist grassland butterfly. *Biological Conservation*, *192*, 200–206. https://doi.org/10.1016/j.biocon.2015.09.028

Kindlmann, P., & Burel, F. (2008). Connectivity measures: a review. *Landscape Ecology, 23* (8), 879–890. https://doi.org/10.1007/s10980-008-9245-4

Kun, Á., & Scheuring, I. (2006). The evolution of density-dependent dispersal in a noisy spatial population model. *Oikos*, *115*(2), 308–320. https://doi.org/10.1111/j.2006.0030-1299.15061.x

Melero, Y., Stefanescu, C., & Pino, J. (2016). General declines in Mediterranean butterflies over the last two decades are modulated by species traits. *Biological Conservation*, *201*, 336–342. https://doi.org/10.1016/j.biocon.2016.07.029

Naujokaitis-Lewis, I.R., Curtis, J.M.R., Tischendorf, L., Badzinski, D., Lindsay, M.J., & Fortin, K. (2013). Uncertainties in coupled species distribution-metapopulation dynamics models for risk assessments under climate change. *Diversity and Distribution*, 19 541-554.

Palmer, S. C. F., Coulon, A., & Travis, J. M. J. (2011). Introducing a "stochastic movement simulator" for estimating habitat connectivity. *Methods in Ecology and Evolution*, *2*(3), 258–268. https://doi.org/10.1111/j.2041-210X.2010.00073.x

Pollard, E. (1988). Temperature, Rainfall and Butterfly Numbers. *The Journal of Applied Ecology*, *25*(3), 819. https://doi.org/10.2307/2403748

Poniatowski, D., Löffler, F., Stuhldreher, G., Borchard, F., Krämer, B., & Fartmann, T. (2016).

Functional connectivity as an indicator for patch occupancy in grassland specialists. *Ecological Indicators*, *67*, 735–742. https://doi.org/10.1016/j.ecolind.2016.03.047

Stevens, V. M., Leboulengé, E., Wesselingh, R. A., & Baguette, M. (2006). Quantifying functional connectivity: experimental assessment of boundary permeability for the natterjack toad (Bufo calamita). *Oecologia*, *150*(1), 161–171. https://doi.org/10.1007/s00442-006-0500-6

Table A1. Reference ID used for the parameterisation of the species-specific emigration probability d and the step mo considered in the studies, their values and their literature reference.

Reference ID	Species	Parameters	Values	Type of study
1	*Plebejus argus*	Emigration Per-step mortality (distance travelled)	1.5% 37-395m	Mark–release–recapture experiment Empirical colonisation Empirical genetics
2	*Plebejus argus*	Emigration Per-step mortality (distance travelled)	31% Mean 86m, max. 660m	Empirical distribution
3	*Plebejus argus*	Per-step mortality (distance travelled)	57.3 ± 52.0 m (max 343.7)	Radiotracking
4	*Maniola jurtina*	Emigration Per-step mortality (distance travelled)	54% 60-1150m, with differing frequencies (Fig.3 reference)	Mark–release–recapture experiment
5	*Maniola jurtina*	Emigration Per-step mortality (distance travelled)	25.7% 0-3000m, with differing frequencies (Table 1 and Fig.4 reference)	Mark–release–recapture experiment
6	*Maniola jurtina*	Emigration	10%	Mark–release–recapture experiment
7	*Maniola jurtina*	Emigration	50.7%	Mark–release–recapture experiment Simulations
8	*Maniola jurtina*	Perceptual range, dispersal cost	60m 0-1000m varying with habitat (See Table 2 reference)	Empirical genetics
9	*Maniola jurtina*	Emigration	42.4%	Mark–release–recapture experiment
10	*Maniola jurtina*	Emigration Per-step mortality	D0 = 0.4, β = 1.0 and α = 5.0 Mortality = 0.0	Simulations
11	*Maniola jurtina*	Emigration Per-step mortality	D0 = 0.4, β = 1.0 and α = 5.0 Mortality = 0.0	Simulations
12	*Pieris brassicae*	Emigration Per-step mortality	24% (density dependent) 50% survival in 500m	Mark–release–recapture experiment
13	*Pieris brassicae*	Emigration	27%	Mark–release–recapture experiment
14	*Pieris brassicae*	Flight direction	100% of individuals with maintained flight direction	Observations in semi-natural habita
15	*Pieris brassicae*	Dispersal distance Flight endurance	0-5000m 0-16 (Table 1 reference)	Release experiments
16	*Pieris brassicae*	Per-step mortality Flight endurance	18m per movement 10-14 days	Release experiments

17	*Pieris brassicae*	Emigration Per-step mortality	73% 700m moved per day. Mortality λ = 0–4.5	Review
18	*Pieris brassicae*	Emigration Per-step mortality	73% 700m moved per day. Mortality λ = 0–4.5	Review
19	*Pieris brassicae*	Per-step mortality (distance travelled)	0-5000m	Review
20	*Pieris brassicae*	Per-step mortality (distance travelled)	3100 m varying with the cover	Release experiments

Table A2. Default and alternative RangeShifter parameter values and references.

Default Parameter	Alternative Parameter	*Plebejus argus*	*Maniola jurtina*	*Pieris brassicae*	References
R_{max}		1.50	1.39	1.69	Melero et al 2016 CBMS, http://www.cata
Q_{garden}		15	12	30	
	$Q_{gardenx1.5}$	22	18	45	
	$Q_{gardenx2}$	30	24	60	
	$Q_{gardenx3}$	45	36	90	
Q_{meadow}		33	44	25	Melero et al 2016 CBMS, http://www.cata
Q_{forest}		12	13	10	
$Q_{arable\ crops}$		2	28	12	
$Q_{woody\ crops}$		2	16	13	
$Q_{built\ matrix}$		0	0	0	
D_0		0.013	0.4	0.7	Table S1
β		5	5	6	
α		0	1	0.1	
sm		0.029	0.007	0.004	
PR		60	60	60	Table S1 Expert opinion
DP		5.0	5.0	5.0	
MemSize		60	60	60	

ρ		*K*	*K*	*K*	Melero et al 2016

R_{max} = Species intrinsic population growth rate, i.e. the number of flying females in the next generation per breeding female, not the number of e
habitat-dependent carrying capacity ind/ha in RS manual; D_0,= maximum emigration probability, β = inflection point, α = slope at the inflection
dependence emigration probability; *sm* = per-step mortality; PR = Perceptual range (m); DP = Directional persistence (number of cells); MemSiz
densit

References

Aviron, S., Kindlmann, P., & Burel, F. (2007). Conservation of butterfly populations in dynamic landscapes: The r
landscape mosaic. Ecological Modelling, 205(1–2), 135–145. https://doi.org/10.1016/j.ecolmodel.2007.02

Bergerot, B., Tournant, P., Moussus, J.-P., Stevens, V.-M., Julliard, R., Baguette, M., & Foltête, J.-C. (2013). Coupling
landscape graph to assess functional connectivity. Population Ecology, 55(1), 193–203. https://doi.org/10.

Ducatez, S., Baguette, M., Trochet, A., Chaput-Bardy, A., Legrand, D., Stevens, V., & Fréville, H. (2013). Flight endu
both latitude and habitat connectivity in a butterfly species. Oikos, 122(4), 601–611. https://doi.org/10.11

Ducátez, S., Legrand, D., Chaput-Bardy, A., Stevens, V. M., Fréville, H., & Baguette, M. (2012). Inter-individual vari
mobility syndrome in the large white butterfly Pieris brassicae? Ecological Entomology, 37(5), 377–385. ht
2311.2012.01375.x

Feltwell, J. (1982). The Biology, Biochemistry and Physiology of Pieris brassicae (Linnaeus). Dordrecht, the Neth
Publishers.

Fernández, P., Rodríguez, A., Obregón, R., de Haro, S., Jordano, D., & Fernández-Haeger, J. (2016). Fine Scale Mov
argus in a Heterogeneous Natural Landscape as Revealed by GPS Tracking. Journal of Insect Behavior, 29(1
https://doi.org/10.1007/s10905-016-9543-7

Gutiérrez, D., León-Cortés, J. L., Menéndez, R., Wilson, R. J., Cowley, M. J. R., & Thomas, C. D. (2001). Metapopulati
on a Single Host Plant, Lotus corniculatus. Ecology, 82(5), 1371–1386. https://doi.org/10.1890/0012-965

Heikkinen, R. K., Bocedi, G., Kuussaari, M., Heliölä, J., Leikola, N., Pöyry, J., & Travis, J. M. J. (2014). Impacts of lanc
parameterisation on dynamic modelling of species' range expansion. PloS One, 9(9), e108436. https://doi.c

Heikkinen, R. K., Pöyry, J., Virkkala, R., Bocedi, G., Kuussaari, M., Schweiger, O., … Travis, J. M. J. (2015). Modelling
translocations of a specialist grassland butterfly. Biological Conservation, 192, 200–206. https://doi.org/1

Legrand, D., Trochet, A., Moulherat, S., Calvez, O., Stevens, V. M., Ducatez, S., … Baguette, M. (2014). Ranking the e
butterfly. Ecography, n/a-n/a. https://doi.org/10.1111/ecog.01283

Lewis, O., Thomas, C., Hill, J., Brookes, M., Crane, T. P., Graneau, Y., … Rose, O. (1997). Three ways of assessing me
butterfly Plebejus argus. Ecological Entomology, 22(3), 283–293. https://doi.org/10.1046/j.1365-2311.19

Melero, Y., Stefanescu, C., & Pino, J. (2016). General declines in Mediterranean butterflies over the last two decac

Biological Conservation, *201*, 336–342. https://doi.org/10.1016/j.biocon.2016.07.029

Öckinger, E., & Smith, H. G. (2007a). Asymmetric dispersal and survival indicate population sources for grasslan
landscapes. *Ecography*, *30*(2), 288–298. https://doi.org/10.1111/j.0906-7590.2007.05048.x

Öckinger, E., & Smith, H. G. (2007b). Do corridors promote dispersal in grassland butterflies and other insects?
https://doi.org/10.1007/s10980-007-9167-6

Rabasa, S., Gutiérrez, D., & Escudero, A. (2007). Metapopulation structure and habitat quality in modelling dispe
Oikos, *116*(5), 793–806. https://doi.org/10.1111/j.0030-1299.2007.15788.x

Schneider, C., Dover, J., & Fry, G. L. A. (2003). Movement of two grassland butterflies in the same habitat networ
of the study area. *Ecological Entomology*, *28*(2), 219–227. https://doi.org/10.1046/j.1365-2311.2003.004

Spieth, H. R., Cordes, R.-G., & Dorka, M. (1998). Flight Directions in the Migratory Butterfly Pieris brassicae: Resu
Ethology, *104*(4), 339–352. https://doi.org/10.1111/j.1439-0310.1998.tb00073.x

Stevens, V. M., Trochet, A., Van Dyck, H., Clobert, J., & Baguette, M. (2012). How is dispersal integrated in life hist
butterflies. *Ecology Letters*, *15*(1), 74–86. https://doi.org/10.1111/j.1461-0248.2011.01709.x

Stevens, V. M., Turlure, C., & Baguette, M. (2010). A meta-analysis of dispersal in butterflies. *Biological Reviews*
Society, *85*(3), 625–642. https://doi.org/10.1111/j.1469-185X.2009.00119.x

Trochet, A., Legrand, D., Larranaga, N., Ducatez, S., Calvez, O., Cote, J., … Baguette, M. (2013). Population sex ratio
patch metapopulations of butterflies. *Journal of Animal Ecology*, *82*(5), 946–955. https://doi.org/10.1111/

Villemey, A., Peterman, W. E., Richard, M., Ouin, A., van Halder, I., Stevens, V. M., … Archaux, F. (2016). Butterfly
landscape genetics study on the meadow brown butterfly (Maniola jurtina). *Landscape Ecology*, 1–13. https
0348-z