Vertical heterogeneity in predation pressure in a temperate forest canopy

The forest canopy offers a vertical gradient across which variation in predation pressure implies variation in refuge quality for arthropods. Direct and indirect experimental approaches were combined to assess whether canopy strata differ in ability to offer refuge to various arthropod groups. Vertical heterogeneity in impact of avian predators was quantified using exclosure cages in the understory, lower, mid, and upper canopy of a north-temperate deciduous forest near Montreal, Quebec. Bait trials were completed in the same strata to investigate the effects of invertebrate predators. Exclusion of birds yielded higher arthropod densities across all strata, although treatment effects were small for some taxa. Observed gradients in predation pressure were similar for both birds and invertebrate predators; the highest predation pressure was observed in the understory and decreased with height. Our findings support a view of the forest canopy that is heterogeneous with respect to arthropod refuge from natural enemies.

1   Vertical heterogeneity in predation pressure in a temperate forest canopy

3   Kathleen R. Aikens, Laura L. Timms*, and Christopher M. Buddle

5   Department of Natural Resource Sciences

6   McGill University, Macdonald Campus

7   21,111 Lakeshore Road, Ste-Anne-de-Bellevue

8   Quebec H9X 3V9 Canada

11   *Author for Correspondence: laura.timms@mail.mcgill.ca, 1-416-660-7096

12   **INTRODUCTION**

13   Temperate forest canopies are heterogeneous environments, where variation in resources,

14   structure, and abiotic conditions exists at even small scales (Parker, 1995). An important

15   resource type that is often overlooked in ecological studies is the refuge – space within a habitat

16   that allows organisms to escape from their natural enemies (Berryman & Hawkins, 2006).

17   Vertical heterogeneity within forest canopies can offer refuge from predators, through the

18   physical properties of the habitat as well as foraging behaviour of both prey and natural enemies

19   (Jeffries & Lawton, 1984). If refuge quality differs across a spatial gradient, predation then

20   becomes an important determinant of local distribution.

21   Arthropods living in trees face strong predation pressure from vertebrate and invertebrate

22   natural enemies (Cornell & Hawkins, 1995; Mooney et al., 2010). Predation can play an

23   important role in shaping the niches of arthropods, particularly insect herbivores, by affecting the

24   choice of feeding location, resource use, and ultimately fitness (Jeffries & Lawton, 1984; Bernays

25   & Graham, 1988; Stamp & Bowers, 1990). These relationships, however, are poorly understood

26   as a function of vertical stratification, even though it is well established that arthropods are

27   structured along vertical gradients in forest (e.g. Larrivée & Buddle, 2009; Pinzon, Spence &

28   Langor, 2013).

29   This research tested vertical heterogeneity in predation pressure in a north-temperate sugar maple (*Acer*

30   *saccharum* Marsh.) forest to determine whether refuge from predators differs by canopy height. Optimal foraging

31   theory predicts that predators should spend more time foraging in areas with higher prey density and reduced search

32   time (Emlen, 1966; MacArthur & Pianka, 1966). These predictions are consistent with the observations of Van Bael,

33   Brawn & Robinson (2003), who found correspondingly higher arthropod abundance and predation pressure in the

34   tropical forest canopy vs. understory. Previous work in our system suggests arthropod abundance decreases with

35   distance from the forest floor (Aikens & Buddle, 2012), which would mean higher pay-off for predators foraging in

36   the understory and lower canopy layers and thus higher predation pressure for arthropods in these strata.

37   Furthermore, increased density and structural complexity of foliage in the upper canopy may provide more

38   camouflage for arthropod prey and increase predator search time. We therefore predict that the upper canopy crown

39   represents a refuge for arthropods and that relative impact of predators will be reduced with increasing canopy

40   height.

41

42   **MATERIALS AND METHODS**

43   **Study site**

44   Experiments were completed at the Morgan Arboretum, a 245-hectare forest reserve near

45   Montréal (Ste-Anne-de-Bellevue, Québec, Canada, (45˚26'N, 73˚57'W)). The Arboretum

46   contains tracts of natural woodland and collections of exotic trees, although most of the forested

47   area is typical temperate beech (*Fagus grandifolia* (Ehrh.)) and sugar maple forest. Natural stands

48   of sugar maple were selected for this study, including mature trees with heights of approximately

49   20-25 meters. Trees were selected on the basis of accessibility of the canopy using a mobile

50   aerial lift platform.

51   To examine differences in predation on arthropods along a vertical gradient, we carried out

52   manipulations in four vertical strata: understory, lower canopy, middle canopy, and upper canopy.

53   We defined strata in relative terms rather than in absolute height because of variance in both absolute tree height and

54   depth of canopy foliage. The lower canopy was defined as the first several layers of branches

55   encountered (~ 10-12 m); the middle canopy as the layers of branches at the mid-point of total

56   tree foliage (~ 15-17 m); and the upper canopy as the several layers of branches at the very top of

57   the foliage (~ 20-25 m). The understory was defined as the first two meters above the forest

58   floor; which, because mature sugar maples do not have foliage at these heights, meant that the

59   understory stratum was composed of sugar maple saplings. We acknowledge that this has the

60   potential to add ontogeny as a confounding factor to our study. However, a recent meta-analysis

61   found no overall preference for insect herbivores between saplings and mature trees, despite

62   significant ontogenetic changes in leaf chemistry (Barton & Koricheva 2010).

63

64   **Bird predation**

65   We used wire exclosure cages to assess differences in vertebrate predation across strata

66   (Figure 1). Cages had a mesh diameter of 2.5 x 3.5 cm, which excludes the majority of vertebrate

67   predators (mainly birds) while still allowing access to most insects. Similar cages have been used

68   elsewhere to assess the effects of predation on arthropod abundance (e.g. Marquis & Whelan,

69   1994; Boege & Marquis, 2006). Each cage measured approximately one meter in length, with a

70   circumference of 1.7 ± 0.11 meters (mean ± SE). Cage design and placement did not compress

71   leaves or deform branches in any way; cages were supported with ropes from above to relieve

72   weight and pressure on the branches and leaves within the enclosure (Figure 1a).   We selected 20

73   mature trees and attached a single cage on one branch in each stratum, for a total of 20 cages per

74   stratum. Sugar maple saplings nearest each tree were selected for understory exclosures. Each

75   cage branch was paired with a control branch of similar size.

76   We completed arthropod censuses at intervals of approximately two weeks, for a total of six sampling periods

77   from June to September 2007. We collected arthropods by shaking each branch onto a stretched canvas collecting

78   frame, identifying all arthropods to the most precise taxonomic level possible and then returning them to the branch.

79   Flies (Diptera), bees and wasps (Hymenoptera, excluding ants), and some groups of true bugs (e.g. Cercopidae) were

80   excluded from collections, as they are too mobile to be accurately censused. All cage and control branches

81   were removed in September, and the dry mass of leaves on each branch was measured.

82   Comparisons between cage and control branches are thus expressed as arthropod density per unit

83   leaf biomass.

84   We tested the effects of vertical stratum and vertebrate exclusion on arthropod density using

85   linear mixed effects models, with stratum and treatment as fixed effects and tree identity

86   (including one understory sapling and the three canopy levels of one mature tree) as a random

87   effect. Modeling tree identity as a random effect within a mixed model allowed us to account for

88   the fact that the data include multiple observations from each of the twenty tree pairs (Lindstrom

89   and Bates 1990; Zuur et al. 2009). Response variables included the density of (i) all arthropods,

90   (ii) spiders (Araneae), (iii) beetles (Coleoptera), (iv) true bugs (Hemiptera), and (v) caterpillars

91   (Lepidoptera), pooled over the six collection periods. Arthropod densities were square-root

92   transformed before analysis to increase normality. One understory cage and one mid-canopy

93   cage from the same tree were lost late in the season, and were excluded from analyses. Model

94   fitting and checking procedures were carried out as recommended in Zuur et al. (2009),

95   including: fitting the full model; finding the optimal random structure; and, finding the optimal

96   fixed structure. The fit of these models to the data was assessed using diagnostic graphical

97   methods, including plots of fitted values versus standardized residuals as well as normal QQ plots

98   for both the fixed and random residual error. Contrasts were defined for each model using backwards

99   difference coding, such that the means for each stratum were compared to the stratum before it – in other words, the

100   lower canopy mean was compared to the understory mean, the middle canopy mean was compared to the lower

101   canopy mean, and the upper canopy mean was compared to the middle canopy mean.

102   We tested the hypothesis that predation pressure would differ between vertical strata using

103   the interaction between exclusion treatment and stratum. However, a non-significant interaction

104   does not exclude the possibility that the magnitude of treatment effects differs between strata (e.g.

105   Boege and Marquis 2006). Thus, we calculated effect sizes (Cohen's d) and their 95% confidence

106   intervals for the vertebrate exclusion treatment in each stratum and for each response group.

107   Means for each stratum-treatment combination were calculated based on the season total density

108   for each branch of that type (n=20). An effect size was considered to be non-significant if its

109   confidence intervals overlapped the value zero. All statistical analyses were carried out in R (R

110   Core Team, 2012), with the use of the packages nlme (Pinheiro et al., 2012) and lme4 (Bates,

111   Maechler & Bolker, 2012).

112

113   **Bird census**

114   Birds were censused within the areas selected for exclosure experiments during mid-May

115   to early June 2007. Five sites were chosen as stationary points, and all individuals within a 100m

116   radius were identified to species by sight or vocalization. We delimited the sites in this way to

117   fully census the experimental area while reducing the potential of recording individuals residing

118   in nearby fields. Censuses occurred over ten days, beginning at dawn and ending approximately

119   2.5-3 hours later. A total of 20.9 survey hours were completed. Efforts were made to ensure that

120   no individual was recorded twice during the same day; however, we cannot guarantee that the

121   same individuals were not counted on multiple days. Therefore, data represent relative

122   frequencies of species and not abundance data.

123

124   **Invertebrate predation**

125   We used bait trials to assess differences in invertebrate predation across vertical strata (see

126   Olson, 1992; Novotny et al., 1999). These trials were completed on 21 sugar maple trees during

127   June and July 2007. In each trial immobilized, but live, mealworm larvae (*Tenebrio molitor* L.)

128   were pinned to the bark of the tree as bait. Five bait mealworms were fastened to the bark in each

129   stratum by puncturing their body with an insect pin and securing the pin into bark. Though these

130   beetle larvae are not naturally found in the forest, they represent a generally palatable prey for

131   many arthropod and bird species (e.g. Uetz, Bischoff & Raver, 1992; Vivan, Torres & Veiga,

132   2003; Grieco, 2003). We chose to use mealworms for these trials as it allowed us to estimate a

133   relative value of predation pressure, comparable across strata and free from idiosyncrasies of prey

134   defense chemicals or behavior. We acknowledge that this does not correspond to predation

135   pressure experienced by any one naturally occurring prey species; however, mealworms are

136   acceptable prey for many generalist predators (e.g. Lymberry & Bailey, 1980).

137   All trials were completed between 0900 and 1700 hours, during which period baits were

138   checked a total of four times over 150 minutes. The first observation was recorded after 60

139   minutes, and each successive observation was taken 30 minutes after the previous one. During

140   each observation period, predator presence and type (e.g., ant, jumping spider, fly, etc.) were

141   recorded. Missing mealworms were also recorded as depredated, as it was observed that large

142   ants (*Camponotus* sp.) were capable of removing mealworms from the pin within minutes. After

143   initial observation, baits were left overnight and examined once more the following morning.

144   We tested the effects of vertical stratum on the proportion of predated mealworms using

145   binomial generalized linear mixed models, with stratum as a fixed effect and tree identity as a

146   random effect. Model fitting and checking procedures were carried out as outlined in Bolker et al.

147   (2009), including: fitting the full model; checking for overdispersion; finding the optimal random

148   structure; and, finding the optimal fixed structure. A priori contrasts between strata were defined

149   as described above. We repeated this analysis both for the proportion of predated mealworms

150   observed during the initial 150 minutes as well as for the proportion removed after the overnight

151   period.

152

153   **RESULTS**

154   **Vertebrate predation**

155   More than 2,600 individual arthropods identified from 49 families were surveyed from

156   June to September 2007. Spiders were the most abundant group (57%), followed by beetles

157   (16%), true bugs (10%), and caterpillars (9%). Other arthropod groups, including ants

158   (Hymenoptera: Formicidae), earwigs (Dermaptera), harvestmen (Opiliones), and booklice

159   (Psocoptera) were observed in small numbers (Table 1).

160   Selection procedures for the mixed effects models found that the best model for all

161   response groups included a weighted variance structure due to differences in residual variances

162   between strata. Exclusion treatment and vertical stratum were significantly related to arthropod

163   density for all response groups, but the interaction between the two was not significant for any

164   response group (Table 2). Mean arthropod density was higher on caged branches than on

165   controls, and in general decreased with increasing height (Figure 2). Density was highest in the

166   understory for all groups except caterpillars, whose density was highest in the lower canopy; the

167   results of comparisons between strata are presented in Table 2.

168   Based on effect sizes, the magnitude of the vertebrate exclusion treatment effect on

169   density was largest in the understory in the analyses for all arthropods, spiders, and beetles;

170   however, for beetles the effect was not significantly different than zero as the 95% confidence

171   intervals just overlap the zero line (Figure 3). None of the effect sizes were significantly different

172   than zero for true bugs or caterpillars (Figure 3).

173   Spring bird censuses yielded a total of 31 species observed or heard vocalizing in and

174   around experimental trees (Table 3). The most frequently recorded species were American Crow

175   (*Corvus brachyrhynchos*), American Goldfinch (*Carduelis tristis*), Red-eyed Vireo (*Vireo*

176   *olivaceus*), Ovenbird (*Seriurus aurocapillus*), Black-throated Green Warbler (*Setophaga virens*),

177   and Black-capped Chickadee (*Poecile atricapillus*). The latter four species are primarily

178   insectivorous in the spring and early summer (Holmes, Bonney & Pacala, 1979; De Graaf,

179   Tilghman & Anderson, 1985).

180

181   **Invertebrate predation**

182   Of 840 mealworm baits, 134 were removed or observed with feeding invertebrate predators.

183   A total of 194 predators were observed, the majority of which were ants (Formicidae) (157, or

184   81%). Also recorded were: 17 muscoid flies (Diptera: Muscidae, Tachinidae, Calliphoridae,

185   Sarcophagidae); 13 harvestman (Opiliones: Phalangidae, Sclerosomatidae); 3 jumping spiders

186   (Araneae: Salticidae); and, 3 predatory bugs (Hemiptera: Reduviidae). Predatory arthropod

187   species that could be reliably identified in the field are listed in Table 4.   The highest number of

188   predators was observed in the understory; however, after excluding a large number of ants (60)

189   observed on a single occasion in the understory, the highest number of observed predators was

190   seen in the lower canopy.

191   The highest proportion of observed daytime predation occurred in the understory, followed

192   by the lower canopy, upper canopy, and middle canopy (Figure 4a). Predation in the middle

193   canopy was significantly lower than both the lower canopy and the upper canopy, however

194   predation in the lower canopy was not significantly lower than the understory (Table 5). The

195   highest proportion of overnight removal of baits also occurred in the understory, followed by

196   lower canopy, middle canopy, and upper canopy (Figure 4b). The lower canopy had significantly

197   lower proportions of overnight bait removal than the understory, however neither of the other

198   stepwise comparisons showed significant differences (Table 5).

199

200   **DISCUSSION**

201   Excluding birds and other vertebrates in our cage treatment resulted in increased density

202   of all study groups, indicating that vertebrate predation has a significant negative impact on

203   arthropod density. In addition, our results demonstrate vertical heterogeneity in both density of

204   arthropods and some aspects of predation pressure on arthropods in mature sugar maple trees. In

205   particular, the understory contained the greatest density of arthropods, showed the greatest

206   predation rates by invertebrate natural enemies, and presented the highest vertebrate predation

207   pressure on spiders and beetles. However, we found no differences in predation pressure between

208   strata for the other arthropod groups in our study.

209   The densities of most arthropod taxa in our study were highest in the understory and

210   decreased with increasing canopy height. These results are consistent with the majority of

211   descriptions of the vertical stratification of arthropods in temperate forests (e.g. Preisser, Smith &

212   Lowman, 1998; Larrivée & Buddle, 2009; Ulyshen, 2011), although it has been noted that certain

213   species and trophic groups that we did not survey (e.g. some parasitoids and predatory wasps) are

214   more abundant in the upper canopy (e.g. Vance et al., 2007; Sobek et al., 2009). The general

215   pattern of higher abundance and richness of temperate forest arthropods near to the forest floor

216   has been explained by a number of factors, including the greater stability of the microclimate

217   nearer to the ground (Parker, 1995) and dispersal limitation after emergence (Brown et al., 1997).

218   Refuge from natural enemies and the distribution and quality of food resources may also explain

219   the pattern.

220   Seasonality in the temperate forest means that most arthropods in these systems likely

221   overwinter at or below ground level, and must recolonize the newly grown canopy habitat every

222   spring. When other factors do not exert strong selection pressure to move further up the tree, this

223   factor alone can provide a reasonable explanation for the greater abundance and diversity of

224   temperate forest arthropods at lower heights. For example, after ruling out a number of other

225   possible factors, including foliage quality, microclimate, leaf phenology, and natural enemies,

226   Brown et al. (1997) concluded that dispersal limitation following spring emergence is the best

227   explanation for the high densities of a leaf mining moth in the lower canopy. Ulyshen (2011)

228   notes that many predators of forest arthropods are generally more abundant in the upper canopy,

229   including birds, parasitoids, and predatory wasps. These two factors might combine to create

230   strong selection for arthropods to forage in the lower canopy or understory, unless there is a large

231   trade-off in resource quality.

232   Foliage within a tree can vary in suitability for herbivorous insects, such that leaf age, size, and position can

233   affect the nutritional quality and quantity of secondary chemicals. Herbivorous insects are commonly thought to

234   optimize their foraging in order to maximize nutrition and minimize attack by natural enemies (e.g. Carroll &

235   Quiring, 1994). However, there are many exceptions to this rule; for example, spruce budworm larvae prefer to feed

236   on the nutritious foliage in the upper canopy of host trees, which is also where they experience the highest parasitism

237   rates and pathogen infection (Dodge, 1961; Regnière, Lysyk & Auger, 1989). Caterpillars in our study were the only

238   group whose density was highest above the understory, although the overall low numbers of caterpillars observed

239   make comparisons difficult. For the other herbivorous groups in our study the high densities observed in the

240   understory may be a result of the quality or diversity of food sources as well as the dilution effect, where individual

241   predation risk decreases as the number of potential prey goes up (e.g. Finkbeiner, Briscoe, & Reed 2012).

242   The majority of the individuals observed in our study are generalist predators of

243   arthropods (i.e. spiders, predatory bugs), and a large part of their within-tree distribution may

244   therefore be influenced by where the bulk of their prey is located. Predators can be flexible in

245   their habitat use, and some species will track the distribution of their prey through space

246   (Murakami, 2002). We also note that spider density increased substantially within cages, and it is

247   possible that increased spider predation may have reduced the effect of the cage treatment for

248   other groups. When intermediate predators are released from predation pressure, populations may

249   increase to the point where they control herbivores more effectively than higher order predators

250   (Tscharntke, 1997), and the removal of vertebrate predators may therefore not always result in

251   decreases of invertebrate herbivore density. However, a recent meta-analysis of predator

252   exclusion studies found that exclusion of vertebrate predators reduced the density of invertebrate

253   predators and herbivores by the same magnitude, indicating that the release of vertebrate

254   predation pressure on invertebrate predators did not result in increased predation by invertebrate

255   predators on herbivores (Mooney et al., 2010). This may be due to intraguild predation, where

256   predators prey on each other; for example, it is estimated that about 20% of the diet of hunting

257   spiders is made of other spiders (Hodge, 1999).

258   Although we found that vertebrate predator exclusion was significantly related to

259   increases in density for all response groups, it is worth noting that the effect size was only

260   significantly different from zero for spider densities in the understory, and not for any other

261   individual response group or stratum (Figure 3). Spiders were also the only response group in

262   which the interaction between treatment and stratum was close to significant (Table 2). In their

263   meta-analysis Mooney et al. (2010) found that caterpillars and spiders exhibited the two strongest

264   responses in density to predator exclusion (based on effect sizes), followed by Hemiptera,

265   Coleoptera, and Hymenoptera. The consistent and strong effect of bird exclusion on caterpillars

266   in the meta-analysis reflects the fact that caterpillars are usually a favoured prey item of birds

267   (Robinson & Holmes, 1982; Marshall et al., 2002). However, during years and periods of the

268   season when caterpillar abundance is low most birds will switch to feeding on other arthropods,

269   including beetles and true bugs, rather than change foraging locations (Sample, Cooper &

270   Whitmore, 1993; Murakami, 2002). In our study, the peak caterpillar density occurred in the

271   lower and middle canopies during the early season and the understory during the mid season

272   (data not shown), which may have contributed to the unclear pattern of vertebrate exclusion on

273   caterpillars. However, we note that the four most abundant common insectivorous bird species observed in

274   our study area includes one ground forager (Ovenbird), one species that gleans in the understory and lower crown

275   (Black-capped Chickadee), and two species that glean in the main canopy (Red-eyed Vireo, Black-throated Green

276   Warbler) (Holmes, Bonney & Pacala 1979; Robinson & Holmes 1984; De Graaf, Tilghman &

277   Anderson, 1985).

278   Under most conditions, birds are able to limit forest arthropod abundance, especially that

279   of herbivorous insects (e.g. Holmes, Schultz & Nothnagle, 1979; Marquis & Whelan, 1994;

280   Philpott et al., 2004). However, there has been no clear consensus when considering differences

281   in bird predation pressure between vertical strata. Van Bael et al. (2003) found the effects of bird

282   predation to be higher in the canopy versus the understory, whereas Boege & Marquis (2006)

283   found that bird exclusion reduced arthropod density by same magnitude in both saplings and

284   mature trees. Our study is the first to consider this question in temperate forests; for most

285   arthropod groups in our survey, vertebrate predation pressure did not differ between vertical

286   strata, including between understory saplings and three levels of mature canopy. However, we did

287   find that vertebrate predation pressure was highest in the understory for spiders, the most

288   abundant arthropods in our system. More distinct differences in vertebrate predation pressure

289   between canopy strata might be seen in forest systems with higher densities of other arthropod

290   groups.

291   The increased arthropod densities that we observed on caged branches may have been due

292   to the exclusion of bats in addition to birds. Several tropical studies have found that using night

293   cage treatments to exclude bats alone resulted in a greater increase in arthropod density than

294   excluding birds only using day cage treatments (Kalka, Smith & Kalko, 2008; Williams Guillén,

295   Perfecto & Vandermeer, 2008), suggesting that measurements of the effects of cage exclosures

296   are actually measuring the effects of birds and bats combined. Bats in temperate forests seem to

297   exhibit some degree of niche partitioning, such that some species are canopy specialists, some are

298   sub-canopy and gap specialists, and some are habitat generalists (Jung et al., 1999). At least four

299   species of bat have been recorded in the Morgan Arboretum (Fabianek, Gagnon & Delorme,

300   2011), and it is therefore possible that bat predation may have contributed to the mortality of

301   arthropods on control branches.

302   We also cannot exclude the possibility that bat predation contributed to mortality in the

303   overnight bait trials; however, we observed no birds feeding near baits in the daytime bait trails

304   and therefore attribute all such predation events to invertebrates. These experiments indicated that

305   invertebrate predators were most active in the understory and lower canopy. This pattern was

306   primarily driven by ants, which accounted for the majority of predation events and whose

307   abundance in our study decreased in abundance with increasing height from the forest floor. Ants

308   may spend more time in the understory and lower canopy because of distance limits from colony

309   nest sites on the ground (Seifert 2008). However, studies in tropical forests have found ant

310   density and predation rates to be higher in the canopy than in the understory (Basset, Aberlenc &

311   Delvare, 1992; Olson, 1992), suggesting that ants will spend more time where their prey are more

312   abundant. Ants are likely to have been responsible a majority of the overnight removal of baits as

313   well; the dominant ant in our sites, *Camponotus pennsylvanicus*, is an aggressive and

314   predominantly a nocturnal forager, especially in late spring and early summer, though it forages

315   in lower numbers during the day (Klotz, 1984).

316   This research supports a view of the forest canopy that is heterogeneous with respect to

317   arthropod densities and refuge from natural enemies. Our study is the first to examine such

318   vertical heterogeneity within temperate forests, and our findings support the view that vertebrate

319   predators can have significant impacts on the densities of forest arthropods. It would be of

320   interest to conduct future research on this topic in other forest types, locations, and years with

321   higher densities of prey arthropods to better understand how these predator effects vary in space

322   and time.

323

ACKNOWLEDGMENTS

325   We thank C. Idziak and the Morgan Arboretum staff, J. F. Aublet, M. Larrivée, and C. Frost. S.C. Walker provided

326   statistical advice and comments. We thank D. Huber, M. Ulyshen, and an anonymous reviewer for comments and

327   suggestions on an earlier draft of this manuscript.

328

LITERATURE CITED

330   Aikens KR, Buddle CM. 2012. Small-scale heterogeneity in temperate forest canopy arthropods:

331   stratification of spider and beetle assemblages. *Canadian Entomologist* 144:526-537.

332   Barton KE, Koricheva J. 2010. The ontogeny of plant defense and herbivory: Characterizing

333   general patterns using meta-analysis. *The American Naturalist* 175:481-493.

334   Basset Y, Aberlenc HP, Delvare G. 1992. Abundance and stratification of foliage arthropods in a

335   lowland rain forest of Cameroon. *Ecological Entomology* 17:310–318.

336   Bates D, Maechler M, Bolker B. 2012. lme4: Linear mixed-effects models using S4 classes. R

337   package version 0.999999-0. http://CRAN.R-project.org/package=lme4

338   Bernays EA, Graham M. 1988. On the evolution of host specificity in phytophagous arthropods.

339   *Ecology* 69:886-892.

340   Berryman AA, Hawkins BA. 2006. The refuge as an integrating concept in ecology and

341   evolution. *Oikos* 115:192-196.

342   Boege K, Marquis RJ. 2006. Plant quality and predation risk mediated by plant ontogeny:

343   Consequences for herbivores and plants. *Oikos* 115:559-572.

344   Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulson JR, Stevens MHH, White JSS. 2009.

345   Generalized liner mixed models: A practical guide for ecology and evolution. *Trends in*

346   *Ecology and Evolution* 24:127-135.

347   Brown JL, Vargo S, Connor EF, Nuckols MS. 1997. Causes of vertical stratification in the density

348   of *Cameraria hamadryadella*. *Ecological Entomology* 22:16-25.

349   Carroll AL, Quiring DT. 1994. Intra-tree variation in foliage development influences the foraging

350   strategy of a caterpillar. *Ecology* 75:1978–1990.

351   Cornell HV, Hawkins BA. 1995. Survival patterns and mortality sources of herbivorous insects:

352   Some demographic trends. *The American Naturalist* 145:563-593.

353   Crawley MJ. 2005. *Statistics: An introduction using R.* West Sussex: John Wiley & Sons Ltd.

354   De Graaf RM, Tilghman NG, Anderson SH. 1985. Foraging guilds of North American birds.

355   *Environmental Management* 9:493-536.

356   Dodge HR. 1961. Parasitism of spruce budworm by *Glypta* and *Apanteles* at different crown

357   heights in Montana. *Canadian Entomologist* 93:222–228.

358   Emlen JM. 1966. The role of time and energy in food preference. *American Naturalist*

359   100:611-617.

360   Fabianek F, Gagnon D, Delorme M. 2011. Bat distribution and activity in Montréal Island green

361   spaces: Responses to multi-scale habitat effects in a densely urbanized area. *Ecoscience*

362   18:9-17.

363   Finkbeiner SD, Briscoe AD, Reed RD. 2012. The benefit of being a social butterfly: Communal

364   roosting deters predation. *Proceedings of the Royal Society B: Biological Sciences* 279:

365   2769-2776.

366   Grieco F. 2003. Greater food availability reduces tarsus asymmetry in nestling Blue Tits. *The*

367   *Condor* 105:599-603.

368   Hodge MA. 1999. The implications of intraguild predation for the role of spiders in biological

369   control. *The Journal of Arachnology* 27:351-362.

370   Holmes RT, Bonney, Jr. RE, Pacala SW. 1979. Guild structure of the Hubbard Brook bird

community: a multivariate approach. *Ecology* 60:512-520.

Holmes RT, Schutlz JC, Nothnagle P. 1979. Bird predation on forest insects: an exclosure experiment. *Science* 206:462-463.

Jeffries MJ, Lawton JH. 1984. Enemy free space and the structure of ecological communities. *Biological Journal of the Linnean Society* 23:269-286.

Jung TS, Thompson ID, Titman RD, Applejohn AP. 1999. Habitat selection by forest bats in relation to mixed-wood stand types and structure in central Ontario. *The Journal of Wildlife Management* 63:1306-1319.

Kalka MB, Smith AR, Kalko EKV. 2008. Bats limit arthropods and herbivory in a tropical forest. *Science* 320:71.

Klotz JH. 1984. Diel differences in foraging in two ant species (Hymenoptera: Formicidae). *Journal of the Kansas Entomological Society* 57:111-118.

Larrivée M, Buddle CM. 2009. Diversity of canopy and understorey spiders in north-temperate hardwood forests. *Agriculture and Forest Entomology* 11:225-237.

Lymberry A, Bailey W. 1980. Regurgitation as a possible anti-predator defensive mechanism in the grasshopper *Goniaea* sp. (Acrididae, Orthoptera). Journal of the Australian Entomological Society 19: 129-130.

MacArthur RH. Pianka ER. 1966. On optimal use of a patchy environment. *American Naturalist* 100:603-609.

Marquis RJ, Whelan CJ. 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. *Ecology* 75:2007-2014.

Marshall MR, Cooper RJ, DeCecco JA, Strazanac J, Butler L. 2002. Effects of experimentally reduced prey abundance on the breeding ecology of the Red-eyed Vireo. *Ecological Applications* 12:261-280.

17   17

395   Mooney KA, Gruner DS, Barber NA, Van Bael SA, Philpott SM, Greenberg R. 2010. Interactions

396   among predators and the cascading effects of vertebrate insectivores on arthropod

397   communities and plants. *Proceedings of the National Academy of Sciences* 107:7335-7340.

398   Murakami M. 2002. Foraging mode shifts of four insectivorous bird species under temporally

399   varying resource distribution in a Japanese deciduous forest. *Ornithological Science* 1:63-69.

400   Novotny V, Basset Y, Auga J, Boen W, Dal C, Drozd P, Kasbal M, Isua B, Kutil R, Manubor M,

401   Molem K. 1999. Predation risk for herbivorous insects on tropical vegetation: A search for

402   enemy-free space and time. *Australian Journal of Ecology* 24:477-483.

403   Olson DM. 1992. Rates of predation by ants (Hymenoptera: Formicidae) in the canopy,

404   understory, leaf litter, and edge habitats of a lowland rainforest in Southwestern Cameroon.

405   In: Hallé F, Pascal O (eds). *Biologie d'une canopée de forêt équatoriale —II. Rapport de*

406   *mission: Radeau des cimes Octobre Novembre 1991, Réserve De Campo, Cameroun*. Lyon :

407   Fondation Elf, 101-109.

408   Parker GG. 1995. Structure and microclimate of forest canopies. In: Lowman M, Nadkarni N

409   (eds). *Forest canopies: A review of research on a biological frontier*. San Diego: Academic

410   Press, 431-455

411   Philpott SM, Greenberg R, Bichier P, Perfecto I. 2004. Impacts of major predators on tropical

412   agroforest arthropods: comparisons within and across taxa. *Oecologia* 140:140-149.

413   Pinheiro J, Bates D, DebRoy S, Sarkar D., R Development Core Team. 2012. nlme: Linear and

414   nonlinear mixed effects models. R package version 3.1-105.

415   Pinzon J, Spence JR, Langor DW. 2013. Diversity, species richness, and abundance of spiders

416   (Araneae) in different strata of boreal white spruce stands. *Canadian Entomologist*

417   145:61-76.

418   Preisser E, Smith DC, Lowman MD. 1998. Canopy and ground level insect distribution in a

419   temperate forest. *Selbyana* 19:141-146.

420   R Core Team 2012. R: A language and environment for statistical computing. R Foundation for

421   Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL

422   http://www.R-project.org/.

423   Régnière J, Lysyk TJ, Auger M. 1989. Population density estimation of spruce budworm,

424   *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae) on balsam fir and white spruce

425   from 45-cm mid-crown branch tips. *Canadian Entomologist* 121:267–281.

426   Robinson SK, Holmes RT. 1982. Foraging behaviour of forest birds: the relationships among

427   search tactics, diet and habitat structure. *Ecology* 63:1918-1931.

428   Robinson SK. Holmes RT. 1984. Effects of plant species and foliage structure on the foraging

429   behavior of forest birds. *The Auk* 101:672-684.

430   Sample BE, Cooper RJ, Whitmore RC. 1993. Dietary shifts among songbirds from a

431   Diflubenzuron-treated forest. *The Condor* 95:616-624.

432   Seifert B. 2008. The ants of Central European tree canopies (Hymenoptera: Formicidae) – an

433   underestimated population? In: Floren A, Schmidl J (eds). *Canopy arthropod research in*

434   *Europe.* Nuremberg: Bioform Entomology, 157-173.

435   Sobek S, Tscharntke T, Scherber C, Schiele S, Steffan-Dewenter I. 2009. Canopy vs. understory:

436   Does tree diversity affect bee and wasp communities and their natural enemies across forest

437   strata? *Forest Ecology and Management* 258:609-615.

438   Stamp NE, Bowers MD. 1990. Variation in food quality and temperature constrain foraging of

439   gregarious caterpillars. *Ecology* 71:1031-1039.

440   Tscharntke T. 1997. Vertebrate effects on plant-invertebrate food webs. In: Gange AC, Brown VK

441   (eds). *Multitrophic interactions in terrestrial systems*. Oxford: Blackwell Science Ltd,

442   277-297

443   Uetz GW, Bischoff J, Raver J. 1992. Survivorship of wolf spiders (Lycosidae) reared on different

444   diets. *The Journal of Arachnology* 20:207-211.

445   Ulyshen MD. 2011. Arthropod vertical stratification in temperate deciduous forests: Implications

446   for conservation-oriented management. *Forest Ecology and Management* 261:1479-1489.

447   Van Bael SA, Brawn JD, Robinson SK. 2003. Birds defend trees from herbivores in a neotropical

448   forest canopy. *Proceedings of the National Academy of Sciences* 100:8304-8307.

449   Van Bael SA, Philpott SM, Greenberg R, Bichier P, Barber NA, Mooney KA, Gruner DS. 2008.

450   Birds as predators in tropical agroforestry systems. *Ecology* 89:928-934.

451   Vance CC, Smith SM, Malcolm JR, Huber J, Bellocq MI. 2007. Differences between forest type

452   and vertical strata in the diversity and composition of Hymenopteran families and Mymarid

453   genera in northeastern temperate forests. *Environmental Entomology* 36:1073-1083.

454   Vivan LM, Torres JB, Veiga AFSL. 2003. Development and reproduction of a predatory stinkbug,

455   *Podisius nigrispinus*, in relation to two different prey types and environmental conditions.

456   *BioControl* 48:155-168.

457   Williams-Guillen K, Perfecto I, Vandermeer J. 2008. Bats limit insects in a Neotropical

458   agroforestry system. *Science* 320:70.

459   Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009. *Mixed effects models and*

460   *extensions in ecology with R*. New York: Springer Science + Business Media, LLC.

461

Figure 1

Exclusion cage design and placement

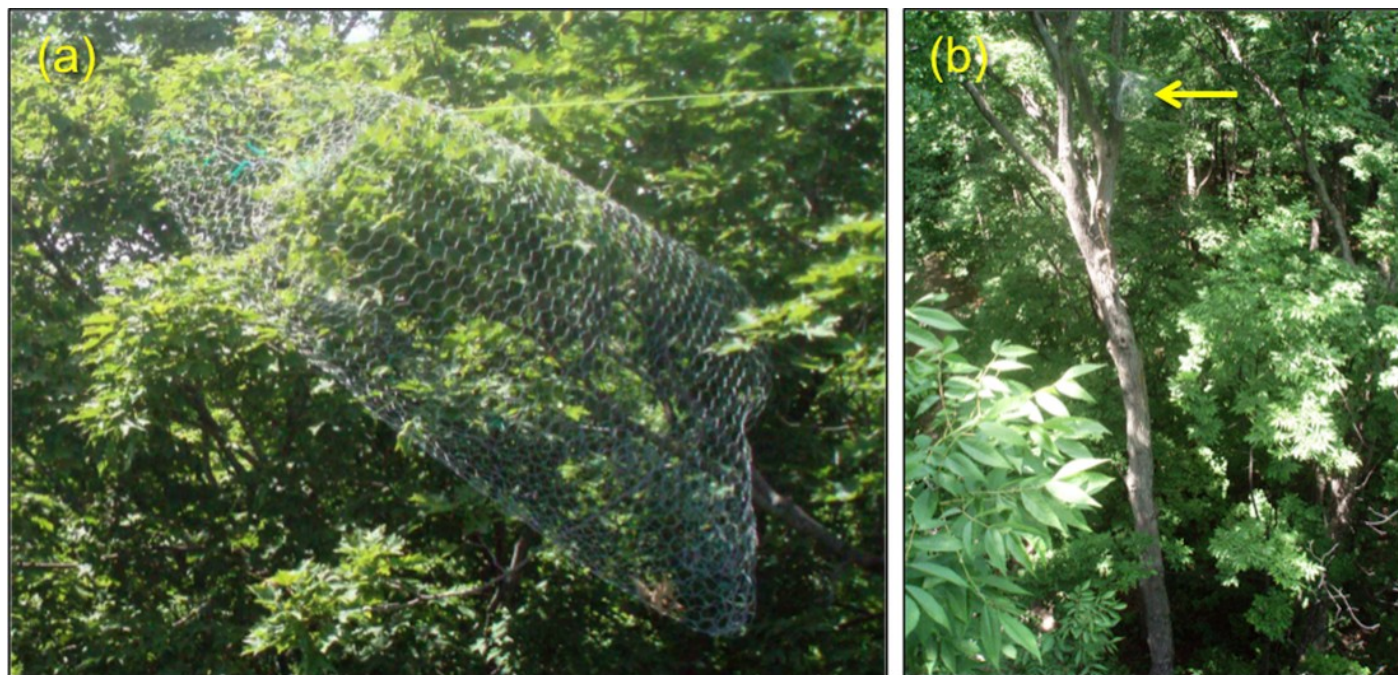
(a) Example of a wire mesh cage used to exclude vertebrate predators, (b) location of cage in the middle canopy of a tree.

Total individuals collected, by order and family

Table 1. Total individuals in arthropod orders and families collected during branch beating surveys in 20 sugar maple (*Acer saccharum* Marsh.) trees in four vertical strata (UN = understory; LC = lower canopy; MC = middle canopy; UC = upper canopy) in the Morgan Arboretum during June – September 2007; rank provides information on the total abundance of families.

Order	Family	UN	LC	MC	UC	TOTAL	Rank
Araneae	Agelenidae	6	0	0	0	6	26
	Araneidae	63	34	26	16	139	5
	Clubionidae	37	36	41	29	143	4
	Dictynidae	15	11	8	4	38	16
	Linyphiidae	24	9	5	7	45	15
	Philodromidae	12	48	25	19	104	7
	Salticidae	216	155	153	263	787	1
	Tetragnathidae	4	0	0	0	4	27
	Theridiidae	59	8	4	3	74	9
	Thomisidae	22	1	2	4	29	17
	Unidentified	48	39	33	12	132	.
Coleoptera	Bostrichidae	2	2	4	0	8	25
	Buprestidae	1	1	2	4	8	25
	Cantharidae	1	9	4	0	14	22
	Carabidae	1	0	0	0	1	30
	Cerambycidae	2	0	1	0	3	28
	Chrysomelidae	8	1	1	1	11	24
	Cleridae	0	1	1	0	2	29
	Coccinellidae	27	10	5	17	59	10
	Curculionidae	20	11	12	6	49	13
	Elateridae	2	0	0	0	2	29
	Lampyridae	18	6	3	0	27	18
	Latridiidae	2	7	2	1	12	23
	Oedomeridae	2	0	1	0	3	28
	Pyralidae	0	1	2	1	4	27
	Scirtidae	10	1	0	0	11	24
	Staphylinidae	1	9	7	1	18	21
	Tenebrionidae	29	56	45	23	153	3
	Unidentified	11	8	18	7	44	.
Dermaptera	Forficulidae	4	21	19	9	53	11
Hemiptera	Aphididae	4	13	4	3	24	19
	Cercopidae	0	0	0	1	1	30
	Lygaeidae	0	1	0	0	1	30
	Miridae	4	7	6	3	20	20
	Nabidae	1	2	1	0	4	27
	Pentatomidae	8	10	16	14	48	14

	Reduviidae	40	35	37	47	159	2
	Thyreocoridae	0	0	1	0	1	30
	Unidentified	1	3	6	4	14	.
Hymenoptera	Formicidae	57	15	3	2	77	8
Lepidoptera	Geometridae	21	42	38	21	122	6
	Lasiocampidae	0	2	1	0	3	28
	Limacodidae	0	2	0	1	3	28
	Lymantriidae	0	1	2	1	4	27
	Noctuidae	3	8	1	2	14	22
	Papillionidae	0	0	1	0	1	30
	Pyralidae	1	5	2	0	8	25
	Tortricidae	2	17	18	14	51	12
	Unidentified	1	10	13	3	27	18
Odonata	.	1	0	0	0	1	30
Opiliones	.	31	11	6	3	51	.
Psocoptera	.	0	0	0	1	1	30
Trichoptera	.	1	0	0	0	1	30
	TOTAL	**824**	**669**	**580**	**547**	**2619**	

Results of mixed effects models testing effects of predator exclusion and vertical stratum

Table 2. Results of mixed effects models testing the fixed effects of predator exclusion (cage vs. control) and vertical stratum (UN = understory; LC = lower canopy; MC = middle canopy; UC = upper canopy) on the density of various groups of arthropods surveyed from June-September 2007 on 20 sugar maple trees (*Acer saccharum* Marsh.), while considering the random effects of tree identification (not shown); comparisons between vertical strata are presented as stepwise contrasts. Bold text indicates significant p-values.

Response Group	Factor	DF	F	p	Comparisons
All arthropods	Treatment	1, 131	174.98	**<0.0001**	Cage > Control ****
	Stratum	3, 131	172.95	**<0.0001**	LC < UN ****
	Trt*Strat	3, 131	1.98	0.1196	MC < LC **
					UC < MC ****
Spiders	Treatment	1, 131	123.90	**<0.0001**	Cage > Control ****
	Stratum	3, 131	106.55	**<0.0001**	LC < UN ****
	Trt*Strat	3, 131	2.49	0.0635	MC < LC **
					UC < MC **
Beetles	Treatment	1, 131	47.55	**<0.0001**	Cage > Control ****
	Stratum	3, 131	43.16	**<0.0001**	LC < UN ****
	Trt*Strat	3, 131	1.55	0.2044	MC < LC
					UC < MC ****
True bugs	Treatment	1, 131	11.76	**0.0008**	Cage > Control ***
	Stratum	3, 131	5.44	**0.0015**	LC < UN *
	Trt*Strat	3, 131	0.24	0.8681	MC < LC
					UC < MC
Caterpillars	Treatment	1, 131	7.98	**0.0055**	Cage > Control **
	Stratum	3, 131	11.04	**<0.0001**	LC > UN
	Trt*Strat	3, 131	0.53	0.6638	MC < LC
					UC < MC **

Comparisons between strata were conducted using contrasts with backwards difference coding, significance of comparisons (t_{134}) designated by **** $p < 0.0001$; *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Figure 2

Mean arthropod density by treatment and stratum

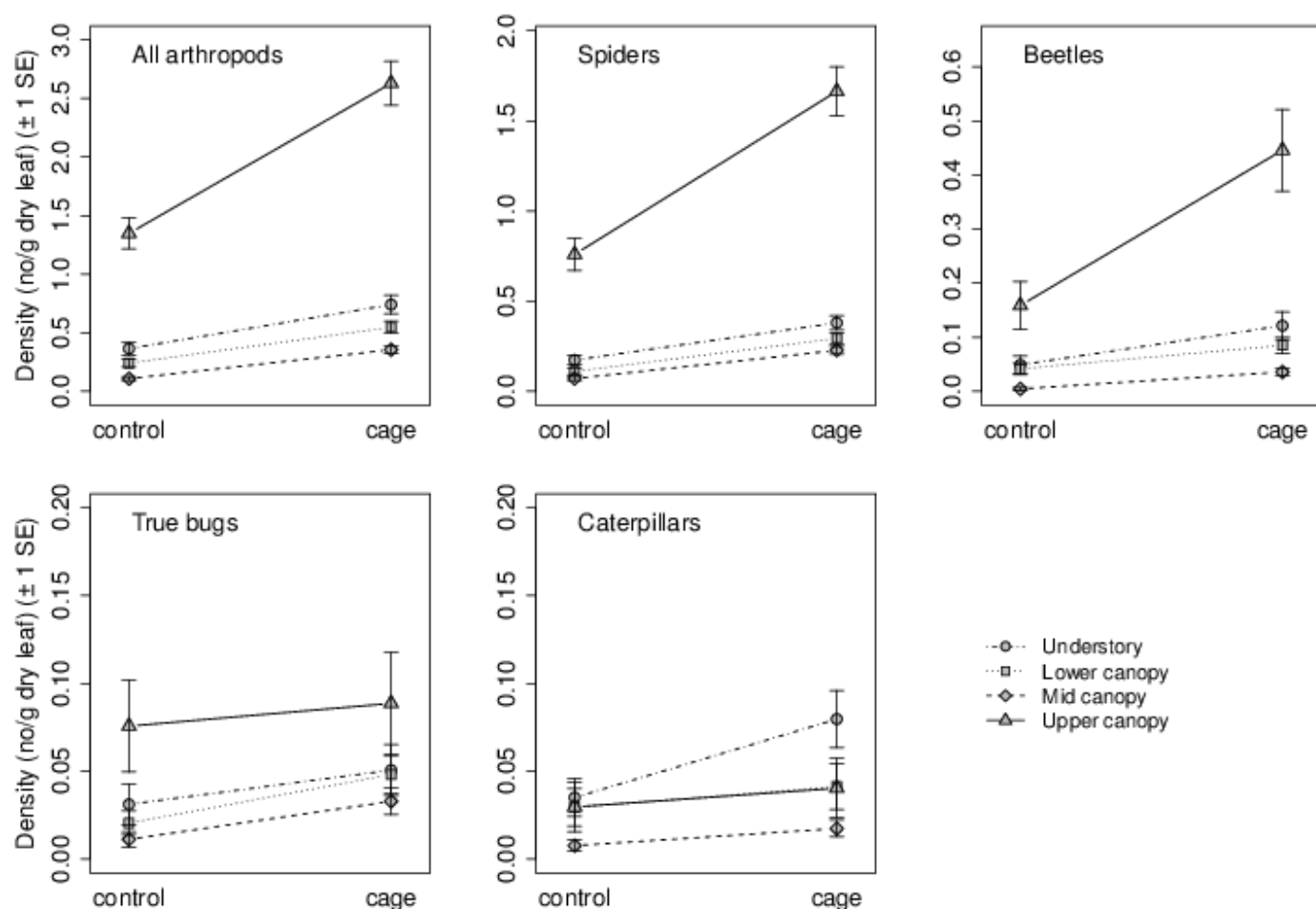
Mean arthropod density (+/- SE) surveyed from June-September 2007 on control and caged branches from 20 sugar maple (*Acer saccharum* Marsh.) trees across four vertical strata: understory (UN); lower canopy (LC); middle canopy (MC); and, upper canopy (UC). Means and standard errors are back-transformed predicted values from mixed effects models with tree identity as a random effect.

Bird species recorded by sight or by vocalizations

Table 3. Bird species recorded by sight or by vocalizations from May 28-June 5, 2007 in sugar maple (*Acer saccharum* Marsh.) stands of the Morgan Arboretum, within 100 m of plots used for predator exclusion trials. Percent relative abundance was calculated as the number of records for a given species divided by the total number of records.

Common name	Scientific name	Records	Rel. abd. (%)
Yellow-bellied Sapsucker	*Sphyrapicus varius*	21	5.7
Downy Woodpecker	*Picoides pubescens*	2	0.5
Northern Flicker	*Colaptes auratus*	5	1.4
Pileated Woodpecker	*Dryocopus pileatus*	5	1.3
Eastern Wood-Peewee	*Contopus virens*	8	2.2
Great-crested Flycatcher	*Myiarchus crinitus*	14	3.8
Empidonax Flycatcher	*Empidonax* sp.	1	0.3
Philadelphia Vireo	*Vireo philadelphicus*	18	4.9
Warbling Vireo	*Vireo gilvus*	1	0.3
Red-eyed Vireo	*Vireo olivaceus*	39	10.5
Bluejay	*Cyanocitta cristata*	10	2.7
American Crow	*Corvus brachyrhynchos*	44	11.9
Black-capped Chickadee	*Poecile atricapillus*	26	7.0
White-breasted Nuthatch	*Sitta carolinensis*	1	0.3
Veery	*Catharus fuscescens*	7	1.9
American Robin	*Turdus migratorius*	3	0.8
Northern Parula	*Setophaga americana*	15	4.1
Yellow Warbler	*Setophaga petechia*	1	0.3
Chestnut-sided Warbler	*Setophaga pensylvanica*	12	3.2
Magnolia Warbler	*Setophaga magnolia*	1	0.3
Cape May Warbler	*Setophaga tigrina*	1	0.3
Black-throated Green Warbler	*Setophaga virens*	27	7.3
Warbler sp.	*Setophaga* sp.	2	0.5
Black-and-white Warbler	*Mniotilta varia*	2	0.5
Ovenbird	*Seiurus aurocapilla*	39	10.5
Scarlet Tanager	*Piranga olivacea*	1	0.3
Rose-breasted Grosbeak	*Pheuticus ludovicianus*	4	1.1
Northern Cardinal	*Cardinalis cardinalis*	3	0.8
Chipping Sparrow	*Spizella passerina*	1	0.3
Red-winged Blackbird	*Agelaius phoeniceus*	9	2.4
American Goldfinch	*Carduelis tristis*	47	12.7

Identifiable arthropod predators observed feeding on mealworm larva baits

Table 4. Identifiable arthropod predators observed feeding on mealworm larva baits in the

Morgan Arboretum during trials conducted in June and July 2007, plus three predatory ant

species collected from foliage on the same trees but not directly observed feeding on baits.

Order	Family	Species
Araneae	Salticidae	*Eris militaris*
Opiliones	Phalangidae	*Odiellus pictus*
	Sclerosomatidae	*Leiobunum aldrichi*
Hemiptera	Reduviidae	*Zelus luridus*
Hymenoptera	Formicidae	*Camponotus pennsylvanicus*
		Aphaenogaster spp.*
		*Lasius alienus**
		*Leptothorax longispinosus**

* These ant species were not directly observed predating mealworm larvae, but were collected from foliage on the same trees and are known to feed on arthropods

Figure 3

Effect sizes by stratum for predator exclusion treatment

Effect sizes (Cohen's d) and 95% confidence intervals for the effects of a predator exclusion treatment on arthropod density surveyed from June-September 2007 on branches from 20 sugar maple (Acer saccharum Marsh.) trees in four vertical strata: understory (UN); lower canopy (LC); middle canopy (MC); and, upper canopy (UC). Effect sizes and 95% CIs were calculated using predicted values from mixed effects models with tree identity as a random effect.

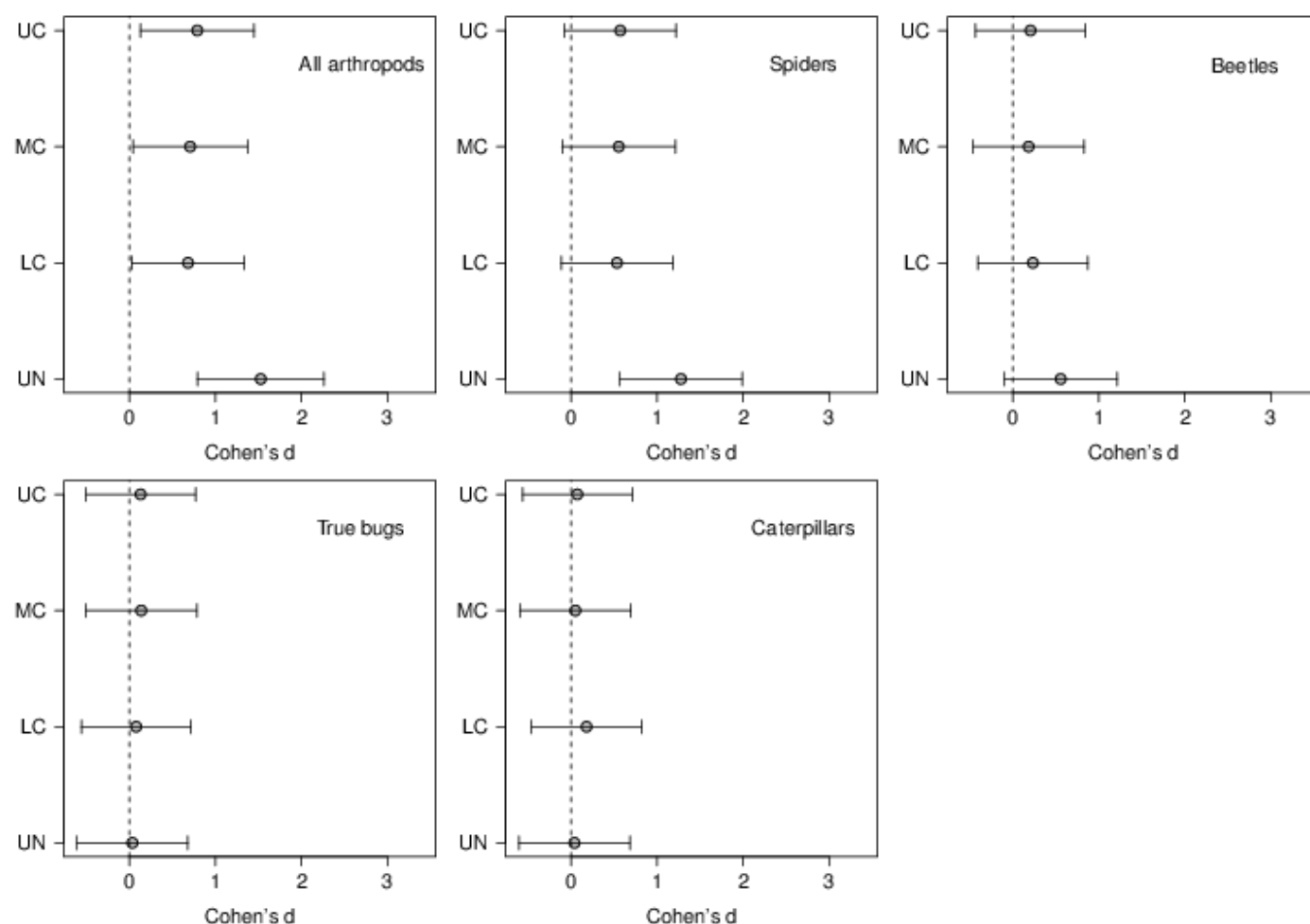



Figure 4

Proportion of mealworm bait predated by stratum

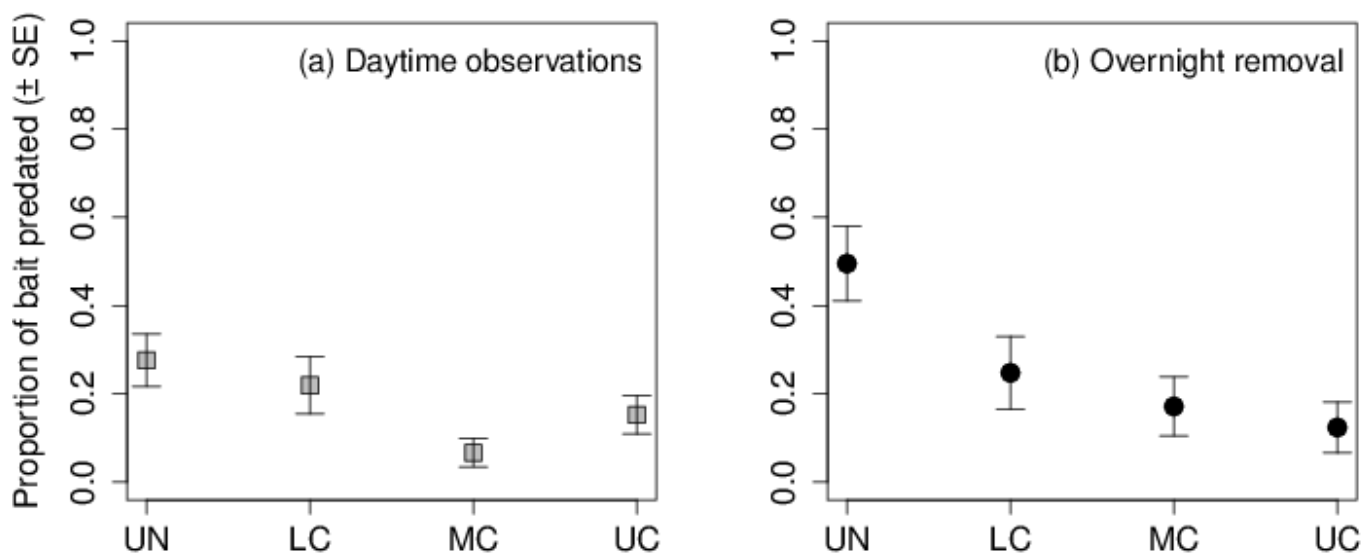
Proportion of mealworm larvae bait predated (± SE) on sugar maple (*Acer saccharum* Marsh.) branches (a) during daytime observations, and (b) removed after an overnight period, in four vertical strata: understory (UN); lower canopy (LC); middle canopy (MC); and, upper canopy (UC).

Results of binomial glm testing the effects of vertical stratum on predation

Table 5. Results of binomial generalized linear mixed effects models testing the fixed effects of vertical stratum (UN = understory; LC = lower canopy; MC = middle canopy; UC = upper canopy) on the proportion of mealworm bait predated during two trial periods, while considering the random effects of tree identification (not shown); comparisons between vertical strata are presented as stepwise contrasts. Bold text indicates significant p-values.

Predation period	Comparison	Est.	SE	Z	p
Daytime	LC < UN	-0.37	0.35	-1.07	0.2849
	MC < LC	-1.59	0.49	-3.20	**0.0014**
	UC > MC	-1.06	0.51	2.06	**0.0397**
Overnight	LC < UN	-1.49	0.35	-4.26	**<0.0001**
	MC < LC	-0.60	0.39	-1.55	0.1220
	UC < MC	-0.54	0.45	-1.20	0.2310