Urbanization and wetland communities: applying metacommunity theory to understand the local and landscape effects

Pieter T. J. Johnson[1]*, Jason T. Hoverman[1]†, Valerie J. McKenzie[1], Andrew R. Blaustein[2] and Katherine L. D. Richgels[1]

[1]*Ecology and Evolutionary Biology, University of Colorado, Boulder, CO, 80309, USA; and* [2]*Department of Zoology, Oregon State University, Corvallis, OR, 97331, USA*

Summary

1. Urbanization is a growing threat to ecological communities and has become a leading cause of population extirpations in a wide range of taxa. Because the effects of urbanization are often multifaceted, identifying the pathways through which changes in communities occur has remained a persistent challenge.

2. We draw upon metacommunity theory to evaluate competing explanations for the effects of urbanization, focusing on the relative importance of processes at local (e.g. abiotic and biotic characteristics) and regional (e.g. habitat connectivity and dispersal) scales. Over 4 years, we sampled 201 wetlands in the Front Range region of Colorado, which is one of the most rapidly developing areas in the USA.

3. Wetlands embedded within urban areas exhibited significantly lower taxonomic richness and diversity compared to those in agricultural or grassland areas. Relative to grassland wetlands, urban wetlands supported a 60% lower richness of amphibians and aquatic reptiles and a 33% lower richness of aquatic insects, molluscs and crayfish. These patterns were associated with changes in biotic factors (introduced fishes and bullfrogs), abiotic factors (nutrients, conductivity and vegetation) and landscape characteristics (road density and surrounding wetland area).

4. The use of an information-theoretic approach and structural equation modelling suggested that the effects of urbanization on richness were mainly driven by changes in road density. Analyses of community composition indicated that discrete communities formed along the urban systems gradient, such that actively dispersing predators associated more negatively with urban system relative to herbivores with passive dispersal.

5. *Synthesis and applications.* These results highlight the importance of considering both local and regional factors in addressing conservation-related challenges and underscore the benefits of linking conceptual work on metacommunity theory with applied efforts to mitigate the effects of urbanization.

Key-words: amphibian decline, aquatic conservation, community ecology, global change, habitat loss, trait-based approach

Introduction

Recognizing that local communities are linked through species dispersal, metacommunity theory has emerged as a powerful tool for advancing our understanding of the joint influences of local and regional processes on ecological communities and biodiversity patterns (Leibold *et al*. 2004; Holyoak, Leibold & Holt 2005). This framework has revealed that the relative importance of local vs. regional influences depends, in part, on system and species' characteristics (e.g. habitat type, dispersal mode, spatial scale; Cottenie 2005). For instance, local processes tend to dominate in metacommunities composed of species with passive dispersal, while those constituted by

primarily active dispersers are strongly influenced by regional processes (Cottenie 2005). Thus far, however, there have been few attempts to apply metacommunity theory to human-modified landscapes, despite an abundance of evidence showing that human activity affects both local and regional processes (Parris 2006; Corbyn 2010; Buczkowski 2011).

Urbanization is an increasing threat to ecological communities and has become a leading cause of population and species extirpations (McKinney 2006). Progressive development can profoundly alter not only the abiotic and biotic characteristics of habitats but also their connectivity across the landscape (McDonnell *et al.* 1997; McKinney 2006). Numerous studies have documented the loss of native species in urban settings, leading to the generalization that urbanization reduces species diversity and promotes homogenization of plant and animal assemblages (Faeth *et al.* 2005; Clergeau *et al.* 2006). Urban environments can also facilitate establishment of invasive species that further contribute to native biodiversity loss (Shochat *et al.* 2006). However, while considerable effort has been directed towards descriptive accounts of ecological responses along urbanization gradients (McDonnell & Pickett 1990; McDonnell *et al.* 1997; Tait, Daniels & Hill 2005), fewer studies have explored the ecological processes underlying observed responses (Croci, Butet & Clergeau 2008).

Recently, Shochat *et al.* (2006, 2010) proposed that the patterns associated with urbanization could result from several mechanisms: (i) alteration of habitat structure and connectivity, (ii) increased productivity and species interactions and (iii) changes in patch quality and stability. These hypotheses align broadly with the local (e.g. resource availability, species interactions) and regional (e.g. habitat structure, connectivity) factors explored in metacommunity research, suggesting a timely opportunity to integrate ecological theory with applied issues such as urbanization. For instance, the predicted effects of urbanization on habitat heterogeneity and connectivity suggest that species-sorting and mass-effects perspectives from metacommunity theory are likely to characterize human-modified landscapes. Tools from metacommunity research can also facilitate comparisons of metrics beyond species richness to examine compositional changes in communities along urbanization gradients. For example, species-specific responses to urbanization could generate strong patterns of turnover as urban-intolerant species are replaced by urban-tolerant species (Kark *et al.* 2007; Croci, Butet & Clergeau 2008), ultimately forming discrete communities across urbanization gradients that are distinguished by variation in traits (e.g. trophic status, dispersal mode, behaviour; Kark *et al.* 2007; Croci, Butet & Clergeau 2008).

Here, we sought to evaluate the relationship between urbanization and aquatic community richness and to explore the local and regional factors contributing to observed changes in biodiversity. We quantified patterns of richness and composition for aquatic vertebrates (amphibians and reptiles) and macroinvertebrates (molluscs, insects and crayfish), each of which are understudied groups in urbanization research (McDonnell & Hahs 2008). Wetland communities have been used increasingly in metacommunity research because of the following reasons: (i) wetlands represent discrete habitats embedded within a terrestrial matrix, (ii) multiple taxa representing different trophic levels and functional groups utilize wetlands, and (iii) many of these taxa use aquatic and terrestrial habitats such that both local and regional processes affect community structure (Van Buskirk 2005; Werner *et al.* 2007; McCauley *et al.* 2008; Hoverman *et al.* 2011). Concurrently, the effects of urbanization on the characteristics of aquatic habitats have been well documented in temperate regions (Rubbo & Kiesecker 2005; Hamer & McDonnell 2008; Gagne & Fahrig 2010). With the goal of providing an empirical bridge between metacommunity theory and urbanization research, we used analytical tools from community ecology to evaluate (i) whether urban wetlands supported lower diversity and more homogenous assemblages relative to other land use types, (ii) the relative contributions of local and regional processes in explaining such patterns, including the hypothesized roles of resource availability, connectivity and invasive species, and (iii) whether community composition changed along the urbanization axis in association with specific organismal traits.

Materials and methods

STUDY REGION AND SITE SELECTION

The Rocky Mountain West is one of the fastest growing regions in the USA and exhibited a 60% population increase from 1980 to 2000 (Vias & Carruthers 2005). Colorado's Front Range region, in particular, is a rapidly developing area along the eastern foothills of the southern Rocky Mountains with several counties that have exhibited growth rates of >50% (Perry & Mackun 2001). We used the National Wetlands Inventory (NWI, United States Fish and Wildlife Service) to identify wetlands in a seven county area of Colorado's Front Range (Fig. 1) that encompasses broad variation in land use types, including row-crop agriculture, pasturelands, native grasslands, open rangelands and a progressively increasing density of urban and suburban areas (Perry & Mackun 2001). We selected wetlands using ArcGIS 9·3 that were 0·05 to 2 ha in surface area, <2300 m in elevation, and then used the National Land Cover Database (Fry *et al.* 2011) to obtain the percentage of land cover types within a 1-km radius of each system (Rubbo & Kiesecker 2005; Van Buskirk 2005; Hamer & Parris 2011). We aggregated among categories to generate three major forms of land use: grassland (combination of grassland/herbaceous and shrub/scrub categories), agricultural (combination of cultivated crops and pasture/hay categories) and urban (combination of low intensity, medium intensity and high intensity development categories). From the resulting list of 4087 wetlands, we randomly selected 100 sites in the uppermost quartile of each land use type and used Google Earth (version 4.0, 2006) to verify that (i) the system was a wetland, (ii) the wetland still existed and (iii) the system was at least 10 years old (using the 'view historical imagery' tool). Ultimately, we selected 70 sites

in each land cover type to sample, including a mixture of publicly and privately owned sites, although the final sample sizes varied as a function of property access and hydroperiod.

SAMPLING METHODS

Between 2007 and 2010, we sampled wetlands in early summer (May–June) to quantify vertebrate (amphibian and reptile) and macroinvertebrate (crayfish, mollusc and aquatic insect) richness and community composition using visual encounter surveys (VES) around the shoreline (0–2 m from shore), standardized (1-m length) dipnet sweeps every 10 m (D-frame dipnet, 1·2-mm mesh) and three to five habitat-stratified seine hauls (1·2 × 1·8 m, 3·18-mm mesh, *c*. 3 m average haul distance) (Johnson *et al.* 2011). All taxa were identified in the field and released; while this created some variation in taxonomic resolution, with groups such as amphibians and reptiles identified to species while macroinvertebrates were identified to genus or family, we analysed vertebrate and invertebrate richness separately for most analyses and, when combined, adjusted to the higher taxonomic level as needed. Alongside native taxa, we also recorded the occurrence of non-native bullfrogs *Lithobates catesbeianus* Shaw, 1802, and introduced fishes. We assessed the efficacy of our methods using species accumulation curves and rarefaction analyses (see Appendix S1, Supporting information). We visually estimated the proportion of the shoreline that was vegetated and the number of trees ≥ 3 m in height within 15 m of the water's edge. Pond surface area was measured using a GPS (Garmin GPSMAP 60CSx), while water temperature and conductivity were quantified using a YSI (Model 556; Yellow Springs Instruments, Yellow Springs,

Ohio, USA) placed 0·5 m below the water's surface. Total nitrogen and phosphorus were measured using standard methods (http://snobear.colorado.edu/Kiowa/Kiowaref/procedure.html). We estimated whether wetlands were permanent or temporary (i.e. held water <4 months in most years) based on water depth, wetland area, and using Google Earth's historical imagery tool.

ANALYSES OF TAXONOMIC RICHNESS

To evaluate the influence of urbanization on aquatic community richness, we used a hierarchical approach involving three steps. First, we assessed the relationship between land use and vertebrate and invertebrate richness, independent of any other variables. This analysis determined whether land usage generally and urbanization in particular correlated with native vertebrate and invertebrate richness. Using abundance data on invertebrates and vertebrates (larval amphibians only) from the dipnet sweeps, we also calculated the Shannon–Wiener diversity index for the entire native community. These measures were generated using data only from the first visit to each wetland to standardize sampling effort. Urbanization, as a proportion, was arcsin-square root transformed prior to analyses, and we used generalized linear models with either a Poisson or Gaussian distribution for count data (taxonomic richness) and diversity estimates (Shannon), respectively. To account for potential effects of sample year, we repeated these analyses using generalized linear mixed models with year as a random effect. We also tested whether the relationships between urbanization and richness were nonlinear using generalized additive models and assessed whether the smoothing function was warranted using ΔAIC and ANOVA (see Zuur *et al.* 2009).

Second, we developed models to explain assemblage richness that included variables to represent abiotic factors, biotic factors and landscape-level factors based on theory and previous literature (Parris 2006; Hamer & Parris 2011). We represented the abiotic environment using wetland area, wetland permanence and the first two factors from a principal components analysis (Appendix S1, Supporting information). The biotic community was represented by the presence/absence of non-native bullfrogs and introduced fishes. Native fishes were largely absent in our sampled wetlands. Finally, to represent changes in urban landscapes likely to influence species colonization and dispersal, we included (i) the total length (km) of paved roads and (ii) the total wetland surface area within 1 km of the study site. Roads more so than simple measures of impervious surfaces have consistently been shown to influence organismal dispersal (Hamer & McDonnell 2008), while nearby wetland area was used as a measure of potential colonization sources (Rubbo & Kiesecker 2005). We compared among models that included abiotic, biotic and dispersal-mediated variables using an AIC model selection approach ('AICCMODAVG' package, R Development Core Team 2008). We further evaluated variable importance using hierarchical partitioning analysis in the R package 'hier.part' using R^2 goodness-of-fit measures for Gaussian responses and the root mean square predictor error for Poisson responses (Mac Nally 2000). We then tested the residuals from the best models to ensure there was no remaining relationship with urbanization, which suggests that the included variables adequately captured the mechanisms through which urbanization affected richness. We also tested the residuals for indications of spatial autocorrelation using Moran's I in the 'spdep' package of R.

Finally, we evaluated which predictors from the models determined the influence of urbanization on aquatic communities. We
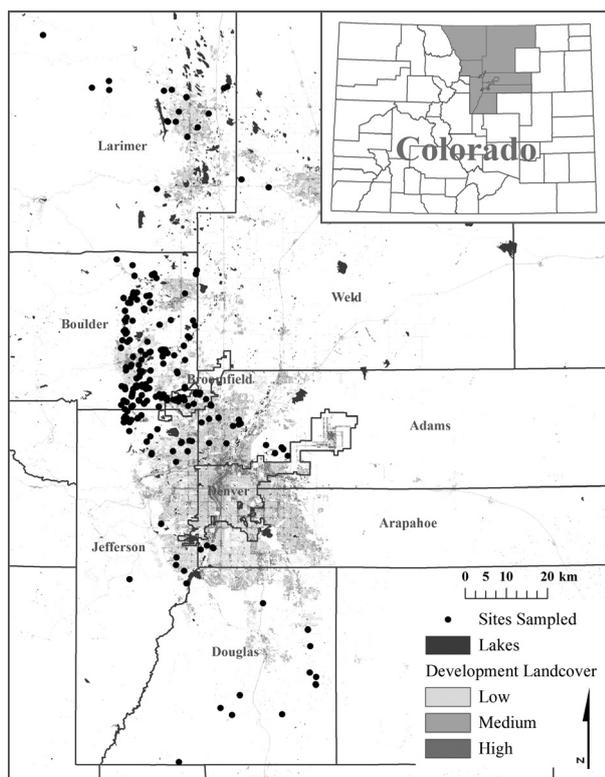

Fig. 1. Map of sampled wetlands in the Front Range region of Colorado. Study sites are depicted as black circles while urban development intensity is reflected by the grey shading.

used structural equation modelling in the software package AMOS 19 to assess the direct and indirect effects of urbanization on each of the response variables (vertebrate richness, invertebrate richness and total diversity). Structural equation modelling (SEM) provides a statistical technique to test the relative importance of direct and indirect effects simultaneously through construction of path diagrams (Pugesek, Tomer & Eye 2003; Byrne 2010). The standardized coefficients of each path can be quantified while the overall fit of the model to the data can be tested using the chi-squared distribution (with the null hypothesis that the model fits the data) alongside other measures of fit that incorporate parsimony (root mean square error of approximation, RMSEA and the comparative fit index, CFI). Thus, this approach built upon the previously described AIC-modelling approach in two important ways: first, we incorporated urbanization into the model as an indirect predictor of proximate variables, and second, we used only the predictor variables identified as important (partitioned variance explained >10%), thus helping to keep models tractable. Urbanization was not included as a direct predictor of richness or diversity owing to its high collinearity with road length, which can inflate type II error in SEM (Grewal, Cote & Baumgartner 2004). We assessed variable importance using standardized coefficients and used a Monte Carlo bootstrapping approach (2000 simulations) to assess the indirect effects of urbanization.

ANALYSES OF ASSEMBLAGE COMPOSITION

We used the methods of Leibold & Mikkelson (2002) to examine the site-by-species incidence matrix for patterns of turnover, nestedness and boundary clumping (Appendix S1, Supporting information). To identify the role of species traits in predicting transitions between communities, we used fourth-corner statistics, which use a site-by-species matrix, a site-by-habitat characteristic matrix and a species-by-trait matrix to evaluate associations between traits and environmental characteristics (Appendix S1, Supporting information; Dray & Legendre 2008). We included urbanization as our main habitat characteristic, while each sampled species was classified by trophic level (herbivore or predator) and dispersal mode (active or passive) to generate the species-by-trait matrix using the 'ape4' package (R Development Core Team 2008) (Urban 2004). Finally, we assessed whether urbanization promoted homogenization of communities by calculating community similarity (Jaccard's index; Magurran 2004) and inter-wetland distance for each pairwise combination of sites using PASSAGE 2.0 (Rosenberg & Anderson 2011). We then used linear regression to compare the relationship between community similarity and distance among land use types, with the hypothesis that urban sites would exhibit greater similarity to one another relative to other land use types (McKinney 2006).

Results

SAMPLING OVERVIEW

Between May 2007 and June 2010, we conducted 466 site-visits to 219 wetlands for an average of 2·13 visits per site (Fig. 1). After excluding duplicate visits and sites with incomplete data, the total wetland sample size was 201. Of these, 30·7% were classified as agricultural, 34·7% as urban/suburban and 34·7% as grassland. Fifty-six percentage of sampled wetlands were on privately owned land. A total of 10 vertebrate species and 19 invertebrate taxa were observed. Among sites, vertebrate and invertebrate taxonomic richness were low overall, averaging 1·18 ± 0·09 and 5·56 ± 0·19, respectively, with ranges of 0–5 vertebrate species and 0–11 invertebrate taxa. Excluding sites at which no native vertebrates were detected ($n = 78$), average vertebrate richness increased to 1·96 ± 0·10. Non-native bullfrogs and introduced fishes were observed at 91 and 120 sites, respectively.

EFFECTS OF URBANIZATION ON AQUATIC ASSEMBLAGES

Aquatic diversity varied significantly with surrounding land use (GLM; vertebrate richness $\chi^2 = 45.99$, d.f. = 3, $P < 0.0001$, $n = 201$; invertebrate richness $\chi^2 = 23.25$, d.f = 3, $P < 0.0001$, $n = 201$; total Shannon diversity $\chi^2 = 15.17$, d.f. = 3, $P < 0.0005$; $n = 189$). For both vertebrates and invertebrates, taxonomic richness was greatest in wetlands surrounded by grasslands and lowest in wetlands embedded in agricultural and especially urban areas (Fig. 2a). The degree of urbanization was a negative predictor of native vertebrate presence ($\chi^2 = 16.93$, d.f. = 1, $P < 0.0001$; $n = 201$), vertebrate richness ($\chi^2 = 34.61$, d.f. = 1, $P < 0.0001$; $n = 201$), invertebrate richness ($\chi^2 = 34.08$, d.f. = 1, $P < 0.0001$; $n = 201$) and total diversity ($\chi^2 = 17.58$, d.f. = 1, $P < 0.0001$; $n = 189$) (Fig. 2b). Residuals from these analyses were not spatially autocorrelated based on Moran's I (all $P > 0.3$), and including year as a random effect did not alter the results (urbanization coefficients differed by <2%). We also found no evidence that the relationship between urbanization and richness or diversity was better fit with a smoothing term.

FACTORS LINKING URBANIZATION AND RICHNESS

While many wetland characteristics varied as a function of land use type (Table S2, Supporting information), AIC-based model selection approaches yielded strongly similar results in explaining vertebrate and invertebrate richness as well as total diversity. For vertebrate and invertebrate richness, the biotic + dispersal models were the 'best-supported' as determined by AIC values and Akaike weights, with the global model also receiving strong support (Table S3, Supporting information). For total diversity, the global model was the most supported with no other models within five AIC units. Based on hierarchical partitioning analysis, the most important variables were roads (dispersal) and fish presence (biotic), each of which explained between 23 and 48% of observed variance (Fig. 3). Other important variables included principal component 1 (vegetation) and bullfrogs for the invertebrate richness models and principal component 2 (productivity) for the total diversity models (Fig. 3). Residuals from the best models were not significantly related to urbanization (all $P > 0.45$), suggesting these
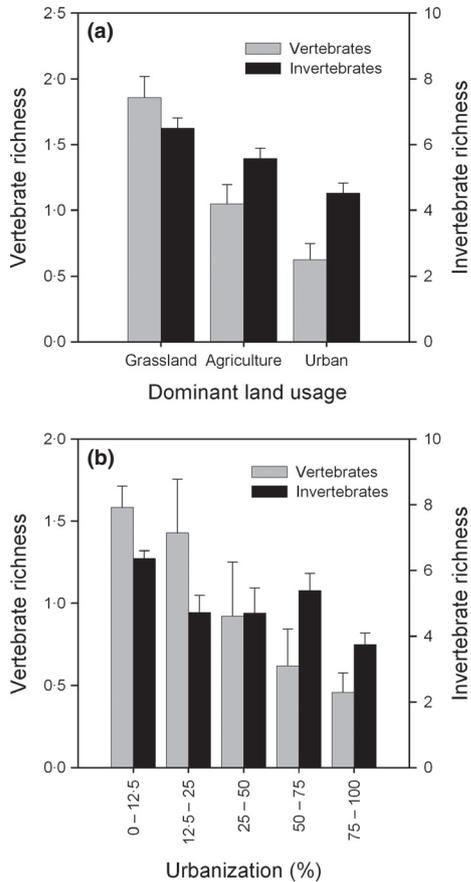
Fig. 2. (a) Vertebrate and invertebrate taxonomic richness among wetlands as a function of the surrounding land cover type. Dominant land usage reflects the primary (>50%) land cover type within a 1-km buffer of each wetland. (b) Relationship between the amount of urbanization around a wetland (%) and its taxonomic richness.
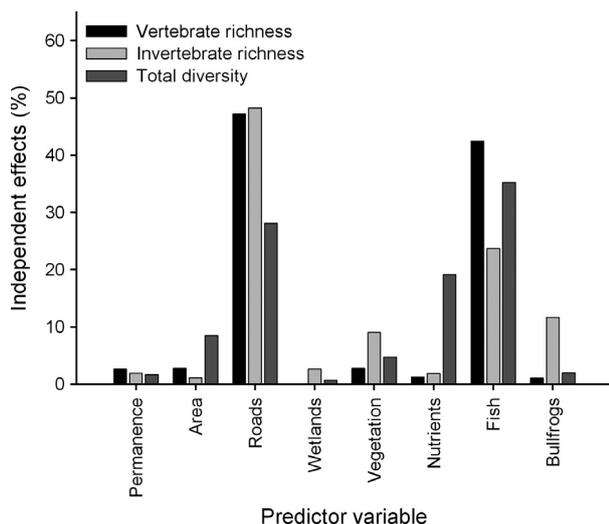

Fig. 3. Relative importance of predictor variables in explaining patterns of vertebrate richness, invertebrate richness and total Shannon diversity. The size of the bar indicates the total amount of variance (%) in each response variable explained by a given predictor. Vegetation and nutrients were derived from PCA.

models did an adequate job capturing the pathways through which urbanization affected richness.

The use of a structural equation modelling approach provided additional information about the pathways through which urbanization likely influenced richness and diversity. Reinforcing results from the AIC model selection approach, both road density and fish occurrence had consistently negative effects on vertebrate and invertebrate richness (Fig. 4 and Fig. S2, Supporting information). For invertebrates, vegetation structure (PC 1) also had a significant positive effect on richness, whereas nutrients (PC 2) had a negative effect on total Shannon diversity. Each of these models provided an adequate fit to the data ($P > 0.05$, RMSEA < 0.05, CFI > 0.98) (Table 1). Based on bootstrapping estimates, urbanization had a negative indirect effect on each measure of richness or diversity ($P < 0.01$). Importantly, urbanization had strong direct effects only on road density, with no significant influence on fish or measures of vegetation and nutrients (Table 1). Results were generally similar for invertebrate richness, although roads had a slightly weaker effect than observed for vertebrates (Table 1). Separation of the data set into wetlands with and without fish revealed that urbanization had negative effects on richness in sites from both conditions, whereas urbanization had non-significant effects on
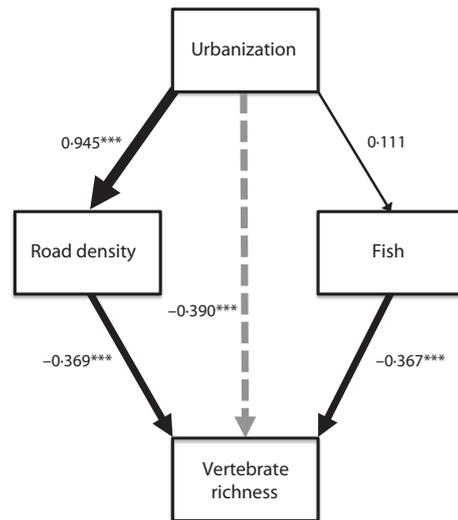

Fig. 4. Representative structural equation model diagram used to evaluate relationships among vertebrate richness and urbanization (arcsin-square root transformed), road density (square root transformed), fish occurrence and local environmental factors. Direct relationships are shown with solid black arrows, whereas indirect effects are depicted using dashed grey arrows. The relative size of each arrow reflects relationship strength; standardized path coefficients and significance values are presented alongside each path ($P < 0.05$ [*], $P < 0.005$ [**], $P < 0.0005$ [***]). The indirect effect of urbanization is driven predominantly through road density, with the following specific contributions: indirect effect through roads: −0.35***; indirect effect through fish: −0.041; total indirect effect: −0.39***. See Fig. S2 for the diagrams involving invertebrate richness and total Shannon diversity.

Table 1. Results from the structural equation models for vertebrate richness, invertebrate richness and total diversity. Presented is the standardized coefficient and *P*-value for each path in the model. Predictor variables varied among models as a function of which variables were identified during the hierarchical partitioning analysis. Model diagnostics were as follows: vertebrates ($\chi^2 = 2.074$, d.f. = 2, *P* = 0.36; RMSEA = 0.014, CFI = 1.0), invertebrates ($\chi^2 = 1.95$, d.f. = 3, *P* = 0.58; RMSEA = 0.0, CFI = 1.0) and diversity ($\chi^2 = 2.8$, d.f. = 3, *P* = 0.42; RMSEA = 0.0, CFI = 1.0)

Model	Predictor	Response	Coefficient	*P*-value
Vertebrates	Urban	Roads	0.945	< 0.0001
	Urban	Fish	0.111	0.124
	Roads	Richness	−0.369	< 0.0001
	Fish	Richness	−0.367	< 0.0001
	Urban	Richness (indirect)	−0.390	0.006
Invertebrates	Urban	Roads	0.945	< 0.0001
	Urban	Fish	0.111	0.124
	Urban	Vegetation	−0.029	0.688
	Roads	Richness	−0.337	< 0.0001
	Vegetation	Richness	0.146	0.024
	Fish	Richness	−0.2	0.002
	Urban	Richness (indirect)	−0.345	0.001
Total diversity	Urban	Roads	0.945	< 0.0001
	Urban	Nutrients	0.05	0.495
	Urban	Fish	0.103	0.157
	Roads	Diversity	−0.238	< 0.0001
	Nutrients	Diversity	−0.250	< 0.0001
	Fish	Diversity	−0.303	< 0.0001
	Urban	Diversity (indirect)	−0.269	0.001

the residuals from a regression between road density and invertebrate or vertebrate richness.

ASSEMBLAGE COMPOSITION AND URBANIZATION

We found coherence in the ordinated site-by-species incidence matrix with 2477 observed embedded absences (expected mean ± 1 SD; 2771 ± 46, *P* < 0.001), indicating that species were not randomly distributed across sites. Species' ranges displayed significant turnover with 67 030 replacements (expected mean ± 1 SD; 26 052 ± 12 429, *P* < 0.001), which was associated with the transition to urban wetlands as evidenced by the positive correlation between wetland ordination scores and urbanization (Pearson's *r* = 0.274, *P* < 0.001). Additionally, species' range boundaries were significantly clumped (Morisita's index = 10.32, *P* < 0.001), suggesting that discrete communities formed along the urbanization gradient (i.e. Clementsian structure). Taxa such as mosquito larvae, dytiscids, notonectids, larvae of *Pseudacris triseriata* (Wied-Neuwied, 1838) and *Ambystoma tigrinum* (Green, 1825) were largely absent from heavily urbanized wetlands, whereas leeches, crayfish and bullfrog larvae were less common among grassland wetlands. Fourthcorner methods indicated that species characterized by passive dispersal modes (*r* = −0.056, *P* = 0.001) and

herbivory (*r* = −0.033, *P* = 0.008) associated positively with urbanized wetlands. Counter to our expectation, however, there was no evidence that the degree of community similarity and homogenization differed among land use categories ($F_{3,184} = 2.6$, $R^2 = 0.041$, *P* = 0.95).

Discussion

Our results revealed a strong, negative relationship between urbanization and aquatic assemblage richness and diversity. Across a mosaic of land use forms in the Front Range region of Colorado, wetlands surrounded by urban areas supported the lowest native richness for both aquatic vertebrates and macroinvertebrates. The degree of urbanization within a 1-km buffer of each pond correlated negatively with the richness of both groups and, when the abundance of specific taxa was incorporated alongside their presence, urbanization also negatively predicted total diversity. While the overall taxonomic richness within these small pond communities was generally low, these patterns are noteworthy given the diversity of surveyed taxa, which included amphibians, turtles, snakes, larval insects, molluscs, crayfishes and other invertebrates, as well as the number of sampled assemblages.

A major goal of the current study was to use a metacommunity approach to explore the pathways through which urbanization – and land use change generally – influenced aquatic community richness. Metacommunity theory provides an important bridge in community ecology by recognizing the joint influence of local factors, such as the biotic and abiotic features of a habitat patch, and the regional or landscape features likely to affect organismal dispersal (Leibold *et al.* 2004; Urban 2004; Cottenie 2005; Holyoak, Leibold & Holt 2005). Our results indicated that urbanization was associated with substantial changes in nearly every wetland characteristic measured. Relative to wetlands embedded within grassland areas, which come closest to approximating native habitats, urban wetlands tended to be warmer, more permanent, with higher conductivity and surrounded by more roads with fewer neighbouring wetlands (Table S2, Supporting information). They were also more likely to support introduced fishes and non-native bullfrogs. These urbanization-associated changes in wetland characteristics and the terrestrial habitat matrix are largely consistent with previous studies (Vos & Chardon 1998; Parris 2006; Hamer & Parris 2011) and underscore the challenges inherent to urban ecology: with so many factors altered in association with development, what are the most important pathways through which observed changes in richness occur?

Results of the AIC model selection approach followed by structural equation modelling suggested two insights into this problem. First, factors associated with the abiotic habitat, the biotic community and the surrounding landscape all contributed to patterns of invertebrate and vertebrate richness generally. In particular, the presence

of introduced fishes and the density of roads surrounding a wetland each had sharply negative effects on assemblage richness and were included in all of the best-supported models. Second, structural equation modelling suggested that, while both fish and roads negatively affected aquatic richness, the effects of urbanization on richness were more likely driven through changes in road density than through changes in fish occurrence. Thus, road development and its likely effects on dispersal and wetland isolation associated intimately with urbanization; non-native fishes, in contrast, which are introduced through a variety of mechanisms, were equally likely to occur in agricultural habitats as in those associated with urban areas (although introduced fishes were rare in the more natural grassland ponds). Notably, the effects of urbanization remained strongly negative if the data set was divided into ponds with and without fish, whereas urbanization became a non-significant predictor of richness after controlling for road density.

Collectively, these findings are consistent with the previously documented effects of roads and introduced fishes on native amphibians and macroinvertebrates (Vos & Chardon 1998; Rubbo & Kiesecker 2005; Schilling, Loftin & Huryn 2009). From a metacommunity perspective, these results correspond with urbanization having effects mediated through the mass-effects perspective, such that urbanization influenced connectance among wetlands and the capacity for immigration to rescue population 'losses', which are especially important to organisms with biphasic life cycles such as many amphibians and aquatic insects that must 'recolonize' systems each year. Fish occurrences, as a biotic limitation on species' occurrences, were superimposed on this pattern as a species-sorting influence (see also Rubbo & Kiesecker 2005; Van Buskirk 2005). However, perfect separation of variables into local (niche) and regional (dispersal) categories is often impossible, particularly for such a diverse set of taxa with difficult to measure dispersal rates (Logue *et al.* 2011). Thus, we cannot rule out the potential contributions of other, unmeasured variables associated with roads that could also have contributed to their observed effects on biodiversity. For instance, beyond their effects on dispersal, roads also influence local habitat characteristics through increased noise, light and pollutant runoff (Warren *et al.* 2006; Horvath *et al.* 2009; Simon *et al.* 2009). Ultimately, a greater focus on quantifying the effects of roads on the dispersal rates of different species will be necessary to fully characterize the contributions of roads to both local and regional processes (Logue *et al.* 2011).

Metacommunity theory also provides a useful framework for examining changes in community composition along habitat gradients. Wetland metacommunities in this study displayed Clementsian structure (i.e. species turnover with boundary clumping), suggesting that distinct communities formed along the urbanization gradient in accordance with the tolerance of different taxa (Hogsden & Hutchinson 2004; Croci, Butet & Clergeau 2008).

Predators and species dependent on active dispersal mechanisms were the most negatively affected by urbanization. Given that urbanization reduces habitat connectivity and the quality of the terrestrial matrix, species with active dispersal may suffer increased mortality during dispersal with fewer opportunities for rescue effects (Alberti *et al.* 2003; Bowne & Bowers 2004; Rubbo & Kiesecker 2005). Because many of the actively dispersing species in our communities were also predatory (e.g. dytiscids, anisopterans), urbanization-mediated losses of predators may also explain the apparent increase in herbivore populations, alongside any increases in nutrient resources. Surprisingly, however, there was no evidence that communities within urban wetlands were more homogeneous than communities within grassland wetlands. Although community homogenization is a proposed outcome of urbanization due to greater uniformity in habitat characteristics at urban sites (Kuhn & Klotz 2006; McKinney 2006), our results suggest caution when applying this generalization across systems.

The current findings have implications for continued research on metacommunities and urbanization. While urbanization is widely recognized as a contributing cause of decreases in aquatic and terrestrial species richness, several competing hypotheses have emerged to explain the mechanisms underlying this pattern: increased fragmentation, increased density of urbanophilic species, including non-natives, increased competition owing to decreases in top predators coupled with greater resource availability and decreased temporal variability (Shochat *et al.* 2006, 2010). Our use of alternative models supported contributing roles for habitat fragmentation in the form of dispersal barriers (roads) and for introductions of non-native predators, including bullfrogs and especially fishes. However, we did not find evidence implicating increased competition as a driver of decreased species richness, which is consistent with general findings from metacommunity research (Hamer & McDonnell 2008; Hoverman *et al.* 2011). Invertebrate and vertebrate biomass tended to decrease or show no effect with increasing urbanization. Rather surprisingly, we also found no effect of urbanization on habitat stability, as we had expected urban wetlands would have more permanent hydroperiods (Rubbo & Kiesecker 2005). However, if we restricted comparisons to urban vs. grassland ponds (omitting agricultural ponds), urbanization associated positively with hydroperiod (94·2% of wetlands were permanent within urban areas vs. 77·1% permanent within grasslands; $\chi^2 = 8·72$, $P = 0·0031$).

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Over the last three decades, it has often been argued that ecologists need to explicitly study modified landscapes associated with urbanization and that urban environments are unique ecosystems with their own set of rules and processes (McDonnell & Pickett 1990; Alberti *et al.* 2003;

Corbyn 2010). Although not all taxa are likely to respond similarly to urbanization (see Tait, Daniels & Hill 2005), we suggest that community ecology in general and meta-community theory in particular provide promising tools to help understand and address the challenges associated with land use transformation. Our results suggest, for instance, that mitigating the effects of urbanization on freshwater communities will require conservation pro-grammes that simultaneously address local and regional processes. At the local scale, the elimination of non-native fish populations can be achieved by draining urban ponds during the winter and restoring the natural hydroperiod (Dodd 2009). At the regional scale, efforts directed towards maintaining habitat connectivity will be vital for maintaining biodiversity on the fringe of urban advance-ment, as has been achieved in some regions using wildlife corridors (Rosenberg, Noon & Meslow 1997) and crossing structures (Clevenger & Wierzchowski 2006). And while research on metacommunities has focused historically on undeveloped areas, particularly with respect to aquatic systems, incorporating modified landscapes into such studies has enormous potential to help inform and advance metacommunity theory. For example, by altering habitat characteristics that influence dispersal, urbaniza-tion can serve to identify the consequences of shifts in the relative importance of regional and local processes within metacommunities.

Acknowledgements

References

Alberti, M., Marzluff, J.M., Shulenberger, E., Bradley, G., Ryan, C. & Zumbrunnen, C. (2003) Integrating humans into ecology: opportunities and challenges for studying urban ecosystems. *BioScience*, **53**, 1169–1179.

Bowne, D.R. & Bowers, M.A. (2004) Interpatch movements in spatially structured populations: a literature review. *Landscape Ecology*, **19**, 1–20.

Buczkowski, G. (2011) Suburban sprawl: environmental features affect col-ony social and spatial structure in the black carpenter ant, Camponotus pennsylvanicus. *Ecological Entomology*, **36**, 62–71.

Byrne, B.M. (2010) *Structural Equation Modeling with AMOS: Basic Con-cepts, Applications, and Programming*, 2nd edn. Routledge, New York.

Clergeau, P., Croci, S., Jokimaki, J., Kaisanlahti-Jokimaki, M.L. & Dinetti, M. (2006) Avifauna homogenisation by urbanisation: analysis at different European latitudes. *Biological Conservation*, **127**, 336–344.

Clevenger, A.P. & Wierzchowski, J. (2006) Maintaining and restoring con-nectivity in landscapes fragmented by roads. *Maintaining Connections for Nature* (eds K.R. Crooks & M. Sanjayan), pp. 502–535. Cambridge University Press, Cambridge.

Corbyn, Z. (2010) Ecologists shun the urban jungle. *Nature News* Nature, doi: 10.1038/news.2010.359.

Cottenie, K. (2005) Integrating environmental and spatial processes in ecological community dynamics. *Ecology Letters*, **8**, 1175–1182.

Croci, S., Butet, A. & Clergeau, P. (2008) Does urbanization filter birds on the basis of their biological traits? *Condor*, **110**, 223–240.

Dodd, C.K. (2009) Conservation and management. *Amphibian Ecology and Conservation: A Handbook of Techniques* (ed. C.K. Dodd). pp. 507–527. Oxford University Press, Oxford.

Dray, S. & Legendre, P. (2008) Testing the species traits-environment relationships: the fourth-corner problem revisited. *Ecology*, **89**, 3400–3412.

Faeth, S.H., Warren, P.S., Shochat, E. & Marussich, W.A. (2005) Trophic dynamics in urban communities. *BioScience*, **55**, 399–407.

Fry, J., Xian, G., Jin, S., Dewitz, J., Homer, C., Yang, L., Barnes, C., Herold, N. & Wickham, J. (2011) Completion of the 2006 national land cover database for the conterminous United States. *Photogrammetric Engineering & Remote Sensing*, **77**, 858–864.

Gagne, S.A. & Fahrig, L. (2010) Effects of time since urbanization on anuran community composition in remnant urban ponds. *Environmental Conservation*, **37**, 128–135.

Grewal, R., Cote, J.A. & Baumgartner, H. (2004) Multicollinearity and measurement error in structural equation models: implications for theory testing. *Marketing Science*, **23**, 519–529.

Hamer, A.J. & McDonnell, M.J. (2008) Amphibian ecology and conserva-tion in the urbanising world: a review. *Biological Conservation*, **141**, 2432–2449.

Hamer, A.J. & Parris, K.M. (2011) Local and landscape determinants of amphibian communities in urban ponds. *Ecological Applications*, **21**, 378–390.

Hogsden, K.L. & Hutchinson, T.C. (2004) Butterfly assemblages along a human disturbance gradient in Ontario, Canada. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **82**, 739–748.

Holyoak, M., Leibold, M.A. & Holt, R.D. (2005) *Metacommunities: Spatial Dynamics and Ecological Communities*. University of Chicago Press, Chicago.

Horvath, G., Kriska, G., Malik, P. & Robertson, B. (2009) Polarized light pollution: a new kind of ecological photopollution. *Frontiers in Ecology and the Environment*, **7**, 317–325.

Hoverman, J.T., Davis, C.J., Werner, E.E., Skelly, D.K., Relyea, R.A. & Yurewicz, K.L. (2011) Environmental gradients and the structure of freshwater snail communities. *Ecography*, **34**, 1049–1058.

Johnson, P.T.J., McKenzie, V.J., Peterson, A.C., Kerby, J.L., Brown, J., Blaustein, A.R. & Jackson, T. (2011) Regional decline of an iconic amphibian associated with elevation, land-use change, and invasive species. *Conservation Biology*, **25**, 556–566.

Kark, S., Iwaniuk, A., Schalimtzek, A. & Banker, E. (2007) Living in the city: can anyone become an 'urban exploiter'? *Journal of Biogeography*, **34**, 638–651.

Kuhn, I. & Klotz, S. (2006) Urbanization and homogenization-comparing the floras of urban and rural areas in Germany. *Biological Conservation*, **127**, 292–300.

Leibold, M.A. & Mikkelson, G.M. (2002) Coherence, species turnover, and boundary clumping: elements of meta-community structure. *Oikos*, **97**, 237–250.

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M. & Gonzalez, A. (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, **7**, 601–613.

Logue, J.B., Mouquet, N., Peter, H., Hillebrand, H. & Grp, M.W. (2011) Empirical approaches to metacommunities: a review and comparison with theory. *Trends in Ecology & Evolution*, **26**, 482–491.

Mac Nally, R. (2000) Regression and model building in conservation biol-ogy, biogeography and ecology: the distinction between and reconcilia-tion of 'predictive' and 'explanatory' models. *Biodiversity and Conservation*, **9**, 655–671.

Magurran, A.E. (2004) *Measuring Biological Diversity*. Blackwell Pub., Malden, MA.

McCauley, S.J., Davis, C.J., Relyea, R.A., Yurewicz, K.L., Skelly, D.K. & Werner, E.E. (2008) Metacommunity patterns in larval odonates. *Oecologia*, **158**, 329–342.

McDonnell, M.J. & Hahs, A.K. (2008) The use of gradient analysis stud-ies in advancing our understanding of the ecology of urbanizing land-scapes: current status and future directions. *Landscape Ecology*, **23**, 1143–1155.

McDonnell, M.J. & Pickett, S.T.A. (1990) Ecosystem structure and function along urban rural gradients - an unexploited opportunity for ecology. *Ecology*, **71**, 1232–1237.

McDonnell, M.J., Pickett, S.T.A., Groffman, P., Bohlen, P., Pouyat, R.V., Zipperer, W.C., Parmelee, R.W., Carreiro, M.M. & Medley, K. (1997) Ecosystem processes along an urban-to-rural gradient. *Urban Ecosystems*, **1**, 21–36.

McKinney, M.L. (2006) Urbanization as a major cause of biotic homogenization. *Biological Conservation*, **127**, 247–260.

Parris, K.M. (2006) Urban amphibian assemblages as metacommunities. *Journal of Animal Ecology*, **75**, 757–764.

Perry, M.J. & Mackun, P.J. (2001) U.S. Census Bureau, population change and distribution: 1990 to 2000. *Census 2000 Brief Series*, **52**, 230.

Pugesek, B.H., Tomer, A. & Eye, A.V. (2003) *Structural Equation Modeling: Applications in Ecological and Evolutionary Biology*. Cambridge University Press, Cambridge; New York.

R Development Core Team (2008) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Rosenberg, M.S. & Anderson, C.D. (2011) PASSaGE: pattern analysis, spatial statistics and geographic exegesis version 2.. *Methods in Ecology and Evolution*, **2**, 229–232.

Rosenberg, D.K., Noon, B.R. & Meslow, E.C. (1997) Biological corridors: form, function, and efficacy. *BioScience*, **47**, 677–687.

Rubbo, M.J. & Kiesecker, J.M. (2005) Amphibian breeding distribution in an urbanized landscape. *Conservation Biology*, **19**, 504–511.

Schilling, E.G., Loftin, C.S. & Huryn, A.D. (2009) Effects of introduced fish on macroinvertebrate communities in historically fishless headwater and kettle lakes. *Biological Conservation*, **142**, 3030–3038.

Shochat, E., Warren, P.S., Faeth, S.H., McIntyre, N.E. & Hope, D. (2006) From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology & Evolution*, **21**, 186–191.

Shochat, E., Lerman, S.B., Anderies, J.M., Warren, P.S., Faeth, S.H. & Nilon, C.H. (2010) Invasion, competition, and biodiversity loss in urban ecosystems. *BioScience*, **60**, 199–208.

Simon, J.A., Snodgrass, J.W., Casey, R.E. & Sparling, D.W. (2009) Spatial correlates of amphibian use of constructed wetlands in an urban landscape. *Landscape Ecology*, **24**, 361–373.

Tait, C.J., Daniels, C.B. & Hill, R.S. (2005) Changes in species assemblages within the Adelaide Metropolitan Area, Australia, 1836–2002. *Ecological Applications*, **15**, 346–359.

Urban, M.C. (2004) Disturbance heterogeneity determines freshwater metacommunity structure. *Ecology*, **85**, 2971–2978.

Van Buskirk, J. (2005) Local and landscape influence on amphibian occurrence and abundance. *Ecology*, **86**, 1936–1947.

Vias, A.C. & Carruthers, J.I. (2005) Regional development and land use change in the Rocky Mountain West, 1982–1997. *Growth and Change*, **36**, 244–272.

Vos, C.C. & Chardon, J.P. (1998) Effects of habitat fragmentation and road density on the distribution pattern of the moor frog *Rana arvalis*. *Journal of Applied Ecology*, **35**, 44–56.

Warren, P.S., Katti, M., Ermann, M. & Brazel, A. (2006) Urban bioacoustics: it's not just noise. *Animal Behaviour*, **71**, 491–502.

Werner, E.E., Skelly, D.K., Relyea, R.A. & Yurewicz, K.L. (2007) Amphibian species richness across environmental gradients. *Oikos*, **116**, 1697–1712.

Zuur, A.F., Leno, E.N., Wlaker, N., Saveliev, A.A. & Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York, NY.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Supplementary information on analyses and model development.

Fig. S1. Rarefaction curves for local and regional richness patterns.

Fig. S2. Structural equation modelling diagrams and path coefficients.

Table S1. Occupancy modelling results.

Table S2. Environmental information on wetlands as a function of surrounding land usage.

Table S3. Ranking and support for competing models used to predict richness and diversity.