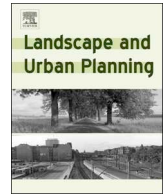




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Research Paper

Moderately urbanized areas as a conservation opportunity for an endangered songbird

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ABSTRACT

Urban sprawl has increased in Western Europe principally due to conversion of farmland areas, which has constrained remaining farmland to more intensive use. Urban densification aims to counteract urban sprawl; however, it threatens urban green spaces that act as sustainable alternative habitats for wildlife. In this study, we used the Common Redstart (*Phoenicurus phoenicurus*) as a model species to develop sustainable planning recommendations for urban green spaces. Using species distribution models (SDMs) in combinations with high-resolution predicting variables (2×2 m grid cell), we defined the suitable habitat of a Common Redstart territory in a moderately urbanized environment. We then predicted how the distribution would be affected under realistic scenarios of land-use modification (termed conservation scenario and threat scenario) in an effort to provide recommendations for urban green space planning. Tree canopy cover was the principal land-cover type in the SDMs that explained the current species distribution followed by impervious surface and short-cut lawn. In the conservation scenario where tree canopy coverage was increased we predicted an increase in optimum habitat for the Common Redstart from 7% to 27% of the study area. In contrast, under a threat scenario based on urban densification, we predicted a decrease in the optimum habitat to only 4% of the study area. The SDMs results were used to highlight the importance of the suitable areas that have a predicted potential to conserve and promote an interconnected urban green space networks to maintain urban biodiversity.

1. Introduction

In Western Europe, urban sprawl has increased up to 80% since the 1950's, largely due to broad-scale conversion of farmlands and agricultural areas (Antrop, 2004). Urbanization in Switzerland represents an extreme example, with an increase in urban areas of 125% between 1935 and 2002 (total surface cover of urban areas increased from 4000 km² to 9000 km²; ARE, 2009b; Hayek, Jaeger, Schwick, Jame, & Schuler, 2011). During the same period, agriculture has intensified in Western Europe, resulting in the loss and degradation of traditional farmland landscapes over large scales (Foley et al., 2005). Consequently, many previously widespread farmland bird species have lost suitable habitat and have shown considerable range and population declines (Donald, Green, & Heath, 2001; Donald, Sanderson, Burfield, & van Bommel, 2006). In this context, moderately urbanized areas

(i.e. sparsely housed areas) with a heterogeneous landscape composed of green spaces (e.g. private gardens and parks) and man-made structures could offer alternative habitats for many wildlife species (Aronson et al., 2014; Ives et al., 2016).

Developing sustainable urban green spaces for conserving native biodiversity and its ecosystem services (according to e.g. URBIO criteria; Müller, Elsner, & Wittmann, 2014) could be undertaken at two different spatial scales: small (i.e. garden and park) versus large spatial extent (i.e. city; Goddard, Dougill, & Benton, 2010). At the local scale, providing a combination of land-cover types within a given bird territory should create suitable habitats and meet resource requirements which is critical for conservation (Daniels & Kirkpatrick, 2006). At the landscape scale, interconnected networks of suitable habitats improve the viability of populations (Douglas & Sadler, 2011). Because urbanized environments are usually

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highly fragmented (Grimm et al., 2008), management effort to build green space networks is needed to support biodiversity (Lepczyk et al., 2017). However, many urban land-use planning strategies in Europe currently seek to mitigate urban sprawl by urban densification (ARE, 2009a; Fatone, Conticelli, & Tondelli, 2011; Maas, Verheij, Groenewegen, de Vries, & Spreuwenberg, 2006). For example, the city of Stockholm aims to increase the density of constructed impervious surfaces during its expected urban sprawl from 2000 to 2050, which will correspond to 90-km² of constructed impervious surface (Schmitt & Schlossman, 2012). Such land-use planning will obviously reduce urban green space and therefore involve trade-offs between future human use (i.e., urban densification) and biodiversity conservation (i.e., maintaining urban green space; Aronson et al., 2017). In the near future, urban sprawl and urban densification will constitute two opposite scenarios for the expansion of cities and will lead to different urban green space management to minimize their impacts on native biodiversity. Land-sharing vs. land-sparing concepts have been proposed as two contrasting urban green space management strategies to maximise urban biodiversity (Soga, Yamaura, Koike, & Gaston, 2014; Stott, Soga, Inger, & Gaston, 2015). In land-sharing, low density constructed impervious surfaces will be interspersed with green spaces (i.e. garden and park) but will lack large continuous green patch. Alternatively, in land-sparing, high density constructed impervious surfaces will have large continuous green spaces. These two concepts could be associate with vertical green infrastructure, such as green wall and roof garden, who may provide additional green spaces for biodiversity (Collins, Schaafsma, & Hudson, 2017). To date, understanding variations in and ecological aspects of intra-urban biodiversity has been obtained by comparing habitat variables within cities (Beninde, Veith, & Hochkirch, 2015), but no predictions have been made on how species distributions will be affected by future urban land-use scenarios.

In this study, we used the Common Redstart (*Phoenicurus phoenicurus*) as a model species to spatially define sustainable urban green space. We posited that the habitat suitability of the Common Redstart could serve as an indicator for sustainable urban green space due to the multiple ecological requirements of this bird (see A1. Table S.1). From a conservation point of view, the Common Redstart is a species of conservation concern in

Switzerland and other countries in Central Europe (BirdLife International, 2004; Spaar, Ayé, Zbinden, & Rehsteiner, 2012). The Common Redstart was originally found in semi-open areas such as orchards and woodland edges. However, in areas where changes from semi-open areas to rural landscapes have occurred, Common Redstart populations in urbanized areas have become of higher relative importance. Nowadays, monitoring programs and regional atlas projects in Europe estimate that between 17 and 59% of Common Redstart populations are located in urbanized areas (Droz, Arnoux, Rey, Bohnenstengel, & Laesser, 2015). This large variation is likely due to non-homogenous land conversion changes across Europe (Verburg & Overmars, 2009).

In this study, we therefore address the following two questions: (1) what is the combination of environmental factors that best defines the suitable habitat of a Common Redstart territory in an urbanized environment?, and (2) how will these suitable habitat conditions be geographically affected under two realistic and contrasting future land-use scenarios? The first question has been qualitatively assessed in term of land-cover (Droz et al., 2015; Fontana, Sattler, Bontadina, & Moretti, 2011; Sedlacek, Fuchs, & Exnerova, 2004), however, the relative importance of topo-climatic environmental factors and the most suitable proportion of each land-cover surfaces within a territory remains to be known. The second question is key to prioritize urban areas and balance future urban development strategies between land-sparing and land-sharing. To address these two questions, we used a collection of species distribution models (SDMs) in combination with high-resolution predicting variables (2 × 2 m grid cell) to analyze data obtained from a medium-sized town in Switzerland. By modelling the habitat of an indicator species and simulating realistic land-use scenarios, our aim was to provide clear recommendations to local authorities and urban planners on management strategies needed to promote and conserve an interconnected urban green space network and thereby biodiversity.

2. Material and methods

Our methodological concept consisted of five steps (Fig. 1). First, species data were acquired and predicting variables were identified as

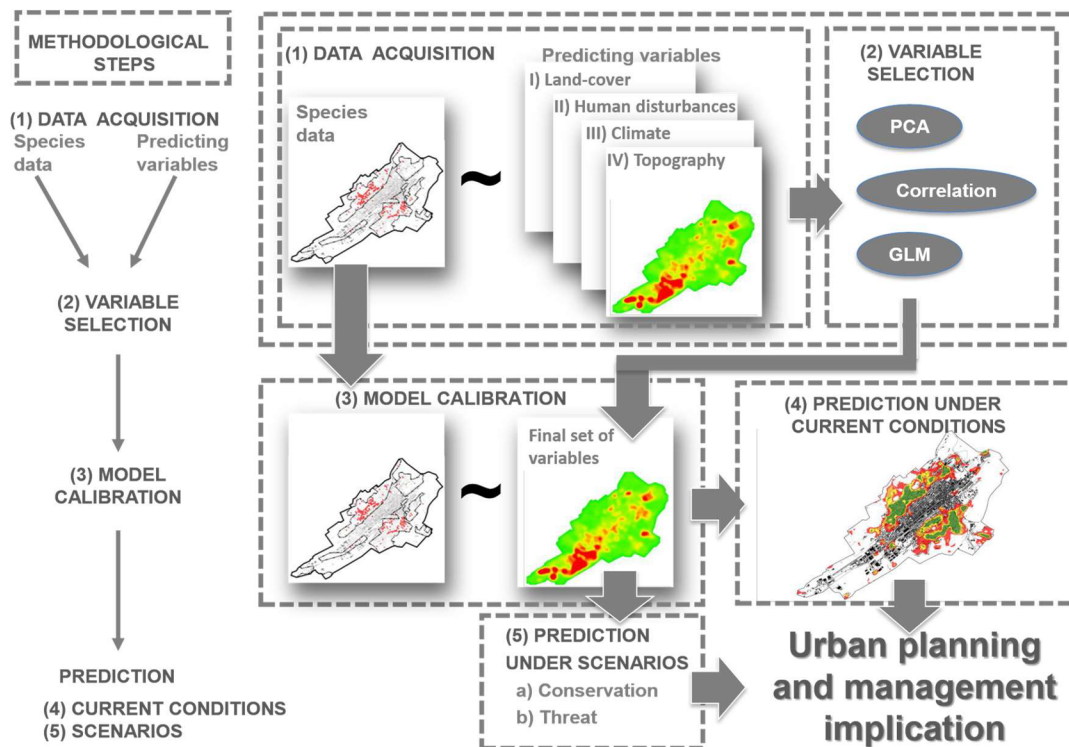


Fig. 1. Conceptual chart summarizing methods. Numbers in the figure correspond to the chapters in the material and method section. PCA refers to principal components analysis, correlation refers to Pearson’s correlation coefficients between predicting variables, and GLM refers to univariate generalized linear models.

specific ecological requirements for the species (step 1). Next, a subset of the predicting variables was selected (step 2) to calibrate SDMs to define the suitable habitat of a Common Redstart territory in an urbanized environment (step 3). The species distribution was then predicted under the current conditions of the study area (step 4). After this, we simulated the changes of species distribution under an increase in tree canopy coverage as a conservation scenario and under an increase in impervious surfaces (i.e. the combination of asphalted surfaces and buildings) as a threat scenario (step 5). Step one was conducted in ArcGIS 9.3 (ESRI, Redlands, CA) and steps two through five were conducted in R (R Development Core Team, Vienna, Austria).

2.1. Data acquisition: species data and predicting variables

We collected 1762 presence data points of Common Redstart from yearly censuses (Droz et al., 2015) and observations of ornithologists collected through the official birding exchange platform in Switzerland (www.ornitho.ch) between 2004 and 2012. Data collection was restricted to the city of La Chaux-de-Fonds (Switzerland; 47°06'N, 6°47'E; Fig. 2a) within a sampling area of 5.4 km² (dashed black line; Fig. 2b). Territory mapping followed the methodology of Bibby et al. (2000). The median northing and easting of all observations within a territory was defined as the territory center, and the corresponding predictive variables were assessed as in Martinez, Jenni, Wyss, and Zbinden (2009) within a 100 m radius around the territory center. This buffer size corresponds to an average territory (i.e. 31400 m²) described for urban populations of Common Redstarts (Sedlacek et al., 2004) and included 95% of our field observations. All grid cells within the 283 resulting circular buffer were considered as presence data in the SDMs analysis.

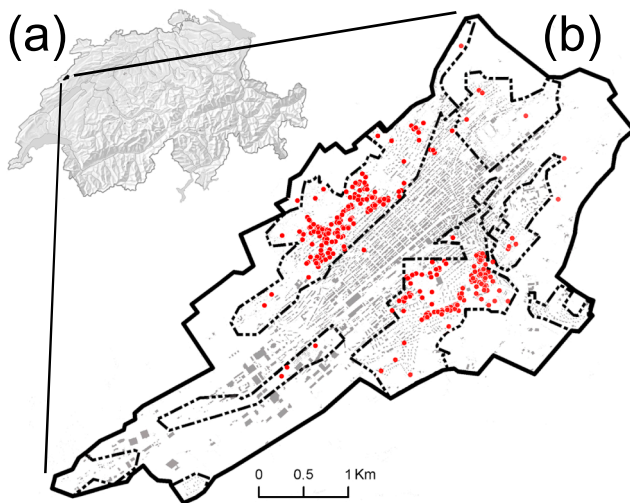


Fig. 2. Geographic location of the study area in Switzerland (a) with a detailed view of the city of La Chaux-de-Fonds (b). In (b), the sampling area (total surface = 5.4 km²) is delimited with dashed black lines. The median of each individual territory recorded between 2004 and 2012 used as presences to calibrate species distribution models (total number of territories, $n = 283$) are represented with red points. The study area (entire surface of the urban area; 14.2 km²) is delimited with a solid line. Geographic data were taken from Système d'Information du Territoire Neuchâtelois (SITN 2008; <http://sitn.ne.ch>). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Literature reviews of the specific ecological requirements (see Appendix A1, Tables S.1 and S.2) for the ecological niche of the Common Redstart and related species with similar requirements of sparse vegetation (Schaub, Martinez, Tagmann-Joset, Weisshaupt, & Maurer, 2010) were used to select 32 variables as potential predicting variables for consideration in the SDMs. The predicting variables belonged to four main categories: land-cover used for nesting and feeding, human disturbances restricting a sustainable occupation of territories, and climatic and topographic conditions required during the breeding period. The basic metrics used to compute this initial set of 32 predicting variables included land-cover categories, a digital elevation model, road traffic counts and human density estimates, as well as long-term mean monthly temperatures at 2 × 2 m resolution grid cells for the totality of the study area (Fig. 2b; 14.2 km²; further detail on building predicting variables can be found in Appendix A1).

2.2. Variable selection

No assumptions were made on the specific ecological requirements of the Common Redstart and its associate set of predicting variables. Therefore, three successive steps were performed independently to identify the most appropriate set of predicting variables and improve the model output. We followed the recommendation made by Araujo and Guisan (2006): (i) ordinary least squares regressions between each pair of variables to remove variables providing the same information, (ii) principal component analysis (PCA) to remove variables that contain the least information (i.e., noise variables); and (iii) univariate generalized linear models (GLM) to select the most appropriate variable response for the generalized regression modeling approach (McCullagh & Nelder, 1989). Presences and pseudo-absences used in (i) to (iii) were randomly selected (see Section 2.3 below), and the three analyses were repeated ten times to minimize spurious effects of geographic autocorrelation and to estimate the sampling bias on model fit and predictive power of univariate GLMs (Guisan & Zimmermann, 2000).

Multicollinearity between two dependent predicting variables was assessed by ordinary least squares regressions. Resulting Pearson's correlations were used to remove one of the predicting variables for each highly correlated (i.e., $|R^2| > 0.7$) variable pair in the next step. The two first principal axes of the PCA matrix were used for analysis because they contained the greatest amount of information within the data set (PCA axe 1: 28.6 ± 0.1%, PCA axe 2: 20.6 ± 0.1%). Next, variable contribution and the relationship of each predictive variable on multiple scales were calculated under a distance biplot on the two first principal axes. Comparison of the Euclidean distance allowed us to remove variables which contained the least information ($|d| < 0.3$; Legendre & Legendre, 1998). Nevertheless, PCA was used with caution in removing variables. In the last step, univariate GLMs with a second-order polynomial function were computed for each continuous predicting variable. The performance of each univariate GLM was evaluated by running a 10-fold cross-validation (Randin et al., 2006) and taking an average of the 10 replicates. Model fit was evaluated by the adjusted geometric mean squared improvement D^2 (i.e. model fit; Nagelkerke, 1991) and the predictive power was evaluated by the area under the curve (AUC; Hanley & McNeil, 1982). Predicting variables with poor fit ($D^2 < 0.07$) and low predicting power (AUC < 0.65) were considered not suitable for modeling purposes and consequently were not retained for the SDMs.

2.3. Models calibration

Nine variables were selected from the initial set of 32 variables and

Table 1

Set of selected predicting variables used for the calibration of species distribution models. Rank (i.e. by the relative importance) and optimum are the average values of the four modeling techniques. Standard deviation is indicated for both the relative importance and the variable optimum.

Rank	Predicting variables	Relative importance	Optimum	Unit
1	Trees canopy coverage	39.8 ± 4.2	20.4 ± 2.3	(%)
2	Impervious surface	24.5 ± 6.0	34.6 ± 3.7	(%)
3	Human population density	11.6 ± 2.7	0.20 ± 0.01	(number of human m-2)
4	Short-cut lawn	7.8 ± 2.8	47.5 ± 2.5	(%)
5	High herbaceous vegetation	7.7 ± 4.6	0.70 ± 0.48	(%)
6	Length of walls	3.2 ± 2.4	0.013 ± 0.002	(m m-2)
7	Traffic volume	2.8 ± 0.7	0.5951 ± 0.0003	(car day-1 m-2)
8	Bare ground	2.5 ± 1.9	5.6 ± 1.6	(%)
9	Solar radiation	0.17 ± 0.15	11177 ± 6257	(kJ m-2 day-1)

were used to calibrate multivariate SDMs (see Table 1: tree canopy coverage, impervious surface, human population density, short-cut lawn, high herbaceous vegetation, length of walls, traffic volume, bare ground and solar radiation). We used a suite of four distinct modeling techniques and calibrated them independently to avoid predictive biases toward one predictive technique (more details about the ensemble approach is provided below in the prediction section). The four models were further combined into an ensemble approach (as recommended in Araujo & New, 2007). These techniques included stepwise GLMs (McCullagh & Nelder, 1989) and general additive models (GAM; Hastie & Tibshirani, 1986), multi-model inference (MMI; Burnham & Anderson, 2002) with GLMs and maximum entropy models (Maxent; Phillips & Dudik, 2008).

For each technique, 10 presences were randomly selected within each territory (i.e. a total of 2830 presences) together with 10000 randomly selected pseudo-absences outside territories within the sampling area (as recommended for the four modeling techniques by Barbet-Massin, Jiguet, Albert, & Thuiller, 2012). This random selection procedure is needed to avoid type I statistical error (Bahn, O'Connor, & Krohn, 2006) due to the spatial autocorrelation occurring between all neighborhood pixels inside a territory (representing 31400 m² and 7850 2 × 2 m resolution grid cells). In this context, our randomly selected presences and absences presented a dispersed spatial pattern without significant spatial correlation for all predictive variables extracted below (Moran's test; $I_{\text{mean}} = -0.29 \pm 0.11$, $P\text{-value}_{\text{mean}} = 0.05 \pm 0.01$). Randomly selected absences were expected to represent true absences due to the large survey effort on the study area (see above Data acquisition: species data), although the entire study area was not covered each year.

Stepwise GLMs and GAMs were calibrated with a logistic link function; a binomial error distribution and presence versus pseudo-absence were weighted. A second-order polynomial function was allowed for each predicting variable, which corresponded to a Gaussian response curve and satisfied the common assumptions of the ecological niche theory and species response along environmental gradients (Austin, Nicholls, Doherty, & Meyers, 1994; Pearman, Guisan, Broennimann, & Randin, 2008). Gaussian response curves were also used to approximate the optimum for each predicting variable (i.e. curve mean), which referred to the position along an environmental gradient producing the highest probability of presence (Oksanen & Minchin, 2002).

A stepwise procedure in both directions was used to select the final set of predicting variables in GLM and GAM and was based on the Akaike information criterion (AIC). This additional variable selection ensured parsimonious models compromising between fit and number of variables. MMI (Burnham & Anderson, 2002) and GLMs were calibrated as in Vicente, Alves, Randin, Guisan, and Honrado (2010) with a set of competing GLMs. Performance of each model technique was evaluated

using a 10-fold cross-validation based on the area under the curve (AUC; Hanley & McNeil, 1982) and the true skill statistics (TSS; Allouche, Tsoar, & Kadmon, 2006).

The relative contribution of each variable and for each modeling technique was calculated as in Thuiller, Lafourcade, Engler, and Araujo (2009): the vector of values of the variable under investigation was randomly permuted 1000 times and the predictions on the training dataset (i.e. probability of occurrence) were re-computed each time on the permuted dataset. Then, the two sets of predictions (original and permuted) were compared using Pearson's correlation. Each value was the Pearson's correlation score between a permuted set of the predictor, and the reference set minus 1. The higher the value, the more influence the predictor had on the model. The contribution was finally reported in relative importance between 0 (no importance) and 100% (high importance).

2.4. Prediction under current condition

Geographic predictions were performed using 2 × 2 m resolution grid cells for the totality of the study area with an ensemble approach combining the four modeling techniques and as recommended by Araujo and New (2007). TSS for each modeling technique was used for the transformation of predicting probabilities into binary presences and absences (Allouche et al., 2006). Reclassified binomial geographic predictions of each of the four techniques were then summed to produce the ensemble of SDMs (Marmion, Hjort, Thuiller, & Luoto, 2009). Ensemble of SDMs combined accuracy and robustness of each technique to reduce the uncertainty of the prediction (Araujo & New, 2007). By consequence, we defined a habitat as suboptimum when the species was predicted to occur by one to three of the modeling techniques and as optimum when it was predicted by all four modeling techniques. Here we considered a relationship between the environmental suitability projected by SDMs and key parameters of fitness (as shown by e.g. Brambilla & Ficetola, 2012 for bird species).

2.5. Predictions under a conservation and under a threat scenario

Two scenarios reflecting potential future land-use outcomes were designed. These scenarios were driven by current national and local laws and regulations in Switzerland and aimed to illustrate: (i) conservation opportunities (Fig. 3b) that refer to an increase in potentially suitable surfaces for the Common Redstarts or (ii) threats (Fig. 3c) that refer to a decrease in potentially suitable surfaces. For both scenarios, modification of land-cover was simulated in areas where the urban development planning of the city of La Chaux-de-Fonds allows it (Le conseil général de la ville de La Chaux-de-Fonds, 1998) considering no building destruction. Under these constraints, modifications were allowed in 60% and 53% of the study area for the conservation and threat

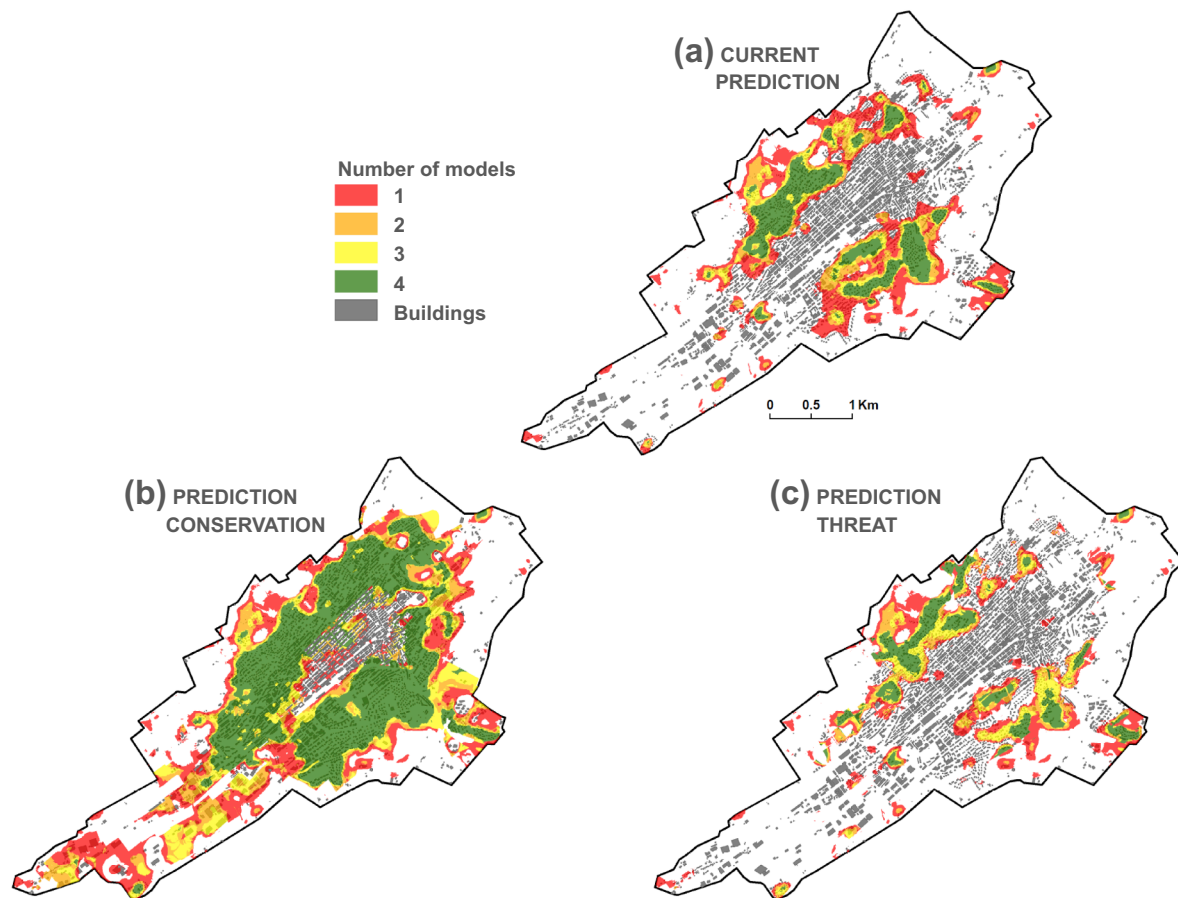


Fig. 3. Geographic prediction of the species distribution models (SDMs). (a) Current prediction, (b) prediction for the conservation scenario with optimisation of the tree canopy coverage until 20%, and (c) prediction for the threat scenario with a mean of impervious surfaces of 53%. Colors show the number of model techniques, which predicted a presence from 1 (one technique predicted a cell (2×2 m) as potentially suitable) to 4 (all techniques predicted a cell as potentially suitable).

scenarios respectively (see area of modification in A1. Fig. S1). In the conservation scenario, tree canopy coverage per grid cell was recalculated for every 2.5% stepwise until the increase reached the optimum values of 20% (optimum calculated in the section 2.3). In the threat scenario, impervious surface cover was increased by 2.5% stepwise per grid cell and the corresponding decrease in the sum of bare ground, high herbaceous vegetation and short-cut lawn was recalculated until the sum of these land-covers reached zero in each grid cell. Due to the restriction made by the urban plan of the city, both scenarios reach saturation before more modification were possible (see A1. Fig. S2).

Additionally, connectivity, which represents the degree to which a habitat is spatially continuous (Goddard et al., 2010), was separately calculated for each grid cell in the study area and each ensemble of modeling techniques. Connectivity was calculated as the total number of suitable cell in a 3×3 -cells window around the focus cell divided by eight (Randin, Jaccard, Vittoz, Yoccoz, & Guisan, 2009). Eight (unitless) constitutes the maximum possible connections to other suitable cells for a focal cell. The connectivity for each modeling was summed to create a global mean connectivity (i.e. connectivity between suitable habitats predicted by at least one of the four modeling techniques). Finally, changes in potentially suitable surfaces and mean connectivity within the study area were assessed for each 2.5% stepwise increase and for each scenario in order to identify at which steps potential thresholds and tipping points in gain or loss of habitat suitability could be detected and to further provide recommendations for an optimum conservation and management strategy.

3. Results

3.1. Predicting variables under current condition

A set of nine predicting variables were retained to calibrate multi-variate species distribution models (SDMs). Of these retained variables (Table 1), tree canopy coverage and impervious surface were the two most important predicting variables. Human population density, short-cut lawn, and high herbaceous vegetation were ranked from three to five in terms of importance (mean importance ranging from 12 to 7%).

The calculated optimum for each of the land-cover variables suggested that the optimum habitat (i.e. mean over the four model techniques) within a territory corresponds to a combination of $47.5 \pm 2.5\%$ short-cut lawn, $34.6 \pm 3.7\%$ impervious surfaces from which $12.5 \pm 1.5\%$ are building coverage, and an overall tree canopy coverage of $20.4 \pm 2.3\%$. Geographic predictions of SDMs under current conditions (Fig. 3a) revealed that optimum habitats (i.e. predicted as potentially suitable by all four modeling techniques) represented only 7% of the study area and were confined within moderately urbanized areas of the city (i.e. with less than 40% of impervious surfaces). Suboptimum habitats (i.e. predicted as suitable by one to three modeling techniques) represented 27% of the study area.

3.2. Predictions under a conservation and threat scenario

Under the conservation scenario within the study area, 57% of suboptimum habitats under current conditions were converted into

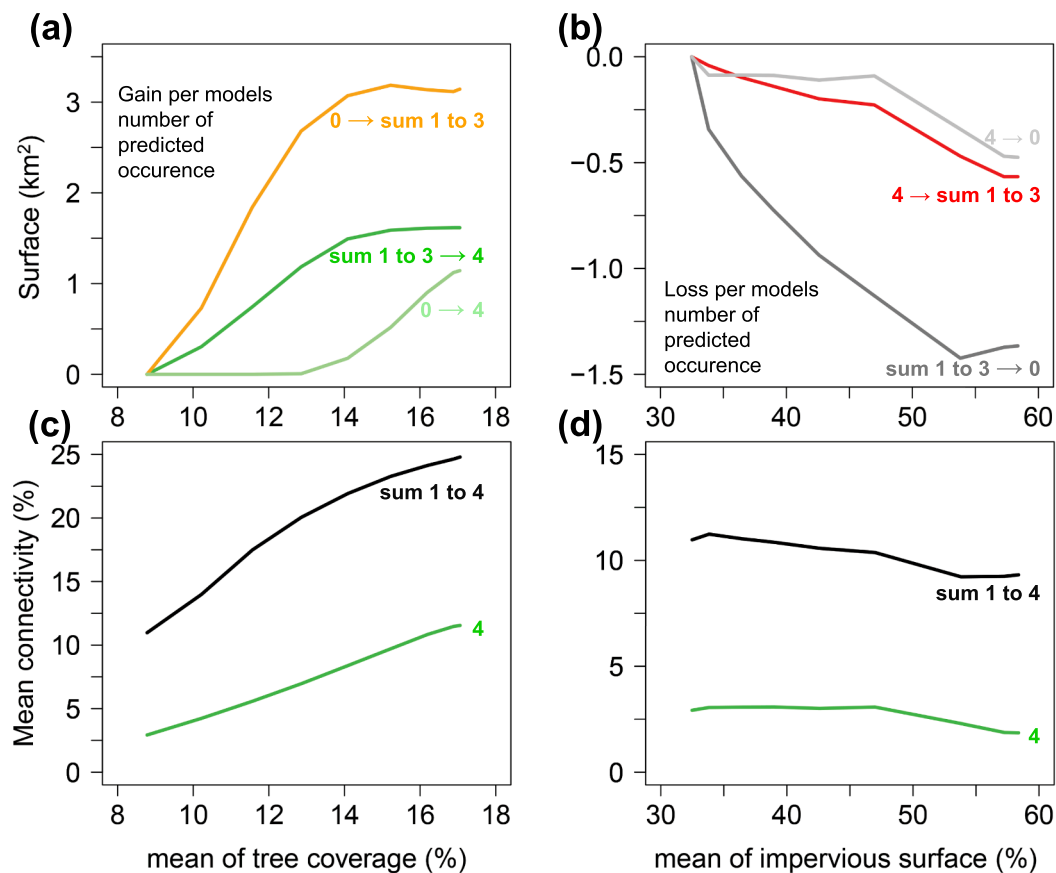


Fig. 4. Modification of the predicted potential suitable areas for the Common Redstart and mean connectivity between suitable habitats in the study area under the conservation (a & c) and the threat (b & d) scenarios driven by a step-wise increase in tree canopy coverage and impervious surface, respectively. In (a), the green line represents the perspective of suboptimum habitats (i.e. predicted as potentially suitable by 1–3 modeling techniques) and optimum habitats (i.e. predicted as potentially suitable by all four modeling techniques) under the conservation scenario. The orange line represents unsuitable areas under the current conditions predicted to become suboptimum habitats under the conservation scenario. Finally, the light green line represents the new optimum habitats. In (b), colors represent the loss of habitat suitability in the reverse process than explained for (a). In (c) & (d), mean connectivity of the four techniques (green) and for the sum of all techniques (black) which predicted a presence are plotted for the two scenarios. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

optimum habitats when the mean tree canopy coverage was forced to reach 20% (Fig. 4a). Furthermore, 11% of unsuitable habitats under current conditions were converted into suboptimum habitats when the mean of tree canopy coverage was increased to 13%. Beyond this value, new suboptimum habitats were then progressively converted into optimum habitats until a plateau for all potentially suitable habitats was reached at 17% of tree canopy coverage. This scenario plateau contained 24.7% of suboptimum and 26.8% of optimum habitats in the study area. In addition, when habitats were promoted to optimal or suboptimal (when mean tree canopy coverage reached 17%), the global mean connectivity (i.e. connectivity between suitable habitats predicted by at least one of the four modeling techniques) was increased from 11 to 25% (Fig. 4c). Overall, the conservation scenario predicted a linear increase in optimum habitats for the Common Redstart from 7 to 27% of the study area when tree canopy coverage was increased to 20%.

The threat scenario predicted a decrease in optimum habitats from 7.1 to 3.5% within the study area when the mean of impervious surface was increased from 25 to 53% (Fig. 4b). Like the conservation scenario, variations in optimum habitats triggered a proportional modification of the global mean connectivity but with only a slight decrease from 11 to 9% (Fig. 4d). However, this decrease occurred only after a 47.5% increase in the mean of impervious surface.

4. Discussion

In this study, our methodological framework (Fig. 1) using species distribution models (SDMs) was able to identify key environmental factors and their optimum combination that promote potential habitats for the Common Redstart. Conservation and threat scenarios for the species allowed us to predict the potential distribution gain or loss under future land-use changes. The optimum combination of land-cover types offering the most suitable habitat within the territory of the Common Redstart in an urbanized environment is composed of 50% short-cut lawn, 35% impervious surfaces and 20% tree canopy within a territory. Under a land-use change scenario focused on conservation, more than half of suboptimum habitats under current conditions could be converted into optimum habitats when the mean tree canopy coverage was forced to reach the optimum value of 20%. In contrast, and under a land-use change scenario focused on densification of constructed surfaces, a significant decrease in suitable habitats and connectivity between these suitable habitats was observed when the proportion of impervious surfaces reached half of the total surface of a territory.

Tree canopy coverage was the most important variable at the territory scale when modeling potential suitable habitats of the Common Redstart in a moderately urbanized environment where the requirement for short-cut

lawn was largely satisfied (Droz et al., 2015). This is not surprising given that Common Redstart's primary habitat is open forest. Glutz von Blotzheim and Bauer (1988) explicitly state: "trees must not be absent". Fontana et al. (2011) suspected that not all tree species and ages contribute to habitat suitability in the same way. In our study area, the importance of trees cannot be explained by nest site availability: tree cavities hosted only 5% of nests found during our survey versus 62% in building cavities (Droz et al., 2015). However, trees indirectly produce an important biomass of soil invertebrates (Smith, Gaston, Warren, & Thompson, 2006) and were generally associated with nearby sparse vegetation under the tree (Manning, Gibbons, & Lindenmayer, 2009), which could increase hunting success of the Common Redstart (Martinez et al., 2009). The species also forages in the canopy of trees (Glutz von Blotzheim & Bauer, 1988; own obs.). Common Redstarts show a preference for habitats including forests, graveyards and others with a high proportion of mature and decaying trees (Glutz von Blotzheim & Bauer, 1988). Additionally, our field observations also confirmed that territories containing large mature trees are favored by Common Redstarts. This strengthens our idea that the Common Redstart acts as an umbrella species.

In European cities, urban green spaces constitute 2–46% of the total surface area (Fuller & Gaston, 2009), including 16–47% of private lawns/gardens (which are generally mowed frequently; Goddard et al., 2010) and 4–70% of trees (Casalegno, 2011). When SDMs were projected under a realistic conservation scenario in our study, potential optimum habitats could be increased by a factor of 3.8 in our study area when increasing tree canopy coverage. Our study shows that there is potential to promote the habitat of the Common Redstart by enhancing the density of trees and promoting large and mature indigenous trees. However, due to slow tree growth, efforts might only become effective several decades after planting (Loram, Warren, & Gaston, 2008), therefore tree management is very important to promote habitat management.

Predictions under the threat scenario with increasing impervious surfaces suggested a certain resilience of habitat suitability for the Common Redstart (Fig. 4.b; conversion of optimal surface into unsuitable or suboptimal). Similar relationships for an insect were obtained at low levels of urbanization (Soga et al., 2014) suggesting that, in our study, urban densification should proceed only with great care and under preservation of green spaces (i.e., land-sharing or vertical green infrastructure) to minimize impacts on native biodiversity. However, it should be noted that our threat predictions underestimate impacts due to removal of mature trees during housing construction or to increased garden size (Daniel, Morrison, & Phinn, 2016; Lambelet-Haueter et al., 2011), and substitutions by young trees, other vegetation types or structures might not alleviate the negative effect of removing mature trees. In addition, the decrease of global mean connectivity predicted after the mean of impervious surfaces reached 47.5% (Fig. 4d) indicated that this proportion should be considered as a limit before isolation and/or fragmentation from other neighboring habitats may damage the habitat for the Common Redstart.

To promote habitats for the Common Redstart under a conservation scenario in moderately urbanized area, we propose several management recommendations. First, we recommend increasing tree canopy coverage to 20% in areas where the proportion of impervious surface is below 35%. In addition, we recommend maintaining an appropriate combination of land-cover types such as the combination defined in our study (see Table 1) to ensure optimum habitat on the territory-scale. We also recommend maintaining connectivity between optimum habitats to satisfy a territory size as well as ensure a stable population dynamic at the city-scale. We have two additional management recommendations related to specific ecological requirements of the Common Redstart (see Appendix A1. Tables S.1 and S.2). First, nesting cavities in new or renovated buildings or nest boxes should be placed to enhance reproduction possibilities. Second, small man-made structures (e.g. wildflower strips, dead trees, woodpile branches, stone walls, bare ground) containing high prey density (e.g. insects, arachnids) within

cities should be made to provide additional food sources to the nearby short-cut lawns (Martinez et al., 2009).

The results of our study (i.e. the importance of a combination of land-cover types to predict the potential distribution of the Common Redstart) corroborate those recommended to enhance global urban biodiversity in Central Europe (Fontana et al., 2011; Sattler, Duelli, Obrist, Arlettaz, & Moretti, 2010). Accordingly, the Common Redstart is a good model species to promote sustainable and green urban planning in moderately urbanized areas. Our management recommendations, based on the optima of land-cover types in SDMs, also fit very well with recent expert recommendations: to ensure functional biodiversity, urban areas require at least 18% of green surfaces of a high landscape quality (Guntern, Lachat, Pauli, & Fischer, 2013). Moreover, a sociologic study (Home, Keller, Nagel, Bauer, & Hunziker, 2009) and citizen science programs (Brossard, Lewenstein, & Bonney, 2005; Sullivan et al., 2009) demonstrated that birds are very popular and therefore are key species to use in raising awareness of and promoting green urban planning to city inhabitants and policymakers (Dunn, Gavin, Sanchez, & Solomon, 2006; Turner, Nakamura, & Dinetti, 2004). In Switzerland, the optima of land-cover types match well with the combination of green land-cover patches containing trees, which is preferred by 60% of the population as a living environment (Obrist et al., 2012). Connectivity and a combination of land-cover types are also crucial for ground-dwelling animals (e.g. European hedgehog *Erinaceus europaeus*; Braaker et al., 2014) and could benefit urban biodiversity in general, such as forest birds which breed regularly in cities (e.g. high priority species in Switzerland: the Fieldfare *Turdus pilaris*; Spaar et al., 2012) as well as insects and spiders (Atkinson et al., 2005; Smith et al., 2006).

Future urban planning should prioritize the conservation, extension, and connection of potential optimum habitats to create an urban green space network as individual green patches are likely too small for hosting viable populations (Goddard et al., 2010). Meta-analysis estimated that sites greater than 50 ha of urban green space are necessary to prevent a rapid loss of area-sensitive species (Beninde et al., 2015). Indeed, the size of suitable habitats is usually correlated with population resilience (Pulliam, 2000) and in turn, small and localized patches could be considered suboptimum for population survival (Dale, 2001). In addition, connectivity was recognized as a key factor for recolonization processes from source populations to newly-created suitable habitats (Taylor, Fahrig, Henein, & Merriam, 1993) and for promoting ecological processes required for population survival such as movement along resource patches (Mimet, Houet, Julliard, & Simon, 2013).

Our predictions under the two scenarios were based on a gradual increase in tree cover or impervious surface in all pixels of the study area that are allowed, until a maximum was reached. However, it is likely that these changes will not be homogeneous in the landscape and that a maximum will be reached with high changes in some regions and only small changes in other regions of our study area, thus also affecting habitat suitability. In addition, in our study, we only used the vertical structure of the trees without any consideration of species identity, which could strongly affect bird's feeding habitat quality. Further studies should consider the identity of tree species when building the scenarios since such data are already available (Andrew & Asner, 2014; van Ewijk, Randin, Treitz, & Scott, 2014) as well as potential changes in species composition. Last, we calculated our connectivity index with a structural measure of connectivity, based on land-cover categories. Considering a functional connectivity that would include information about species movement and e.g. the crossing capacity (Awade & Metzger, 2008) will likely provide better ecological information.

5. Conclusion

Similar to many other cities in Europe, La Chaux-de-Fonds contains moderately urbanized areas. However, since the 1950s, city municipalities have promoted urban densification, which was recently

enforced by country and regional policy in Europe to mitigate urban sprawl, reduce energy consumption (ARE, 2009a; Fatone et al., 2011), and by consequence reduce the loss of native ecosystem (i.e. woodlands and farmlands). However, moderately urbanized areas with green space networks have a high potential for hosting some species of birds that are threatened due to habitat degradation in their native ecosystems. As a paradoxical consequence, the urban densification planned in many European countries could penalize some endangered urban ecosystems and reduce biodiversity. In this context, the methodology developed in this study could help urban planning and policy makers to better target areas where urban densification could be performed and where the structure of green spacing and housing should be conserved. Future sustainable urban planning should both mitigate urban sprawl and reduce impacts on existing and future urban biodiversity (Haaland & van den Bosch, 2015).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.landurbplan.2018.09.011>. These data include Google maps of the current and conservation scenarios described in this article.

References

BirdLife International (Ed.). (2004). *Birds in Europe: population estimates, trends and conservation status*, BirdLife Conservation serie n°12. Cambridge: BirdLife International.

Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, 43(6), 1223–1232. <https://doi.org/10.1111/j.1365-2664.2006.01214.x>.

Andrew, D. B., & Asner, G. P. (2014). Advances in animal ecology from 3D-LiDAR ecosystem mapping. *Trends in Ecology & Evolution*, 29(12), 681–691. <https://doi.org/10.1016/j.tree.2014.10.005>.

Antrop, M. (2004). Landscape change and the urbanization process in Europe. *Landscape and Urban Planning*, 67(1–4), 9–26. [https://doi.org/10.1016/S0169-2046\(03\)00026-4](https://doi.org/10.1016/S0169-2046(03)00026-4).

Araujo, M. B., & Guisan, A. (2006). Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, 33(10), 1677–1688. <https://doi.org/10.1111/j.1365-2699.2006.01584.x>.

Araujo, M. B., & New, M. (2007). Ensemble forecasting of species distributions. *Trends in Ecology & Evolution*, 22(1), 42–47. <https://doi.org/10.1016/j.tree.2006.09.010>.

ARE (2009a). *Concept pour un développement urbain vers l'intérieur: Aide de travail pour l'élaboration des projets d'agglomération transport et urbanisation (Concept for inside urban development - working support for the development of the agglomeration programs*

traffic and settlement). Berne: Office fédéral du développement territorial.

ARE (2009b). *Monitoring de l'espace urbain suisse – Analyses des villes et agglomérations (Monitoring on the Swiss urban space - Analysis of town and surrounding)*. Bern: Office fédéral du développement territorial.

Aronson, M. F. J., La Sorte, F. A., Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., ... Winter, M. (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B-Biological Sciences*, 281(1780), 20133330. <https://doi.org/10.1098/Rspb.2013.3330>.

Aronson, M. F. J., Lepczyk, C. A., Evans, K. L., Goddard, M. A., Lerman, S. B., MacIvor, J. S., ... Vargo, T. (2017). Biodiversity in the city: Key challenges for urban green space management. *Frontiers in Ecology and the Environment*, 15(4), 189–196. <https://doi.org/10.1002/fee.1480>.

Atkinson, P. W., Fuller, R. J., Vickery, J. A., Conway, G. J., Tallowin, J. R. B., Smith, R. E. N., ... Brown, V. K. (2005). Influence of agricultural management, sward structure and food resources on grassland field use by birds in lowland England. *Journal of Applied Ecology*, 42, 932–942. <https://doi.org/10.1111/j.1365-2664.2005.01070.x>.

Austin, M. P., Nicholls, A. O., Doherty, M. D., & Meyers, J. A. (1994). Determining species response functions to an environmental gradient by means of a β -function. *Journal of Vegetation Science*, 5(2), 215–228. <https://doi.org/10.2307/3236167>.

Awade, M., & Metzger, J. P. (2008). Using gap-crossing capacity to evaluate functional connectivity of two Atlantic rainforest birds and their response to fragmentation. *Austral Ecology*, 33(7), 863–871. <https://doi.org/10.1111/j.1442-9993.2008.01857.x>.

Bahn, V., O'Connor, R. J., & Krohn, W. B. (2006). Importance of spatial autocorrelation in modeling bird distributions at a continental scale. *Ecography*, 29(6), 835–844. <https://doi.org/10.1111/j.2006.0906-7590.04621.x>.

Barbet-Massin, M., Jiguet, F., Albert, C. H., & Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: How, where and how many? *Methods in Ecology and Evolution*, 3(2), 327–338. <https://doi.org/10.1111/j.2041-210X.2011.00172.x>.

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>.

Bibby, C. J., Burgess, N. D., Hill, D. A., & Mustoe, S. (Eds.). (2000). *Bird census techniques*. Academic press.

Braaker, S., Moretti, M., Boesch, R., Ghazoul, J., Obrist, M. K., & Bontadina, F. (2014). Assessing habitat connectivity for ground-dwelling animals in an urban environment. *Ecological Applications*, 24(7), 1583–1595. <https://doi.org/10.1890/13-1088.1>.

Brambilla, M., & Ficetola, G. F. (2012). Species distribution models as a tool to estimate reproductive parameters: A case study with a passerine bird species. *Journal of Animal Ecology*, 81(4), 781–787. <https://doi.org/10.1111/j.1365-2656.2012.01970.x>.

Brossard, D., Lewenstein, B., & Bonney, R. (2005). Scientific knowledge and attitude change: The impact of a citizen science project. *International Journal of Science Education*, 27(9), 1099–1121. <https://doi.org/10.1080/09500690500069483>.

Burnham, K. P., & Anderson, D. R. (Eds.). (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). New York: Springer Verlag.

Casalegno, S. (2011). Urban and peri-urban tree cover in European Cities: Current distribution and future vulnerability under climate change scenarios. In S. Casalegno (Ed.), *Global warming impacts – Case studies on the economy, human health, and on urban and natural environments*. Italy: InTech.

Collins, R., Schaafsma, M., & Hudson, M. D. (2017). The value of green walls to urban biodiversity. *Land Use Policy*, 64, 114–123. <https://doi.org/10.1016/j.landusepol.2017.02.025>.

Dale, S. (2001). Female-biased dispersal, low female recruitment, unpaired males, and the extinction of small and isolated bird populations. *Oikos*, 92(2), 344–356. <https://doi.org/10.1034/j.1600-0706.2001.920217.x>.

Daniel, C., Morrison, T. H., & Phinn, S. (2016). The governance of private residential land in cities and spatial effects on tree cover. *Environmental Science & Policy*, 62, 79–89. <https://doi.org/10.1016/j.envsci.2016.01.015>.

Daniels, G. D., & Kirkpatrick, J. B. (2006). Does variation in garden characteristics influence the conservation of birds in suburbia? *Biological Conservation*, 133(3), 326–335. <https://doi.org/10.1016/j.biocon.2006.06.011>.

Donald, P. F., Green, R. E., & Heath, M. F. (2001). Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society B-Biological Sciences*, 268(1462), 25–29. <https://doi.org/10.1098/rspb.2000.1325>.

Donald, P. F., Sanderson, F. J., Burfield, I. J., & van Bommel, F. P. J. (2006). Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. *Agriculture Ecosystems & Environment*, 116(3–4), 189–196. <https://doi.org/10.1016/j.agee.2006.02.007>.

Douglas, I., & Sadler, J. (2011). Urban wildlife corridors: Conduits for movement or linear habitat? In I. Douglas, D. Goode, M. Houck, & R. Wang (Eds.), *Handbook of urban ecology* (pp. 274–288). Routledge.

Droz, B., Arnoux, R., Rey, E., Bohnenstengel, T., & Laesser, J. (2015). Characterizing the habitat requirements of the Common Redstart *Phoenicurus phoenicurus* in moderately urbanized areas. *Ornis Fennica*, 92(3), 112–122.

Dunn, R. R., Gavin, M. C., Sanchez, M. C., & Solomon, J. N. (2006). The pigeon paradox: Dependence of global conservation on urban nature. *Conservation Biology*, 20(6), 1814–1816. <https://doi.org/10.1111/j.1523-1739.2006.00533.x>.

Fatone, S., Conticelli, E., & Tondelli, S. (2011). Environmental sustainability and urban densification. In M. Pacetti, G. Passerini, C. A. Brebbia, & G. Latini (Eds.), *The sustainable city VII: Urban regeneration and sustainability* (pp. 217–228). Southampton, UK: WIT Press.

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., ... Snyder, P. K. (2005). Global consequences of land use. *Science*, 309(5734), 570–574. <https://doi.org/10.1126/science.1111772>.

Fontana, S., Sattler, T., Bontadina, F., & Moretti, M. (2011). How to manage the urban

- green to improve bird diversity and community structure. *Landscape and Urban Planning*, 101(3), 278–285. <https://doi.org/10.1016/j.landurbplan.2011.02.033>.
- Fuller, R. A., & Gaston, K. J. (2009). The scaling of green space coverage in European cities. *Biology Letters*, 5(3), 352–355. <https://doi.org/10.1098/rsbl.2009.0010>.
- Glutz von Blotzheim, U., & Bauer, K. M. (Eds.). (1988). *Handbuch der Vögel Mitteleuropas Band 11/1: Gartenrotschwanz *Phoenicurus phoenicurus* (Handbook of European Birds: the Common Redstart)*. Wiesbaden: Aula Verlag.
- 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>.
- Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X., & Briggs, J. M. (2008). Global change and the ecology of cities. *Science*, 319(5864), 756–760. <https://doi.org/10.1126/science.1150195>.
- Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling*, 135(2–3), 147–186. [https://doi.org/10.1016/S0304-3800\(00\)00354-9](https://doi.org/10.1016/S0304-3800(00)00354-9).
- Gunter, J., Lachat, T., Pauli, D., & Fischer, M. (2013). *Surface requise pour la sauvegarde de la biodiversité en Suisse (Area requirement to protect biodiversity in Switzerland)*. Berne: Forum Biodiversité Suisse.
- Haaland, C., & van den Bosch, C. K. (2015). Challenges and strategies for urban green-space planning in cities undergoing densification: A review. *Urban Forestry & Urban Greening*, 14(4), 760–771. <https://doi.org/10.1016/j.ufug.2015.07.009>.
- Hanley, J. A., & McNeil, B. J. (1982). The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology*, 143(1), 29–36. <https://doi.org/10.1148/radiology.143.1.7063747>.
- Hastie, T., & Tibshirani, R. (1986). Generalized additive models. *Statistical Science*, 1(3), 297–318.
- Hayek, U. W., Jaeger, J. A. G., Schwick, C., Jarne, A., & Schuler, M. (2011). Measuring and assessing urban sprawl: What are the remaining options for future settlement development in Switzerland for 2030? *Applied Spatial Analysis and Policy*, 4(4), 249–279. <https://doi.org/10.1007/s12061-010-9055-3>.
- Home, R., Keller, C., Nagel, P., Bauer, N., & Hunziker, M. (2009). Selection criteria for flagship species by conservation organizations. *Environmental Conservation*, 36(2), 139–148. <https://doi.org/10.1017/S0376892909900051>.
- Ives, C. D., Lentini, P. E., Threlfall, C. G., Ikin, K., Shanahan, D. F., Garrard, G. E., ... Kendal, D. (2016). Cities are hotspots for threatened species. *Global Ecology and Biogeography*, 25(1), 117–126. <https://doi.org/10.1111/geb.12404>.
- Lambelet-Haueyer, C., Burgisser, L., Clerc, P., Gloor, S., Moeschler, P., Monney, J.-C., ... Zbinden, N. (2011). Evolution du milieu urbain (Urban environment change). In T. Lachat, D. Pauli, Y. Gonseth, G. Klaus, C. Scheidegger, P. Vittoz, & T. Walter (Eds.). *Evolution de la biodiversité en Suisse depuis 1900. Avons-nous touché le fond?*. Berne: Haupt Verlag.
- Le conseil général de la ville de La Chaux-de-Fonds. (1998). Règlement d'aménagement (Planning regulations). <http://www.chaux-de-fonds.ch/fr/administration> (Accessed on 1st December 2009).
- Legendre, P., & Legendre, L. (Eds.). (1998). *Numerical ecology*. Elsevier.
- Lepczyk, C. A., Aronson, M. F. J., Evans, K. L., Goddard, M. A., Lerman, S. B., & MacIvor, J. S. (2017). Biodiversity in the city: Fundamental questions for understanding the ecology of urban green spaces for biodiversity conservation. *BioScience*, 67(9), 799–807. <https://doi.org/10.1093/biosci/bix079>.
- Loram, A., Warren, P. H., & Gaston, K. J. (2008). Urban domestic gardens (XIV): The characteristics of gardens in five cities. *Environmental Management*, 42(3), 361–376. <https://doi.org/10.1007/s00267-008-9097-3>.
- Maas, J., Verheij, R. A., Groenewegen, P. P., de Vries, S., & Spreeuwenberg, P. (2006). Green space, urbanity, and health: How strong is the relation? *Journal of Epidemiology and Community Health*, 60(7), 587–592. <https://doi.org/10.1136/jech.2005.043125>.
- Manning, A. D., Gibbons, P., & Lindenmayer, D. B. (2009). Scattered trees: A complementary strategy for facilitating adaptive responses to climate change in modified landscapes? *Journal of Applied Ecology*, 46(4), 915–919. <https://doi.org/10.1111/j.1365-2664.2009.01657.x>.
- Marmion, M., Hjort, J., Thuiller, W., & Luoto, M. (2009). Statistical consensus methods for improving predictive geomorphology maps. *Computers & Geosciences*, 35(3), 615–625. <https://doi.org/10.1016/j.cageo.2008.02.024>.
- Martinez, N., Jenni, L., Wyss, E., & Zbinden, N. (2009). Habitat structure versus food abundance: The importance of sparse vegetation for the common redstart *Phoenicurus phoenicurus*. *Journal of Ornithology*, 151, 297–307. <https://doi.org/10.1007/s10336-009-0455-6>.
- McCullagh, P., & Nelder, J. A. (Eds.). (1989). *Generalized linear models*. London: Chapman and Hall.
- Mimet, A., Houet, T., Julliard, R., & Simon, L. (2013). Assessing functional connectivity: A landscape approach for handling multiple ecological requirements. *Methods in Ecology and Evolution*, 4(5), 453–463. <https://doi.org/10.1111/2041-210x.12024>.
- Müller, N., Elsner, K., & Wittmann, A. (2014). Der URBIO Index – ein Bewertungssystem zur Nachhaltigkeit von Grünflächen (The URBIO Index – an evaluation system for the sustainability of green spaces). In U. Feit, & H. Korn (Vol. Eds.), *Treffpunkt biologische Vielfalt XIII, BfN Skripten: 370*, (pp. 181–190). Bundesamt für Naturschutz.
- Nagelkerke, N. J. D. (1991). A note on a general definition of the coefficient of determination. *Biometrika*, 78(3), 691–692. <https://doi.org/10.1093/biomet/78.3.691>.
- Obrist, M. K., Sattler, T., Home, R., Gloor, G., Bontadina, F., Nobis, M., ... Moretti, M. (2012). La biodiversité en ville – pour l'être humain et la nature (Biodiversity in the city - for humans and nature). *Notice pour le praticien* (pp. 12). Birmensdorf: Institut fédéral de recherches WSL.
- Oksanen, J., & Minchin, P. R. (2002). Continuum theory revisited: What shape are species responses along ecological gradients? *Ecological Modelling*, 157(2), 119–129. [https://doi.org/10.1016/S0304-3800\(02\)00190-4](https://doi.org/10.1016/S0304-3800(02)00190-4).
- Pearman, P. B., Guisan, A., Broennimann, O., & Randin, C. F. (2008). Niche dynamics in space and time. *Trends in Ecology & Evolution*, 23(3), 149–158. <https://doi.org/10.1016/j.tree.2007.11.005>.
- Phillips, S. J., & Dudik, M. (2008). Modeling of species distributions with Maxent: New extensions and a comprehensive evaluation. *Ecography*, 31(2), 161–175. <https://doi.org/10.1111/j.0906-7590.2008.5203.x>.
- Pulliam, H. R. (2000). On the relationship between niche and distribution. *Ecology Letters*, 3(4), 349–361. <https://doi.org/10.1046/j.1461-0248.2000.00143.x>.
- Randin, C. F., Dirnbock, T., Dullinger, S., Zimmermann, N. E., Zappa, M., & Guisan, A. (2006). Are niche-based species distribution models transferable in space? *Journal of Biogeography*, 33(10), 1689–1703. <https://doi.org/10.1111/j.1365-2699.2006.01466.x>.
- Randin, C., Jaccard, H., Vittoz, P., Yoccoz, N., & Guisan, A. (2009). Land use improves spatial predictions of mountain plant abundance but not presence-absence. *Journal of Vegetation Science*, 1–13. <https://doi.org/10.1111/j.1654-1103.2009.01098.x>.
- Sattler, T., Duelli, P., Obrist, M. K., Arlettaz, R., & Moretti, M. (2010). Response of arthropod species richness and functional groups to urban habitat structure and management. *Landscape Ecology*, 25(6), 941–954. <https://doi.org/10.1007/s10980-010-9473-2>.
- Schaub, M., Martinez, N., Tagmann-Ioset, A., Weisshaupt, N., & Maurer, M. (2010). Patches of bare ground as a staple commodity for declining ground – Foraging insectivorous farmland birds. *PLoS One*, 5(10), e13115. <https://doi.org/10.1371/journal.pone.0013115>.
- Schmitt, P., & Schlossman, A. L. (2012). Sustainable urban growth through densification and regional governance: The Stockholm Case. *Nordregio Policy Brief*, 1, 1–4.
- Sedlacek, O., Fuchs, R., & Exnerova, A. (2004). Redstart *Phoenicurus phoenicurus* and black redstart *P. ochrurus* in a mosaic urban environment: neighbours or rivals? *Journal of Avian Biology*, 35(4), 336–343. <https://doi.org/10.1111/j.0908-8857.2004.03017.x>.
- Smith, R. M., Gaston, K. J., Warren, P. H., & Thompson, K. (2006). Urban domestic gardens (VIII): Environmental correlates of invertebrate abundance. *Biodiversity and Conservation*, 15(8), 2515–2545. <https://doi.org/10.1007/s10531-005-2784-y>.
- Soga, M., Yamaura, Y., Koike, S., & Gaston, K. J. (2014). Land sharing vs. land sparing: does the compact city reconcile urban development and biodiversity conservation? *Journal of Applied Ecology*, 51(5), 1378–1386. <https://doi.org/10.1111/1365-2664.12280>.
- Spaar, R., Ayé, R., Zbinden, N., & Rehsteiner, U. (2012). Eléments pour les programmes de conservation des oiseaux en Suisse. Actualisation 2011 (Element for the Swiss species Recovery Programme for Birds, 2011 Update). Association Suisse pour la Protection des Oiseaux ASPO/BirdLife Suisse et Station ornithologique suisse, Zurich et Sempach, pp. 92.
- Stott, I., Soga, M., Inger, R., & Gaston, K. J. (2015). Land sparing is crucial for urban ecosystem services. *Frontiers in Ecology and the Environment*, 13(7), 387–393. <https://doi.org/10.1890/140286>.
- Sullivan, B. L., Wood, C. L., Iliff, M. J., Bonney, R. E., Fink, D., & Kelling, S. (2009). eBird: A citizen-based bird observation network in the biological sciences. *Biological Conservation*, 142(10), 2282–2292. <https://doi.org/10.1016/j.biocon.2009.05.006>.
- Taylor, P. D., Fahrig, L., Henein, K., & Merriam, G. (1993). Connectivity is a vital element of landscape structure. *Oikos*, 68(3), 571–573. <https://doi.org/10.2307/3544927>.
- Thuiller, W., Lafourcade, B., Engler, R., & Araujo, M. B. (2009). BIOMOD – A platform for ensemble forecasting of species distributions. *Ecography*, 32(3), 369–373. <https://doi.org/10.1111/j.1600-0587.2008.05742.x>.
- Turner, W. R., Nakamura, T., & Dinetti, M. (2004). Global urbanization and the separation of humans from nature. *Bioscience*, 54(6), 585–590. [https://doi.org/10.1641/0006-3568\(2004\)054\[0585:GUATSO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054[0585:GUATSO]2.0.CO;2).
- van Ewijk, K. Y., Randin, C. F., Treitz, P. M., & Scott, N. A. (2014). Predicting fine-scale tree species abundance patterns using biotic variables derived from LiDAR and high spatial resolution imagery. *Remote Sensing of Environment*, 150, 120–131. <https://doi.org/10.1016/j.rse.2014.04.026>.
- Verbürg, P. H., & Overmars, K. P. (2009). Combining top-down and bottom-up dynamics in land use modeling: Exploring the future of abandoned farmlands in Europe with the Dyna-CLUE model. *Landscape Ecology*, 24(9), 1167. <https://doi.org/10.1007/s10980-009-9355-7>.
- Vicente, J., Alves, P., Randin, C., Guisan, A., & Honrado, J. (2010). What drives invasibility? A multi-model inference test and spatial modelling of alien plant species richness patterns in northern Portugal. *Ecography*, 33(6), 1081–1092. <https://doi.org/10.1111/j.1600-0587.2010.6380.x>.