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# No overall effect of urbanization on nest-dwelling arthropods of great tits (*Parus major*).

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## Abstract

Urbanization has been shown to strongly affect community composition of various taxa with potentially strong shifts in ecological interactions, including those between hosts and parasites. We investigated the effect of urbanization on the composition of arthropods in nests of great tits in Flanders, Belgium. These nests contain taxonomically and functionally diverse arthropod communities including parasites, predators, detritivores and accidental commensals. Using a standardized hierarchical sampling design with subplots (200m x 200m) nested in plots (3km x 3km) of varying urbanization levels, we collected arthropods from nests of resident great tits after young had fledged. Arthropods were extracted, identified to Primary Taxonomical Groups (PTG) and counted. Using generalized linear mixed models (GLMMs) we found diverging effects of urbanization on PTG occurrences and abundances at various levels, but we did not find an overall signal in arthropod diversity or richness. Also, visual inspection of non-metric multidimensional scaling (NMDS) plots did not reveal any community differences between urbanization levels at plot or subplot scales. Land use and environmental variables at different distances around nestboxes did not contribute much to the variation between communities. Our results indicate that arthropod nestbox communities are generally not adversely affected by urbanization, and even city gardens and parks harbor comparable communities to forests and suburban areas. We thus found

no evidence for a parasite release effect due to urbanization, nor an increased risk of parasitism in human-dominated environments.

## Introduction

The process of urbanization refers to the creation of dense human habitats dominated by buildings, roads and infrastructure ([Johnson and Munshi-South 2017](#)). In addition to these structural changes, urbanization prompts changes in abiotic factors such as temperature, loss of waterbodies and increase of light, noise and air pollution ([McIntyre 2000](#); [Gil and Brumm 2014](#)). Some of the major changes in the biotic environment are size and isolation of natural areas, abundance and predictability of food sources for wildlife, increase of nonnative species and decrease of phylogenetic diversity ([Grimm et al. 2008](#)). The effects of urbanization are relatively predictable, rendering distant cities more similar to each other than to the natural environment surrounding them, also known as homogenization. Biotic homogenization in urban areas, or an increase in similarity between communities due to the combined effects of loss of native species and invasion by nonnatives, has received much attention ([Clergeau et al. 2006](#); [Kuhn and Klotz 2006](#); [McKinney 2006](#)). However, a recent review by [Olden et al. \(2018\)](#) questions our current comprehension of causes and consequences of the phenomenon and urges more integrative research including multiple taxa and different spatial and temporal scales. Urban ecosystems are temporally dynamic and can be very spatially heterogeneous within a short space ([McIntyre 2000](#); [Savard et al. 2000](#); [Thompson et al. 2003](#)), with land uses ranging from buildings and infrastructure to green spaces (gardens, parks, waterbodies, verges of infrastructure) which are often rich in microhabitats ([Cornelis and Hermy 2004](#); [Beninde et al. 2015](#)). Owing to this spatial heterogeneity, as well as differences among taxa in traits such as mobility and specialization, effects of urbanization may differ according to the scale and taxa examined ([Clergeau et al. 2006](#); [Concepcion et al. 2015](#); [Rega-Brodsky and Nilon 2017](#)).

The effect of urbanization on species diversity and community composition has been studied in a multitude of taxa such as plants ([Kowarik 2011](#); [Concepcion et al. 2015](#); [Malkinson et al. 2018](#)), birds ([Blair 1999](#); [Imai and Nakashizuka 2010](#); [Dale 2018](#)), reptiles ([Germaine and Wakeling 2001](#); [Ljustina and Barrett 2018](#)) and arthropods: ([Sattler et al. 2011](#); [Vergnes et al. 2014](#); [Concepcion et al. 2015](#); [Nagy et al. 2018](#)), but has commonly focused on single species groups ([Cornelis and Hermy 2004](#); [Nielsen et al. 2014](#)). Findings vary depending on the focal taxa. Non-avian vertebrate richness tends to peak at low urbanization, while richness of plants ([McKinney 2008](#)), and birds ([Jokimaki et al. 2018](#)) have been found to be highest at intermediate levels of urbanization. Studies of arthropod taxa are less conclusive with some showing no difference or even an

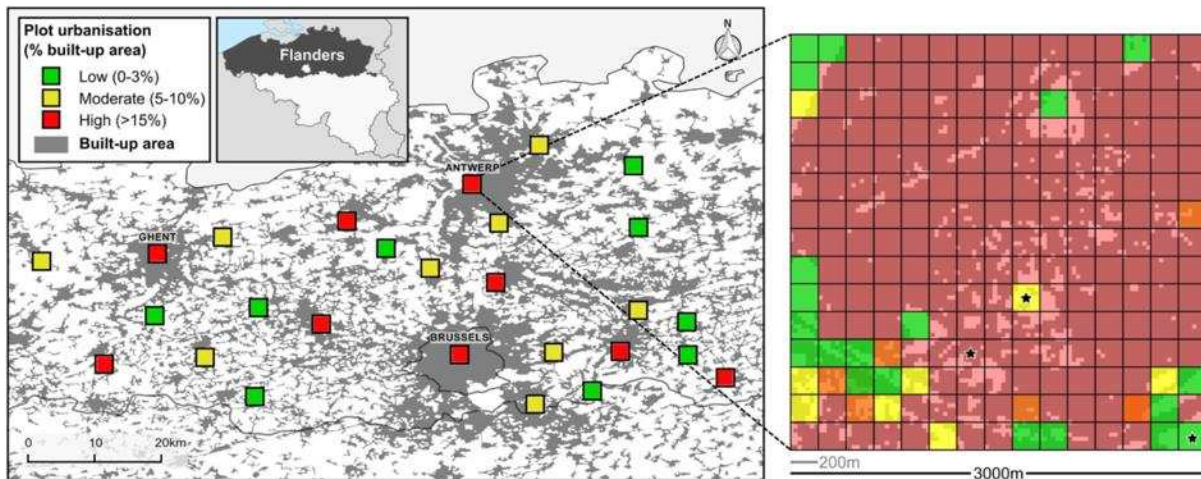
increase in richness over the urbanization gradient, reviewed by [Jones and Leather \(2012\)](#). Since arthropods and plants require relatively little space, the increased microhabitat diversity in urban areas may still support an increased beta-diversity, defined as variation in species communities between (micro)habitats ([Niemela 1999](#)). However, shifts in community composition have also been reported in arthropod studies, such as replacement of forest specialized species by generalist species as urbanization increases ([Deichsel 2006](#); [Faeth et al. 2011](#); [Magura et al. 2013](#)), or selection for smaller or more mobile species ([Merckx et al. 2018](#)).

Urbanization can also have strong effects on species interactions, such as predation, competition and host-parasite interactions. Host-parasite interactions are particularly important in anthropogenic environments as parasites not only affect host population dynamics, but can also act as vectors of diseases, potentially affecting humans ([Rizzoli et al. 2014](#); [LaDeau et al. 2015](#)). There are several mechanisms that could lead to changes in host-parasite interactions over an urbanization gradient. Examples include “spill-over” of non-native parasites from introduced species, or “spill-back” effects where introduced species act as reservoirs hosts for native generalist parasites and diseases that are transferred back to the native fauna ([Kelly et al. 2009](#); [Strauss et al. 2012](#)). Alternatively, hosts could experience a “parasite release” in urban areas induced by spatial or temporal barriers reducing prevalences of parasites ([Torchin et al. 2003](#)). Studies indicate that environmental stressors can affect host-parasite interactions through changes in immune responses and thereby tolerance and/or resistance of hosts to parasites ([Oppliger et al. 1998](#); [Dittmar et al. 2014](#); [Conroy et al. 2016](#)). For example, higher temperatures in cities, known as the urban heat island effect ([Oke 1982](#); [Youngsteadt et al. 2015](#); [Merckx et al. 2018](#)), might produce changes in parasite life histories such as increased growth rates ([Macnab and Barber 2012](#)), longer activity periods ([Wall et al. 2011](#)) or increased capacity for overwintering ([Trajer et al. 2014](#)).

Arthropod communities in natural nest cavities and nestboxes specific for small birds offer an interesting system to study how urbanization affects trophic interactions and host-parasite interactions in particular. These communities are often highly diverse in terms of species, body sizes, dispersal abilities and trophic levels ([Tomas et al. 2007](#); [Roy et al. 2013](#); [Masan et al. 2014](#)). Birds provide food resources directly for nest parasites but also indirectly for detritivores, predators and hyperparasites. With specialist and generalist predators controlling abundances of parasites and detritivores, bird nest communities can be rich and stable, potentially lowering the stress on birds induced by parasitism ([Lesna et al. 2009](#); [Hanmer et al. 2017](#); [Kristofik et al. 2017](#)). From a practical point of view, nestboxes provide a highly standardized study system that can be easily sampled with high reproducibility, and may therefore function as a dispersed mesocosm setup.

Predicting how individual arthropod groups react to urbanization is difficult, not only because outcomes from studies diverge but also because of the variability in ways of defining urbanization and spatial scales. However, one can assume that arthropods that are commonly associated with human produce or waste can be expected to have higher abundances in urban areas. Some examples include dust and storage mites (e.g. Acaridae and Glycyphagidae) and their predators (e.g. *Cheyletus eruditus*), as well as highly mobile flies that lay their eggs in decaying organic matter and sap-feeding Hemiptera that may benefit from the lack of natural predators as well as the large diversity of well-kept ornamental plants in urban gardens. Another general expectation is that generalist arthropods would be more common in urban areas ([Knop 2016](#); [Merckx and Van Dyck 2019](#); [Rocha and Fellowes 2020](#)). On the other hand, some will be less suited to urban living on account of their specialized nature. Dead tree trunks, decomposing leaves, high grass and fungi are resources that may be less plentiful in urban spaces, on account of greenspace management, and thus not well suited for supporting high abundances of specialist species. For parasitic species it is also not straightforward to predict the effect of urbanization on diversity or abundance. On one hand, hosts might be fewer and further apart, vegetation might be less suited for aiding transfer (e.g. limited patches of higher grass for questing ticks) and making cities more of a sink for parasitic individuals. But parasites might also find lowered predator pressure and high local density of hosts, boosting their numbers.

[McIntyre \(2000\)](#) points out the lack of studies showing how urbanization affects abundance and diversity of arthropods that are not specifically linked to human activity. Certainly at this moment, facing the global decline in arthropods ([Vergnes et al. 2014](#); [Hallmann et al. 2017](#); [Sanchez-Bayo and Wyckhuys 2019](#)) it is important to assess a broad spectrum of arthropods to better understand which groups are most vulnerable to increased severity and spread of urbanization. In this study we examine how urbanization at different scales affects richness and diversity, as well as occurrence and abundance of functional arthropod groups, in nests of great tits breeding in nestboxes, with special attention to the parasite groups. We collected data from the highly urbanized Flanders and Brussels regions in a strict sampling design allowing us to disentangle effects of urbanization at different spatial scales. We test whether arthropod community composition changes along urbanization gradients and explore at which spatial scale habitat and land-use variables most strongly affect community composition.



**Fig. 1** Overview of spatial setup, taken from De Satgé et al. (2019) with permission from the authors. Left: Map of central part of northern Belgium. Squares on the map show position of the plots (3km x 3km - not to scale) with colors indicating level of urbanization as explained in the top-left information box. Right: Magnification of the Antwerp plot divided into subplots of 200m x 200m. Colors of subplots indicate the same urbanization levels with the exception of orange, an intermediate category (10-15% build-up) not included in the study. Star symbols indicate the sampling sites – including all three subplot urbanization levels. Note that one nestbox location was in the wrong position in De Satgé et al. 2019, and is shown correctly here.

## Methods

### Study sites

This study covers an area of ca 5000 km<sup>2</sup> within the Belgian regions of Flanders and Brussels, which combined comprise one of the most urbanized areas in north-west Europe with population densities at 477/km<sup>2</sup> and 7,025/km<sup>2</sup>, respectively. Study sites were chosen as part of a multi-taxon research project (see [Piano et al. 2017](#); [Gianuca et al. 2018](#); [Merckx et al. 2018](#)) and based on the degree of urbanization at two hierarchical spatial scales. Initially, the study area (Flanders plus Brussels) was divided in non-overlapping plots of 3 x 3 km. Using GIS tools on a vectorial layer of all buildings, each plot was assigned to one of three urbanization levels according to percentage build-up; rural: 0-3%, semi-urban: 5-10% and urban: >15%. Plots with build-up percentages falling between these ranges were excluded. 27 plots (9 per urbanization level) were selected, covering urbanization gradients radiating from the cities of Gent (51°03'N, 3°44'E), Antwerp (51°13'N, 4°24'E), Brussels (50°51'N, 4°21'E) and Leuven (50°53'N, 4°42'E). The 27 plots were then sub-divided into 225 subplots of 200 x 200 m, and urbanization levels were again calculated the same way for each subplot. See Fig. 1 for a schematic overview of the spatial setup. Within each of the 27 plots, we selected three subplots, one of each urbanization level, henceforth known as sites. Site urbanization level was therefore of a hierarchical nature, with nine possible combinations of plot and subplot urbanization. All sites were chosen to contain a minimum of suitable vegetation for breeding great tits. For logistic reasons, a few sites consisted of multiple subplots – not

necessarily adjacent, but with the same urbanization levels. This design resulted in 81 sampling sites. In 20 of the sites, more or less evenly spread over the nine plot-subplot combinations, we installed or located 15 nestboxes. In the remaining 61 sites we installed or located 3 nestboxes. Installed nestboxes were either never used before, or sterilized in an oven of 70°C for 3 hours to prevent introduction of arthropods from its former location. Nestboxes already present (ca 23% of the boxes) were manually cleaned out the autumn before use. For the analysis we distinguished between first use (first nesting attempt after sterilization) and older (second nest after sterilization or boxes already in use before). This will be referred to as HNB (“Had Nest Before”) with levels “Yes” and “No”.

### **Sample selection**

A total of 483 nestboxes were monitored over one, or both, breeding seasons (2014 and 2015). Monitoring included a weekly visit to register nest building, first egg date, hatching date, number of eggs and chicks ([see Matthysen et al. 2011](#)). Overall, 447 breeding attempts successfully fledged first broods. Since collecting, sorting and identifying nest material is extremely time consuming, we had to take a subsample based on following criteria:

- a) Only first breeding attempt per nest box per season;
- b) Only nests with at least two fledglings to exclude nests that had too few parasites and other arthropods because hardly any chicks survived (only 3 were nests excluded);
- c) Only nests of great tits (24% of the nestboxes were occupied by blue tits);
- d) For each site, both sampling years were included, but never the same nestbox twice;
- e) From the 20 sites with 15 nestboxes, we randomly selected 4 or 5 nests; from the remaining 55 sites we selected all that met criteria a-d (1-3 nests).

This subsampling resulted in 186 nests sampled from 75 of the 81 subplots. 105 nests were from 2014 and 81 from 2015. Nest material was collected in individual zip-lock bags between 1 and 4 days after the estimated date of fledging.

### **Arthropod data**

Nests were extracted over 10 days in a modified Berlese-Tullgren funnel, which, simply put, works by drying out the nest material from the top towards the bottom, forcing arthropods to flee the downwards and eventually ending up in a vial filled with ethanol. Wet (pre-extraction) and dry (post-extraction) weight of nest material

was noted. The extracted arthropods were sorted and counted into “Primary Taxonomical Groups” (PTGs), following [Roy et al. \(2013\)](#). PTGs are higher level identification groups based on taxonomy, ecological role and overall abundance that allow us to focus on functional diversity and trophic guilds. We removed PTGs that occurred in less than 5% of nests from all further analyses to prevent influence of rare groups. In the end, 18 PTGs were differentiated (see Online resource 1 for a detailed list and information on their trophic position).

### **Field-survey environmental data**

All field-based environmental data were collected in the fall (91% of the samples) and early winter of 2014 and 2015. We first estimated the percentage land cover within a 3 and 10 meter radius around each nestbox for the following categories: lawn, planted vegetation, natural vegetation, leaf litter, bare soil, water and hard surfaces (buildings, pavement and gravel). Since we use easily identifiable vegetation categories and the typical plants are perennials that do not wither during autumn and winter, we are confident that our data describe the situation during the breeding season accurately. Additional variables describing the immediate surroundings of the nestbox, hereafter named “outside-box variables”, included area type (6 categories: forest (>100ha), large woodlot (10-100ha), small woodlot (<10ha), rural garden, city park, city garden), nestbox height and substrate (tree or wall), average height of undergrowth, percentage of shrubs and canopy cover, all at 3 meter radius, and sun exposure (mostly sun, some sun, full shade). Variables connected to the interior nestbox environment, hereafter known as “within-box variables”, included dry weight of nest material, number of chicks fledged, number of chicks found dead in the nest, timing of egg laying and HNB (“Had Nest Before”, as explained above).

### **GIS-derived environmental (land cover) data**

Land cover data at 30, 100, 500 and 1000 meter radius around each nestbox were based on the combination of two land cover data layers (1x1 m) from the Flemish Agency for Geographical Information ([www.geopunt.be](http://www.geopunt.be)). Vegetation data were obtained from the “Groenkaart” (classes: agricultural land; vegetation below 3 meters; vegetation above 3 meters). Hard surfaces (classes: buildings; transport infrastructure including roads, parking lots, railways, paths) and water bodies were obtained from the GRBgis map. For the Brussels region layers with similar information were obtained from the Brussels Environmental Agency (Brussels Ecological Network) and URBISonline, respectively.



## Statistical analysis

We tested whether PTG Richness and Shannon Diversity, as well as occurrences and abundances of all individual PTGs, were related to the level of urbanization at the two spatial scales using generalized linear mixed models (GLMMs). For this we used model selection by AICc (Akaike information criterion with correction for small sample sizes). Our full model included plot and subplot urbanization, their interaction, year and HNB as main effects. To account for the fact that 1 to 5 nests were included per site and that up to 3 sites were within the same plot, we included SiteID nested in PlotID as random effect in all models. Occurrence data were analyzed with binomial distributions with a logit link function, richness with Poisson distribution with log link function and Shannon Diversity with normal distribution and identity link function. For the analyses of individual PTG abundances we selected the best fitted full model showing lowest AICc value by comparing models with negative binomial and quasi-poisson distributions, as well as with and without a zero-inflation parameter applying to all observations ([Brooks et al. 2017](#)).

The most complex additive model (i.e. full model without interaction but plot and subplot urbanization as additive main effects in addition to year and HNB) was investigated for variance inflation factors (VIFs) and dropped if exceeding 3 to reduce collinearity ([Zuur et al. 2010](#)). Extreme outliers were checked for validity and removed if their presence changed the outcomes compared to the dataset without them. For each response variable (Shannon diversity, Richness, individual PTG abundances and occurrences), the full model and subsets using all possible combinations of the main effects of the full model, were ranked. Models that had a  $\Delta$ AICc value of less than 2, compared to the best model (lowest AICc), were considered further. Within this competitive set we investigated whether simpler models (also null model if present) nested in more complex models were more parsimonious, using ANOVAs (analysis of variance). By this method we ended up with one (or sometimes more) best model(s). For occurrence data, we then examined the fit of the best models using ROC (receiver operating characteristic) curves. For abundance, diversity and richness data we plotted residuals against fitted values to examine fit of best models. The residuals of the best models were also tested on potential remaining spatial autocorrelation by plotting variograms. Best models were then inspected for significance between model terms, using the Bonferroni correction for multiple testing. GLMMs were performed with the R package glmmTMB. Packages used were “lme4” and “car” for checking VIF’s, “glmmTMB” for GLMMs used in model selection, “DHARMA” and “pROC” for residual diagnostics and “sp” and “gstat” for variograms.

We tested whether species composition changed over the urbanization levels by utilizing non-metric multidimensional scaling (NMDS). We first standardized the dataset by dividing abundances by column

maxima (Faith et al. 1987). Then, a Bray-Curtis dissimilarity matrix was calculated and NMDS technique applied using metaMDS from the *vegan* package (Oksanen et al. 2018). Pairwise plots were produced depicting axes 1, 2 and 3 with ellipses representing 95% confidence intervals around urbanization category centroids and vectors representing gradients in the PTG variables. The stress value, indicating the disagreement between distances in the reduced dimension compared to the predicted values from the regression, was calculated. Stress values of more than 0.2 would indicate unreliability of the NMDS visualization, while values approaching 0.3 suggest randomness (Clarke 1993). To formally test differences in species composition between categories, permutational multivariate analysis of variance (PERMANOVA) was performed on the same Bray-Curtis dissimilarity matrix, using 999 permutations. This is a non-parametric test considering the null hypothesis that centroids and dispersion of groups are similar. Although this function allows for the inclusion of random effects, it does not accommodate for nestedness in random effects. Therefore we performed the test with both random effects separately and reported the most conservative outcome.

To examine at what spatial scale the environment affects PTG composition we performed Canonical Correspondence Analyses (CCA). With this multivariate constrained ordination method we combined the PTG abundances with a corresponding matrix of environmental variables (constraints). Analyses were performed separately on land cover data at all radii (field survey: 3 & 10 m; GIS-derived: 30, 100, 500 and 1000m) and on within-box and outside-box variables (as defined above). Variance inflation factors of the full model were investigated and removed if above 3. Because CCA does not allow any missing values one nestbox was dropped in the analyses at 3 and 10 meter radius, while five nests were dropped from within-box and outside-box analyses. Using ANOVA with 999 Monte Carlo permutations we formally tested whether the variation in community composition explained by the environmental variables was more than expected by chance.

All statistical analyses were performed with R version 4.0.0 (R Core Team).

## Results

### Occurrence and abundance of Primary Taxonomic Groups.

A total of 186728 arthropods from 186 nests were collected and assigned to PTGs. Most PTGs were found in all urbanization level combinations, and those that were not (ticks, moths, springtails, earwigs, ants and booklice) were missing in maximum two of the nine combinations. For complete data on occurrence and abundances per plot level urbanization, see Online resource 2. Best models that included urbanization are illustrated in Fig. 2 (occurrence data) and Fig. 3 (abundance data). The competitive sets of models ( $\Delta\text{AICc}$  within 2 of best model),

and estimates of best models are presented in table 1 and 2, respectively, for occurrence data, and table 3 and 4, respectively, for richness, Shannon diversity and abundance data. These tables are found in Online resource 3. Here, we present the results of the GLMMs by main effects of urbanization, plot and subplot, followed by year and HNB.

Plot urbanization was featured in the best models of tick occurrence as well as in hematophagous mite, tick and saprophagous beetle abundance models. The chance of finding ticks decreased with plot level urbanization and was significantly lower in urban plots compared to rural. Similarly, their abundances were significantly lower in urban plots compared to both rural and semi-urban plots. The abundance of hematophagous mites was lowest in semi-urban plots but only rural plots had significantly higher mean abundances. Also the best models for saprophagous beetle occurrence and moth abundance included plot urbanization, but these models showed a less than acceptable fit and were therefore excluded.

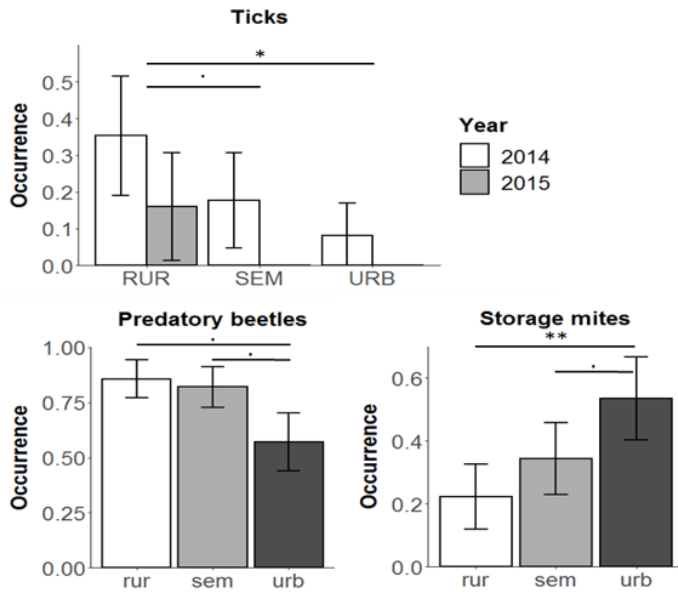
Both the occurrence and abundance of predatory beetles and storage mites included subplot urbanization in their best models. For both indices of predatory mites, urban subplots had the lowest means, but whereas their abundance was significantly higher in rural subplots, there were no significant differences found in their occurrence, after correcting for multiple testing. Storage mite occurrence was significantly lower in rural subplots compared to urban, and their abundances were also significantly lower in rural subplots compared to semi-urban ones.

Year was included in the best models of flea and tick abundance, as well as tick, wasp and phytophagous Hemipteran occurrences. While tick occurrence and abundances were higher in 2014, flea abundances as well as wasp and phytophagous Hemipteran occurrences were higher in 2015. However, when tested for statistical significance the year effect was only confirmed for flea abundance.

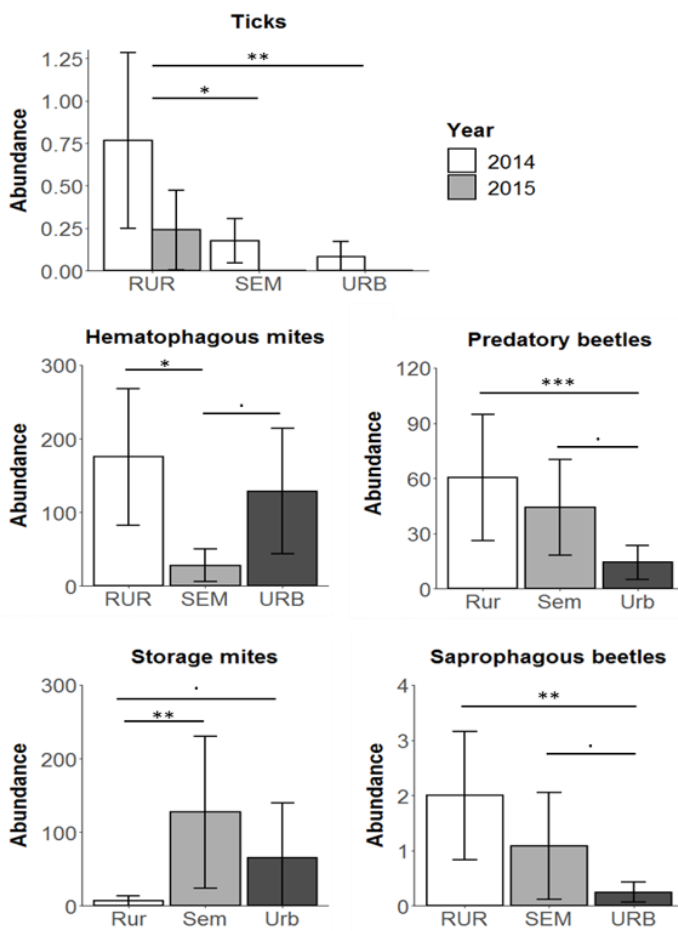
The best models including HNB (Had Nest Before) were found for hematophagous mite and saprophagous beetle occurrences as well as predatory mite, wasp and booklice abundances. Hematophagous mites were more abundant in new nests while the other PTGs were more plentiful in boxes that had been previously occupied. However, none of these differences between used and unused nestboxes were significant after correcting for multiple testing.

For parasitic flies, scavenger flies, beetle mites, spiders and earwigs, the best model turned out to be the null model both in terms of occurrence and abundance. The null model was also the best model for the occurrence of fleas, moths, springtails and booklice, as well as the abundance of phytophagous Hemiptera. For

ant occurrence and abundance, as well as springtail abundance, no single best model could be selected, but upon inspection, also none of the candidate models contained any significant terms.



**Fig. 2** Effects of urbanization at two spatial scales on occurrences of primary taxonomic groups. Only best models including urbanization are illustrated. Plot-level urbanization (3km x 3km) is indicated in capital letters, subplot-level urbanization (200m x 200m) in lower case letters. RUR/rur = Rural, SEM/sem = Semi-urban, URB/urb = Urban. Error bars show 95% confidence intervals. Significance indicated by asterisk: 0 '\*\*\*\*' 0.0001 '\*\*\*' 0.001 '\*\*' 0.0027 '.' 0.05



**Fig. 3** Effects of urbanization at two spatial scales on mean abundances of primary taxonomic groups. Only best models including urbanization are illustrated. Plot-level urbanization (3km x 3km) is indicated in capital letters, subplot-level urbanization (200m x 200m) in lower case letters. RUR/rur = Rural, SEM/sem = Semi-urban, URB/urb = Urban. Error bars show 95% confidence intervals. Significance indicated by asterisk: 0 '\*\*\*\*' 0.0001 '\*\*\*' 0.001 '\*\*' 0.0027 '.' 0.05

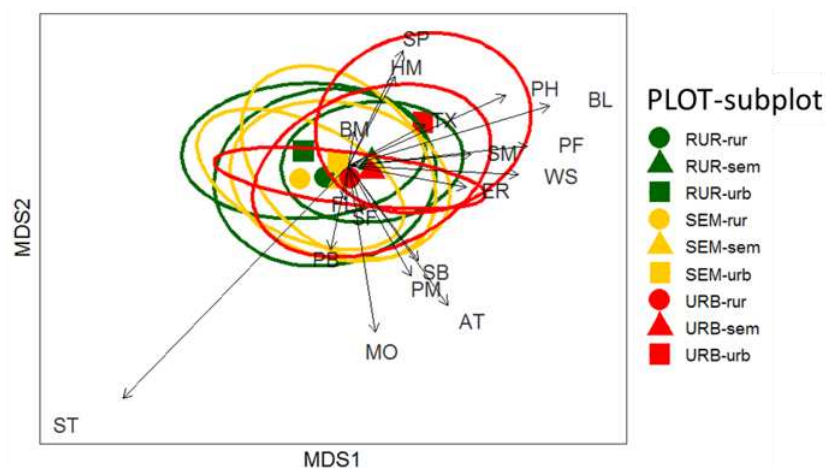
### Species richness and diversity

The number of PTGs per nest varied from 2 to 14 of the 18 PTGs found. The best model for PTG richness was the null model, indicating no effect of urbanization, year or HNB. Shannon Diversity index of the PTGs ranged from 0.008 to 1.92. Here, the best model included year. Shannon diversity was lower in 2015 compared to 2014, but on further inspection we saw that the difference was not significant.

### Community composition

The NMDS plots did not visually indicate a significant separation among the urbanization levels at plot or subplot scale. Stress values were 0.21 for both analyses, indicating that community data did not effectively compress into the 2-D ordination (Clarke 1993). The PERMANOVA analysis did not show significant results on either subplot scale ( $R^2 = 0.02$ ,  $p = 1$ ), nor plot scale ( $R^2 = 0.019$ ,  $p = 1$ ), considering both random effects.

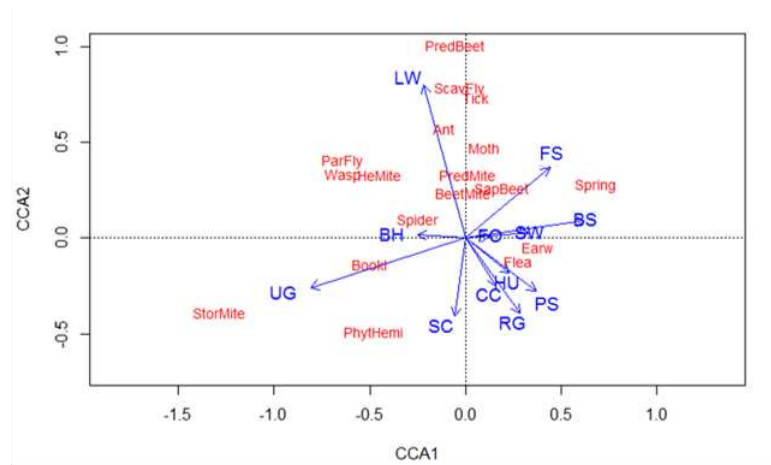
The NMDS was illustrated in one figure (Fig. 4) with the nine plot and subplot combinations.



**Fig. 4** NMDS plot showing centroids and ellipses for the nine combinations of plot and subplot urbanization levels. PTG abbreviations: AT = Ant, BL = Booklouse, BM = Beetle mite, ER = Earwig, FL = Flea, HM = Hematophagous mites, MO = Moth, PB = Predatory beetle, PF = Parasitic flies, PH = Phytophagous Hemiptera, PM = Predatory mite, SB = Saprophagous beetle, SF = Scavenger fly, SM = Storage mite, SP = Spider, ST = Springtail, TX = Tick, WS = Wasp.

CCA analyses showed that land cover variables explained only limited variation in the arthropod community, varying from 2.9% at 100m radius to 6.6% at 30m radius. The accompanying ANOVA test on the joint effect of land cover variables was significant at 3m radius ( $df = 6$ ,  $\chi^2 = 0.21$ ,  $F = 1.78$ ,  $p = 0.05$ ), 10 meter radius ( $df = 6$ ,  $\chi^2 = 0.23$ ,  $F = 1.96$ ,  $p = 0.027$ ) and 30 meter radius ( $df = 5$ ,  $\chi^2 = 0.25$ ,  $F = 2.54$ ,  $p = 0.023$ ), but not at 100, 500 and 1000m radius. Within-box variables explained 4.2% of the variation, and showed non-significant ANOVA results ( $df = 5$ ,  $\chi^2 = 0.16$ ,  $F = 1.54$ ,  $p = 0.076$ ). Outside-box variables explained somewhat more variation (13.4 %) with a significant ANOVA test ( $df = 12$ ,  $\chi^2 = 0.46$ ,  $F = 2.17$ ,  $p = 0.009$ ). Among the

constraining variables the area type, sun exposure and what the box was hanging on (substrate) were the most important (Fig. 5).



**Fig. 5** CCA triplot of primary taxonomic groups constrained by outside-box environmental variables. PTG abbreviations: BeetMite = Beetle mite, Bookl = Booklouse, Earw = Earwig, HeMite = Hematophagous mite, ParFly = Parasitic fly, PhytHem = Phytophagous hemipteran, PredBeet = Predatory beetle, PredMite = Predatory mite, SapBeet = Saprophagous beetle, ScavFly = Scavenger fly, Spring = Springtail, StorMite = Storage mite. Environmental abbreviations: HU = Height of undergrowth, SC = Shrub cover, CC = Canopy cover, FO = Forest, LW = Large woodlot, SW = Small woodlot, RG = Rural garden, UG = Urban garden, PS = Partial sun, FS = Full shade, BS = Box substrate

## Discussion

In this study, we found that different primary taxonomic groups (PTGs) of arthropods in bird nests responded idiosyncratically to urbanization, but that there was no overall effect of urbanization on taxonomic richness or diversity. This indicates that urban greenspaces are able to support a multitude of functional arthropod groups, comparable to rural areas. Multivariate analysis (NMDS) likewise suggest that overall arthropod community composition did not differ notably between urbanization levels at the two spatial scales of 3 by 3 km and 200 by 200m, respectively (“plot” and “subplot”). Also, the measured environmental and landcover variables associated with the nestboxes and their surroundings explained only little variation in community structure.

Despite the overall weak effects of urbanization on community composition as shown through multi-dimensional community analysis (NMDS), several arthropod groups did show responses to urbanization - but in idiosyncratic ways. The high heterogeneity of group-specific responses likely explains the lack of trends reflected by richness and diversity measures. The PTGs with the clearest negative effect of urbanization were parasitic ticks, predatory and saprophagous beetles. These groups displayed marked declines in abundances, and occurrences from rural to urban, albeit on different spatial scales. The effect of urbanization that we saw in ticks in our system is in line with several studies showing that urban areas have lower frequency of questing ticks ([Maetzel et al. 2005](#); [Heylen et al. 2019](#)) and lower prevalence of ticks on birds ([Gregoire et al. 2002](#); [Evans et](#)

[al. 2009](#)). However, caution has to be applied in extrapolating our results to ticks in general, since some of the ticks we found in the nests were habitat-specific species (*Ixodes arboricola* - depending on tree-holes, and *I. frontalis* – specialized on birds) with a highly divergent ecology from the more common generalist species (*Ixodes ricinus*) ([Heylen and Matthysen 2010](#); [Heylen et al. 2014](#)). Saprophagous beetles also reacted negatively to urbanization on plot scale. This is a diverse group of mostly small bodied fungivores, necrophages and detritivores. [Pilskog et al. \(2016\)](#) found that richness of saproxylic beetles in hollow oaks responded strongest to habitat quality, while abundances were linked to patch size. They are also likely to be affected by management practices common in cities such as removal of rotting trees, carrion and fungi, and treatment of wood. However, our results suggest that their occurrence in urban areas may be driven by larger-scale factors such as dispersal and landscape permeability, rather than local habitat quality ([Beninde et al. 2015](#)). The predatory beetles included mainly histerid beetles (family Histeridae) and rove beetles (family Staphylinidae), both of which have good dispersal capabilities ([Bajerlein 2009](#); [Nagy et al. 2018](#)). This group was affected on a subplot scale, possibly indicating that it is the intensive management activities (such as cutting, pruning, paving, raking, removal of fungi and dead trees etc.) in urban subplots, generally comprised of gardens and smaller inner city parks, that affect predatory beetles, rather than isolation of green spaces at landscape scale. The marked decrease seen here can relate to findings of lower diversity reported for Staphylinid beetles over an urbanization gradient in Hungary ([Magura et al. 2013](#); [Nagy et al. 2018](#)) and abundance of Carabid beetles in Finland ([Venn et al. 2003](#)).

Hematophagous mites and storage mites seemed to respond more positively to urbanization. Hematophagous mite occurrences were fairly even. However, abundances were conspicuously low in semi-urban plots. One of the most researched parasitic mite species, *Dermanyssus gallinae*, is a common pest in laying hen farms and coops of domestic chickens, thus one could expect them to be abundant in wild bird nests in rural areas and larger semi-urban gardens, as a result of spill over. However this was not supported here. One reason might be that the *Dermanyssus* mites in our samples were mostly other species, i.e. *D. carpathicus* and *D. longipes* (Baardsen et al., unpublished). To our knowledge there are no previous studies investigating the effect of urbanization on these mite species.

Storage mites contain species generally known as grain-, storage- or dust mites which thrive in anthropogenic environments ([Colloff 1998](#); [Kosik-Bogacka et al. 2010](#)). As such, there's no surprise that their occurrences were the highest in urban subplots. However, their abundance peaked in semi-urban subplots. Storage mites were first noticed as involved in occupational allergies in the agricultural sector, but within the

past few decades focus has also been given to their role in urban homes ([Franz et al. 1997](#); [Vidal et al. 2004](#)). As semi-urban subplots are found either at the outskirts of cities, bordering farmlands or at the interface between forests and small villages, these subplots would undoubtedly provide ample habitats for these prolific mites, in barns with cattle or grain stores, wild animal nests and burrows and old damp houses.

Many of the PTGs proved unaffected by urbanization. Fleas, being parasitic in their adult form, were overall very common and abundant, and not influenced by urbanization. This is in general agreement with [Reynolds et al. \(2016\)](#) who found no difference in flea loads in blue tit nests between urbanization categories in Birmingham. However, [Hanmer et al. \(2017\)](#) found that flea abundances in great tit nests decreased with increasing urbanization, but increased with the percentage inclusion of anthropogenic materials in the nest, showing that the two environmental variables were unrelated. Beetle mites (Oribatida), is a group of detritivores and fungivores found in the litter layer, and are generally common in various habitats ([Rota et al. 2015](#); [Caruso et al. 2017](#)) and our findings are in tune with studies such as [Caruso et al. \(2017\)](#). Very few studies have studied predatory mites (e.g. prostigmata & mesostigmata) in direct relation to urbanization. However, [Mizser et al. \(2016\)](#) showed that prevalence and abundances of mesostigmata phoretic on carabid beetles were higher in a rural forest compared to urban parks. We also know that one of the most common species in this group, *Androlaelaps casalis*, is a common nidicole in various habitats (e.g. [Pung et al. 2000](#); [Wolfs et al. 2012](#); [Kristofik et al. 2013](#); [Bloszyk et al. 2016](#)). Also, studies of pests on stored products, often found in more urbanized spaces, identify prostigmatic mites of the genus *Cheyletide* as prolific predators in these systems ([Zdarkova 1979](#); [Lukas et al. 2007](#); [Palyvos et al. 2008](#)). [Fenoglio and Salvo \(2010\)](#) reviewed the studies focusing on how parasitoid wasp community composition changed with various measures of urbanization and found that urbanization generally had neutral or negative impacts on parasitoid richness and parasitism rates. More recent studies similarly found no impact of urbanization ([Rocha and Fellowes 2018](#)) or negative effects on parasitoid diversity ([Bennett and Gratton 2012](#); [Burks and Philpott 2017](#)). Scavenger flies include detritivorous Diptera species known to be associated with human environments and manure, garbage and decaying organic matter produced here, and are found to be more abundant in fragmented landscapes ([Gibbs and Stanton 2001](#)). However, we found they were not significantly affected by our urbanization levels. The lack of response of moths to urbanization is in contrast to [Lagucki et al. \(2017\)](#) who found that moth abundances positively increased with the distance from urban centers. Another study, by [Rice and White \(2015\)](#), found that richness was higher in urban woodlots compared to residential gardens, a pattern not seen in our data. Contrary to our predictions, we did not find more phytophagous Hemiptera in urban areas. Studies of Hemiptera have revealed



contrasting results, both greater abundances in urban gardens ([Philpott et al. 2014](#)), and decreasing abundance with increasing impervious surface cover ([Lagucki et al. 2017](#)). As such, and given the accidental nature of phytophagous Hemipteran presence in the nestboxes, we cannot make any inference as to their robustness to urbanization.

Predatory mite and wasps abundances, as well as saprophagous beetles and booklice occurrences were higher in nestboxes that had been used in previous breeding season(s). Comparing our results to other findings is however difficult as most studies focused on the abundances of ectoparasites, and compared nests where the nest material was left from the previous breeding season to those that were cleaned out ([Mazgajski 2007](#); [López-Arrabé et al. 2012](#)). We, on the other hand, compare nests that were effectively sterile to those that were cleaned out. However, among the parasitic PTGs we saw that the occurrence of hematophagous mites was higher in new nests compared to older nests. We can only speculate on possible reasons for this, such as increased visitation rates by birds carrying parasites to novel boxes or preferences to clean boxes for roosting ([Christe et al. 1994](#)).

One of our aims in this study was to examine how parasite communities may change with urbanization. Urbanization may free hosts from their parasites (“parasite release hypothesis”) through several mechanisms, e.g. isolation of host populations from larger rural populations, by providing an inhospitable environment for particular life-stages or increased abundances of predators preying on the parasites. Given the contrasting patterns in the four parasitic groups we studied (fleas, ticks, mites, parasitic flies), we found no evidence for parasite release in nest of urban great tits. Rather, our results indicate prevalences comparable to those in rural areas, the main exception being ticks. We also found substantial abundances of fleas, hematophagous mites and parasitic flies in urban bird nests. Our results are therefore in tune with those of [Le Gros et al. \(2011\)](#) who found no evidence for parasite release in urban nests of northern mockingbirds (*Mimus polyglottos*) and their dipteran parasite, as well as studies of blood parasites in lizards ([Lazic et al. 2017](#)) but contrast with other studies such as [Geue and Partecke \(2008\)](#) that did find lower blood parasite prevalence in urban blackbirds (*Turdus merula*). In their review of urbanization effects on bird-parasite interactions, [Delgado and French \(2012\)](#) found conflicting trends in parasite prevalence with results apparently varying with type of host and parasite studied, as well as differences between cities. It is predicted that urbanization can have a larger impact on parasite species with more complex life cycles, such as reliance on multiple hosts during the lifecycle, or strong host specificity ([Delgado and French 2012](#); [Calegario-Marques and Amato 2014](#)). In our study, most parasites had simple life-cycles and moderate to low host specificity, many being able to infest many bird species or even vertebrates. The only species relying on multiple different hosts is the common sheep tick

(*Ixodes ricinus*) which indeed is absent from urban centers ([Heylen et al. 2019](#)), but this species is only rarely found in bird nests since it searches for hosts in the open field ([Heylen et al. 2014](#)).

One factor that could potentially affect our findings is host health. Urban-related stressors such as light pollution ([Bedrosian et al. 2011](#); [Raap et al. 2016](#)), reduction in food availability or quality ([Blondel 2007](#); [Bailly et al. 2016](#); [Seress et al. 2018](#); [de Satge et al. 2019](#), but see also [Oro et al. 2013](#)), pollution ([Chatelain et al. 2016](#)) or even presence of other parasites ([Krasnov et al. 2005](#)) could lead to a reduced health state, such as lower immune responses ([Wegmann et al. 2015](#)) and thereby attract more parasites and/or increase parasite success. For example, parasite preference for low quality nestlings has been found ([Roulin et al. 2003](#); [Tschirren et al. 2007](#); [Owen et al. 2010](#)). Using data from the same nests as in this study, ([de Satge et al. 2019](#)) found lower breeding success and lower mean nestling mass in urban broods, at both spatial scales. Reduced reproductive success in urban tits has also been found in other studies, (e.g. [Horak 1993](#); [Solonen 2001](#); [Kalinski et al. 2009](#); [Bailly et al. 2016](#)). However, since we here only include successful nests, we cannot test for any causal relations between urbanization, parasitism and breeding success. The indicated reduction in breeding success did not translate to overall higher parasite abundances in urban areas in our study. Moreover, it does not explain the different patterns observed in different parasites. One explanation could be that early nestling mortality, as regularly observed in urban great tits, actually reduces parasite success rather than boosting it ([Tschirren et al. 2007](#)).

Conversely, the absence of a general trend in parasitism rates means that parasites cannot explain the low breeding success in urban areas. Some, but not all, studies show increased mortality and adverse effects in passerine birds as a direct result of ectoparasites such as parasitic flies ([Merino and Potti 1995](#); [Hurtrez-Bousses et al. 1997](#)), parasitic *Muscidae* ([Fessl and Tebbich 2002](#); [O'Connor et al. 2010](#)), fleas ([Richner et al. 1993](#); [Fitze et al. 2004](#)) and mites ([Merino and Potti 1995](#)). Tick infestations have been reported to show little impact (e.g. [Heylen et al. 2009](#); [Heylen and Matthysen 2011](#); [Castano-Vazquez et al. 2018](#)). It has been suggested that negative effects of parasites are more likely to be translated to higher nestling mortality when environmental factors inhibit sufficient parental compensation, which may be the case in city environments (e.g. [de Lope et al. 1993](#); [Merino and Potti 1995](#); [Christe et al. 1996](#); [Dufva and Allander 1996](#); [Tripet and Richner 1997](#)). In any case, we cannot draw an inference between the increases in some parasites (notably hematophagous mites) we see in our urban areas with the lowered reproductive success reported, without further study.

The inclusion of spatial scales is important in detecting effects of urbanization on species with differing habitat dependencies and mobility. A multi-scale approach could potentially also allow for extracting

information on where to focus efforts when it comes to conservation of species or communities. In our data, there was little evidence for land-use variables shaping community composition at spatial scales larger than 30 meters. At 30 meters and less, including our outside-box variables, the environmental constraints had some influence, indicating that nest arthropod communities were more affected by habitat disturbances at small distances rather than large. Overall, and despite the differences found in some primary taxonomic groups, our multidimensional approach (NMDS) showed very little structuring in community composition along the urbanization gradient at either spatial scales. This general absence of urbanization effects is in contrast with other studies showing clear community differentiation. For example, [Bang and Faeth \(2011\)](#) found significant arthropod community differentiation with urbanization on all taxonomical levels tested, probably driven by losses of specialized species in the urban mesic gardens. In the same system as our study, [Piano et al. \(2017\)](#) found that species composition of carabid beetles differed significantly among urbanization categories at both plot and subplot scale. This comparison shows that results found in free-living arthropod communities cannot be extrapolated to nest-associated arthropods; or generally, that strong caution should be taken in generalizing effects of urbanization across species groups fulfilling different ecological roles.

A general explanation why urbanization effects appear to be weak on nest arthropods may be the buffering effect of the sheltered nestbox environment, where resources are predictable and provided by the host. Moreover, arthropods specialized in nest environments are already adapted to exploiting highly dispersed resources, either by moving phoretically with the host (such as mites, ticks and fleas ([Smith et al. 1996](#); [Tripet et al. 2002](#); [Heylen and Matthysen 2010](#))) or being active flyers in at least one life-stage (such as parasitic flies and predatory beetles). Thus, these species groups may be pre-adapted to overcome the isolation and fragmentation of urban green spaces, explaining their overall success in penetrating the urban environment.

It is worth mentioning that the density of occupied natural nest cavities, of great tits and other birds, as well as private nestboxes are unknown variables that could affect our findings. However, this is a challenging parameter to produce, given the mosaic nature of the habitat, but also the cryptic nature of natural nest cavities. We should also note that, while nestboxes offer a highly useful system for systematic comparison of arthropod communities across the urbanization gradient, they also represent an element of anthropogenic disturbance, and hence may be somewhat biased towards disturbance-tolerant species. Unfortunately, very little information, if any, is available on arthropod communities in natural cavities versus man-made boxes.

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**Online resource 1** List of arthropods grouped by firstly by guild and PTG, followed by order, family, genus and species where possible. Identification based on morphology for all groups except Hematophagous mites, Parasitic flies and Scavenger flies where most identification was done by DNA barcoding.

**GUILD: Ectoparasites**

**PTG: Fleas<sup>1</sup>**

**Order: Siphonaptera**

**Family: Ceratophyllidae**

*Ceratophyllus gallinae* (Schrank, 1803)

*Ceratophyllus garei* (Rothschild, 1902)

*Dasypsyllus gallinulae* (Dale, 1878)

**PTG: Hematophagous mites**

**Order: Mesostigmata**

**Family: Dermanyssidae**

*Dermanyssus carpathicus* (Zeman, 1979)

*Dermanyssus longipes* (Berlese & Trouessart, 1889)

*Dermanyssus* sp. (Dugès, 1834)

**PTG: Parasitic flies<sup>2</sup>**

**Order: Diptera**

**Family: Calliphoridae**

*Protocalliphora azurea* (Fallen, 1817)

**Family: Carnidae**

Carnidae sp. (Newman, 1834)

**PTG: Ticks**

**Order: Ixodida**

**Family: Ixodidae**

*Ixodes arboricola* (Schulze & Schlotke, 1930)

*Ixodes frontalis* (Panzer, 1798)

*Ixodes ricinus* (Linnaeus, 1758)

**GUILD: Predators**

**PTG: Parasitoid wasps**

**Order: Hymenoptera**

**Family: Braconidae**

Braconidae sp. (Latreille, 1829)

**Family: Pteromalidae**

Pteromalidae sp. (Dalman, 1820)

*Nasonia* sp. (Ashmead, 1904)

*Nasonia vitripennis* (Walker, 1836)

**PTG: Predatory beetles**

**Order: Coleoptera**

**Family: Staphylinidae**

*Aleochara sparsa* (Heer, 1839)

*Atheta harwoodi* (Williams, 1930)

*Atheta nigricornis* (Thomson, 1852)

*Bisnius subuliformis* (Gravenhorst, 1802)

*Haploglossa villosula* (Stephens, 1832)

*Haploglossa* sp. (Kraatz, 1856)

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<sup>1</sup> Both flea adults and larvae were included in the PTG although their larvae stage is non-parasitic.

<sup>2</sup> Both *Protocalliphora* adults and larvae were included in the PTG although their adult stage is non-parasitic.

*Philonthus politus* (Linnaeus, 1758)  
*Tachinus bipustulatus* (Fabricius, 1793)

**Family: Histeridae**

*Gnathoncus buyssoni* (Auzat, 1917)  
*Gnathoncus* sp. (Jacquelin-Duval, 1858)

**Family: Carabidae**

*Dromius quadrimaculatus* (Linnaeus, 1758)

**Family: Coccinellidae**

Coccinellidae sp. (Latreille, 1807)

**Family: Trichogrammatidae**

*Trichogramma pretiosum* (Riley, 1879)

**PTG: Predatory mites**

**Order: Mesostigmata**

**Family: Laelaptidae**

Laelaptidae sp. (Berlese, 1892)  
*Androlaelaps casalis*<sup>3</sup>(Berlese, 1887)  
*Androlaelaps* sp. (Berlese, 1903)  
*Hypoaspis* sp. (G. Canestrini, 1884)

**Family: Macrochelidae**

Macrochelidae sp. (Vitzthum, 1930)  
*Macrocheles* sp. (Latreille, 1829)

**Family: Parasitidae**

*Poecilochirus* sp. (G. & R. Canestrini, 1882)

**Family: Uropodidae**

Uropodidae sp. (Kramer, 1881)

**Order: Prostigmata**

**Family: Anystidae**

Anystidae sp. (Oudemans, 1936)

**Family : Cheyletidae**

Cheyletidae sp. (Leach, 1815)  
*Cheyletus eruditus* (Schrank, 1781)

**Order: Trombidiformes**

**Family: Bdellidae**

Bdellidae sp. (Dugès, 1834)

**Family: Trombidiidae**

Trombidiidae sp. (Leach, 1815)

**GUILD: Detritivores**

**PTG: Storage mites**

**Order:Orbatida**

**Cohort: Astigmatina**

Astigmatina sp. (Canestrini, 1891)

**Family: Acaridae**

Acaridae sp. (Latreille, 1802)  
*Acarus siro* (Linnaeus, 1758)  
*Tyrophagus putrescentiae* (Schrank, 1781)

**Family: Glycyphagidae**

Glycyphagidae sp. (Berlese, 1887)  
*Glycyphagus domesticus* (De Geer, 1778)

**PTG: Scavenger flies**

**Order: Diptera**

**Family: Calliphoridae**

Calliphoridae sp. (Hough, 1899)

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<sup>3</sup> The trophic role of this mite in bird nests is much debated. However, as we observed no gut coloration indicating hematophagy in the *A. casalis* found in our nests, we assume their role to be predatory.

*Calliphora vicina* (Robineau-Desvoidy, 1830)  
*Lucilia ampullacea* (Villeneuve, 1922)  
*Lucilia sericata* (Meigen, 1826)  
*Lucilia* sp. (Robineau-Desvoidy, 1830)

**Family: Drosophilidae**

*Zaprionus vittiger* (Coquillett, 1902)

**Family: Heleomyzidae**

*Tephrochlamys rufiventris* (Meigen, 1830)  
*Tephrochlamys tarsalis* (Zetterstedt, 1847)

**Family: Muscidae**

Muscidae sp. (Latreille, 1802)  
*Fannia aequilineata* (Ringdahl, 1945)  
*Fannia* sp. (Robineau-Desvoidy, 1830)  
*Hydrotaea armipes* (Fallen, 1825)  
*Muscina prolapsa* (Harris, 1780)  
*Potamia littoralis* (Robineau-Desvoidy, 1830)

**Family: Phoridae**

*Megaselia longicostalis* (Wood, 1912)  
*Megaselia scalaris* (Loew, 1866)  
*Megaselia* sp. (Róndani, 1856)

**Family: Psychodidae**

Psychodidae sp. (Newman, 1834)

**Family: Sarcophagidae**

*Sarcophaga argyrostoma* (Robineau-Desvoidy, 1830)  
*Sarcophaga caerulescens* (Zetterstedt, 1838)  
*Sarcophaga pyrenaica* (Séguy, 1941)

**Family: Stratiomyidae**

*Microchrysa polita* (Linnaeus, 1758)

**Family: Syrphidae**

*Cheilosia rita* (Curran, 1922)

**PTG: Saprophagous beetles**

**Order: Coleoptera**

Coleoptera sp.

**Family: Cerylonidae**

*Cerylon* sp. (Latreille, 1802)

**Family: Corylophidae**

Corylophidae sp. (LeConte, 1852)  
*Orthoperus* sp. (Stephens, 1829)  
*Sericoderus lateralis* (Gyllenhal, 1827)

**Family: Cryptophagidae**

*Atomaria* sp. (Stephens, 1829)

**Family: Curculionidae**

Curculionidae sp. (Latreille, 1802)

**Family: Dermestidae**

Dermestidae sp. (Latreille, 1804)  
*Anthrenus pimpinellae* (Fabricius, 1775)  
*Dermestes undulatus* (Brahm, 1790)

**Family: Latridiidae**

*Dienerella clathrata* (Mannerheim, 1844)  
*Dienerella vincenti* (Curtis, 1830)

**Family: Leiodidae**

Leiodidae sp. (Fleming, 1821)  
*Catops* sp. (Paykull, 1798)  
*Sciodrepoides watsoni* (Spence, 1815)

**Family: Mycetophagidae**

*Litargus connexus* (Geoffroy, 1785)

**Family: Ptinidae**

*Ptinus fur* (Linnaeus, 1758)

**Family: Silphidae**

*Nicrophorus vespilloides* (Herbst, 1783)  
**Family: Tenebrionidae**  
*Nalassus laevicostriatus* (Goeze, 1777)

**PTG: Moths**

**Order: Lepidoptera**

Lepidoptera sp. (Linnaeus, 1758)

**Family: Oecophoridae**

*Hofmannophila pseudospretella* (Stainton, 1849)

**Family: Tineidae**

Tineidae sp. (Latreille, 1810)

**Guild: Others**

**PTG: Ants**

**Order: Hymenoptera**

**Family: Formicidae**

Formicidae sp. (Latreille, 1809)

*Lasius brunneus* (Latreille, 1798)

*Lasius niger* (Linnaeus, 1758)

**PTG: Beetle mites<sup>4</sup>**

**Order: Sarcoptiformes**

**Suborder: Oribatida**

Oribatida sp.

**Family: Achipteridae**

*Achipteria coleoprata* (Linnaeus, 1758)

*Achipteria* sp. (Berlese, 1885)

*Parachipteria punctata* (Nicolet, 1855)

**Family: Ameronothridae**

*Ameronothrus maculatus* (Michael, 1882)

**Family: Carabodidae**

*Carabodes coriaceus* (C.L. Koch, 1835)

*Carabodes labyrinthicus* (Michael, 1879)

*Odontocephus elongatus* (Michael, 1879)

**Family: Ceratozetidae**

*Melanozetes mollicomus* (C.L. Koch, 1839)

*Trichoribates trimaculatus* (C.L. Koch, 1836)

**Family: Chamobatidae**

*Chamobates pusillus* (Berlese, 1895)

**Family: Damaeidae**

*Kunstdamaeus* sp. [nidicola] (Willmann, 1936)

**Family: Galumnidae**

Galumnidae sp. (Jacot, 1925)

*Galumna* sp. (Heyden, 1826)

*Pilogalumna tenuiclava* (Berlese, 1908)

**Family: Hemileiidae**

*Dometorina plantivaga* (Berlese, 1895)

**Family: Humerobatidae**

*Humerobates rostromellatus* (Grandjean, 1936)

**Family: Hypochthoniidae**

*Hypochthonius rufulus* (C.L. Koch, 1835)

**Family: Liacaridae**

*Xenillus clypeator* (Robineau-Desvoidy, 1839)

*Xenillus* sp. (Robineau-Desvoidy, 1839)

*Xenillus tegeocranus* (Hermann, 1804)

**Family: Liebstadiidae**

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<sup>4</sup> Following the classification of Krantz & Walter (2009) "A manual of Acarology"

*Liebstadia similis* (Michael, 1888)

**Family: Malaconothridae**

Malaconothridae sp. (Berlese, 1916)

**Family: Micreremidae**

*Micreremus gracilior* (Willmann, 1931)

**Family: Nothridae**

Nothridae sp. (Berlese, 1896)

*Nothrus* sp. (C.L. Koch, 1836)

*Nothrus silvestris* (Nicolet, 1855)

**Family: Oribatellidae**

*Oribatella calcarata* (C.L. Koch, 1835)

*Oribatella quadricornuta* (Michael, 1880)

*Oribatula tibialis* (Nicolet, 1855)

**Family: Oribatulidae**

*Phauloppia lucorum* (C. L. Koch, 1841)

*Zygoribatula exilis* (Nicolet, 1855)

**Family: Phenopelopidae**

*Eupelops occultus* (C.L. Koch, 1835)

*Eupelops strenzkei* (Knülle, 1954)

**Family: Phthiracaridae**

Phthiracaridae sp. (Perty, 1841)

*Phthiracarus laevigatus* (C. L. Koch, 1841)

**Family: Punctoribatidae**

*Minunthozetes semirufus* (C. L. Koch, 1841)

**Family: Scheloribatidae**

*Hemileius initialis* (Berlese, 1908)

**Family: Scutoverticidae**

*Scutovertex sculptus* (Michael, 1879)

**Family: Tectocephidae**

*Tectocephus velatus* [sarekensis] (Trägårdh, 1910)

*Tectocephus velatus* [velatus] (Michael, 1880)

**PTG: Boolice**

**Order: Psocoptera**

Psocoptera sp.

**Family: Trogiidae**

Trogiidae sp. (Roesler, 1944)

**Family: Psoquillidae**

Psoquillidae sp. (Lienhard & Smithers, 2002)

**PTG: Earwigs**

**Order: Dermaptera**

Dermaptera sp. (De Geer, 1773)

**Family: Forficulidae**

Forficulidae sp. (Latreille, 1810)

*Forficula auricularia* (Linnaeus, 1758)

**PTG: Phytophagous Hemiptera**

**Order: Hemiptera**

Hemiptera sp. (Linnaeus, 1758)

**Family: Aphididae**

Aphididae sp. (Latreille, 1802)

**Family: Cicadellidae**

Cicadellidae sp. (Latreille, 1802)

**PTG: Spiders**

**Order: Araneae**

Araneae sp. (Clerck, 1757)

**Family: Araneidae**

*Araneus diadematus* (Clerck, 1758)

**Family: Clubionidae**

Clubionidae sp. (Wagner, 1887)

*Clubiona comta* (C. L. Koch, 1839)

*Clubiona similis* (L. Koch, 1867)

*Clubiona* sp. (Latreille, 1804)

*Clubiona subsultans* (Thorrell, 1875)

**Family: Philodromidae**

*Philodromus* sp. (Walckenaer, 1826)

**Family: Tetragnathidae**

*Meta* sp. (C. L. Koch, 1836)

**Family: Thomisidae**

*Ozyptila praticola* (C. L. Koch, 1837)

**PTG: Springtails**

**Order: Entomobryomorpha**

Entomobryomorpha sp.

**Family: Entomobryidae**

*Entomobrya albocincta* (Templeton, 1835)

*Entomobrya nivalis* (Linnaeus, 1758)

*Willowsia platani* (Nicolet, 1842)

**Family: Tomoceridae**

*Tomocerus vulgaris* (Tullberg, 1871)

**Order: Poduromorpha**

Poduromorpha sp.

**Order: Symphypleona**

Symphypleona sp.

**Online resource 2** Total percentage occurrence, and occurrence, mean, maximum and median (0's excluded) abundances of PTG's by plot scale urbanization levels

| PTG  | Guild                  | ALL    | RURAL  |       |      | SEMI-URBAN |        |       |      | URBAN |        |       |      |     |
|--|------------------------|--------|--------|-------|------|------------|--------|-------|------|-------|--------|-------|------|-----|
|  |                        | Occ(%) | Occ(%) | Mean  | Max  | Med        | Occ(%) | Mean  | Max  | Med   | Occ(%) | Mean  | Max  | Med |
| <b>Parasites: 81% of all arthropods</b>          |                        |        |        |       |      |            |        |       |      |       |        |       |      |     |
|  | Fleas                  | 91.4   | 94.9   | 640.0 | 3990 | 459        | 90.0   | 612.0 | 3310 | 293   | 89.2   | 743.0 | 7039 | 471 |
|  | Hematophagous mites    | 74.2   | 81.4   | 175.0 | 1746 | 67.5       | 69.4   | 27.9  | 568  | 5     | 72.3   | 182.0 | 3617 | 11  |
|  | Parasitic flies        | 31.2   | 28.8   | 1.8   | 23   | 3          | 19.4   | 1.0   | 9    | 5     | 44.6   | 4.8   | 38   | 7   |
|  | Ticks                  | 13.4   | 27.1   | 0.5   | 7    | 1          | 9.7    | 0.1   | 1    | 1     | 4.6    | 0.05  | 1    | 1   |
| <b>Predators: 6% of all arthropods</b>           |                        |        |        |       |      |            |        |       |      |       |        |       |      |     |
|  | Predatory beetles      | 75.8   | 72.9   | 24.9  | 285  | 18         | 82.3   | 69.0  | 926  | 17    | 72.3   | 28.8  | 650  | 11  |
|  | Predatory mites        | 48.4   | 50.8   | 10.7  | 183  | 8.5        | 45.2   | 12.2  | 301  | 4.5   | 49.2   | 32.2  | 1244 | 4.5 |
|  | Wasps                  | 18.8   | 18.6   | 0.30  | 6    | 1          | 19.4   | 5.3   | 167  | 1     | 18.5   | 3.9   | 164  | 1   |
| <b>Detritivores: 12% of all arthropods</b>       |                        |        |        |       |      |            |        |       |      |       |        |       |      |     |
|  | Scavenger flies        | 58.6   | 47.5   | 13.9  | 234  | 10         | 58.1   | 50.7  | 589  | 50    | 69.2   | 26.1  | 205  | 15  |
|  | Storage mites          | 36.0   | 35.6   | 43.7  | 2000 | 4          | 32.3   | 87.9  | 2210 | 62.5  | 40.0   | 131.0 | 4000 | 10  |
|  | Saphrophagous beetles  | 28.5   | 39     | 2.7   | 42   | 3          | 30.6   | 1.1   | 29   | 1     | 16.9   | 0.3   | 5    | 1   |
|  | Moths                  | 8.2    | 15.3   | 0.2   | 4    | 1          | 1.6    | 0.2   | 9    | 9     | 7.7    | 0.5   | 14   | 3   |
| <b>Accidental visitors: 1% of all arthropods</b> |                        |        |        |       |      |            |        |       |      |       |        |       |      |     |
|  | Beetle mites           | 71.5   | 69.5   | 2.2   | 12   | 2          | 69.4   | 2.5   | 42   | 2     | 75.4   | 3.0   | 30   | 3   |
|  | Phytophagous hemiptera | 19.9   | 16.9   | 0.7   | 26   | 1          | 14.5   | 0.3   | 6    | 1     | 27.7   | 3.6   | 122  | 2   |
|  | Spiders                | 12.9   | 11.9   | 0.1   | 1    | 1          | 11.3   | 0.2   | 5    | 1     | 15.4   | 0.4   | 8    | 2   |
|  | Springtails            | 12.4   | 18.6   | 0.7   | 10   | 2          | 6.5    | 0.2   | 6    | 1.5   | 12.3   | 2.1   | 124  | 1   |
|  | Booklice               | 9.2    | 5.1    | 0.4   | 20   | 2          | 6.5    | 0.2   | 8    | 2     | 15.4   | 1.5   | 50   | 3.5 |
|  | Earwigs                | 9.1    | 15.3   | 1.0   | 31   | 3          | 3.2    | 0.3   | 19   | 10    | 9.2    | 1.6   | 80   | 2   |
|  | Ants                   | 8.1    | 5.1    | 0.2   | 5    | 4          | 9.7    | 0.6   | 29   | 1.5   | 9.2    | 1.0   | 32   | 4   |



### Online resource 3

Set of models with  $\Delta\text{AICc}$  within 2 of best model, and estimates of best models are presented in table 1 and 2, respectively, for occurrence data, and table 3 and 4, respectively, for Shannon diversity, richness and PTG abundance data.

**Table 1** Competitive models of the occurrence of PTGs, with  $\Delta\text{AICc}$  (Akaike information criterion with modifications for small samples sizes) within 2 of best model, presented with models main effect(s), degrees of freedom and loglikelihood as well as  $\text{AICc}$ .

| Response variable      | Model            | df       | logLik         | AICc          |
|------------------------|------------------|----------|----------------|---------------|
| Flea                   | Null             | 3        | <b>-54.04</b>  | <b>114.22</b> |
|                        | HNB              | 4        | -53.71         | 115.64        |
|                        | Year             | 4        | -53.74         | 115.7         |
|                        | Sub              | 5        | -52.84         | 116.02        |
| Hematophagous mite     | <b>HNB</b>       | <b>4</b> | <b>-101.63</b> | <b>211.48</b> |
|                        | Year+HNB         | 5        | -101.44        | 213.21        |
|                        | Null             | 3        | -103.63        | 213.38        |
| Parasitic diptera      | Year             | 4        | -107.43        | 223.08        |
|                        | Plot+Year        | 6        | -105.48        | 223.42        |
|                        | <b>Null</b>      | <b>3</b> | <b>-108.76</b> | <b>223.66</b> |
|                        | Year+HNB         | 5        | -106.78        | 223.89        |
|                        | Plot             | 5        | -106.83        | 223.99        |
|                        | Plot+Year+HNB    | 7        | -105.03        | 224.69        |
| Tick                   | <b>Plot+Year</b> | <b>6</b> | <b>-61.17</b>  | <b>134.81</b> |
| Predatory beetle       | <b>Sub</b>       | <b>5</b> | <b>-91.9</b>   | <b>194.13</b> |
|                        | Sub+HNB          | 6        | -91.53         | 195.53        |
|                        | Sub+Year         | 6        | -91.68         | 195.83        |
| Predatory mite         | <b>Null</b>      | <b>3</b> | <b>-128.83</b> | <b>263.79</b> |
|                        | HNB              | 4        | -128.24        | 264.69        |
| Wasp                   | <b>Year</b>      | <b>4</b> | <b>-87.59</b>  | <b>183.39</b> |
|                        | Sub+Year         | 6        | -86.28         | 185.02        |
| Scavenger fly          | <b>Null</b>      | <b>3</b> | <b>-117.54</b> | <b>241.2</b>  |
|                        | Year             | 4        | -116.9         | 242.02        |
|                        | Plot             | 5        | -115.96        | 242.25        |
|                        | Sub+Year         | 6        | -114.94        | 242.35        |
|                        | Sub              | 5        | -116.14        | 242.61        |
|                        | HNB              | 4        | -117.43        | 243.09        |
|                        | Plot+Year        | 6        | -115.35        | 243.17        |
| Storage mite           | Sub+HNB          | 6        | -113.35        | 239.17        |
|                        | <b>Sub</b>       | <b>5</b> | <b>-115.14</b> | <b>240.61</b> |
| Saprophagous beetle    | <b>Plot+HNB</b>  | <b>6</b> | <b>-106.62</b> | <b>225.7</b>  |
|                        | Plot+Year+HNB    | 7        | -106.42        | 227.46        |
| Moth                   | <b>Null</b>      | <b>3</b> | <b>-45.87</b>  | <b>97.87</b>  |
|                        | Year             | 4        | -45.69         | 99.6          |
| Beetle mite            | <b>Null</b>      | <b>3</b> | <b>-111.15</b> | <b>228.43</b> |
|                        | Year             | 4        | -110.63        | 229.49        |
|                        | HNB              | 4        | -110.94        | 230.11        |
| Phytophagous hemiptera | <b>Year</b>      | <b>4</b> | <b>-89.56</b>  | <b>187.34</b> |
|                        | Plot+Year        | 6        | -87.51         | 187.5         |
|                        | Plot*Sub+Year    | 12       | -81.62         | 189.03        |

| <b>(Cont.)</b>           |               |           |               |               |
|--------------------------|---------------|-----------|---------------|---------------|
| <b>Response variable</b> | <b>Model</b>  | <b>df</b> | <b>logLik</b> | <b>AICc</b>   |
| <b>Spider</b>            | <b>Null</b>   | <b>3</b>  | <b>-71.14</b> | <b>148.41</b> |
|                          | HNB           | 4         | -70.26        | 148.74        |
|                          | Year+HNB      | 5         | -69.58        | 149.49        |
|                          | Year          | 4         | -70.92        | 150.06        |
| <b>Springtail</b>        | Sub           | 5         | -63.89        | 138.1         |
|                          | Sub+HNB       | 6         | -63.16        | 138.8         |
|                          | Plot+Sub      | 7         | -62.25        | 139.13        |
|                          | Plot*Sub+HNB  | 12        | -56.78        | 139.36        |
|                          | HNB           | 4         | -65.82        | 139.85        |
|                          | <b>Null</b>   | <b>3</b>  | <b>-66.96</b> | <b>140.04</b> |
| <b>Earwig</b>            | <b>Null</b>   | <b>3</b>  | <b>-54.56</b> | <b>115.25</b> |
|                          | Sub           | 5         | -52.74        | 115.81        |
|                          | Sub+Year      | 6         | -51.74        | 115.95        |
|                          | Plot          | 5         | -52.85        | 116.02        |
|                          | Year          | 4         | -54.1         | 116.42        |
|                          | Plot+Sub+Year | 8         | -49.84        | 116.5         |
|                          | Plot+Sub      | 7         | -50.95        | 116.53        |
|                          | HNB           | 4         | -54.34        | 116.9         |
|                          | Sub+Year+HNB  | 7         | -51.24        | 117.11        |
|                          | Plot+Year     | 6         | -52.32        | 117.11        |
| <b>Booklouse</b>         | <b>Null</b>   | <b>3</b>  | <b>-48.76</b> | <b>103.65</b> |
|                          | HNB           | 4         | -48.39        | 105           |
|                          | Year          | 4         | -48.69        | 105.61        |
| <b>Ant*</b>              | <b>Sub</b>    | <b>5</b>  | <b>-48.58</b> | <b>107.49</b> |
|                          | <b>Year</b>   | <b>4</b>  | <b>-49.79</b> | <b>107.79</b> |
|                          | <b>HNB</b>    | <b>4</b>  | <b>-49.95</b> | <b>108.12</b> |
|                          | Sub+Year      | 6         | -48.33        | 109.12        |

\*No top model was selected because the set of models included different single main effects, and were not nested, but within 2 units of AICc from each other.

**Table 2** Estimates, standard errors and significance of predictor levels in 'best' models of PTG occurrences. Significance indicated by asterisk: 0 '\*\*\*' 0.0001 '\*\*' 0.001 '\*' 0.0027 '.' 0.05 'NS' 1

| <b>Response variable</b>      | <b>Model</b> | <b>Predictor level</b> | <b>Estimate</b> | <b>Std. Error</b> | <b>Sign.</b> |
|-------------------------------|--------------|------------------------|-----------------|-------------------|--------------|
| <b>Flea</b>                   | Null         | Intercept              | 2.870           | 0.665             | ***          |
| <b>Hematophagous mite</b>     | HNB          | Intercept              | 1.511           | 0.299             | ***          |
|                               |              | HNB: Yes               | -0.848          | 0.420             | .            |
| <b>Parasitic fly</b>          | Null         | Intercept              | -1.146          | 0.354             | *            |
| <b>Tick</b>                   | Plot + Year  | Intercept              | -0.443          | 0.337             | NS           |
|                               |              | Plot: SEMI-URBAN       | -1.292          | 0.537             | .            |
|                               |              | Plot: URBAN            | -2.138          | 0.674             | *            |
|                               |              | Year: 2015             | -1.667          | 0.585             | .            |
| <b>Predatory beetle</b>       | Sub          | Intercept              | 0.382           | 0.436             | NS           |
|                               |              | Sub: Rural             | 1.853           | 0.661             | .            |
|                               |              | Sub: Semi-urban        | 1.457           | 0.626             | .            |
| <b>Predatory mite</b>         | Null         | Intercept              | -0.065          | 0.147             | NS           |
| <b>Wasp</b>                   | Year         | Intercept              | -1.872          | 0.287             | ***          |
|                               |              | Year: 2015             | 0.822           | 0.383             | .            |
| <b>Scavenger fly</b>          | Null         | Intercept              | 0.375           | 0.300             | NS           |
| <b>Storage mite</b>           | Sub          | Intercept              | 0.143           | 0.268             | NS           |
|                               |              | Sub: Rural             | -1.396          | 0.405             | **           |
|                               |              | Sub: Semi-urban        | -0.792          | 0.372             | .            |
| <b>Saprophagous beetle</b>    | Plot + HNB   | Intercept              | -0.595          | 0.284             | .            |
|                               |              | Plot: SEMI-URBAN       | -0.308          | 0.390             | NS           |
|                               |              | Plot: URBAN            | -1.393          | 0.462             | *            |
|                               |              | HNB: Yes               | 0.752           | 0.374             | .            |
| <b>Moth</b>                   | Null         | Intercept              | -7.149          | 1.673             | ***          |
| <b>Beetle mite</b>            | Null         | Intercept              | 0.920           | 0.162             | ***          |
| <b>Phytophagous hemiptera</b> | Year         | Intercept              | -1.872          | 0.287             | ***          |
|                               |              | Year: 2015             | 0.947           | 0.378             | .            |
| <b>Spider</b>                 | Null         | Intercept              | -2.135          | 0.382             | ***          |
| <b>Springtail</b>             | Null         | Intercept              | -3.103          | 1.245             | .            |
| <b>Earwig</b>                 | Null         | Intercept              | -2.944          | 0.628             | ***          |
| <b>Booklouse</b>              | Null         | Intercept              | -7.855          | 1.664             | ***          |

**Table 3** Competitive models of Shannon diversity, richness and PTG abundances, with  $\Delta\text{AICc}$  (Akaike information criterion with modifications for small samples sizes) within 2 of best model, presented with models main effect(s), degrees of freedom and loglikelihood as well as AICc.

| <b>Response variable</b>   | <b>Model</b>       | <b>df</b> | <b>logLik</b>   | <b>AICc</b>    |
|----------------------------|--------------------|-----------|-----------------|----------------|
| <b>Shannon diversity</b>   | <b>Year</b>        | <b>5</b>  | <b>-94.53</b>   | <b>199.39</b>  |
| <b>Richness</b>            | <b>Null</b>        | <b>3</b>  | <b>-405.43</b>  | <b>816.99</b>  |
|                            | Year               | 4         | -404.87         | 817.97         |
|                            | Plot               | 5         | -403.82         | 817.98         |
|                            | HNB                | 4         | -405.30         | 818.82         |
|                            | Plot + Year        | 6         | -403.22         | 818.91         |
| <b>Flea</b>                | Sub + Year         | 7         | -1272.69        | 2560.01        |
|                            | <b>Year</b>        | <b>5</b>  | <b>-1275.31</b> | <b>2560.95</b> |
| <b>Hematophagous mite</b>  | Plot + Sub         | 8         | -796.27         | 1609.36        |
|                            | <b>Plot</b>        | <b>6</b>  | <b>-799.26</b>  | <b>1611.00</b> |
|                            | Plot + Sub + Year  | 9         | -796.11         | 1611.25        |
|                            | Plot + Sub + HNB   | 9         | -796.16         | 1611.35        |
| <b>Parasitic fly</b>       | <b>Null</b>        | <b>4</b>  | <b>-290.92</b>  | <b>590.07</b>  |
|                            | Plot               | 6         | -288.84         | 590.15         |
|                            | Year               | 5         | -289.92         | 590.18         |
|                            | Plot + Year        | 7         | -287.80         | 590.24         |
|                            | Year + HNB         | 6         | -289.37         | 591.21         |
|                            | Plot + Year + HNB  | 8         | -287.49         | 591.80         |
|                            | HNB                | 5         | -290.80         | 591.93         |
| <b>Tick</b>                | <b>Plot + Year</b> | <b>7</b>  | <b>-84.41</b>   | <b>183.44</b>  |
| <b>Predatory beetle</b>    | <b>Sub</b>         | <b>6</b>  | <b>-718.47</b>  | <b>1449.41</b> |
|                            | Sub + HNB          | 7         | -718.28         | 1451.18        |
|                            | Sub + Year         | 7         | -718.30         | 1451.23        |
|                            | Plot + Sub         | 8         | -717.22         | 1451.26        |
| <b>Predatory mite</b>      | <b>HNB</b>         | <b>5</b>  | <b>-471.45</b>  | <b>953.23</b>  |
|                            | Sub + HNB          | 7         | -470.09         | 954.81         |
| <b>Wasp</b>                | <b>HNB</b>         | <b>5</b>  | <b>-457.34</b>  | <b>925.02</b>  |
| <b>Scavenger fly</b>       | Sub                | 6         | -610.89         | 1234.24        |
|                            | <b>Null</b>        | <b>4</b>  | <b>-613.02</b>  | <b>1234.27</b> |
|                            | Plot               | 6         | -611.51         | 1235.50        |
|                            | Plot + Sub         | 8         | -609.46         | 1235.73        |
|                            | Sub + Year         | 7         | -610.76         | 1236.16        |
| <b>Storage mite</b>        | <b>Sub</b>         | <b>6</b>  | <b>-438.91</b>  | <b>890.29</b>  |
|                            | Sub + HNB          | 7         | -438.71         | 892.04         |
|                            | Sub + Year         | 7         | -438.82         | 892.26         |
| <b>Saprophagous beetle</b> | Plot + HNB         | 7         | -204.16         | 422.94         |
|                            | Plot + Year + HNB  | 8         | -203.43         | 423.67         |
|                            | Plot               | 6         | -205.77         | 424.02         |
| <b>Moth</b>                | Plot + Year        | 7         | -74.63          | 163.89         |
|                            | <b>Plot</b>        | <b>6</b>  | <b>-76.04</b>   | <b>164.54</b>  |
|                            | Plot + Year + HNB  | 8         | -74.51          | 165.84         |
| <b>Beetle mite</b>         | <b>Null</b>        | <b>4</b>  | <b>-388.71</b>  | <b>785.65</b>  |
|                            | Plot               | 6         | -387.55         | 787.56         |

| (Cont.)                |                    |          |                |               |
|------------------------|--------------------|----------|----------------|---------------|
| Response variable      | Model              | df       | logLik         | AICc          |
| Phytophagous hemiptera | Plot               | 6        | -169.21        | 350.88        |
|                        | HNB                | 5        | -170.34        | 351.02        |
|                        | Plot + HNB         | 7        | -168.21        | 351.06        |
|                        | <b>Null</b>        | <b>4</b> | <b>-172.09</b> | <b>352.41</b> |
| Spider                 | Year + HNB         | 6        | -100.30        | 213.07        |
|                        | <b>Null</b>        | <b>4</b> | <b>-102.84</b> | <b>213.90</b> |
|                        | Plot + Year + HNB  | 8        | -98.59         | 213.99        |
|                        | HNB                | 5        | -101.85        | 214.04        |
|                        | Plot + HNB         | 7        | -99.73         | 214.10        |
|                        | Year               | 5        | -101.99        | 214.30        |
| Springtail*            | Sub + HNB          | 7        | -110.33        | 235.29        |
|                        | <b>HNB</b>         | <b>5</b> | <b>-112.70</b> | <b>235.74</b> |
|                        | <b>Sub</b>         | <b>6</b> | <b>-112.09</b> | <b>236.64</b> |
| Earwig                 | <b>Null</b>        | <b>5</b> | <b>-93.35</b>  | <b>197.04</b> |
|                        | HNB                | 6        | -92.79         | 198.04        |
| Booklouse              | Sub + HNB          | 7        | -93.92         | 202.47        |
|                        | Sub + Year + HNB   | 8        | -93.27         | 203.35        |
|                        | <b>HNB</b>         | <b>5</b> | <b>-96.68</b>  | <b>203.70</b> |
| Ant*                   | <b>Year + HNB</b>  | <b>7</b> | <b>-83.99</b>  | <b>182.60</b> |
|                        | <b>Plot + Year</b> | <b>8</b> | <b>-83.83</b>  | <b>184.46</b> |

\* No top model was selected because the set of models included different single or additive main effects and were not nested, but within 2 units of AICc from each other.

**Table 4** Estimates, standard errors and significance of predictor levels in 'best' models of Shannon diversity, richness and PTG abundances. Significance indicated by asterisk: 0 '\*\*\*\*' 0.0001 '\*\*' 0.001 '\*' 0.0027 '.' 0.05 'NS' 1

| <b>Response variable</b>      | <b>Model</b> | <b>Predictor level</b> | <b>Estimate</b> | <b>Std. Error</b> | <b>Sign.</b> |
|-------------------------------|--------------|------------------------|-----------------|-------------------|--------------|
| <b>Shannon diversity</b>      | Year         | Intercept              | 0.746           | 0.040             | ***          |
|                               |              | Year: 2015             | -0.151          | 0.060             | .            |
| <b>Richness</b>               | Null         | Intercept              | 1.838           | 0.029             | ***          |
| <b>Flea</b>                   | Year         | Intercept              | 6.107           | 0.160             | ***          |
|                               |              | Year: 2015             | 0.520           | 0.167             | *            |
| <b>Hematophagous mite</b>     | Plot         | Intercept              | 2.723           | 0.4493            | ***          |
|                               |              | Plot: RURAL            | 2.0058          | 0.6205            | *            |
|                               |              | Plot: URBAN            | 1.4686          | 0.6131            | .            |
| <b>Parasitic fly</b>          | Null         | Intercept              | 0.418           | 0.330             | NS           |
| <b>Tick</b>                   | Plot + Year  | Intercept              | -0.253          | 0.402             | NS           |
|                               |              | Plot: SEMI-URBAN       | -1.754          | 0.557             | *            |
|                               |              | Plot: URBAN            | -2.492          | 0.689             | **           |
|                               |              | Year: 2015             | -1.579          | 0.539             | .            |
| <b>Predatory beetle</b>       | Sub          | Intercept              | 1.671           | 0.400             | ***          |
|                               |              | Sub: Rural             | 2.099           | 0.456             | ***          |
|                               |              | Sub: Semi-urban        | 1.105           | 0.448             | .            |
| <b>Predatory mite</b>         | HNB          | Intercept              | 2.052           | 0.265             | ***          |
|                               |              | HNB: Yes               | 1.389           | 0.520             | .            |
| <b>Wasp</b>                   | HNB          | Intercept              | -1.153          | 0.616             | NS           |
|                               |              | HNB: Yes               | 0.940           | 0.844             | NS           |
| <b>Scavenger fly</b>          | Null         | Intercept              | 2.839           | 0.261             | ***          |
| <b>Storage mite</b>           | Sub          | Intercept              | 1.498           | 0.923             | NS           |
|                               |              | Sub: Semi-urban        | 3.130           | 0.864             | **           |
|                               |              | Sub: Urban             | 2.190           | 0.888             | .            |
| <b>Saprophagopus beetle</b>   | Plot         | Intercept              | -1.567          | 0.442             | **           |
|                               |              | Plot: RURAL            | 2.094           | 0.550             | **           |
|                               |              | Plot: SEMI-URBAN       | 1.267           | 0.564             | .            |
| <b>Moth</b>                   | Plot         | Intercept              | -6.174          | 1.744             | **           |
|                               |              | Plot: SEMI-URBAN       | -1.919          | 2.135             | NS           |
|                               |              | Plot: URBAN            | -0.512          | 1.613             | NS           |
| <b>Beetle mite</b>            | Null         | Intercept              | 0.837           | 0.110             | ***          |
| <b>Phytophagous hemiptera</b> | Null         | Intercept              | -0.669          | 0.403             | NS           |
| <b>Spider</b>                 | Null         | Intercept              | -1.651          | 0.445             | **           |
| <b>Earwig</b>                 | Null         | Intercept              | -0.725          | 0.737             | NS           |
| <b>Booklouse</b>              | HNB          | Intercept              | -2.502          | 0.817             | *            |
|                               |              | HNB: Yes               | 1.544           | 0.682             | .            |