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RESEARCH

Older urban forest fragments support parasitoid wasp spillover into adjacent landscapes

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Abstract

Urban reforestation programs seek to offset the detrimental effects of urbanization on tree cover and associated ecosystem services. One understudied ecosystem service that urban forests may provide is biological control of insect pests in adjacent managed landscapes by providing habitat for natural enemy arthropods. As forest fragments mature, ecosystem services such as biological control may accrue within fragments and in adjacent landscapes. We measured arthropod natural enemy abundance within and surrounding 20 urban forest fragments in Lexington, Kentucky, USA, that were each planted between 1999 and 2019, representing a 20-year chronosequence. We collected natural enemies at three locations within fragments and at 0, 5, and 10 m away from fragment edges using yellow pan traps. We also measured fragment size and impervious surface cover surrounding each fragment at a 100 m and 1000 m radius. Fragment size and surrounding impervious cover did not influence natural enemy abundance within or outside fragments. Parasitoid wasp spillover was higher outside of older relative to newer fragments while no other natural enemy group was affected by forest age either inside or outside fragments. Natural enemy abundance was greater outside fragments relative to the interior, and natural enemy abundances were similar at edges and 10 m away from edges in adjacent lawns or meadows. Our findings indicate that reforestation in urban areas can support natural enemy spillover to adjacent landscapes and this effect appears to increase over time since establishment. Urban forest fragments may reduce the severity of pest outbreaks in adjacent managed landscapes.

Keywords Urban forest · Natural enemy · Biological control · Spillover · Parasitoid

Introduction

Creating and maintaining urban forests is necessary for conserving wildlife and ecosystem services in the face of increasing urbanization. Urban landcover worldwide increased by 1 million km^2 between 1992 and 2018 (Radwan et al. 2021), and urban land expansion is a major driver of deforestation (Radwan et al. 2021; Clement et al. 2015; Nowak and Greenfield 2020). Forests within urban matrices are typically fragmented (e.g. Porter et al. 2001) and dominated by invasive plant species (e.g. Blood et al. 2016; Londe et al. 2017), however, they provide numerous ecosystem services such as pollution and temperature reduction, carbon sequestration, flood control, and recreation opportunities while providing habitat for wildlife (Escobedo et al. 2011; Weissert et al. 2014; Medina Camarena et al. 2022; Arnberger 2006; O'Brien et al. 2022; Ziter et al. 2019). Trees in urban forest fragments may provide additional unrealized ecosystem services for humans such as supporting populations of arthropod natural enemies that regulate pests found within urban landscapes. For example, Hanks and Denno (1993) found that the increased natural enemy diversity found within forests relative to landscape trees was associated with increased predation and lower incidence of white peach scale (*Pseudaulacaspis pentagona* Targioni Tozzetti) on mulberry trees. Whether or not natural enemies spillover from forest fragments into adjacent landscapes is unclear, but if such effects occur, forest fragments may function analogously to hedgerows in agroecosystems which support natural enemy spillover, and biological control of pests

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in nearby crops (e.g. Rand et al. 2006; Inclan et al. 2015; González et al. 2015).

The natural enemy communities supported by forest fragments likely regulate common pests in urban landscapes. Natural enemy abundance and/or diversity in unmanaged forest trees in woodlots is typically higher relative to nearby planted urban landscape trees which can correlate with reduced pest density or increased biological control (Hanks and Denno 1993, Tooker and Hanks 2000; Garcia et al. 2022). Common natural enemies that have been recorded as more prevalent in unmanaged forest trees relative to planted urban landscape trees include parasitoid wasps, ladybeetles, lacewing larvae, spiders, harvestmen, and earwigs (Hanks and Denno 1993; Tooker and Hanks 2000; Sobek et al. 2009; Serée et al. 2020; Prieto-Benitez and Mendez, 2011; Stašiov et al. 2021). There are many different urban landscape pests which might be managed by these natural enemies. For example, scale insects are pests on landscape trees surrounded by impervious surfaces and limited vegetation cover (Dale and Frank 2014; Wilson et al. 2023). However, parasitoid wasps, lady beetles, lacewing larvae, and spiders can all regulate scale populations (e.g., Golan et al. 2023; Kapranas and Tena 2015; Hodek and Honek 2009, Miller et al. 2004; Wilson and Frank 2023). Similarly, common shrub pests such as lace bugs are killed by spiders, earwigs, and parasitoids (Balsdon et al. 1996; Shrewsbury and Raupp 2006). Turfgrass lawns comprise as much as 160,000 km^2 across the United States alone (Milesi et al. 2005) and certain pests such as fall armyworm, Japanese beetle larvae, and chinch bugs are common pests of turfgrass (Potter and Braman 1991). Fall armyworm is attacked by a diverse array of natural enemies including dipteran and hymenopteran parasitoids, ants, and earwigs (Canas and O'Neill 1998, Sisay et al. 2018; Abang et al. 2021). *Tiphia* spp. wasps are introduced parasitoids that can parasitize 33–58% of beetle grubs in turfgrass lawns (Rogers and Potter 2004). Finally, chinch bugs are consumed by big-eyed bugs, parasitoid wasps, damsel bugs, minute pirate bugs, ants, spiders, assassin bugs, and earwigs (Reinert 1978; Carstens et al. 2008). Spillover of natural enemy taxa supported by urban forest fragments could therefore potentially regulate many important pests of urban landscapes.

Resources such as supplemental prey, floral resources, or nesting habitat can attract natural enemies and result in greater biological control of pests (Gurr et al. 2017), and urban forest fragments likely provide these resources. For example, maintaining flowering plants adjacent to pest infested shrubs can increase parasitism of evergreen bagworm [*Thyridopteryx ephemeraeformis* (Haworth)] (Ellis et al. 2005) but had inconsistent effects on euonymus scale [*Unaspis euonymi* (Comstock)] (Rebek et al. 2005). Shrewsbury and Raupp (2000, 2006) found that azalea shrubs surrounded by complex vegetation cover hosted greater natural enemy abundance and fewer azalea lace bugs [*Stephanitis pyrioides* (Scott)] relative to shrubs with limited surrounding vegetation cover. These effects were linked to shade produced by tall trees and predation resulting from ghost spiders [*Anyphaena celer* (Hentz)] supported by greater vegetation complexity (Shrewsbury and Raupp 2000, 2006). It is unclear if urban plants closer to forest fragments are visited more frequently by natural enemies due to spillover, and if such plants host fewer pests due to increased biological control. For example, Long et al. 2019 found that gloomy scales [*Melanaspis tenebricosa* (Comstock)], a common red maple pest, were least abundant on forest fragment trees, in comparison to forest edge trees and street trees, but that these effects were best explained by heat island effects on scale fitness instead of the activity of scale parasitoids. In contrast, Long and Frank 2020 found greater caterpillar abundance in forest fragment trees compared to street trees and that biological control services provided by birds were highest in street trees compared to forest trees. These studies suggest that while forest fragments can aid in regulation of nearby pests, these effects vary across pest taxa and are not always attributable to natural enemy activity.

The age of forest fragments may influence their suitability as habitat for natural enemies and the degree to which spillover occurs from these fragments into adjacent landscapes. Sena et al. (2023) reported substantial shifts in plant communities in an urban forest chronosequence as planted trees grew, established a canopy, and shaded out shade-intolerant plants. While species diversity did not necessarily increase with forest age in these parks, planted forests developed vertical forest structure over time, increasing structural complexity in overstory and midstory layers. Vegetation structural complexity supports natural enemy abundance through multiple mechanisms such as by reducing intraguild predation and by increasing the availability of supplemental resources (Langellotto and Denno 2004). In a chronosequence analysis of developing urban forest patches in New Zealand, Wallace et al. (2022) reported thresholds in some aspects of ecosystem structure and function around 10–11 years after planting, including shifts in litter cover, native tree seedling abundance, and canopy openness. While these aspects of forest growth are typical of forest development in general, successional processes in urban forest fragments may be limited by seed sources and invasive species (Ettinger et al. 2017; Clements and Bierzychudek 2017; Sena et al. 2021, 2023; Oldfield et al. 2018), and factors such as site suitability and pollution may further constrain forest development in such patches (Hilbert et al. 2019; Doroski et al. 2018). Given major shifts in plant community structure over time since planting, we anticipate that forest age will play a key role in structuring habitat suitability for

natural enemies, but the degree to which forest age will be further modified by site factors and plant species composition is not well understood.

Ecosystem service delivery from forest fragments further depends on patch size, structure, and connectivity (Gaublomme et al. 2008; Burkman and Gardiner 2014; Kang et al. 2015; Parsons and Frank 2019; Doroski et al. 2021). For example, Garcia et al. (2022) found greater abundance of herbivorous insects and natural enemies in monospecific forest patches than isolated trees. Similarly, Burks and Philpott (2017) found that parasitoids were positively associated with urban garden size. Generally, larger forest patches with more diverse plant communities support more diverse natural enemy communities (Burkman and Gardiner 2014; Jordani et al. 2015). Furthermore, Barr et al. (2021) found that spatial connectivity of habitat patches was a key factor structuring herbivorous insect communities in an urban forest, and Peng et al. (2020) reported that human structures may limit arthropod dispersal, particularly for nonflying taxa. Thus, in a landscape context, we anticipate that larger forest patches and well-connected patches will support more diverse and abundant natural enemy communities than smaller and more isolated patches.

One dominant feature in all urban landscapes is widespread impervious surface cover (Arnold and Gibbons 1996; Nowak and Greenfield 2020). Impervious surface cover is an effective proxy for heat island effects, habitat fragmentation, soil compaction, and increased runoff (Weng and Lu 2008; Miller et al. 2014; Ziter et al. 2019). Impervious surface area can also be an effective predictor for effects of urban development on plant communities. For example, Yan et al. (2019) found that impervious surface area exceeding 40% was associated with decreased plant diversity and increased importance of non-native species. The extent and intensity of impervious surface cover surrounding an urban forest fragment may be a useful proxy for the effect of urban development on the taxa found within forest fragments as well as those which disperse from fragments to nearby landscapes (Parsons and Frank 2019). For example, Parker et al. (2020) reported decreased native and exotic lady beetle abundance in vacant lots surrounded by greater impervious surface area, and Korányi et al. (2021) found that aphid abundance was positively associated, and predatory arthropods were negatively associated, with impervious surface area. Parsons and Frank (2019) also found greater aphid abundance in crape myrtles when surrounded by extensive impervious surface area, but noted that local landscape complexity can buffer this effect on natural enemy abundance.

In this study we examined the effects of forest age, size, and surrounding impervious surface cover on spillover of natural enemies from forests into adjacent urban landscapes. We did this work on reforested fragments located in city parks in central Kentucky. Our goal was to determine if reforested fragments support natural enemy spillover into adjacent landscapes and what factors mediate these effects.

Methods

We collected arthropods from 20 different forest fragments located within 12 parks in Lexington, Kentucky between June 16th −26th, 2024 (Fig. S1). In 13 planting periods, plantings were spread across more than one fragment located within the same park, while in seven planting periods, plantings occurred within one fragment in one park (Table 1). All fragments were planted from 1999 to 2019; with one park representing each year except 2015. Fragments were established in city parks as part of Reforest the Bluegrass (RTB), an annual community reforestation event initiated in 1999 and coordinated by the Lexington-Fayette Urban County Government (LFUCG). As part of this program, community members plant native trees into mowed grassland parks. In each planting year approximately 20 species of bare root native tree seedlings were planted at each park and the species selection varied year to year. Trees were sourced from the Kentucky Department of Forestry and nearby nurseries. Some fragments had walking trails passing through them while others were established away from nearby trails and had limited accessibility, but none were surrounded by fencing. The distribution of fragments at one park are shown in Fig. 1A. Previous work on these fragments found that planted trees establish a canopy and drive shifts in understory plant communities, including recruitment of native herbs, shrubs, and trees, but that invasive plants including Amur honeysuckle [*Lonicera maackii* (Rupr.) Maxim.] and purple wintercreeper [*Euonymus fortunei* (Turcz.) Hand.-Maz.] present significant challenges to forest development (Sena et al. 2021, 2023).

The boundaries for each fragment at each park were delineated with polygons in Google Earth Pro v 7.3.6 (Google Inc. 2022) and we used these polygons to calculate fragment size. At parks where we sampled across multiple fragments within the same year, we averaged the area of all sampled fragments if the distance between fragments was greater than 10 m and used this value to represent total fragment size for that planting year. If multiple fragments planted in the same year were sampled but were separated by a distance of less than 10 m, we summed the area of all sampled fragments to represent total fragment size for that planting year (Table 1). Three fragments planted at Veterans Park in 2010 were connected to fragments planted in 2021 within the same park to form a continuous fragment, and we therefore included the area of these younger fragments in total fragment area in this planting year.

Table 1 List of all parks sampled for this project. Most sampling locations consisted of multiple small fragments which were planted in the same year. The size of all sampled fragments within each planting year were summed for analyses when fragments were separated by less than 10 m and averaged when greater than 10 m apart. Impervious surface values were first recorded at 100 m and 1000 m radii surrounding each fragment and then averaged across all fragments

Park	Planting year	Number of fragments sampled	Average distance between sampled fragments (m)	Average size of sampled fragments (m^2)	Total size of sampled fragments (m^2)	Percent impervious cover at a 100 m radius	Percent impervious cover at a 1000 m radius	Total natural enemies collected
Coldstream campus	1999	1	NA	68,158	68,158	2.6%	15.3%	417
Masterson station park	2000	2	16.4	23,018	46,035	2.4%	22.4%	174
Masterson station park	2001	2	391.2	17,114	34,227	2.5%	8.9%	170
Shilito park	2002	1	NA	23,225	23,225	32.0%	57.3%	181
Veterans park	2003	2	6.7	13,517	27,033	7.8%	34.6%	205
Veterans park	2004	2	6.5	5,607	11,213	10.7%	35.3%	241
Wellington park	2005	2	13.1	13,742	27,483	18.5%	33.8%	154
Mary Todd Lincoln estate	2006	2	7.0	11,420	22,839	6.9%	16.5%	157
Town Branch	2007	3	112.3	4,250	12,750	33.3%	14.3%	131
Jacobson park	2008	2	106.9	7,807	15,614	5.4%	18.2%	178
Shilito park	2009	1	NA	34,194	34,194	5.7%	52.9%	247
Veterans park	2010	3	94.6	4,275	22,742	43.6%	58.7%	292
Liberty park	2011	1	NA	13,419	13,419	45.3%	61.8%	70
Legacy trail	2012	1	NA	6,044	6,044	0%	2.2%	117
Hisle farm	2013	1	NA	16,658	16,658	0	0.1%	121
Hisle farm	2014	2	68.1	17,696	35,391	0	0.6%	143
Bryan station	2016	2	87.9	2,728	6,240	30.6%	27.5%	132
Hisle farm	2017	2	4.5	12,426	24,852	0	0	160
Veterans park	2018	2	27.3	2,613	5,225	4.7%	20.7%	123
Masterson station	2019	1	NA	18,701	18,701	0.7%	22.0%	147

We created a 100 m and 1000 m buffer around all fragments and used the 2023 Annual National Land Cover Database (NLCD) (USGS 2024) to record percent impervious surface coverage within buffers. Our measurement of impervious surface cover was calculated by summing all pixels represented by the medium and high-density development classes in the NLCD legend and dividing this sum by the total number of pixels, as has been done in other studies (e.g. Glaum et al. 2017; Fitch et al. 2019). For parks where we sampled more than one fragment, surrounding percent impervious cover was averaged across all fragments. We then created a 25 × 25 m grid over the extent of each fragment in ArcGIS Pro v. 2.5.1 (Esri 2020) to select sampling locations within fragments. We also created an extra layer of grid cells surrounding the outside of each fragment to select sampling locations outside of fragments. In each planting year, we randomly selected two grid cells within and two cells outside of fragments to sample within. For parks with multiple fragments planted in the same year, we randomly selected 2 cells within fragments and 2 cells outside of fragments using the full set of cells across all fragments in the same park and planting year (Table 1, Table S1). In total, we placed traps in more than one fragment in nine planting years (Table S1). Only one fragment in the same planting year was not sampled in two different planting years using this random assignment protocol – Veterans park 2018 and Veterans park 2010 (Table S1). Prior to conducting analyses we decided to remove observations collected from the outside of four fragments (Veterans park 2004, Hisle Farm 2013, Bryan Station 2016, and Veterans park 2018) because these traps were within 10 m of another forest fragment, while all other traps outside of all other fragments had no nearby fragments near the traps. In all planting years at all parks, traps collected within fragments were retained for analysis.

To sample arthropods within fragments, one yellow pan trap was placed in the centroid of selected grid cells, 5 m away from the center in a random direction, and 10 m away from the center in a random direction (Fig. 1B). In cells outside of fragments, pan traps were placed 0 m, 5 m, and 10 m away from the forest edge (Fig. 1C). Thus in each planting year a total of 12 pan traps were placed out to collect arthropods. Pan traps consisted of a plastic yellow soup bowls filled $2/3^{rds}$ full with soapy water and were held in place with three 0.3 m bamboo stakes. We used yellow pan traps because they can effectively sample multiple natural enemy taxa from different orders (e.g. Leksono et al. 2005; Shweta and Rajmohana 2016; Tenguri et al. 2024). Traps were left for 48 h and all arthropods collected were stored in 70% ethanol until processing could occur in the lab.

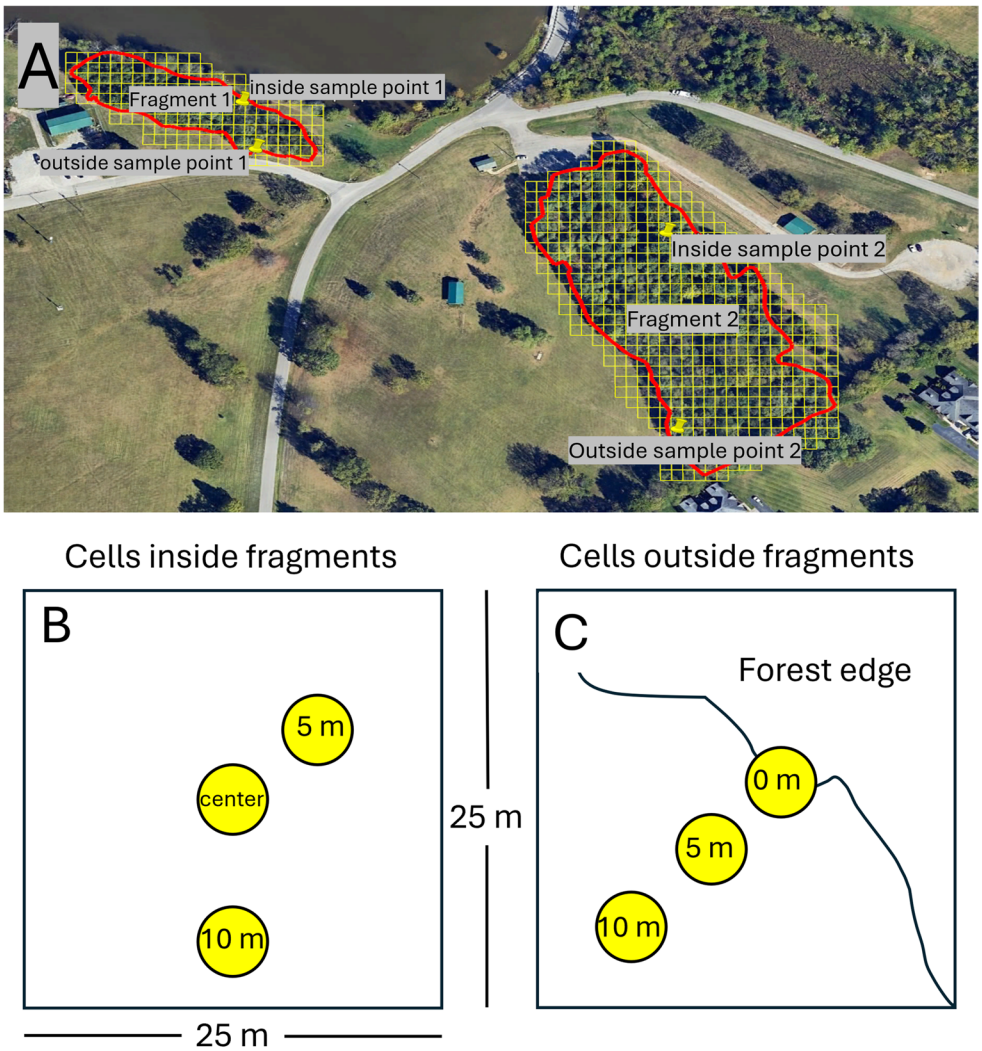

Fig. 1 (**A**) An overhead image of two fragments sampled at Jacobson Park that were both planted in 2008. Two grid cells were sampled within and two grid cells were sampled outside of fragments in each planting year. Cells were randomly selected. Image was sourced from Google Earth Pro (Google Inc. 2022, Imagery date: 10/23/2023). (**B**) In selected cells within fragments, yellow pan traps were placed at the centroid and at 5 m and 10 m away from the center in a random direction. (**C**) In grid cells outside of forest fragments, one trap was placed at the forest edge, one was placed 5 m away from the edge, and another was placed 10 m away from the edge. Traps were placed in lawns or meadows adjacent to fragments

We sorted natural enemies from pan traps into the following groups: Ants (Formicidae), parasitoid wasps (Ichneumonoidea, Proctotrupomorpha, Chrysidoidea, Tiphioidea, Scoliidae, or Apoidea), spiders (Araneae), lady beetles (Coccinellidae), earwigs (Dermaptera), lacewings (Chrysopidae or Hemerobiidae), long-legged flies (Dolichopodidae), predatory wasps (Pompiloidea or Vespoidea), predatory beetles (Carabidae or Staphylinidae), damselflies (Zygoptera), and robber flies (Asillidae), and crickets (Grylloidea).

Statistical analysis

We scaled and centered all predictor variables prior to analysis to improve model fit. We first fit a generalized linear model (negative binomial, log-link function) to determine if natural enemy abundance across all fragments differed inside and outside of fragments. To determine how forest age, size, and surrounding impervious cover influenced natural enemy abundance within and outside of fragments we fit two generalized linear models (negative binomial, log-link function for both). In these models, the response terms were total natural enemy abundance (either inside or outside fragments) and the predictors were forest fragment age, forest fragment size, the interaction between age and size, and percent impervious surface cover within a 100 m buffer surrounding each fragment. We also fit a second model which included impervious surface cover within a 1,000 m buffer as opposed to a 100 m buffer as a predictor. We used AIC values to choose the model in each case with the impervious surface buffer that explained the most variation in the response variable. We also used AICs to determine if including an interaction term between fragment size and age improved model fit. We calculated variance inflation factors (VIFs) for all models and all variables were <2 prior to including interactions, and in one model two terms had VIFs <5 after including interactions. We consider these VIF values to be within acceptable thresholds based on established guidelines (Zuur et al. 2010). To account for the non-independence of forest fragments of different ages sampled within the same park, we used cluster-robust standard

errors with park as the clustering unit ("vcovCL" function in the "sandwich" package Zeileis et al. 2020). This approach adjusts standard error estimates for potential within-park correlation without requiring assumptions about the structure of that correlation, while coefficient estimates remain those of the underlying negative binomial GLM. Given the relatively small number of parks (G = 12), we applied a bias-corrected cluster-robust variance estimator (HC3) to avoid underestimation of standard errors associated with few-cluster settings (Zeileis et al. 2020). We used this approach instead of fitting park as a random intercept term in the model because such an approach created singular fits or prevented models from converging. We used a negative binomial GLMM (log-link function) to determine if natural enemy abundance recorded outside of fragments was influenced by sampling location − 0 m, 5 m, 10 m. We included a random intercept term for each planting year within each park to account for the repeated measures data structure. Follow-up Tukey's HSD test was used to detect significant differences between sampling locations.

We used the "many.glm" function in the "mvabund" package (Wang et al. 2012) to determine if natural enemy group composition (using the abundances of each group) recorded inside and outside of fragments was influenced by fragment age, size, surrounding impervious cover (using the radius selected via model selection) and the park fragments were within. We used follow-up univariate tests with a p-value correction factor to determine which natural enemy taxa drove the significant effect of predictor variables on community composition.

Results

We collected 3,171 natural enemies across all 20 planting years. We collected more natural enemies outside of fragments (Mean ± SE = 115.4 ± 10.4) than within fragments (66.2 ± 11.1) (Fig. 2, $\chi^2 = 10.051$, df = 1, $P = 0.002$). The most common natural enemy arthropods were ants (29.4% of all specimens), parasitoid wasps (27.9%), long-legged flies (26.9%), and spiders (8.3%). Fragment size ranged from 68,158 to 2728 m^2 (18,534 ± 3,214 m^2). Percent impervious cover surrounding fragments ranged from 0% to 45.6% (12.6 ± 3.4%) at a 100 m buffer, and 0 to 61.8% (25.2 ± 4.5%) at a 1000 m buffer. The model containing impervious surface cover at a 100 m radius explained greater variation in natural enemy abundance within frag, emts (AIC = 201.5 compared to 201.7), while the model containing impervious cover at a 1000 m radius explained greater variation in abundance outside of fragments (AIC = 159.8 compared to 160.4), however; in both cases ΔAIC values were < 2, indicating both explained similar variation in response variables. An

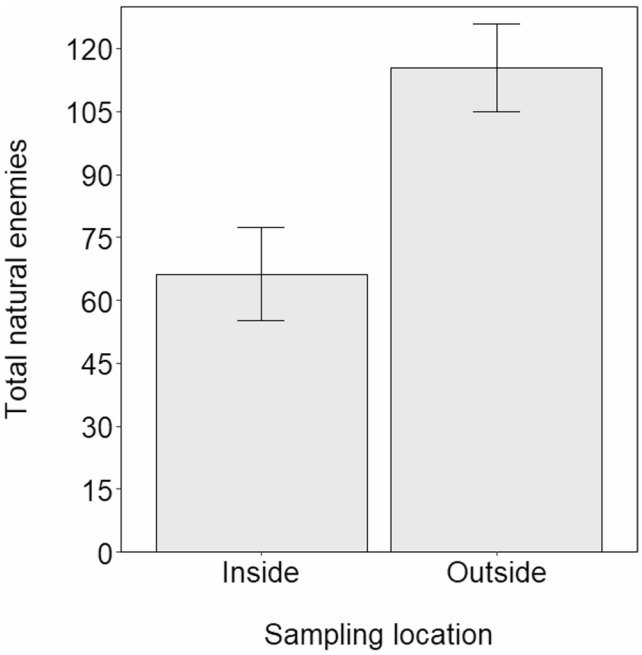

Fig. 2 Significantly more natural enemies were collected on average from traps located outside fragments compared to traps within fragments. $N = 20$ inside fragments and $N = 16$ outside fragments

interaction between fragment size and age was included in the model for natural enemy abundance outside fragments (ΔAIC = 2.1), but not within fragments (ΔAIC = 0.7) based on ΔAIC threshold of 2. Fragment size, age, or impervious surface cover did not influence natural enemy abundance within or outside of fragments (Table 2).

There was a significant effect of sampling location on natural enemy abundance recorded outside fragments ($\chi^2 = 6.281$, df = 2, $P = 0.043$). Average natural enemy abundance was significantly different between the 0 m and 5 m sapling locations (β = −0.370 ± 0.157, Z = −2.356, $P = 0.048$)

Table 2 Results from statistical tests determining the influence of predictors on total natural enemy abundance (NE) recorded within and surrounding fragments. Significance was evaluated with Wald tests. Significant predictors are in bold-face text

Response	Predictor	Estimate ± S.E.	Z	*P*
NE abundance outside fragments	Intercept	4.710 ± 0.093	50.319	< 0.001
	Fragment age	0.115 ± 0.105	1.092	0.275
	fragment size	0.345 ± 0.192	1.791	0.073
	Impervious cover (1 km)	0.069 ± 0.134	0.513	0.608
	Age * size	−0.187 ± 0.255	−0.731	0.465
NE abundance inside fragments	Intercept	4.106 ± 0.149	27.520	< 0.001
	Fragment age	−0.013 ± 0.147	−0.090	0.929
	Site size	0.335 ± 0.211	1.586	0.113
	Impervious cover (100 m)	−0.060 ± 0.194	−0.308	0.758

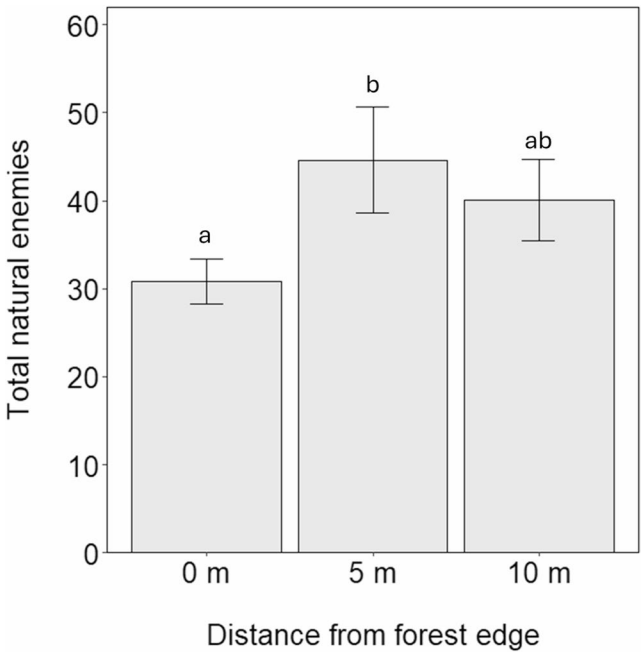

Fig. 3 Natural enemy abundance outside of fragments was influenced by sampling location. Bars with different letters above them are significantly different from each other

while the 10 m and 0 m (β = −0.263 ± 0.158, Z = −1.665, P = 0.219), and 10 m and 5 m locations did not differ (β = −0108 ± 0.156, z = −0.693 P = 0.768) (Fig. 3). Average natural enemy abundance at 0 m was 30.8 ± 2.6 and 44.6 ± 6.0 at 5 m, and 40.1 ± 4.6 at 10 m.

Natural enemy community composition within fragments was influenced by fragment size and the park fragments were within (Table 3). The effect of size on community composition was driven by long-legged flies and spiders as both groups were positively associated with fragment size (Fig. 4; Table 4). However these relationships were driven by an influential outlier, as removal of the Coldstream campus 1999 location (the oldest and largest fragment where the most long-legged flies, spiders, and parasitoids were collected) made the effects of fragment size on spider (χ^2 = 0.839, P = 0.934), long-legged fly abundance (χ^2 = 1.221, P = 0.813) non-significant. Outside fragments, natural enemy composition was influenced by impervious surface cover and the interaction of fragment size and age (Table 3). The impervious surface effect was driven by predatory wasps which were positively associated with impervious surface cover, however; removal of an influential outlier made the effect non-significant (Fig. 4, χ^2 = 0.085, P = 0.981). No natural enemy group outside fragments was significantly associated with the interaction of fragment size and age, however, parasitoid wasp abundance outside of fragments was positively associated with fragment age (Fig. 5; Table 4).

Table 3 Results of multivariate tests of how natural enemy (NE) composition is influenced by predictor variables. Significant predictors are in bold-face text

Response	Res.df	Df.diff	Wald chi square	P
NE composition outside of fragments				
Intercept	15			
Fragment age	14	1	4.308	0.135
Size	13	1	3.233	0.521
1 km impervious	**12**	**1**	**5.669**	**0.041**
Park	2	10	17.056	0.540
Age * size	**1**	**1**	**5.809**	**0.034**
NE composition within fragments				
Intercept	19			
Fragment age	18	1	2.322	0.650
Size	**17**	**1**	**7.882**	**<0.001**
100 m impervious	16	1	3.836	0.115
Park	**5**	**11**	**17.072**	**0.043**

Discussion

Although urban forests are usually fragmented and small in extent, they can provide important habitat for wildlife and ecosystem services for humans (Stagoll et al. 2012; Mullaney et al. 2015). The quality of reforested habitat in urban landscapes may be expected to increase over time post-planting as trees mature and understory plant communities change. These changes would likely result in greater vegetation complexity (e.g. Reyes-Palomeque et al. 2021) which is associated with increased natural enemy abundance (Langellotto and Denno 2004) and insect species richness and abundance (Beninde et al. 2015; Knuff et al. 2020). Although fragment size or age did not influence total natural enemy abundance within fragments, we found parasitoid spillover was greater outside of older relative to younger fragments. Therefore, the ability of urban forests to support spillover biological control may also change as forest fragments age. Creating and maintaining urban forest fragments may provide biological control benefits to nearby landscapes, regardless of fragment size, and these effects may accrue over time.

Both the size and the age of forest fragments may influence their ability to support diverse arthropod taxa and subsequent spillover into adjacent landscapes (Burkman and Gardiner 2014; Chase et al. 2020). Larger urban forests often host more arthropod species than smaller fragments and increasing isolation surrounding forests (usually associated with surrounding impervious surface cover) typically decreases species richness or biomass within fragments (Beninde et al. 2015; Fattorini et al. 2018; Svenningsen et al. 2022). Similarly, older forest fragments have a more developed canopy structure (e.g. Sena et al. 2021) and would be expected to host more plant species and vegetation to support diverse herbivore species and their natural

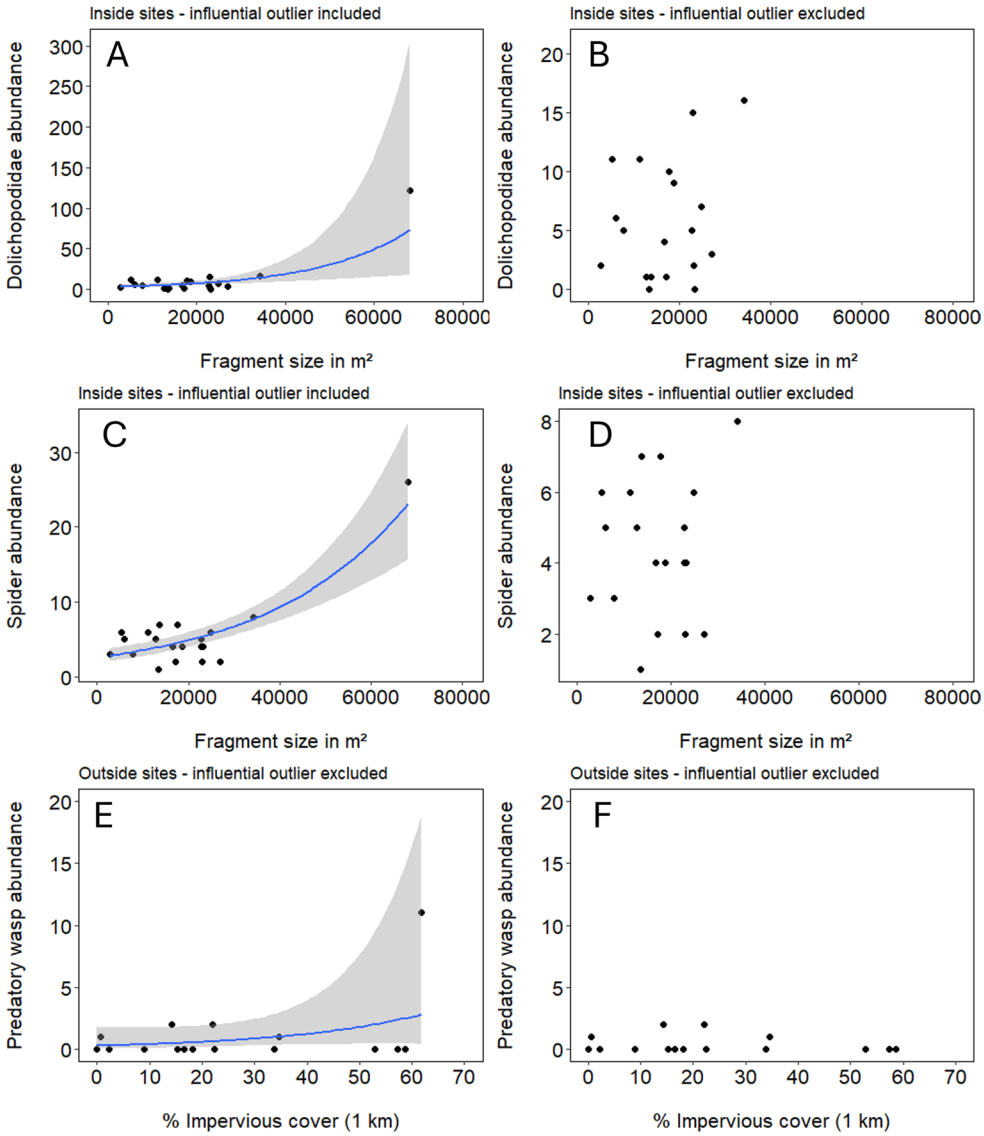

Fig. 4 Certain significant relationships in univariate tests were driven by influential outliers. Best fit lines are plotted for significant effects and shaded regions represent the 95% confidence interval. (**A**) and (**B**) The effect of fragment size on long-legged fly (Dolichopodidae) abundance recorded within fragments was driven by an influential outlier from one planting year (**C**) Spider abundance within fragments was positively associated with fragment size. (**D**) However removal of one data point made the relationship no longer significant. Finally (**E**) predatory wasp abundance collected outside of fragments was associated with impervious surface cover at a 1000 m radius, but (**F**) this effect was no longer significant when an influential outlier was removed

enemies. However, we did not find any effect of forest size or age on total natural enemy abundance recorded within fragments. The abundances of spiders and long-legged flies within fragments were both positively associated with fragment size, although this effect was driven by our oldest and largest fragment which was 22,123 m^2 larger than the next largest fragment. In an urban landscape, fragments may need to reach a certain size threshold before positive effects on natural enemy abundance can be detected, as removal of our largest fragment from the dataset made the aforementioned relationships non-significant. Studies which have documented positive effects of fragment size on arthropod abundance and/or diversity have used a greater range of fragment sizes such as 0.3 to 71 ha (Bolger et al. 2000) or 5.2 to 4,383 ha (Glaubomme et al. 2008). Thus the range of fragments we sampled may have been too limited to document a significant effect of fragment size on natural enemies. A meta-analysis of 123 studies on plant and animal response to fragment size found that the positive effect of fragment size on species abundance and diversity was stronger where the surrounding matrix was largely inhospitable, such as an intensely urbanized location, relative to fragments surrounded by more hospitable fragments, such as a secondary forest (Chase et al. 2020). Given that most of our fragments were within parks surrounded by lightly to moderately urbanized landscapes, the beneficial effect of fragment size on natural enemy abundance may be weaker and require a greater sample size to detect.

Greater natural enemy abundance found outside compared to inside fragments, along with similar natural enemy abundance at edges and 10 m away from edges, may indicate natural enemies are moving between fragments to surrounding habitats to find resources based upon seasonal shifts in availability (e.g. Rand et al. 2006). It is unclear

Table 4 Output from univariate tests on natural enemy (NE) abundance within and outside of fragments. Significant predictors are in bold-face text

NE taxa	Predictor	Wald	*P*
NE abundance outside of fragments			
Ants	Fragment age	0.852	0.914
	Fragment size	0.339	0.952
	1 km impervious	1.435	0.682
	Park	11.205	0.457
	Age * size	0.621	0.641
Long-legged flies	Fragment age	0.676	0.926
	Fragment size	2.191	0.407
	1 km impervious	1.829	0.592
	Park	4.937	0.936
	Age * size	2.620	0.225
Parasitoids	**Fragment age**	**3.313**	**0.046**
	Fragment size	0.573	0.952
	1 km impervious	1.057	0.842
	Park	6.619	0.816
	Age * size	2.568	0.225
Spiders	Fragment age	0.223	0.932
	Fragment size	1.161	0.903
	1 km impervious	0.014	0.996
	Park	8.093	0.730
	Age * size	3.149	0.143
Crickets	Fragment age	0.754	0.926
	Fragment size	0.344	0.952
	1 km impervious	0.345	0.983
	Park	3.873	0.936
	Age * size	2.736	0.212
Predatory beetles	Fragment age	0.329	0.932
	Fragment size	0.889	0.952
	1 km impervious	0.080	0.994
	Park	2.845	0.936
	Age * size	1.578	0.241
Earwigs	Fragment age	1.520	0.655
	Fragment size	0.867	0.952
	1 km impervious	1.758	0.592
	Park	2.927	0.936
	Age * size	0.007	0.641
Predatory wasps	Fragment age	1.833	0.524
	Fragment size	1.484	0.803
	1 km impervious	**4.732**	**0.013**
	Park	0.146	0.936
	Age * size	0.019	0.641
NE abundance within fragments			
Ants	Fragment age	0.131	1.00
	Size	2.383	0.137
	100 m impervious	1.468	0.508
	Park	11.139	0.072
Long-legged flies	Fragment age	1.617	0.639
	Size	**4.04**	**0.006**
	100 m impervious	2.595	0.148
	Park	6.598	0.409
Parasitoids	Fragment age	1.024	0.785
	Size	1.272	0.538
	100 m impervious	0.015	0.986
	Park	7.122	0.417
Spiders	Fragment age	1.306	0.705

Table 4 (continued)

NE taxa	Predictor	Wald	*P*
	Size	**6.186**	**0.001**
	100 m impervious	0.784	0.798
	Park	3.767	0.606
Crickets	Fragment age	0.033	1.000
	Size	0.433	0.915
	100 m impervious	2.131	0.260
	Park	3.828	0.606
Predatory beetles	Fragment age	0.054	1.000
	Size	0.239	0.915
	100 m impervious	0.817	0.798
	Park	6.653	0.409

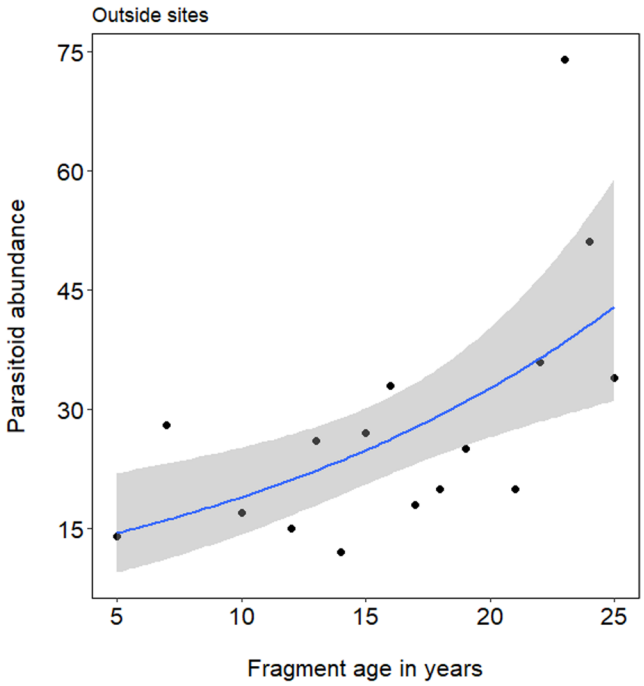

Fig. 5 More parasitoids were collected outside of older forest fragments (χ^2 = 3.313, P=0.046**)**. The best fit line is plotted and shaded regions represent the 95% confidence interval

how far into adjacent landscapes spillover effects may occur as our sampling locations for traps extended only 10 m from edges due to constraints from property boundaries. Nonetheless, these effects likely operate on larger spatial scales as edge effects on arthropod communities can permeate as far as 1 km into forest fragments (Ewers and Didham 2008). Our findings suggest that low to moderately urbanized landscapes surrounding forest fragments are not an inhospitable matrix and the movement of arthropods between these locations drives landscape-wide community structure (Tscharntke et al. 2012). Since older fragments supported parasitoid spillover, changes in plant communities within fragments over time likely enhance host diversity available to parasitoids at or near forest edges due to the different plant communities within adjacent landscapes relative to forests. Resources surrounding forest fragments that could support parasitoids include pollen and nectar from blooming flowers in nearby yards, nesting habitat, or emerging herbivore populations in lawns and ornamental plants that could serve as prey or hosts at the time of year we collected data. All forest fragments were surrounded by turfgrass lawns which can host caterpillars such as fall armyworm [*Spodoptera frugiperda* (J.E. Smith)] or beetle larvae such as masked chafers (*Cyclocephala* spp. Dejean) and Japanese beetles (*Popilla japonica* Newman) which can host large parasitoid populations (Redmond and Potter 2010; Hay-Roe et al. 2016). Fescues (*Festuca* spp.) and Kentucky bluegrass (*Poa pratensis* L.) are also commonly found within RtB fragments and likely support grub populations within fragments (Sena et al. 2023). Many other non-pest arthropods found within lawns such as spiders, ants, or crickets can also serve as hosts for many parasitoid species (Thomson et al. 2012; Fei et al. 2023) and may explain why parasitoid wasps can be abundant in residential lawns (Joseph and Braman 2011). Additionally, common urban landscape tree species in central Kentucky are often infested with scale insects such as calico scale [*Eulecanium cerasorum* (Cockerell)], tulip tree scale [*Toumeyella liriodendri* (Gmelin)], oak lecanium scale (*Parthenolecanium* spp. Šulc), or gloomy scale [*Melanaspis tenebricosa* (Comstock)], each of which can be hosts for multiple parasitoid species (Hubbard and Potter 2005; Dale and Frank 2014; Myartseva et al. 2016; Robayo Camacho et al. 2018). Other pests such as native holly leafminer (*Phytomyza ilicicola* Loew), western flower thrips (*Frankliniella occidentalis* Pergande), evergreen bagworms [*Thyridopteryx ephemeraeformis* (Haworth)], tulip tree aphids [*Illinoia liriodendri* (Monell)], linden aphids (*Eucallipterus tiliae* L.), and silverleaf whiteflies (*Bemisia tabaci* (Gennadius)] are common urban landscape pests in Kentucky that can be hosts for parasitoids (Stegmaier 1971; Potter 1985; Hajek 1986; Zuparko and Dahlsen 1993; Gerling et al. 2001; Ellis et al. 2005; Mouden et al. 2017). Therefore, the yards surrounding our forest fragments could

have contained many potential hosts to support parasitoid populations. Trees commonly found within RtB fragments such as American sycamore (*Platanus occidentalis* L.), black locust (*Robinia pseudoacacia* L.), and hackberry (*Celtis occidentalis* L.) (Sena et al. 2023) can host herbivores such as fall webworm [*Hyphantria cunea* (Drury)], locust leafminer [*Odontota dorsalis* (Thunberg)], and calico scales [*Eulecanium cerasorum* (Cockerell)], respectively, that are each used as hosts by multiple parasitoid species (Weaver and Dorsey 1965; Hubbard and Potter 2005; Cao et al. 2024). Future studies which compare both natural enemy and herbivore abundance across multiple sampling periods, along with biological control services, within and surrounding urban forest fragments may better explain spillover patterns observed in this study.

Impervious surfaces fragment urban greenspaces and hinder the movement of arthropods with limited dispersal capabilities, such as ground beetles or spiders, to habitat patches (Perry et al. 2020; Delgado de la Flor et al. 2020; Fenoglio et al. 2021). Abiotic factors such as pollution or heat island effects associated with urbanization can also negatively affect natural enemy fitness (Gardiner and Harwood 2017; Meineke et al. 2017). As a result, urbanization filters insect communities and selects for those tolerant of urban conditions which can also weaken biological control of pests by natural enemies (Beninde et al. 2015; Fenoglio et al. 2020, 2021, Korányi et al. 2021, 2022). Surprisingly, we found no effect of imperious cover on the abundance of any natural enemy group within fragments. Since we grouped natural enemies into coarse taxonomic categories, these groupings may not accurately reflect differences in functional response to urbanization such as thermal tolerance, dispersal ability, or prey/host range which would be expected to vary considerably at a lower taxonomic resolution (Meineke et al. 2023; Piano et al. 2017). Additionally, the extent of impervious cover at a 1000 m radius surrounding most fragments was low to moderate (mean ± SE = 25.2 ± 4.5%) and detrimental effects of urbanization on arthropod communities within our forest fragments may not be apparent as is usually the case at higher values (e.g. Glaubomme et al. 2008). However, there is typically limited land available for cities to establish forest fragments at heavily urbanized areas relative to larger suburban parks. Thus, deleterious effects of urbanization on arthropod communities may have limited influence in the locations where city governments may be most likely to establish forest fragments. Finally, we detected a significant effect of the park that fragments were within on natural enemy composition, but this effect was not driven by any specific natural enemy group in univariate tests. Multiple environmental factors that we did not measure besides impervious cover such as vegetation diversity and composition within fragments, management practices within and surrounding fragments, soil conditions, and local hydrology would aid in understanding park-specific effects on natural enemy composition.

Our study is a starting point that future researchers could build upon to characterize natural enemy associations with urban forest fragments to inform conservation measures. Limitations of our study are that we characterized natural enemies at one sampling point in time, used only one trap type, and identified natural enemies to coarse categories. Natural enemy community composition shows considerable temporal variation in urban landscapes as their host or prey populations similarly fluctuate (Gardiner et al. 2014; Rocha et al. 2018; Parker et al. 2020). Therefore, community response to forest age, size, and surrounding impervious cover likely also fluctuates depending on what taxa are dominant within communities when samples are collected. Additionally, while yellow pan traps are effective at sampling flying arthropods, they capture fewer ground-dwelling taxa in comparison to pitfall traps (Crowley et al. 2023). Many studies of arthropods in forest fragments use pitfall traps exclusively and focus on ground-dwelling taxa such as spiders or ground beetles (e.g. Myers and Marshall 2021; Gallé et al. 2022). Since traps vary in their ability to sample different arthropod groups, multiple trap types are necessary to quantify the full community of natural enemies that may be affected by forest fragment, age, size, and surrounding impervious cover. Finally, coarse arthropod identifications are useful for understanding the response of smaller taxonomic groups with similar biology to environmental variables (e.g. Wilson and Frank 2022, 2023). However, coarse groups become less predictive for diverse groups such as parasitoid wasps which vary substantially across species in host preference and habitat use. Our approach collected a snapshot estimate of natural enemy community response to urban forest fragment age, size, and surrounding impervious cover in mid-summer using a sampling technique that effectively captures multiple natural enemy taxa, and coarse identifications allowed for quick assessments. Even with the aforementioned limitations, we gained knowledge on natural enemy response to urban forest age and size. Future studies which address the limitations of this project will better inform sustainable urban forest management for natural enemy conservation.

Creating and maintaining urban forest fragments has already been associated with numerous benefits for humans and wildlife, and in this study, we document that forest fragments can also support parasitoid wasp spillover into adjacent landscapes. The coarse taxonomic resolution of our data makes it unclear if the parasitoids we collected outside of fragments are targeting landscape pests or other arthropod taxa. Nonetheless, our results suggest that the age of urban forest plantings may contribute to pest regulation

in nearby landscapes. Future studies which examine forest fragments across a larger urbanization gradient, as well as studies which test spillover effects at larger spatial scales will better explain what parameters support or hinder natural enemy spillover from forests into adjacent landscapes.

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Authors' contributions All authors designed the study. Zoe and Zachary McComas collected all field data and identified arthropods to taxonomic groups. CJW conducted statistical and geospatial analyses. All authors contributed to the writing and editing of the manuscript.

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Data availability Data used in statistical analyses are publicly available at the following link: https://doi.org/10.6084/m9.figshare.31018258.

Declarations

Competing interests The authors declare no competing interests.

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