

# Temporal effects on biodiversity and composition of arthropod communities along an urban–rural gradient

Michael E. Van Nuland · W. Lindsay Whitlow

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**Abstract** Global urbanization is rapidly increasing, yet the prevalence of single order and time point studies likely miss important temporal effects of urbanization on entire communities. We studied three sites along a rural–urban gradient in the Seattle metropolitan area with three sampling periods from 2009–2011 to examine how arthropod communities respond to increasing levels of urbanization in a similar habitat type through time. Consistent with previous studies, urban areas contained altered environmental conditions relevant for litter arthropods, and arthropod biodiversity decreased with urbanization. However, urban arthropod biodiversity was not influenced by environmental measures, supporting the idea of an “urban-filter”. Urbanization was not a factor influencing how communities responded to the effect of time, suggesting that other factors (e.g. disturbance) may ultimately be more important for determining patterns of biodiversity through time in urban areas. Finally, our study illustrates urbanization forces can structuring entire arthropod communities similarly through time, having important consequences for our understanding of urbanization’s temporal effects and indirect influence on community interactions and ecosystem processes. As the effects of urbanization will inevitably vary through time, we suggest that multiple time point studies are required to increase our ability to accurately describe arthropod community responses to increasing urbanization.

**Keywords** Arthropods · Biodiversity · Fragmentation · Temporal effect · Urban–rural gradient · Urbanization

## Introduction

As projections indicate 70 % of the nearly 9 billion people on earth will reside in urban areas by 2050 (Cohen 2003, United Nations 2004) the effects of anthropogenic land-use alterations on ecological processes are becoming more common and acute (McDonnell et al. 1997;

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M. E. Van Nuland (✉)

Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA  
e-mail: mvannula@utk.edu

W. L. Whitlow

Department of Biology, Seattle University, Seattle, WA 98122, USA  
e-mail: whitlowl@seattleu.edu

McKinney 2002; Shochat et al. 2004; Meyer et al. 2005; Urban et al. 2006). Investigating the dynamics of urban terrestrial ecosystems provides valuable information considering urban land use comprises greater than 500,000 km<sup>2</sup> in the United States alone - more than the combined total area of national and state parks preserved by the Nature conservancy (McKinney 2002). Urbanization, the process through which urban ecosystems are created (McIntyre 2001), has been shown to increase temperature (heat-island effect; Terjung and Louie 1973, Yow 2007), modify patterns of precipitation and evapotranspiration (Changnon and Huff 1986, Zhang et al. 2009), alter nutrient flow and energy cycles (Alberti et al. 2003), and fragment and degrade natural habitats (Alberti 2005). Habitat fragmentation and degradation are among the leading global drivers of biodiversity loss (Fahrig 2003), and habitat loss associated with urbanization can threaten ecosystems due to loss of species with high extinction rates, declines in native species, and increases in invasive species (Czech et al. 2000; Cassey et al. 2006). Furthermore, urban environments provide an important and novel habitat to test general ecological theories that have largely been developed in rural or agricultural settings (Niemelä 1999, Gerht and Chelsvig 2004, Shochat et al. 2004, Forman 2008). With twenty-five percent of the nation's total canopy cover comprised of trees in urban counties (Dwyer et al. 2000), urban forests are critical areas to understand how urbanization influences biodiversity within these patches.

Urban forests harbor remnant hot spots of species abundance and diversity within an urban landscape matrix (Miyashita 1998, Fujita et al. 2008), highlighting important areas for urban foresters and city planners to preserve and promote biodiversity (Alvey 2006). Urban forests (i.e. any publicly or privately owned urban trees in an urban area, Nowak and Greenfield 2010) exist as natural forest fragments, parks, recreation areas, or trees spread through neighborhoods (Bolger et al. 2000; McIntyre 2000; Pachecho and Vasconcelos 2007). These forests are often highly fragmented as development expands, producing a gradient of forest types related to urbanization (McDonnell et al. 1997). Urban forest patches have typically been studied as operating similar to islands (MacArthur and Wilson 1963; Gibb and Hochuli 2002; Marzluff 2005), but recent urban ecology theory suggests cities may act as “pseudo-tropical bubbles”. For example, resources in urban areas (e.g. water in desert cities or nutrients in temperate cities) may be subject to less spatial and temporal variation than their natural analogs due to urban management strategies (Shochat et al. 2006). Additionally, seasonal variation is reduced and growing seasons are lengthened in temperate cities (Imhoff et al. 2001), perhaps as an indirect effect of increasing temperature, which acts to stabilize primary productivity (Faeth et al. 2011). Alternate productivity dynamics in urban areas could have differential consequences for urban ecosystem processes and communities than those found in a natural, non-urban system. Moreover, since underlying processes influencing the biodiversity and function of urban ecosystems are not constant through time (Collins et al. 2000), it is important to understand temporal effects of urbanization for effective management strategies. Urban forest fragments are becoming increasingly important for current and future reservoirs of biodiversity, yet general patterns of urban biodiversity responses to temporal effects of increasing urbanization remain relatively untested.

Forest floor litter arthropods provide ideal taxa to investigate the effects of urbanization due to their ease of accessibility, abundance, rapid generation time, and importance for ecosystem processes. Relatively simple collection strategies can obtain large samples of arthropods (both in abundance and diversity) in urban and rural areas, allowing for robust sample sizes and potentially serving as a sample of overall biodiversity in an area (McIntyre 2000). Additionally, most arthropod populations span multiple trophic levels and provide a critical foundation to urban forest food webs (Faeth et al. 2005). Arthropods have short generation times, giving their populations the capacity to respond rapidly to anthropogenic alterations of habitats

(McIntyre 2001). Perhaps most importantly, arthropods regulate ecosystem processes such as carbon and nitrogen cycling (Erwin 1982; Seastedt and Crossley 1984, Jouquet et al. 2006), with consequences for ecosystem function from their influence on soil respiration and understory plant photosynthetic rates (McDonnell et al. 1997), as well as economically important ecosystem services (e.g. pollination; Levin 1983). This diversity of roles highlights the importance of examining entire arthropod community assemblages in rural and urban areas, especially considering that habitat alterations from urbanization are a leading cause in global declines of arthropod biodiversity (Pyle et al. 1981, Clark and Samways 1997).

Research examining arthropods in an urban ecology framework rarely has simultaneously accounted for multiple factors relevant to understanding how arthropods respond to increasing urbanization. Previous work examining arthropod responses to urban development has largely focused on single taxa (Thompson and McLachlan 2007, ants; Uno et al. 2010, ants; Wojcik and McBride 2012, bees; Niemelä et al. 2002, beetles; Venn et al. 2003, beetles; Miyashita et al. 1998, spiders; Shochat et al. 2004, spiders). Fewer studies have examined entire arthropod communities, and general patterns of community responses to urbanization remain scarce. However, previous work indicates that habitat type and land use can be correlated with arthropod community assemblages (McIntyre et al. 2001, Gibb and Hochuli 2002). While these studies examine arthropods with a major factor of urbanization, to predict how communities will respond to increasing anthropogenic changes it may be useful to utilize a continuum of urbanization within a single habitat type. Similarly, few studies have investigated temporal effects of urbanization on arthropods (Magura et al. 2008), carabid beetles; Bang and Faeth 2011, desert ecosystems). As such, our understanding and predictions for arthropod responses to urbanization can benefit from repeated monitoring of communities along gradients of urbanization in a single habitat type over time.

We studied three sites along a rural–urban gradient in a temperate ecosystem with three sampling periods from 2009–2011 to examine how arthropod communities respond to increasing levels of urbanization in a similar habitat type over time. We hypothesized that the level of urbanization would alter environmental conditions and affect patterns of arthropod biodiversity, while temporal effects would alter community composition as arthropods continually respond to urban pressures. Specifically, we predict: i) environments will be more harsh in urban areas (increased temperature, and decreased canopy density, litter mass, depth, and moisture), ii) arthropod biodiversity will decline from rural to urban sites and iii) environmental variables differing along the gradient will be correlated with declines in biodiversity, iv) more urban areas will record greater declines in arthropod biodiversity over time, and v) arthropod community composition will differ by site and over time as communities shift towards dominance by urban-tolerant (e.g. generalist) arthropods from rural to urban areas.

## Methods

### Gradient sites and sampling timeline

Three sites were established in the Seattle metropolitan area (47°, 40' N; 122°, 20' W), located in the Pacific Northwest's Western Hemlock (*Tsuga heterophylla*) zone (Franklin and Dyrness 1988). A rural–urban gradient based on ratios of vegetation versus developed landcover was constructed from Cougar Mountain Regional Wildland Park (84:16 %, 1260 ha, henceforth, “forest”), Seward Park (74:26 %, 121 ha, henceforth, “urban forest”), and Seattle University (9:91 %, 20 ha, henceforth, “urban”). The use of three disturbance levels when constructing

sites encompassing an urban–rural gradient is a standardized protocol utilized by GLOBENET (Helsinki, Finland) that has been utilized to survey anthropogenic effects on arthropods communities across 4 continents. Moreover, Forest, urban forest, and urban site descriptions align with previously used characterizations of habitats within the Seattle metro area (Marzluff 2005), and all sites contained similar vegetation appropriate to the habitat type of the region (Franklin and Dyrness 1988). Percent cover of vegetation and development were determined using iTree Vue analysis of National Land Cover Database 2001 data ([www.itreetools.org](http://www.itreetools.org)) by defining a set boundary around each site (~500 m) and measuring both within-site and edge cover characteristics. Sampling was conducted with no bias towards geography or particular areas within a site, allowing for accurate representations of average environments and arthropod communities. A general survey was performed in July of 2009 to identify environmental and community patterns along the gradient (Cougar,  $n=25$ ; Seward,  $n=24$ ; SU,  $n=25$ ). An identical sampling procedure was repeated in August of 2010 (Cougar,  $n=30$ ; Seward,  $n=30$ , SU,  $n=15$ ), and a third in April of 2011 (Cougar,  $n=24$ ; Seward,  $n=29$ , SU,  $n=15$ ). To avoid confounding natural population dynamics with temporal effects, sampling dates were arranged within periods over which previous work has shown relatively little change in dominant arthropod orders (Wiwatwitaya and Takeda 2005). Importantly, we use the gradient as a “space-for-time substitution”, in which more urban areas are treated as harbingers of future ecosystem and community dynamics in more rural areas under the assumption of increasing urbanization. In this sense, differences in arthropod patterns along the gradient (within a given year) represent the response to increasing urbanization pressures. The novel approach of this study involves examining patterns along the same gradient across multiple years. As a result, if arthropod patterns along the gradient differ between time periods, this indicates variation in their response to increasing urbanization though time.

### Environmental measurements

To examine abiotic effects on arthropods communities along the urbanization gradient, we measured the following environmental variables at each location of litter collection: canopy density (% cover), litter temperature ( $^{\circ}\text{C}$ ), depth (cm), litter moisture (%), soil moisture (%), soil pH, and litter dry mass (g). Canopy density was measured using a spherical crown densiometer (Forestry Suppliers Inc., Jackson, MS) at waist height above each area of litter collection (Engelbrecht and Herz 2001). To measure an appropriate temperature for litter arthropods in this study, a metal probe thermometer was inserted through the leaf litter and partially submerged in the soil. As a result, temperature measurements reflect a combination of soil and litter temperature. Litter depth was measured by inserting a ruler through the litter to the top of the O horizon, taking the average of 5 measurements evenly distributed throughout the collection area. Litter moisture was measured by the difference between initial sample weight and dry sample weight, with dry sample weight serving as the dry mass value. Soil moisture and pH were measured with a Kelway soil pH and moisture meter (Forestry Suppliers Inc., Jackson, MS).

### Arthropod sampling

Leaf litter and woody debris samples were collected by removing a  $0.25\text{ m}^2$  quadrat of leaf litter (to the top of the O horizon) and placing in cloth drawstring bags before transportation and extraction within 6 hours. A standard Berlese apparatus was used for arthropod extraction from leaf litter (Sabu and Shiju 2009): metal funnels were placed on three-ring stands and  $4\text{ cm}^2$  mesh screens were placed at the bottom of the funnel to ensure sample retention while

allowing space for invertebrates to exit. A lamp placed above the funnel provided a heat and light source, driving invertebrates out of the litter into glass jars containing 75 % ethanol for preservation. Samples were subject to extraction for ~24 hours. Harvested invertebrates were separated initially by morphology, and then identified to order, sub-order, or family via microscopy (Table 1; Milne and Milne 1980; White 1983; Alden et al. 1998; Acorn and Sheldon 2002; Haggard and Haggard 2006; Eaton and Kaufman 2007; Nardi 2007), which has been shown to be adequate taxonomic resolution to detect community patterns between rural and urban areas (Bang and Faeth 2011). It should be noted that two separate analyses were performed on leaf litter samples after 10 trials to independently assess the effectiveness of the Berlese technique, comparing hand sorted litter samples and those collected through Berlese extraction, and no significant difference between arthropod measures were observed between methods (unpublished data). Finally, measures of evenness were calculated (assessed by the quotient of the number of individuals by the number of orders) as it is often an overlooked measure of biodiversity, but has been identified as important for accurately describing urban communities (Shochat et al. 2010).

## Analysis

For each environmental measure we used one-way ANOVAs with site as a fixed factor to determine how response variables differed between gradient sites averaged over the three sampling time points. Similarly, differences in arthropod abundance, richness, and evenness (averaged over three years) were tested using one-way ANOVAs with site as a fixed factor. Linear regressions were performed to examine the influence of environmental factors (independent) on arthropod abundance, richness, and evenness (dependent) by site. To examine the effect of site, time, and their interaction on mean abundance, richness, and evenness of arthropods, two-way ANOVAs were performed with site and time as fixed factors. All data were tested to meet assumptions of normality, and Tukey HSD tests were used to identify differences between groups where appropriate. Analysis was performed using JMP Pro 10 (SAS Institute, Cary, NC, USA).

Arthropod community composition was analyzed using Primer 6.1 (Plymouth, USA). Resemblance matrices were constructed with Bray-Curtis similarity using arthropod abundance data. One-way ANOSIMs (with 999 permutations and site as a fixed factor) were performed to determine differences in arthropod community composition between sites at each sampling time point. A PERMANOVA was performed to examine the interaction between site and time for communities. We used a Mantel spatial autocorrelation test with 9999 permutations comparing the dissimilarity matrices between sampling years to determine whether the composition of arthropod communities at different time periods were correlated (i.e. if current community structure was determined by historical communities). While Mantel analyses do not infer the direction of a correlation between matrices, we reasoned that current communities could not influence previous communities in our interpretations.

## Results

### Environment and arthropod communities

Measures of environmental variables were consistent with previous studies indicating anthropogenic effects on habitats relevant to arthropods (Table 2). Following general trends of increasing temperature with urbanization, samples from the urban site were 1.4° C and 0.8°

**Table 1** Arthropod taxa collected from 2009 – 2011 across all sites

Taxa	Forest	Urban forest	Urban	Total
Acari	3887	2478	3534	9899
Araneae	378	74	25	477
Chilopoda	58	16	39	113
Coleoptera	70	57	47	174
Collembola	1654	1364	1225	4243
Diplopoda	79	61	53	193
Diptera	24	24	38	86
Formicidae	29	51	8	88
Isopoda	169	40	54	263
Isoptera	3	1	0	4
Opiliones	10	14	6	30
Pseudoscorpionida	267	169	0	436
Siphonaptera	3	1	0	4
Symphyta	91	62	20	173
Total	6722	4412	5049	16183

C warmer than forest and urban forest sites, respectively ( $F_{2,221}=5.66$ ,  $p=0.004$ ). Additionally, litter mass ( $F_{2,137}=5.54$ ,  $p=0.005$ ), and litter moisture ( $F_{2,137}=6.60$ ,  $p=0.002$ ) increased from forest to urban sites. Litter depth decreased from forest to urban sites by 0.7 cm ( $F_{2,149}=3.33$ ,  $p=0.039$ ), potentially reducing levels of habitat complexity for arthropods in urban environments. Canopy density ( $F_{2,221}=2.38$ ,  $p=0.095$ ) showed no significant effect of gradient site. While our observations and other studies indicate tree abundance and density decreased from rural to urban sites (Seattle urban tree canopy analysis project

**Table 2** Average site environments and linear regression results for arthropod biodiversity x environment relationships

	Temperature (°C)	Canopy density (%)	Litter depth (cm)	Litter Mass (g)	Litter Moisture (g)
<b>Forest</b>	10.9±0.6 <sup>a</sup>	92.5±1.4 <sup>a</sup>	3.4±0.2 <sup>a</sup>	434.8±27.1 <sup>a</sup>	70.2±3.9 <sup>a</sup>
Abundance	0.001	0.012	0.182**	0.049	0.134**
Richness	0.022	0.003	0.000	0.124**	0.046
Evenness	0.009	0.010	0.211***	0.014	0.114*
<b>Urban forest</b>	12.4±0.4 <sup>ab</sup>	90±1.3 <sup>a</sup>	3.0±0.2 <sup>a</sup>	360.7±19.5 <sup>ab</sup>	67±10.0 <sup>a</sup>
Abundance	0.111**	0.008	0.002	0.003	0.253***
Richness	0.013	0.000	0.009	0.030	0.063
Evenness	0.052*	0.007	0.005	0.017	0.218***
<b>Urban</b>	13.3±0.4 <sup>b</sup>	94±1.0 <sup>a</sup>	2.5±0.2 <sup>b</sup>	501.9±37.4 <sup>b</sup>	100.3±7.4 <sup>b</sup>
Abundance	0.056	0.004	0.010	0.012	0.004
Richness	0.041	0.028	0.011	0.079	0.008
Evenness	0.008	0.004	0.021	0.002	0.001

2009 – 2011 average site environments (bold)±1 SE; letters depict significant differences between sites (Tukey's HSD) Linear regression results depict  $r^2$  values. \*  $p<0.05$ , \*\*  $p<0.01$ , \*\*\*  $p<0.001$

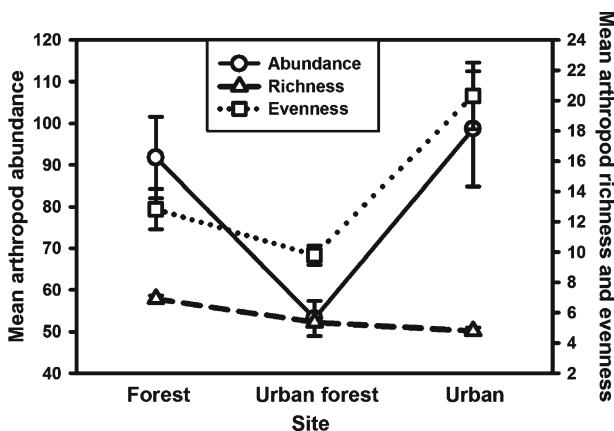
report), our focus on leaf litter arthropods likely influenced our measure of canopy density at urban sites.

A total of 16,183 arthropods belonging to 14 orders were collected across all sites and sampling periods (Table 1). Mean arthropod abundance, richness, and evenness were affected by gradient site (Fig. 1). Cumulatively from 2009–2011, mean arthropod abundance was lowest at the urban forest by 56 % compared to forest and urban sites ( $F_{8,211}=8.03$ ,  $p=0.0004$ ) exhibiting a U-shaped relationship with urbanization. Mean richness declined from the forest to urban forest by 23 %, and from the urban forest to urban site by 10 % ( $F_{8,211}=25.30$ ,  $p<0.001$ ). Mean evenness was highest at the urban site by 44 % compared to the forest and urban forest sites ( $F_{8,211}=13.29$ ,  $p<0.0001$ ), likely due to the combination of increased abundance and decreased richness (the loss of more rare orders allows common orders to dominate more equally).

Overall, arthropods were weakly correlated with the environment, and urban arthropods were not affected by variables we measured (Table 2). Forest arthropod abundance and evenness showed negative relationships with litter depth ( $r^2=0.182$ ,  $p=0.001$  and  $r^2=0.211$ ,  $p<0.001$ , respectively), positive relationships with litter moisture ( $r^2=0.134$ ,  $p=0.006$  and  $r^2=0.114$ ,  $p=0.012$ , respectively), and richness showed a positive relationship with litter mass ( $r^2=0.124$ ,  $p=0.008$ ). Negative correlations with litter depth and positive correlations with litter mass illustrate a complex dynamic with habitat and resource by arthropods in forest areas. Urban forest arthropod abundance and evenness had positive relationships to temperature ( $r^2=0.111$ ,  $p=0.002$  and  $r^2=0.052$ ,  $p=0.038$ , respectively) and negative relationships with litter moisture ( $r^2=0.253$ ,  $p=0.001$  and  $r^2=0.218$ ,  $p=0.002$ , respectively). It is interesting to note that urban forest communities responded oppositely than forest communities to litter moisture, suggesting urbanization may differentially affect how arthropods interact with their environment. Arthropod biodiversity in urban areas were not affected by environmental variables in our study, suggesting alternative factors may be more important for structuring urban communities.

#### Arthropod communities and composition over time

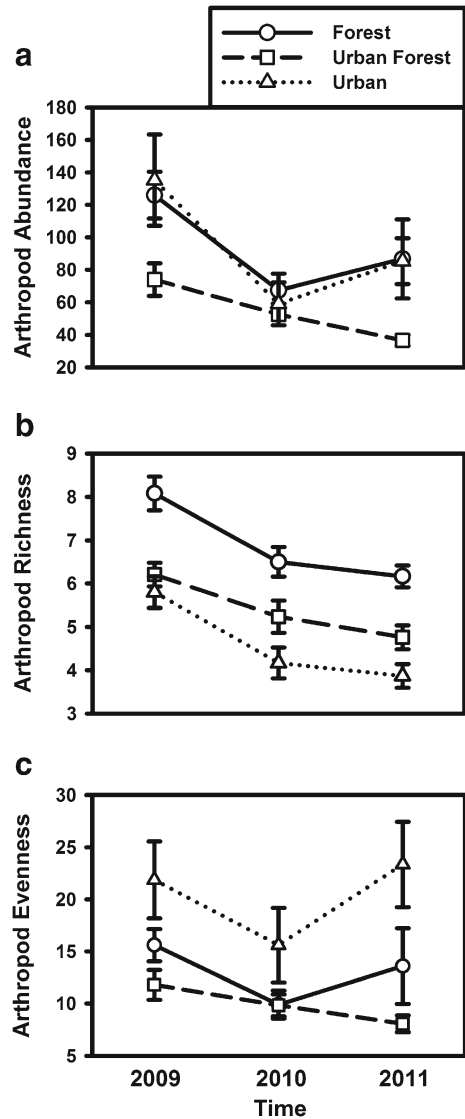
Arthropod communities across all sites changed over time (Fig. 2). All sites declined in mean abundance ( $F_{8,211}=11.43$ ,  $p<0.0001$ ) and richness ( $F_{8,211}=8.23$ ,  $p=0.0004$ ) from 2009 to 2010



**Fig. 1** Mean arthropod biodiversity is affected by urbanization. 2009–2011 mean arthropod abundance (circle), richness (triangle), and evenness (square)  $\pm$  1 SE



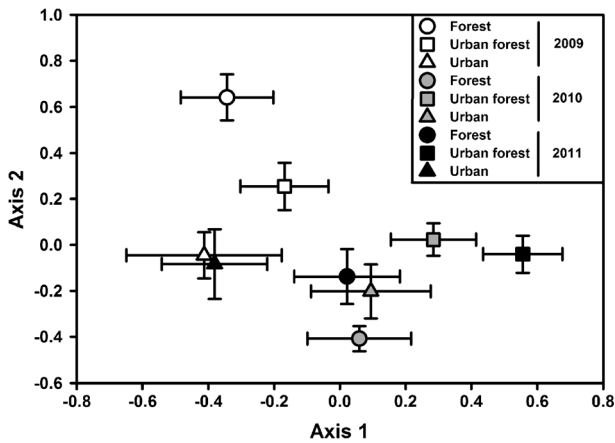
**Fig. 2** Arthropod biodiversity declines over time at all sites. **a** Arthropod abundance, **b** arthropod richness, and **c** arthropod evenness from 2009–2011 by forest (circle), urban forest (square), and urban (triangle) sites  $\pm 1$  SE of the mean



by an average of 47 % and 18 %, respectively, with no difference observed between 2010 and 2011. No significant site by time interactions were observed for abundance ( $F_{8,211}=1.032$ ,  $p=0.392$ ) richness ( $F_{8,211}=1.367$ ,  $p=0.945$ ), or evenness ( $F_{8,211}=0.883$ ,  $p=10.475$ ). Interestingly, similar to our predictions for urban sites, forest communities were subject to equivalent losses of biodiversity through time. All sites declined in evenness from 2009 to 2010 by an average of 32 %, reaching an intermediate level in 2011 ( $F_{8,211}=3.36$ ,  $p<0.037$ ), indicating communities were likely becoming increasingly dominated by a few arthropod orders (notably, acari and collembola).

Arthropod communities composition differed between sites and over time along the gradient (Fig. 3), and past community structure did not predict future composition. Forest,





**Fig. 3** Arthropod community composition is affected by site and time. Nonmetric multidimensional scaling (NMDS) ordination of arthropod communities for forest (circle), urban forest (square), and urban (triangle) sites in 2009, 2010, and 2011 sampling periods. Points represent the centroid for all communities within a group  $\pm 1$  SE of the centroid mean along both axes. In ordination space, points closer together have more similar communities

urban forest, and urban sites had distinct arthropod community compositions at all sample times (ANOSIM; 2009, global  $R=0.111$ ,  $p=0.001$ ; 2010, global  $R=0.076$ ,  $p=0.001$ ; 2011, global  $R=0.134$ ,  $p=0.001$ ) with a significant site by time interaction (PERMANOVA;  $F_{\text{pseudo}}=0.270$ ,  $p=0.0003$ ). Gradient sites are grouped in 2009 and 2010, with communities in 2011 varying between years. With the exception of 2009 communities, forest and urban forest communities are more similar to one another than to urban communities, suggesting consistent effects of urbanization on arthropod community structure. Dissimilarity matrices between sample periods were not correlated with one another (Mantel; 2009–2010,  $p=0.862$ ; 2010–2011,  $p=0.490$ , 2009–2011,  $p=0.063$ ), indicating historical community structure was not a factor influencing future community compositions.

## Discussion

Consistent with established patterns, urban areas contained altered environmental conditions relevant for litter arthropods (Alberti et al. 2003), and arthropod biodiversity declined from rural to urban sites (McKinney 2008). However, urban arthropod biodiversity was not influenced by environmental measures in this study, supporting the idea of an “urban-filter” selecting for generalist or more urban-tolerant arthropods in these habitats. Urbanization was not a factor influencing how communities responded to the effect of time (i.e. no site  $\times$  time interaction), suggesting that even if cities contain reduced spatial and temporal variation of resources and habitat (Shochat et al. 2006; cities as “pseudo-tropical bubbles”), other factors (e.g. disturbance) may ultimately be more important for determining patterns of biodiversity. Finally, our study is the first that illustrates urbanization can exert consistent forces structuring entire arthropod communities similarly through time, with important consequences for our understanding of urbanization’s temporal effects and indirect influence on community interactions and ecosystem processes. As the effects of urbanization will inevitably vary through time (Collins et al. 2000), we suggest that multiple time point studies will increase our ability to accurately describe and predict how arthropod communities respond to urban effects.

## Environmental patterns and arthropod responses to increasing urbanization

Environmental patterns along the rural–urban gradient show urban sites contain more harsh environmental conditions for arthropods. Higher temperatures (likely from a heat-island effect, Terjung and Louie 1973) and lesser habitat complexity (e.g. litter depth; Melles et al. 2003) are consistent with environmental characterizations of urban environments. Although canopy density, an indicator for urban forests (Berland 2012), did not follow a clear pattern along our gradient, this measure was likely influenced by the focus on leaf litter in this study. However, decreasing litter depth from forest to urban sites indirectly supports the pattern of lower canopy cover and vegetation in urban areas (Zipperer et al. 1997). Increased litter mass with urbanization might be explained by common landscape management practices (e.g. leaf-blowing and mulching), and greater litter moisture most likely covaries with greater litter mass in urban areas.

Mean arthropod abundance was highest at the least and most urban sites, and mean richness decreased at more urban sites, supporting previous arthropod biodiversity patterns (Faeth et al. 2011). One explanation for the increasing abundance pattern with urbanization is the simultaneous loss of rare taxa (typically predator species; Shochat et al. 2004) and the increase in populations of more common arthropods (i.e. omnivores and urban exploiters), likely through greater resource and habitat availability or release from predators. Additionally, the increase in mean arthropod evenness for urban areas is likely attributed to the simultaneous increase in abundance and decrease in richness for urban arthropods, resulting in a more even community (i.e. a large amount of a few different taxa). In this study, arachnids and springtails were observed to greatly increase in arthropod community proportion from rural to urban sites, and their relatively equal abundances (given higher evenness values) suggests little competition between the two for resources or habitat.

Urban arthropod communities were not correlated with environmental variables in our study (see Table 2), suggesting alternative factors are more important for explaining patterns of arthropod biodiversity in urban environments. Preliminary evidence from a small-scale pilot experiment suggests habitat and resource disturbance (often higher in urban areas; McKinney 2006) may be important for explaining arthropod community patterns along this urban–rural gradient. Specifically, litter disturbance appeared to interact with arthropod community recolonization by urbanization, but these patterns were found at marginal levels of significance (Van Nuland and Whitlow 2011, *unpublished data*). Alternatively, taxa in the urban site may have passed through an “urban filter” such that only arthropods with a higher tolerance to urban conditions are found in these habitats (McIntyre et al. 2001), thus explaining how these taxa appear to be uninfluenced by urban environmental conditions. Previous studies have shown urban resources can influence urban communities (Rodewald and Shustack 2008), however our results do not support this pattern. For example, forest arthropod richness increased with litter mass, mean litter mass increased from forest to urban sites, yet mean arthropod richness decreased from forest to urban sites. As a result, additional work is required to understand the interactive effects of abiotic and urbanization factors on arthropod communities, and what consequences this has for city managers.

Despite consistent vegetation type (i.e. *T. heterophylla* zone), arthropod community composition varied along the urban–rural gradient. In general, forest arthropod communities had more similar composition compared to urban forest communities, and urban forest communities had more similar composition to urban communities. To our knowledge, only one previous study has found a relatively similar pattern using an urban–rural gradient with a similar habitat type at all sites. Specifically, Hornung et al. (2007) found that urban sites contained different isopod assemblages compared to suburban and rural sites, and this pattern was attributed to

differential tolerances between species. In our study, the combined patterns of decreased richness and altered community composition support the hypothesis of an arthropod community better suited (i.e. more urban-tolerant) to urban areas. Specifically, we noted a shift from more balanced predator–prey communities to largely prey-dominated communities along the gradient (acarid and collembola, also driving the pattern of increasing evenness along the gradient; see Table 1). This effect of urbanization altering trophic webs is also consistent with previous work which found land use and habitat structure altered trophic dynamics with shifts towards omnivore-dominant communities in urban areas (McIntyre et al. 2001). While the rate of litter decomposition may be reduced in urban areas (Carreiro et al. 1999), little is known about the indirect consequences of urbanization altering arthropod communities and potential ramifications for ecosystem function. Our results indicate urbanization affects lesser-studied measures of biodiversity (Faeth et al. 2011), and that shifting community composition may have implications for trophic interactions and the critical ecosystem processes arthropods mediate.

### Temporal effects of urbanization on arthropods

Few studies have examined temporal aspects of urbanization or how arthropod biodiversity along an urban–rural gradient responds over time, and results from our study indicate the utility of monitoring urbanization effects on arthropod communities over time. Previous work examining temporal patterns of arthropods have been limited to single taxa over short time periods (Magura et al. 2008), or use a variety of habitat types outside a continuum of urbanization (Bang and Faeth 2011). Such studies have found inconsistent temporal patterns, ranging from no temporal differences to variation based on habitat and taxa. Our study shows decreasing arthropod biodiversity at all sites between 2009 and 2011, with no major or obvious modifications to habit or resources for arthropods along the gradient. While previous work suggests cities may act as “pseudo-tropical bubbles” mitigating temporal variation through artificially constant resources and habitat (Shochat et al. 2006), our results do not support this hypothesis as we observed a 45 % decline in abundance and 40 % decline in richness for urban arthropod between 2009 and 2011. It should be noted that reduced richness in urban environments at the order level (notably in our study, pseudoscorpionida), translates to large modifications of the phylogenetic structure of arthropod communities (i.e. drastic reductions in evolutionary history), with potentially major alterations to community and trophic dynamics. Urban arthropod communities did show an increase in evenness over time, and likely due to the previously described declining ratio of abundance to richness. Overall, our results suggest that single-year studies may not be sufficient to accurately describe arthropod response to increasing urbanization. Moreover, we highlight that efforts for preserving biodiversity should not be limited to most-urban areas, but adequate focus should be given to natural areas in cities (i.e. urban parks) and at the edges of expanding urban areas (i.e. regional wildland parks).

Although arthropod biodiversity was not differentially affected over time by increasing urbanization effects, arthropod community composition did vary by year. The absence of historical dependency (i.e. previous communities did not predict future communities) and continual differences in composition between sites indicates time consistent effects of urbanization structuring communities. Previous studies have found similar patterns (Magura et al. 2008), in which carabid beetle assemblages exhibited time consistent arrangements along an urban–rural gradient. Our study expands on these findings by showing that the entire arthropod community, even at the relatively coarse taxonomic resolution of order, can exhibit time consistent arrangements and that such assemblages are not a product of historical dependency. For example, 2010 and 2011 urban forest sites contained similar arthropod compositions, but

given the lack of historical dependency, the 2011 community is likely subject to similar factors (e.g. disturbance, resource levels, habitat quality) influencing arthropod composition in order to observe this pattern. Interestingly, forest communities became more similar to urban communities over time, despite any signs of altered land-use during our sampling periods, which may highlight the potential for litter arthropods to be indicators of urbanization or reduced ecological health of ecosystems before any noticeable landscape changes have occurred (Kremen et al. 1993).

Despite our attempts to control for factors that vary through time (see Methods), there may be alternative explanations for temporal effects on arthropod communities in this study. For instance, although we used relatively large sample sizes to account for within-site variation in populations, community and trophic dynamics of arthropods may be driving some of the temporal patterns we observe. This may be less likely as major arthropod orders can exhibit relatively small changes in population sizes over our sampling periods (Wiwatwitaya and Takeda 2005), however future work should account for these and other potential confounding factors when studying urbanization effects on arthropod communities through time.

## Conclusions

Urbanization is increasing, and, with forest fragments serving as critical habitats for urban biodiversity, these areas will likely be impacted with greater intensity. Patterns of arthropod responses to urbanization through time remain unclear, but are important for understanding long-term effects and how communities will respond to increasing urban pressures. We found consistent trends with previous work illustrating harsher environmental conditions and altered biodiversity patterns as a result of urbanization. Additionally, our findings that urban arthropods were uninfluenced by environmental variables, as well as the temporal effect of urbanization on biodiversity and community composition, has consequences for understanding temporal variation in factors structuring urban communities. Future studies would benefit from exploring biodiversity and community responses to urbanization over longer temporal scales, in addition to examining how ecosystem processes and services may be altered in urban environments from differing arthropod communities than are found in natural areas of similar habitat type.

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## References

- Acorn J, Sheldon I (2002) Bugs of Washington and Oregon. Lone Pine Publishing, Washington
- Alberti M, Marzluff JM, Shulenberg E, Bradley G, Ryan C, Zumbrennen C (2003) Integrating humans into ecology: Opportunities and challenges for studying urban ecosystems. *Bioscience* 53:1169–1179
- Alberti M (2005) The effects of urban patterns on ecosystem function. *Int Reg Sci Rev* 28:168–192
- Alden P, Paulson D, Gregoret A, Mathews D, Keen R, Oches E.A, et al. (1998). National Audobon Society Field Guide to the Pacific Northwest. Alfred A. Knopf Inc, New York pp 187–219
- Alvey AA (2006) Promoting and preserving biodiversity in the urban forest. *Urban For Urban Green* 5:195–201
- Bang C, Faeth S (2011) Variation in arthropod communities in response to urbanization: Seven years of arthropod monitoring in a desert city. *Landsc Urban Plan* 103:383–399

- Berland A (2012) Long-term urbanization effects on tree canopy cover along an urban–rural gradient. *Urban Ecosyst* 15:721–738
- Bolger DT, Suarez AV, Crooks KR, Morrison SA, Case TJ (2000) Arthropods in urban habitat fragments in Southern California: Area, age and edge effects. *Ecol App* 10:1230–1248
- Carreiro MM, Howe K, Parkhurst DF, Pouyat RV (1999) Variations in quality and decomposability of red oak litter along an urban–rural land use gradient. *Biol Fert Soils* 30:258–268
- Cassey P, Blackburn TM, Lockwood JL, Sax DF (2006) A stochastic model for integrating changes in species richness and community similarity across spatial scales. *Oikos* 115:207–218
- Changnon S, Huff F (1986) The urban-related nocturnal rainfall anomaly at St. Louis. *J Appl Meteorol Clim* 25:1985–1995
- Clark TE, Samways MJ (1997) Sampling arthropod diversity for urban ecological landscaping in a species-rich southern hemisphere botanic garden. *J Insect Conserv* 1:221–234
- Cohen JE (2003) Human population: The next half century. *Science* 302:1172–1175
- Collins JP, Kinzig A, Grimm NB, Fagan WF, Hope D, Wu J, Borer ET (2000) A new urban ecology. *Am Sci* 88:416–425
- Czech B, Krausman PR, Devers PK (2000) Economic associations among causes of species endangerment in the United States. *BioScience* 50:593–601
- Dwyer JF, Nowak DJ, Noble MH, Sisinni SM (2000) Connecting people with ecosystems in the 21<sup>st</sup> century: An assessment of our nation's urban forests. Pacific Northwest Research Station, USDA
- Eaton ER, Kaufman K (2007) Kaufman Field Guide to Insects of North America. Houghton Mifflin Co, New York
- Engelbrecht B, Herz H (2001) Evaluation of different methods to estimate understorey light conditions in tropical forests. *J Trop Ecol* 17:207–224
- Erwin TL (1982) Tropical forests: Their richness in Coleoptera and other arthropod species. *Coleopt Bull* 36:74–75
- Faeth SH, Warren PS, Shochat E, Marussich WA (2005) Trophic dynamics in urban communities. *Bioscience* 55:399–407
- Faeth SH, Bang C, Saari S (2011) Urban biodiversity: patterns and mechanisms. *Ann NY Acad Sci* 1223:69–81
- Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Ann Rev Ecol Evol Syst* 34:487–515
- Forman RTT (2008) Urban regions: Ecology and planning beyond the city. Cambridge University Press, New York
- Franklin JF, Dymess CT (1988) Natural vegetation of Oregon and Washington. Oregon State University Press, Oregon
- Fujita A, Maeto K, Kagawa Y, Ito N (2008) Effects of forest fragmentation on species richness and composition of ground beetles (Coleoptera: Carabidae and Brachinidae) in urban landscapes. *Entomol Sci* 11:39–48
- Gerth SD, Chelvig JE (2004) Species-specific patterns of bat activity in an urban landscape. *Ecol App* 14:625–635
- Gibb H, Hochuli DF (2002) Habitat fragmentation in an urban environment: Large and small fragments support different arthropod assemblages. *Biol Conserv* 106:91–100
- Haggard P, Haggard J (2006) Insects of the Pacific Northwest. Timber Press Inc, Oregon
- Homung E, Tóthmérész B, Magura T, Vilisics F (2007) Changes of isopod assemblages along an urban-suburban-rural gradient in Hungary. *Eur J Soil Biol* 43:158–165
- Imhoff ML, Lawrence WT, Tucker CJ, Stutzer D (2001) A satellite survey of the impact of urban sprawl on agriculture and primary productivity in the United States: Is our style of development sustainable? *T N M Wildl Nat Res* 66:392–404
- Jouquet P, Dauber J, Lagerlöf LP, Lepage M (2006) Soil invertebrates as ecosystems engineers: Intended and accidental effects on soil and feedback loops. *Appl Soil Ecol* 32:153–164
- Kremen C, Colwell RK, Erwin TL, Murphy DD, Noss RF, Sanjayan MA (1993) Terrestrial arthropod assemblages: Their use in conservation planning. *Conserv Biol* 7:796–808
- Levin MD (1983) Value of bee pollination to US agriculture. *Bull Entomol Soc Am* 29:50–51
- MacArthur RH, Wilson EO (1963) An equilibrium theory of insular biogeography. *Evolution* 17:373–387
- Magura T, Lövei G, Bela T (2008) Time-consistent rearrangement of carabid beetle assemblages by an urbanisation gradient in Hungary. *Acta Oecol* 34:233–243
- Marzluff J (2005) Island biogeography for an urbanizing world: how extinction and colonization may determine biological diversity in human-dominated landscapes. *Urban Ecosyst* 8:157–177
- McDonnell MJ, Pickett STA, Groffman P, Bohlen P, Pouyat RV, Zipperer WC, Parmelee RW, Carreiro MM, Medley K (1997) Ecosystem processes along an urban-to-rural gradient. *Urban Ecosyst* 1:21–36
- McIntyre NE (2000) Ecology of urban arthropods: A review and a call to action. *Ann Entomol Soc Am* 93:825–835
- McIntyre NE, Rango J, Fagan WF, Faeth SH (2001) Ground arthropod community structure in a heterogeneous urban environment. *Landsc Urban Plan* 52:257–274

- McKinney ML (2002) Urbanization, biodiversity, and conservation. *Bioscience* 52:883–890
- McKinney ML (2006) Urbanization as a major cause of biotic homogenization. *Biol Conserv* 127:247–260
- McKinney ML (2008) Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosyst* 11:161–176
- Melles S, Glenn S, Martin K (2003) Urban bird diversity and landscape complexity: Species-environment associations along a multiscale habitat gradient. *Conserv Ecol* 7: <http://www.consecol.org/vol7/iss1/art5/>
- Meyer JL, Paul MJ, Taulbee WK (2005) Stream ecosystem function in urbanizing landscapes. *J N Am Benthol Soc* 24:602–612
- Milne L, Milne M (1980) National Audobon Society Field Guide to Insects & Spiders (North America). Alfred A. Knopf Inc, New York
- Miyashita T, Shinkai A, Chida T (1998) The effects of forest fragmentation on web spider communities in urban areas. *Biodiv Conserv* 86:357–364
- Nardi JB (2007) *Life in the Soil: A Guide for Naturalists & Gardeners*. The University of Chicago Press, Illinois pp 22–197
- Niemelä J (1999) Is there a need for a theory of urban ecology? *Urban Ecosyst* 3:57–65
- Niemelä J, Kotze J, Venn S, Penev L, Stoyanov I, Spence J, Hartley D, Montes de Oca H (2002) Carabid beetle assemblages (Coleoptera, Carabidae) across urban–rural gradients: An international comparison. *Landscape Ecol* 17:387–401
- Nowak DJ, Greenfield EJ (2010) Evaluating the National Land Cover Database tree canopy and impervious cover estimates across the conterminous United States: A comparison with photo-interpreted estimates. *Environ Manage* 46:378–390
- Pachecho R, Vasconcelos HL (2007) Invertebrate conservation in urban areas: Ants in the Brazilian Cerrado. *Landscape Urban Plan* 81:193–199
- Pyle R, Bentzien M, Opler P (1981) Insect conservation. *Annu Rev Entomol* 26:233–258
- Rodewald AD, Shustack DP (2008) Consumer resource matching in urbanizing landscapes: Are synanthropic species over-matching? *Ecology* 89:515–521
- Sabu TK, Shiju RT (2009) Efficacy of pitfall trapping, Winkler, and Berlese extraction methods for measuring ground-dwelling arthropods in moist-deciduous forests in the Western Ghats. *J Insect Sci* 10:98 available online: [insectscience.org/10.98](http://insectscience.org/10.98)
- Seastedt TR, Crossley DA Jr (1984) The influence of arthropods on ecosystems. *Bioscience* 34:157–161
- Shochat E, Stefanov WL, Whitehouse MEA, Faeth SH (2004) Urbanization and spider diversity: Influences of human modification of habitat structure and productivity. *Ecol App* 14:268–280
- Shochat E, Warren PS, Faeth SH, McIntyre NE, Hope D (2006) From patterns to emerging processes in mechanistic urban ecology. *Trends Ecol Evol* 21:186–91
- Shochat E, Lerman SB, Anderies JM, Warren PS, Faeth SH, Nilon CH (2010) Invasion, competition, and biodiversity loss in urban ecosystems. *Bioscience* 60:199–208
- Terjung W, Louie S (1973) Solar radiation and urban heat islands. *Ann Assoc Am Geogr* 63:181–207
- Thompson B, McLachlan S (2007) The effects of urbanization on ant communities and myrmecochory in Manitoba, Canada. *Urban Ecosyst* 10:43–52
- U.N. Secretariat. Office of Legal Affairs, Population Division (2004) *World population to 2300*. New York
- Uno S, Cotton J, Philpott SM (2010) Diversity, abundance, and species composition of ants in urban green spaces. *Urban Ecosyst* 13:425–441
- Urban MC, Skelly DK, Burchsted D, Price W, Lowry S (2006) Stream communities across a rural–urban landscape gradient. *Diversity Distrib* 12:337–350
- Venn SJ, Kotze DJ, Niemelä J (2003) Urbanization effects on carabid diversity in boreal forests. *Eur J Entomol* 100:73–80
- White, RE (1983). *A Field Guide to the Beetles of North America*. Houghton Mifflin Co. New York, New York
- Wiwatwitaya D, Takeda H (2005) Seasonal changes in soil arthropod abundance in the dry evergreen forest of northeast Thailand, with special reference to collembolan communities. *Ecol Re* 20:59–70
- Wojcik VA, McBride JR (2012) Common factors influence bee foraging in urban and wildland landscapes. *Urban Ecosyst* 15:581–598
- Yow DM (2007) Urban heat islands: Observations, impacts, and adaptation. *Geography Compass* 1:1227–1251
- Zhang CL, Chen F, Miao SG, Li QC, Xia XA, Xuan CY (2009) Impacts of urban expansion and future green planting on summer precipitation in the Beijing metropolitan area. *J Geophys Res* 114, D02116
- Zipperer WC, Sisinni SM, Pouyat RV (1997) Urban tree cover: An ecological perspective. *Urban Ecosyst* 1:229–246