How to manage the urban green to improve bird diversity and community structure

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ABSTRACT

Urbanization is a fundamental environmental change, today happening at accelerated speed worldwide. Despite the strong and permanent human impact, urban biodiversity has generally proved to be surprisingly high. Quantitative information on the effect of management actions on biodiversity is often lacking but is an indispensable basis for decisions by urban planners and managers. We therefore quantified key urban variables to predict changes in avian biodiversity when their urban habitat is modified. We analysed species richness, diversity (Simpson index) and community composition of 63 bird species with reference to major urban environmental gradients at 96 sampling points in three Swiss cities. Best explanatory models were selected from candidate models following information theory, and their respective predictions were averaged based on AICc-weights. Bird species richness and diversity are negatively affected by increasing fractions of sealed area or buildings, while increasing vegetation structures, in particular trees, show positive effects. Our models predict an increase from 13 species in the absence of trees to 20 species with 46% tree cover (+54%). Coniferous trees help to maximize bird species richness, with the models predicting an increase from 14 species at sites with only deciduous woody plants to 20 species (+43%) at places with equal representation of coniferous and deciduous plants. While the analysis of the Simpson index did not show any influence of the coniferous and broadleaf woody plants mixture, partial redundancy analysis revealed such an influence on bird community composition, highlighting the importance to consider several measures when analyzing biodiversity.

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1. Introduction

Nowadays, the majority of the world's human population lives in cities. The fraction of these urban inhabitants is constantly growing on all continents and is expected to reach 70% by 2050 (United Nations, 2008). Furthermore, the urban environment has recently gained broad attention by an increasing number of ecologists. Although the urbanization process is wide-spread, high-impact environmental transformation (Grimm et al., 2008), many studies show that cities host a surprisingly high number of species and individuals (e.g. Sukopp, 1998; Marzluff, 2001; Palomino and Carrascal, 2006; Sattler et al., 2010a,b). Moderately urbanized areas often support higher species richness than rural zones (Blair, 1996; Blair and Launer, 1997). Species richness and species diversity are generally considered good indicators of the quality of nature and

ecosystem health (Rapport, 1999). However, they have limitations and do not elucidate all aspects of the community dynamic: species richness does not consider the differences in species composition and diversity metrics have a limited comparability between points (Jost, 2006). Community analyses are used to explain changes in community composition (e.g. Moretti et al., 2006).

The importance to identify thresholds of particular habitat variables which, if exceeded or undercut would cause biodiversity to be maintained or even enhanced in the urban environment, has been highlighted by several studies (e.g. Marzluff and Ewing, 2001). Such predicted thresholds are important tools for convincing environmental managers and politicians of the effectiveness of specific measures. In addition, there is an increasing consensus that biodiversity is important for the quality of life of the people in general, and of urban inhabitants in particular. Sandström et al. (2006) claimed that perceived life quality of citizens might improve when the fraction of nature in urban areas increases. Natural areas and conservation practices in cities give the opportunity for citizens to directly experience nature (Miller, 2006), which is a crucial aspect for restoration in a world with a high urban population (Home et al., 2009a).

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Birds are often chosen as indicators of habitat quality. Their ecology is well known and species respond well to the availability of habitat structures (Clergeau et al., 1998; Evans et al., 2009). In cities, birds are widely considered as an optimal model group to study the ecological effect of urbanization (McDonnell and Hahs, 2008). Strong inter-specific differences in the response of birds to urbanization are known (Møller, 2009), thus, it is expected that increasing urban densification modifies both bird community compositions and structure. Nevertheless, abiotic conditions are similar between cities (Grimm et al., 2008) and thus avian communities are often comparable, independent from latitude (Clergeau et al., 2006; Evans et al., 2009). The following general patterns have been identified on how urbanization influences avian biodiversity: (1) bird species richness and diversity decrease along urbanization gradients ranging from moderately urbanized to densely built-up areas (Clergeau et al., 1998, 2006). (2) Avian abundance tends to increase along the same gradient (Clergeau et al., 1998; Palomino and Carrascal, 2006; Grimm et al., 2008), which reflects the overall dominance of few synantrophic species (omnivorous and ubiquitous) contributing to biotic homogenization (e.g. Clergeau et al., 2006; La Sorte and McKinney, 2007). (3) Specialist species (e.g. woodland and farmland species with narrow ecological requirements, often insect feeders and ground nesters) decrease with increasing urbanization (e.g. Clergeau et al., 1998; Fernández-Juricic, 2004; Devictor et al., 2007).

Several studies provide evidence that site-specific environmental factors (e.g. size of residential house properties) influence avian species occurrence in urban areas (e.g. McKinney, 2002; Sattler and Tobler, 2004; Evans et al., 2009), which suggests that already management decisions by inhabitants and property owners on the site scale can affect nesting and feeding habitats for urban birds (McKinney, 2002; Grimm et al., 2008). The following management actions have been devised with the aim of enhancing urban bird populations: (1) providing additional food resources (Gaston et al., 2007; Evans et al., 2009); (2) enhancing reproduction possibilities with nest boxes (Gaston et al., 2007); (3) increasing structural vegetation diversity (Böhning-Gaese, 1997; Chace and Walsh, 2004; Evans et al., 2009); (4) planting native rather than exotic woody plants (Chace and Walsh, 2004; Daniels and Kirkpatrick, 2006; Burghardt et al., 2009); (5) preserving woodland patches in urban developments (Croci et al., 2008); (6) increasing connectivity among green structures within and around cities (Marzluff and Ewing, 2001; Fernández-Juricic, 2004).

These studies usually indicate the direction of influence (positive/negative) of such management decisions on avian biodiversity, but in addition to this important information there is an urgent need for knowledge on the extent of effects of single factors (Kim and Byrne, 2006). Quantification of the respective influence of single factors on species numbers, diversity and composition facilitates the communication with policy makers, urban planners and builders (e.g. McDonnell and Hahs, 2008; Stagoll et al., 2010). In this way, closer collaboration between the different stakeholders is fostered which is urgently needed with increasing urbanization.

Therefore, in the present study, we calculated model predictions for human-influenced factors such as structural elements to sustain and possibly even enhance bird biodiversity despite increasing expansion and densification of cities. For the same goal of effective planning measures for avian biodiversity, we also analysed the influence of the composition of woody plants which are an important part of the urban green. In particular, we aim to answer the following questions: (A) Structural elements—Which are the most important urban elements that affect bird species richness (species number) and diversity (representing species richness and community evenness) and what are their effect sizes? Do we also find a pre-eminent influence of trees, as revealed by previous studies and, if yes, what is the predicted influence of this variable? (B1) Woody plant composition—Which composition of tree and bush species, with regard to foliage type (coniferous, broadleaf), origin (native, exotic) and woody plant species richness, maximize bird species richness and diversity? (B2) Woody plant composition and bird community—Which additional information is obtained by community analysis? How do different bird species react to changes in woody plant composition?

2. Materials and methods

2.1. Study sites and sampling design

We chose the three Swiss cities of Zurich, Lucerne (both North of the Alps) and Lugano (South of the Alps) as study areas (further details in Appendix S1a). With >73% of the population living in cities (Schuler et al., 2004), Switzerland provides plentiful opportunities to study the effect of small to medium sized cities in central Europe on avian biodiversity. The three cities consist of historical centres, residential areas, business quarters, public green areas, historical parks and cemeteries, and former industrial areas that have been developed for new apartments and office buildings. All three cities are characterized by a temperate climate (North: average January temperature 1 °C, July 17 °C; South: January 3 °C, July 20 °C) with a yearly precipitation of 1000 mm for Zurich, 1150 mm for Lucerne and 1600 mm for Lugano. Within each of the three cities 32 sampling points (total 96) were selected along a continuous urbanization gradient, which was measured as the fraction of sealed and built area in the 50 m radius around the sampling points. The selection of the individual sampling points followed a reasoned choice sampling strategy to cover the entire urbanization gradient (3–92% sealed and built area). We included a wide range of urban habitat types (private gardens, semi-public spaces of apartment buildings, public parks and courtyards of industrial buildings) at different developmental stages into the study (detailed locations in Germann et al., 2008). The mean distance of 388 m (±21 m SE) between sampling points inhibited spatial auto-correlation, which was confirmed using the Moran's Index (Legendre and Legendre, 1998; data not shown). A minimal distance of 250 m was kept between sampling points and the city fringe.

2.2. Bird survey

We used the point count method in the early morning to record birds at sampling points (Bibby et al., 2000) during the breeding season (April 15th–June 13th 2007). Each of the 96 points was visited six times, over the two months (mean interval between visits: 10.6 days, range 4–15 days). Considering that the time of day affects bird activity, which in turn affects detection probability, the order of sampling points during one morning tour was alternated between start (1 h before sunrise) and finish (at the latest 5 h after sunrise) of each tour. Each visit lasted 15 min to give a total of $6 \times 15 = 90$ min per sampling point (144 h overall). Presence of bird species was recorded visually and acoustically in a radius of 50 m, with the first 10 min of observations at the centre and the remaining 5 min checking areas hidden from the observer (e.g. behind buildings). When counting birds, we took special care that individuals were counted once only. We did not distinguish between breeders and other visitors as distinction is difficult, and over-flying birds were counted only when they were flying low and/or showed connection to the ground environment (i.e. searching for food). Species richness for each sampling point was defined as the total number of species detected during the six visits. Abundance for each species and sampling point was defined as the maximum number of individuals present in any of the six visits. We chose Simpson index as measure of species diversity. The Simpson index emphasizes the

Table 1
Continuous habitat variables according to the main study questions on structural elements (analysis A) and woody plant composition (analysis B).

Variable	Mean (min–max)	Units	Definition
Analysis (A) structural elements			
BUILDING	0.23 (0.00–0.65)	Relative coverage in radius 50 m	Buildings
SEALED AREA	0.26 (0.00–0.78)		Asphalted surfaces (roads, spots), diverse anthropogenic features (i.e. gazebos, statues, fountains)
GRASS	0.30 (0.03–0.76)		Short grass, long grass and native flowers
BUSH	0.13 (0.00–0.36)		Woody plants (<5 m high)
TREE	0.13 (0.00–0.47)		Woody plants (>5 m high)
Analysis (B) woody plant composition[a]			
CONIFEROUS	0.05 (0.00–0.35)	Relative coverage in radius 50 m	Coniferous woody plants cover (trees and bushes)
DECIDUOUS	0.21 (0.03–0.65)		Deciduous woody plants cover (trees and bushes)
EXOTIC	0.12 (0.00–0.33)		Exotic woody plants cover (trees and bushes)
NATIVE	0.14 (0.01–0.59)		Native woody plants cover (trees and bushes)
WOODY SPECIES RICHNESS	2.14 (1.00–4.54)	n	Mean number of woody plants species

[a] In analysis B1 the following ratios of the coverage were used: CONIFEROUS/DECIDUOUS (Mean, 0.25; Min 0.00; Max 2.91) and EXOTIC/NATIVE (1.95; 0.00; 13.93).

evenness of a community, being less sensitive to species richness. It is meaningful, very robust, widely used and allows comparisons with the results of other studies (Magurran, 2004):

$$\text{Simpson} = 1 - \sum_{i=1}^{n} p_i^2$$

where n is the number of species observed at the sampling point and p_i is the relative abundance of species i.

Bird community composition at the different sampling points was expressed by the abundance (see definition in the previous paragraph) of each species, obtaining a 'species by sites' matrix.

2.3. Habitat variables

According to the main research questions, ten habitat variables (Table 1) were recorded at or within a 50 m radius of the sampling points and were digitized using Geographic Information Systems (ArcGIS 9.2, ESRI Redlands, USA):

(A) Structural elements – Detailed structural habitat variables were expressed as relative area coverage (=fraction; $100\% = 7854\,\text{m}^2$ for a single location).

(B1) Woody plant composition – We were especially interested in the influence of different types of woody plants (foliage, origin, species richness) on avian biodiversity. Opposed to analysis A, where we distinguished between trees and bushes based on an arbitrary height limit of 5 m, we renounced this distinction in analysis B and considered the type of the tree and bush continuum as 'woody plant composition'. Two habitat variables are expressed as ratios (CONIFEROUS/DECIDUOUS and EXOTIC/NATIVE) as (a), in this analysis, we were not interested in the absolute woody plant coverage which would have dominated the effect of composition and (b) to minimize the number of variables in the candidate models. We calculated mean species richness of woody plants (WOODY SPECIES RICHNESS), using the following formula:

$$\text{WSR} = \sum_{i=1}^{n} \text{SR}_i \frac{\text{area}_i}{\text{area}_{\text{TOT}}}$$

where n is the number of different woody plants patches within a 50 m radius, SR_i is the estimated number of woody plants species within patch i (three categories: 1 species ($\text{SR}_i = 1$), 2–3 species (=2.5), ≥4 species (=5)), area_i is the area of woody plants patch i and area_{TOT} is the total woody plants area within 50 m radius (sum of all area_i).

(B2) Woody plant composition and bird community – The analysis is based on the same variables as analysis B1, but CONIFEROUS, DECIDUOUS, EXOTIC and NATIVE are expressed as relative area coverage.

2.4. Statistical analysis

For the two study questions A and B1, we analysed the correlation of bird species richness and diversity with the habitat variables with linear mixed-effects models (Laird and Ware, 1982; Crawley, 2007), separating random effects (cities) from fixed effects (habitat variables). We found a normal distribution of the model residuals of both response variables (bird species richness and Simpson index) and thus used linear models.

We regressed species richness and Simpson index as a measure for species diversity on two different sets of explanatory variables corresponding to the two study questions (A and B1). All variables are continuous. Pair-wise correlation analysis showed that correlation coefficients r were below 0.7 which was defined as the maximal accepted limit of correlation.

For each of the two analyses, we formulated a priori models including all possible combinations of the variables. A total of 32 pre-defined models were tested for the structural elements analysis (analysis A) and eight models for the woody plant composition analysis (analysis B1). All composition models related to analysis B1 contained the area fraction of woody plants as a co-variable to account for the total cover at each sampling point. We expected a curvilinear relation (optimum curve) for the variable CONIFEROUS/DECIDUOUS (ratio), so we included its quadratic function into the modeling for species richness and species diversity. For the variable BUILDING we only expected a curvilinear relationship for the response variable bird species richness, because moderately built areas can host building dwelling species that profit from artificial rocks without necessarily losing the species already present at sampling locations with less buildings. On the other hand, for species diversity we expected BUILDING to exhibit a linear effect, as the Simpson index might be negatively affected by newly dominant building dwelling species. Consequently, we included the quadratic function of BUILDING into the modeling for species richness but not for species composition.

Models were ranked according to the small-sample unbiased Akaike's Information Criterion (AICc). AICc weights and evidence ratios were calculated (Burnham and Anderson, 2002; Johnson and Omland, 2004). Models with evidence ratios <10 were defined as the most parsimonious set of models. These selected models were predicted individually for all of the independent variables varying between the minimum and maximum value of the data set, while the remainder were kept constant at their mean value. By bootstrapping (1000 repetitions), standard deviations were calculated for the predicted values. Predicted values were then averaged on the basis of their AICc weights (Burnham and Anderson, 2002). The explained variation of every model was calculated using the generalized form of R^2 for linear mixed effects models proposed by Xu (2003). All statistical calculations were carried out with the pro-

Table 2
Selected linear mixed-effects models (most parsimonious set of models with evidence ratio smaller than 10), relating species richness to five environmental variables (estimates and SD are indicated). (A) Structural elements analysis; (B1) Woody plant composition analysis.

Model	Intercept	Tree	Bush	Grass	Sealed area	Building	Building²	Δ-AICc[a]	AICw[b]	ER[c]	k[d]	R²[e]
(A)												
8	15.6 (1.0)	16.3 (3.2)			−9.7 (2.4)			0.0	45.0%	1.0	5	41.3%
17	14.6 (1.2)	15.8 (3.2)	6.4 (4.3)		−8.8 (2.4)			2.0	17.0%	2.7	6	42.6%
16	9.5 (1.0)	12.7 (3.6)	13.2 (4.2)	7.6 (2.2)				2.8	11.3%	4.0	6	42.0%
21	17.7 (1.7)	11.3 (4.0)			−9.7 (2.3)	−5.8 (8.6)	−3.2 (14.8)	3.5	7.9%	5.7	7	44.3%
19	15.0 (1.5)	15.5 (3.5)		1.5 (2.7)	−8.7 (3.0)			4.0	6.2%	7.3	6	41.5%
26	12.4 (2.0)	13.4 (3.6)	9.5 (4.8)	4.2 (3.0)	−5.6 (3.4)			4.3	5.4%	8.4	7	43.7%

Model	Intercept	Coniferous/deciduous	(Coniferous/deciduous)²	Exotic/native	Woody species richness	Δ-AICc[a]	AICw[b]	ER[c]	k[d]	R²[e]
(B1)										
1	10.2 (0.8)	6.0 (1.9)	−1.1 (0.8)			0.0	61.6%	1.0	6	16.1%
4	10.7 (0.9)	6.6 (1.9)	−1.3 (0.8)	−0.2 (0.1)		1.8	25.7%	2.4	7	19.9%
5	9.6 (1.2)	6.3 (2.0)	−1.2 (0.8)		0.3 (0.5)	3.9	8.6%	7.2	7	16.3%

[a] Difference compared to small-sample unbiased Akaike's Information Criterion of the best model.
[b] Model weight.
[c] Evidence ratio.
[d] Number of parameters.
[e] Adjusted R^2 (Xu, 2003).

gram R v2.6.0 (R Development Core Team, 2007) using library nlme (Pinheiro et al., 2008).

For the study question B2, partial Redundancy Analysis of bird community composition (pRDA; Legendre and Legendre, 1998) was performed using the CANOCO software (Microcomputer Power, Ithaca, NY, USA) and referring to Lepš and Šmilauer (2003). As a multivariate analysis of variance, pRDA tests the linear relationship between a response matrix (i.e. abundance of bird species by 96 sampling points) and the explanatory variables (i.e. five woody plant composition variables; Table 1), while controlling for co-variables (i.e. the three cities, alike to the linear mixed-effects models above). Monte Carlo permutation tests (999 permutations) were performed to assess the significance of the different canonical axes. Species that were observed only few times and/or only at one sampling point (singletons) can cause problems in the analysis, because their occurrence could be accidental and not due to environmental reasons. Therefore, only species observed at least 5 times and at more than one sampling point were included in the pRDA analysis (39 species).

3. Results

We recorded 4120 individuals of 63 species within a radius of 50 m from the 96 sampling points. Overall, we recorded an average of 15.2 species per sampling point (SD = 3.9; range = 7–25) with only small variation between the three cities (Appendix S1b). For species identity and frequencies per city see Appendix S2.

3.1. Structural elements

For bird species richness, six out of the initial 32 models were found by the evidence ratios as the most parsimonious set of models (Table 2A). The explanatory power of the selected models is very high with an average R^2 of 42.6% per selected model. The variable *TREE* is contained in all six selected models (sum of AICc weights = 92.7%) and shows the highest positive correlation with bird species richness. *SEALED AREA* (in five selected models; sum of weights = 81.4%) shows the highest negative correlation. *BUSH* and *GRASS* exhibit a moderately positive influence on bird species richness (each in three selected models; sum of weights = 33.7% and 22.9%, respectively) while *BUILDING* (linear and quadratic term) shows a negative correlation with bird species richness (in one selected model; weight = 7.9%).

For bird species diversity (Simpson index), nine out of the initial 32 models were defined as the most parsimonious set of models (Table 3A). With an averaged R^2 of 21.0%, their explanatory power is about half that of the models that explained species richness. Again, *TREE* is contained in eight of the nine selected models (sum of weights = 84.0%) and shows the highest positive correlation with species diversity. *BUILDING* shows a moderate negative correlation (in four selected models; sum of weights = 23.4%), *BUSH* has a moderate positive correlation (in three selected models; sum of weights = 25.4%), whereas there is hardly any correlation for *GRASS* and *SEALED AREA* (in two selected models each; sum of weights = 13.8% and 9.5%, respectively).

The averaged predictions of the selected models illustrate the outstanding and positive influence of *TREE* on both bird species richness and diversity (Fig. 1): a 20% increase of tree area results in an average of three additional bird species and an increase of Simpson index of about 0.24 (i.e. 24% increase in the probability that two randomly chosen birds belong to two different species). Considering their standard deviations (SD), species richness predictions are reasonably reliable along the entire tree gradient under study, whereas the predictions for species diversity become less reliable for tree coverage above 30% of the total area. The variables *BUSH* and *GRASS* have a moderate and similar positive effect on bird species richness and diversity (although considerably less important than variable *TREE*). The predictions for *SEALED AREA* (Fig. 1) yield a contrasting picture for species richness (negative influence) and for species diversity (no influence). A 40% increase of the sealed area causes a loss of three bird species, whereas predictions become less reliable when the fraction of sealed area is above 50%. In contrast to the influence of sealed area, species richness is not greatly influenced by the fraction of area covered by buildings, while a 25% increase in built area decreases the Simpson index by about 0.01. In this case, species diversity predictions become less reliable for buildings fraction above 40%.

3.2. Woody plant composition

For bird species richness, three models were defined as the most parsimonious set of models (Table 2B1). The explanatory power of these models, with the averaged R^2 of 17.4%, is lower than in the analysis of the structural elements. The variable *CONIFEROUS/DECIDUOUS* (including its quadratic term) occurs in all the three selected models (sum of weights = 95.9%) and reveals a curvilinear response of bird species richness. The variables

Table 3
Selected linear mixed-effects models (most parsimonious set of models with evidence ratio smaller than 10), relating species diversity to five environmental variables (estimates and SD are indicated). (A) Structural elements analysis; (B1) Woody plant composition analysis.

Model	Intercept	Tree	Bush	Grass	Sealed area	Building	Δ-AICc[a]	AICw[b]	ER[c]	k[d]	R^{2e}
(A)											
1	0.81 (0.01)	0.28 (0.06)					0.0	28.4%	1.0	4	19.4%
6	0.80 (0.02)	0.26 (0.06)	0.14 (0.08)				1.3	14.9%	1.9	5	21.6%
9	0.85 (0.03)	0.20 (0.07)				−0.11 (0.07)	1.5	13.4%	2.1	5	21.8%
7	0.80 (0.02)	0.23 (0.07)		0.05 (0.04)			2.7	7.3%	3.9	5	20.7%
8	0.83 (0.02)	0.25 (0.06)			−0.05 (0.05)		2.9	6.6%	4.3	5	20.4%
16	0.78 (0.02)	0.20 (0.07)	0.16 (0.08)	0.07 (0.04)			3.0	6.5%	4.4	6	23.7%
18	0.83 (0.03)	0.20 (0.07)	0.11 (0.08)			−0.09 (0.07)	3.9	4.0%	7.1	6	23.0%
5	0.90 (0.02)					−0.22 (0.05)	4.5	3.0%	9.3	4	15.7%
21	0.86 (0.03)	0.18 (0.08)			−0.05 (0.05)	−0.11 (0.07)	4.5	2.9%	9.7	6	22.7%

Model	Intercept	Coniferous/deciduous	(Coniferous/deciduous)^2	Exotic/native	Woody species richness	Δ-AICc[a]	AICw[b]	ER[c]	k[d]	R^{2e}
(B)										
0	0.79 (0.02)					0.0	71.3%	1.0	4	0.0%
2	0.80 (0.02)		0.00 (0.00)			3.6	11.6%	6.2	5	0.9%
3	0.80 (0.02)				−0.01 (0.01)	3.9	10.3%	6.9	5	0.6%

[a] Difference compared to small-sample unbiased Akaike's Information Criterion of the best model.
[b] Model weight.
[c] Evidence ratio.
[d] Number of parameters.
[e] Adjusted R^2 (Xu, 2003).

EXOTIC/NATIVE and WOODY SPECIES RICHNESS (one model each; weight = 25.7% and 8.6%, respectively) do not exhibit a strong influence on bird species richness.

For bird species diversity, three models were defined as the most parsimonious set of models (Table 3B1). The explanatory power of these models is virtually inexistent with an averaged R^2 of 0.5%. The best model is the null model (AICc weight = 71.3%) indicating random distribution (only the control variable total woody plants cover was included). Consequently, none of the analysed variables (CONIFEROUS/DECIDUOUS, EXOTIC/NATIVE and WOODY SPECIES RICHNESS) affects species diversity.

The averaged predictions of the selected models (Fig. 2) on woody plant composition illustrate that only the variable CONIFEROUS/DECIDUOUS has a considerable (positive) influence on only bird species richness. This variable shows a quadratic curve that probably has not yet reached its optimum. If all woody plants are deciduous, bird species richness is expected to be at

its minimum value of about 14 species (=intercept). If deciduous and coniferous woody plants reach the same coverage (1:1 ratio), six additional bird species are predicted to be present. Predictions become less reliable for ratios >1 and thus the prediction of the maximum is doubtful. It is questionable whether a higher fraction of area covered by coniferous species would still increase bird species numbers. Bird species diversity does not respond to any variable included in the composition analysis (Fig. 2).

3.3. Woody plant composition and bird community

The five habitat variables included in the pRDA analysis (Table 1) explained 15.1% of the total variance in bird community composition. Fig. 3 depicts the results with respect to the first two (and most important) canonical axis. The first axis alone explained 9.9% of the variance ($p \leq 0.001$). When moving along the first axis from left (low
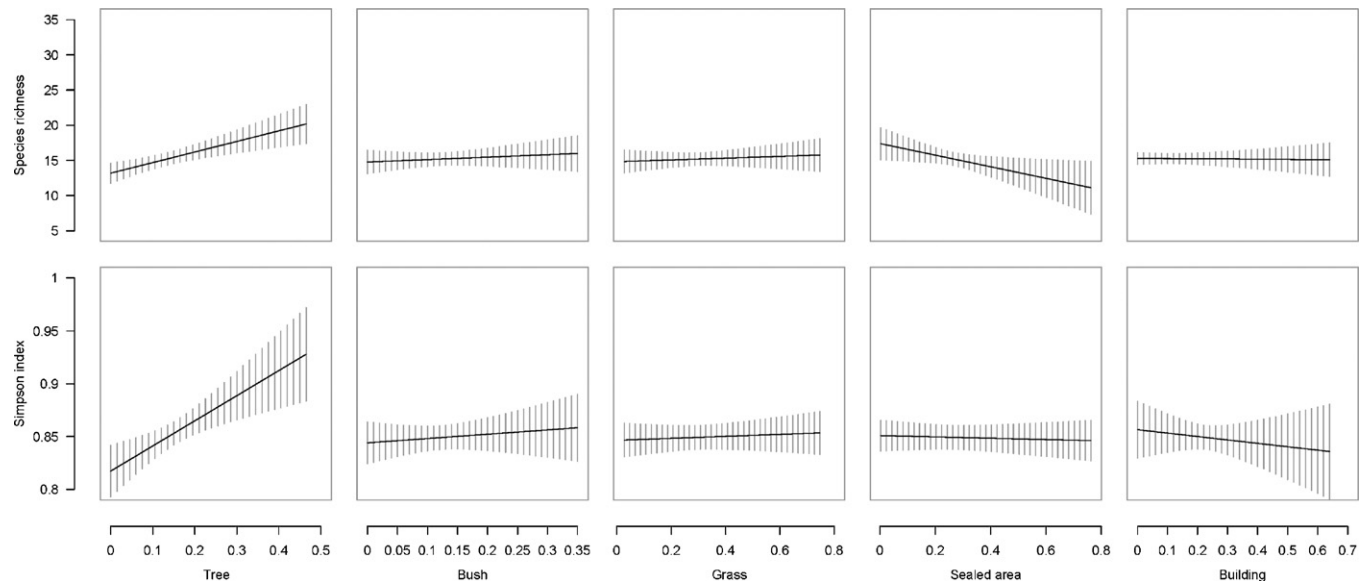

Fig. 1. Model averaged predictions (mean and SD) of bird species richness (above) and bird species diversity (below) on the basis of the most parsimonious set of models for structural elements analysis (A).
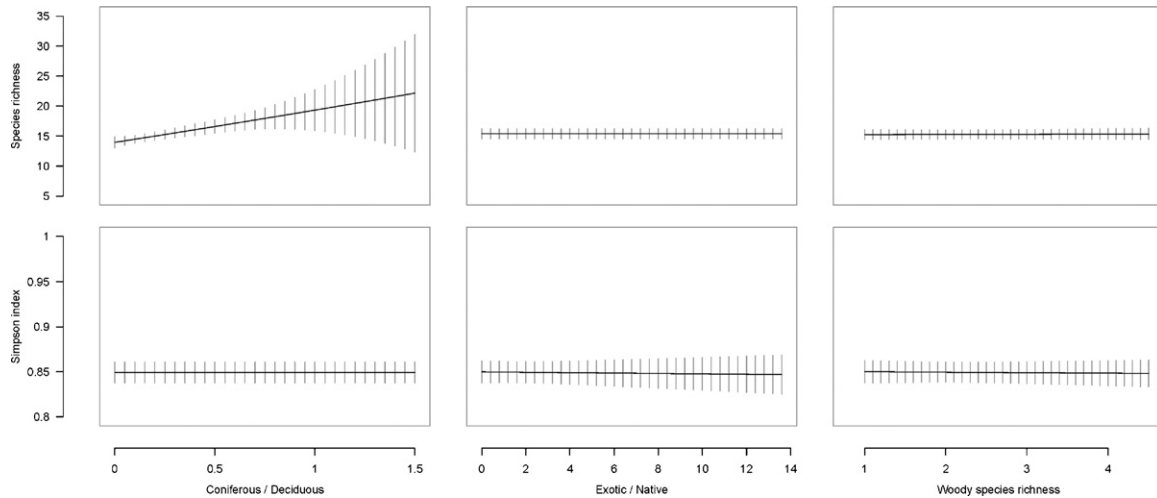
Fig. 2. Model averaged predictions (mean and SD) of bird species richness (above) and bird species diversity (below) on the basis of the most parsimonious set of models for woody plant composition analysis (B1).

fraction of woody plants) to right (high fraction) many bird species become more abundant; in particular, woody plants positively affected *Dendrocopos major*, *Columba palumbus*, *Fringilla coelebs* and *Cyanistes caerulus* as shown by the similar direction of the species arrows and the first axis. Only a few species are negatively correlated with woody plants (e.g. *Passer domesticus/hispaniolensis italiae*, *Streptopelia decaocto*, *Columba livia domestica* and *Apus apus*). The right hand side of the first axis represents a mixture of coniferous and broadleaf woody plants. The arrows of coniferous and broadleaf trees and bushes illustrate that these woody plant types, when dominant, potentially differentiate bird communities. Most species, however are placed in intermediate positions and do not show evident preference for either foliage type. Some species (e.g. *Regulus ignicapilla*, *Periparus ater*, *Turdus merula*, *Certhia brachydactyla*) prefer coniferous woody plants to broadleaf ones. Exotic and native woody plants seem to have similar directions, but the different length of the arrows indicates that native woody plants correlate better with the first and the second canonical axes than the exotic ones (Fig. 3). However, hardly any species correlates with any of the two variables (with the exception of *Parus major* with native woody plants). In our study sites, the fraction of exotic and native woody plants as well as woody plant species richness do not influence urban bird communities.

4. Discussion and conclusions

Most studies on urban birds have considered the classical rural–urban gradient approach as proposed by McDonnell and Pickett (1990), which has generally revealed a negative impact of urbanization (i.e. increasing sealed area) on bird species richness and diversity (e.g. Clergeau et al., 1998; Palomino and Carrascal, 2006). Our study, focusing on gradients within cities, found that three species are lost when sealed area increases by 40%, confirming the general negative pattern of urbanization also on the intra-urban scale. The positive effects of increasing area coverage and of higher complexity of urban green structures on species richness and diversity on our comparatively small 50 m radius illustrates the strong effect of fine scale composition of urban green and they are similar to results obtained at larger scales (Lancaster and Rees, 1979; Clergeau et al., 2001).

4.1. Pre-eminent positive influence of trees

Our results suggest that the amount of trees is the most important habitat variable enhancing bird species richness and diversity in cities, confirming previous studies (Goldstein et al., 1986; Clergeau et al., 1998; Palomino and Carrascal, 2006; Sandström et al., 2006; Evans et al., 2009). We predict an increase from 13 bird species in the absence of trees to 20 species with 46% tree cover (+54%), keeping other model variables constant. The positive effect of trees outweighs the negative effect of sealed area and buildings, probably because trees open up the vertical dimension and thereby substantially increase both habitat dimensions and available niches. Therefore, increasing the fraction of tree cover in the urban matrix seems to be the most promising and efficient measure to enhance bird species richness and diversity.

While sealed area decreases overall bird species richness but not species diversity, an increasing building fraction has the opposite effect, i.e. leads to a reduction in bird diversity but not in rich-
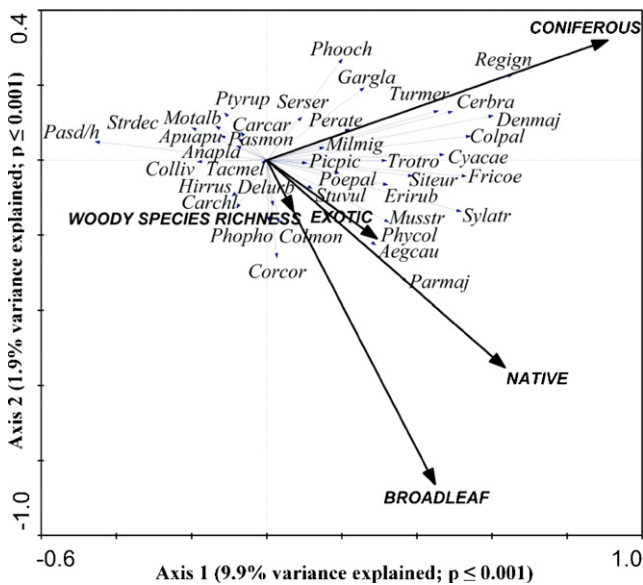

Fig. 3. Species community analysis by pRDA depicting 39 species (black arrows) in the environmental space of the first two canonical axis. The five explanatory variables are in bold and capital letters. Longer arrows illustrate a higher correlation of the species with one of the main axis and/or explanatory variables. Species names are composed by the first three letters of the genus and the first three letters of the species name, for species list see Appendix S2. Two pairs of ecologically equivalent species were summarized in species complexes (*Corvus corone + Corvus cornix = Corcor*; *Passer domesticus + Passer hispaniolensis italiae = Pasd/h*).

ness. In highly urbanized areas, only few species (e.g. *Apus apus*, *Passer domesticus*, *Columba livia* f. *domestica*) profit from buildings as secondary rock habitats and from abundant food resources, and thus dominate the community (Clergeau et al., 2006; La Sorte and McKinney, 2007). Prior to our study and based on the intermediate disturbance hypothesis (Connell, 1978) and results of other studies and taxa (Blair, 1996; Marzluff, 2005; Tratalos et al., 2007; Lepczyk et al., 2008; Sanford et al., 2009), we had expected bird species richness to attain its maximum at an intermediate state of building density. However, our study reveals that buildings do not affect bird species richness, in that the loss of sensitive species is compensated by the appearance of generalist building dweller species (same species as above).

4.2. The influence of woody plant composition on urban avian diversity and species communities

We found that woody plant composition is important for bird richness reaching the maximum number of species with equal representation of coniferous and deciduous plants. At a ratio of 1:1 we predict the occurrence of 20 species although Fig. 2 suggests that more coniferous woody plants could enhance bird species richness even more (note increased SD, however). These results are confirmed by the community analysis, which shows that most species correlate with both coniferous and broadleaf woody plants indicating that the presence of both type of vegetation is favorable to many urban birds. While bird species relying on trees in general profit from the presence of either coniferous and deciduous trees, some specialist species will make use of the habitat only when their preferred foliage type covers a sufficient area. A balanced mixture of both habitat types thus maximizes the total number of species, as indicated by Palomino and Carrascal (2006). Our result contradicts Thompson et al. (1993) who found that bird species richness is highest in gardens with higher ratios of deciduous to coniferous trees. As indicated by the community analysis, the availability of coniferous and broadleaf woody plants does not only affect the presence/absence of species, but also their abundance: some species seem to prefer increased area coverage of coniferous trees, e.g. *Regulus ignicapilla*, *Periparus ater* and *Certhia brachydactyla*. Such changes in abundance of some species due to alterations in the foliage composition of woody plants may not be unraveled when using Simpson index only; the changes may be counterbalanced by abundance shifts of other species resulting in limited or no changes in Simpson index. Our results of the community analysis show that sometimes a constant Simpson index masks complex shifts in community composition.

With regard to the effect of native vs. exotic plants on urban birds, Donnelly and Marzluff (2004) in North America and Daniels and Kirkpatrick (2006) in Australia found a higher correlation of native bird species with native plants than with exotic plants. Again in Australia, White et al. (2005) found lower bird species richness and a modified community composition in areas dominated by exotic vegetation compared to areas where native vegetation prevails. In our fine-scaled study in Switzerland, we found no influence of exotic and native woody plants on neither bird species richness, nor species diversity, nor community composition. We neither found an influence of woody plant species richness on any avian biodiversity measure, which contradicts the results of Shwartz et al. (2008), who found a positive influence of the number of woody plant species on avian species richness in urban areas in Tel Aviv (Israel).

The lack of relationship between any of the woody plant characteristics and species diversity suggests that in areas with high tree fraction no single bird species reaches dominance and thereby greatly impacts Simpson index. Simpson index is mainly influenced by dominant species. Increasing built area, results in few species becoming dominant. This result is confirmed by the community analysis (Fig. 3): the first canonical axis describes a general gradient from areas with a high fraction (right) to areas with a low fraction of woody plants (left), where a limited number of species tends to dominate (e.g. *Passer domesticus/hispaniolensis italiae*, *Streptopelia decaocto*, *Columba livia domestica* and *Apus apus*; see also Appendix S2).

4.3. Conclusions and perspectives

Human requirements for more buildings and transport infrastructure put high pressure on urban green space (densification). While it seems illusive and may be even contra-productive to stop this process (with regard to general conservation efforts: when densification is stopped, urban sprawl is likely to increase) it should be a goal to plan and manage urban green in a way to compensate for the loss of green area as habitats for birds. Our results lead us to two quantitative recommendations for vegetation structures that positively influence avian biodiversity in cities:

(1) The conservation or re-planting of trees and large bushes optimizes vertical vegetation structure and is regarded as the most effective long-term measure to enhance both bird species richness and diversity. Our models predict a 54% increase from 13 bird species in the absence of trees to 20 species with 46% tree cover.
(2) A well-balanced mixture of coniferous and deciduous woody plants maximizes bird species richness. Our models predict a 43% increase from 14 bird species at places with the presence of only deciduous woody plants to 20 species at places with equal representation of coniferous and deciduous plants.

We want to stress that urban planning and management decisions are already effective at comparatively fine scales (<1 ha).

More than 60 bird species can breed in Swiss cities, which is approximately one third of all regularly breeding species of Switzerland. Nevertheless Red List species (11 species, Keller et al., 2001), priority species (9 species, Bollmann et al., 2002) and specialists are underrepresented among urban birds (Appendix S2). Thus, offering optimal habitats in cities cannot replace bird protection measures outside the city fringe (Miller, 2006). From a social science perspective, a recent study has shown the popularity of birds in the public (Home et al., 2009b). So, urban birds and their diversity represent a crucial element on how people can experience urban nature. Such experiences are essential for the individual well-being of city inhabitants (Fuller et al., 2007) and for political decisions regarding environmental conservation since personal experiences influence people's opinion (Turner et al., 2004; Dunn et al., 2006).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.landurbplan.2011.02.033.

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List of Appendices

Appendix S1: Information about the three cities considered: a) information on location, geographical extent and human population; b) bird species richness in the three cities (total, mean, range).

	Zurich	Lucerne	Lugano
a)			
Geographical coordinates	47°22′N, 8°33′E	47°03′N, 8°18′E	46°00′N, 8°57′E
Area	91.88 km²	24.15 km²	26.2 km²
Elevation	408 m a.s.l.	436 m a.s.l.	273 m a.s.l.
Residents	367'000	58'000	49'000
b)			
Total bird species richness	42	51	40
Mean (SD) per sampling point	14.0 (3.7)	16.4 (4.4)	15.1 (3.2)
Range	9-25	9-25	7-21

Appendix S2: List of all bird species according to the three cities considered (n locations = 32 per city, total 96).

Scientific Name	English Name	Species status [a]	Steadiness and dominance (%) [b]			
			Zurich	Lucerne	Lugano	Overall
Accipiter nisus	Eurasian Sparrowhawk		1 (0.1)	1 (0.1)	0 (0.0)	2 (0.0)
Acrocephalus scirpaceus	Eurasian Reed Warbler		0 (0.0)	1 (0.1)	0 (0.0)	1 (0.0)
Aegithalos caudatus	Long-tailed Tit		5 (0.9)	14 (2.3)	10 (1.9)	29 (1.7)
Anas platyrhynchos	Mallard		1 (0.1)	5 (0.8)	0 (0.0)	6 (0.3)
Apus apus	Common Swift	#, §	28 (18.4)	29 (12.2)	25 (7.0)	82 (12.4)
Ardea cinerea	Grey Heron		0 (0.0)	1 (0.1)	0 (0.0)	1 (0.0)
Buteo buteo	Common Buzzard		0 (0.0)	1 (0.1)	0 (0.0)	1 (0.0)
Carduelis cannabina	Common Linnet		0 (0.0)	0 (0.0)	1 (0.1)	1 (0.0)
Carduelis carduelis	European Goldfinch	§	15 (1.7)	19 (2.5)	25 (3.7)	59 (2.7)
Carduelis chloris	European Greenfinch	§	30 (4.6)	26 (3.1)	30 (4.5)	86 (4.1)
Certhia brachydactyla	Short-toed Treecreeper		4 (0.3)	5 (0.4)	2 (0.1)	11 (0.3)
Coccothraustes coccothraustes	Hawfinch		1 (0.1)	0 (0.0)	0 (0.0)	1 (0.0)
Coloeus monedula	Western Jackdaw	VU, #	1 (0.3)	5 (0.7)	0 (0.0)	6 (0.3)
Columba livia f. domestica	Common Pigeon		12 (3.3)	8 (1.8)	22 (5.6)	42 (3.6)
Columba palumbus	Common Wood Pigeon		3 (0.2)	10 (1.0)	0 (0.0)	13 (0.4)
Corvus cornix	Hooded Crow		0 (0.0)	0 (0.0)	32 (6.9)	
Corvus corone	Carrion Crow		28 (4.9)	28 (5.0)	0 (0.0)	88 (5.6) [c]
Cyanistes caeruleus	Eurasian Blue Tit		28 (3.9)	26 (4.3)	16 (1.4)	70 (3.2)
Delichon urbicum	Common House Martin	§	1 (0.1)	0 (0.0)	9 (2.4)	10 (0.8)
Dendrocopos major	Great Spotted Woodpecker		7 (0.6)	7 (0.6)	2 (0.1)	16 (0.4)
Emberiza cirlus	Cirl Bunting	VU, #	0 (0.0)	1 (0.1)	0 (0.0)	1 (0.0)
Erithacus rubecula	European Robin		12 (1.1)	11 (0.9)	14 (1.2)	37 (1.1)
Fringilla coelebs	Common Chaffinch		26 (3.6)	30 (4.8)	28 (3.7)	84 (4.1)
Garrulus glandarius	Eurasian Jay		3 (0.4)	5 (0.5)	0 (0.0)	8 (0.3)
Hippolais polyglotta	Melodious Warbler	NT	0 (0.0)	0 (0.0)	1 (0.1)	1 (0.0)
Hirundo rustica	Barn Swallow		1 (0.2)	1 (0.1)	4 (0.4)	6 (0.2)
Jynx torquilla	Eurasian Wryneck	VU, #	0 (0.0)	0 (0.0)	1 (0.1)	1 (0.0)
Larus michahellis	Yellow-legged Gull	NT	0 (0.0)	1 (0.1)	0 (0.0)	1 (0.0)
Locustella naevia	Common Grasshopper Warbler	VU, #	0 (0.0)	1 (0.1)	0 (0.0)	1 (0.0)
Lophophanes cristatus	European Crested Tit		0 (0.0)	2 (0.2)	0 (0.0)	2 (0.1)
Loxia curvirostra	Red Crossbill		0 (0.0)	0 (0.0)	1 (0.1)	1 (0.0)
Mergus merganser	Common Merganser	VU	0 (0.0)	2 (0.1)	0 (0.0)	2 (0.0)
Milvus migrans	Black Kite		2 (0.2)	2 (0.2)	0 (0.0)	4 (0.1)
Motacilla alba	White Wagtail		7 (0.7)	10 (1.0)	11 (0.9)	28 (0.9)
Muscicapa striata	Spotted Flycatcher	§	7 (0.6)	15 (1.5)	10 (1.0)	32 (1.0)
Oenanthe oenanthe	Northern Wheatear		0 (0.0)	0 (0.0)	1 (0.1)	1 (0.0)
Parus major	Great Tit		29 (5.9)	32 (6.4)	24 (3.0)	85 (5.1)
Passer domesticus	House Sparrow	§	32 (24.1)	29 (16.7)	0 (0.0)	
Passer hispaniolensis italiae	Spanish Sparrow	§	0 (0.0)	0 (0.0)	32 (29.4)	93 (23.5) [c]
Passer montanus	Eurasian Tree Sparrow		1 (0.2)	1 (0.1)	2 (0.4)	4 (0.2)
Periparus ater	Coal Tit		3 (0.2)	6 (0.6)	7 (0.7)	16 (0.5)
Phalacrocorax carbo	Great Cormorant		0 (0.0)	1 (0.1)	0 (0.0)	1 (0.0)
Phoenicurus ochruros	Black Redstart		19 (1.8)	28 (3.3)	14 (1.2)	61 (2.1)
Phoenicurus phoenicurus	Common Redstart	NT, #	2 (0.2)	1 (0.1)	18 (1.8)	21 (0.7)
Phylloscopus collybita	Common Chiffchaff		5 (0.5)	10 (0.9)	2 (0.1)	17 (0.5)

Phylloscopus trochilus	Willow Warbler	NT, #	0 (0.0)	0 (0.0)	1 (0.1)	1 (0.0)
Pica pica	Eurasian Magpie		19 (2.3)	11 (1.4)	0 (0.0)	30 (1.2)
Picus viridis	European Green Woodpecker		1 (0.1)	1 (0.1)	2 (0.1)	4 (0.1)
Poecile palustris	Marsh Tit		1 (0.1)	3 (0.3)	0 (0.0)	4 (0.1)
Ptyonoprogne rupestris	Eurasian Crag Martin		0 (0.0)	0 (0.0)	2 (0.4)	2 (0.1)
Pyrrhula pyrrhula	Eurasian Bullfinch		0 (0.0)	1 (0.1)	0 (0.0)	1 (0.0)
Regulus ignicapilla	Common Firecrest		6 (0.6)	15 (1.6)	9 (0.8)	30 (1.0)
Regulus regulus	Goldcrest		1 (0.2)	0 (0.0)	0 (0.0)	1 (0.0)
Saxicola rubetra	Whinchat	NT, #	0 (0.0)	0 (0.0)	1 (0.1)	1 (0.0)
Serinus serinus	European Serin	§	8 (0.6)	15 (1.5)	24 (2.7)	47 (1.6)
Sitta europaea	Eurasian Nuthatch		8 (0.7)	10 (1.0)	7 (0.6)	25 (0.8)
Streptopelia decaocto	Eurasian Collared Dove	§	14 (1.9)	5 (0.6)	19 (2.7)	38 (1.7)
Sturnus vulgaris	Common Starling		20 (3.4)	19 (3.3)	10 (1.4)	49 (2.7)
Sylvia atricapilla	Eurasian Blackcap		21 (3.2)	27 (3.3)	28 (4.8)	76 (3.8)
Tachymarptis melba	Alpine Swift	NT, #	2 (0.4)	2 (0.7)	1 (0.1)	5 (0.4)
Troglodytes troglodytes	Winter Wren		3 (0.4)	5 (0.4)	4 (0.4)	12 (0.4)
Turdus merula	Common Blackbird		31 (7.1)	32 (12.5)	31 (8.1)	94 (9.2)
Turdus philomelos	Song Thrush		0 (0.0)	2 (0.1)	0 (0.0)	2 (0.0)
Turdus viscivorus	Mistle Thrush		0 (0.0)	1 (0.1)	0 (0.0)	1 (0.0)

[a] Conservation status according to the Red List of birds of Switzerland (Keller et al. 2001): VU = vulnerable, NT = near threatened; # = indicates whether a species was considered as a priority species for Switzerland (Bollmann et al. 2002); § identifies indicator species for urban habitats (Zbinden et al. 2005).

[b] Steadiness expresses the number of sampling points with the presence of the species. Dominance indicates the fraction (%) of individuals of a single species on the total individual number of birds.

[c] As *Passer hispaniolensis italiae and Corvus cornix* occupy the ecological niche of *P. domesticus* and *C. corone* in Lugano, we calculate the overall steadiness and dominance as if they were the same species.

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