COMMUNITY ASSEMBLY OF SAPROPHAGOUS ARTHROPODS OF BIRD NEST BOXES

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ABSTRACT

The patterns of community assembly of saprophagous arthropods in bird nest boxes are poorly understood. Saprophagous arthropods from nest boxes of House Sparrows (*Passer domesticus* L.) and Tree Swallows (*Tachycineta bicolor* (Vieillot)) in southern Quebec were collected over two sampling periods (immediately post-fledging, and 60 days post-fledging) in 2007. A total of 5366 specimens (10 families, 15 species) were collected at the first sampling period and 3794 specimens (seven families, 11 species) at the second sampling period. For both sampling periods, two different methods of null model analyses revealed different patterns of community structure; random in one case, and positive co-occurrence in the other. Stochastic colonization processes probably explain the apparent random patterns and deterministic processes, such as facilitation by early colonizing species explain some of the patterns of species co-occurrence. However, a larger spatial and temporal scale of study is necessary to understand them more fully.

RÉSUMÉ

Les modèles des communautés d'arthropodes saprophages dans les nids des maisons d'oiseaux sont faiblement compris. Les arthropodes saprophages retrouvés dans les nids des maisons habitées par les moineaux (*Passer domesticus* L.) et les hirondelles bicolores (*Tachycineta bicolor* (Vieillot)) dans le Sud de la province de Québec ont été collectés à travers deux périodes d'échantillonnage (immédiatement après maturation, et 60 jours après maturation) au cours de l'année 2007. Un total de 5 366 spécimens (10 familles, 15 espèces) ont été collectés durant la première phase d'échantillonnage et 3 794 spécimens (sept familles, 11 espèces) lors de la seconde phase. Pour les deux périodes d'échantillonnage, deux différentes méthodes d'analyses de modèles nul ont révélé des modèles de structure des communautés différents; la première aléatoire et la seconde de co-occurrence positive. Le processus de la colonisation stochastique explique probablement le modèle aléatoire apparent et le processus déterminant comme la colonisation hâtive des espèces pourrait expliquer certains modèles de co-occurrence des espèces. Toutefois, une étude plus étendue dans l'espace et le temps serait nécessaire pour les comprendre entièrement.

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INTRODUCTION AND LITERATURE REVIEW

One of the principal goals of community ecology is to understand how the diversity (species richness) and abundance of species come together to structure species assemblages (MacArthur 1960, MacArthur & Wilson 1963, Diamond 1975, Connor & Simberloff 1979, Weiher & Keddy 1999, Gotelli & Ellison 2002). Even before MacArthur & Wilson's (1963) work on island biogeography, there were questions related to how many species exist in one place at any given moment and the numbers of individuals of these species (e.g. Gleason 1922, Fisher et al. 1943, Preston 1948). These questions translate directly to the processes that create these communities; that is, how are these communities assembled and structured, and what are the reasons for the resultant patterns of assembly and structure?

Patterns and Processes of Community Assembly

Initially, community assembly was deemed to be the result of competition that manifests itself in niche-based models of structure (Hutchinson 1957). Beginning with Diamond's (1975) assembly rules, there has been a constant debate between advocates of deterministic or stochastic processes that form species assemblages. Diamond (1975) posited that species assemblages were primarily formed by competition; communities in which species competed for limited resources were structured according to the varying competitive abilities of those species. The resulting pattern was non-random. The community assembly rules included checkerboard patterns of distribution; certain species that almost always occurred together, and, at the other end of the spectrum were species that never co-occurred, producing “forbidden species combinations” (Diamond 1975).

In response to Diamond’s assembly rules and the non-random patterns of assembly that were the result of these rules, Connor & Simberloff (1979) questioned whether or not the patterns of assembly that Diamond attributed to interspecific competition could not equally probably be the result of random processes. By using randomizations in the form of Monte Carlo simulations, Connor & Simberloff demonstrated that the same patterns could also result from the random assembly of the community.

Since that time, many studies have equivocally supported either the non-random or random patterns of assembly. The advent of Hubbell’s (2001) unified neutral theory has only added to the debate. Essentially the ecological equivalent of genetic drift, it argues that the assemblies are created by stochastic processes. However, unlike previous theories describing stochastic processes, Hubbell’s theory does not argue that species are treated equally, but rather that individuals are treated as equal. All individuals are seen has having the same probability of procreating or dying, and that the varying dispersal ability of individuals is one important factor responsible for patterns of abundance (Bell 2000, Hubbell 2001). In this context, dispersal is viewed as a stochastic event that is not tied to species or individual interactions. As with earlier theories of biogeography, dispersal plays an important role in the structuring of communities. There has been a large body of literature that has examined the role of dispersal, and, more recently, the importance of historical contingency in the structuring of communities. Recently, studies have attempted to demonstrate that both stochastic (random) and deterministic (non-random) processes occur when structuring communities (Gravel et al. 2006, Ellwood et al. 2009). The joint structuring of the communities by both deterministic and stochastic processes is largely dependent upon scale, both in space and time, with stochastic (dispersal) processes at one end of the continuum and deterministic (niche) processes at the other (Gravel et al. 2006)..

The importance of dispersal in the structuring of communities has long been recognized. The order of arrival of a species (or an individual of a species) has been shown to have direct consequences on the species that arrive thereafter (Sutherland 1974, Connell & Slayter 1977, Shulman et al. 1983, Almany 2003, Collinge & Ray 2009, Geange & Stier 2009). First studied as an element of succession, the concept that the order of arrival (priority effects) influences the structure of communities, and that it is possibly a stochastic process was investigated thoroughly by Drake (1990, 1991). He theorized that, all factors being equal, varying dispersal would result in initially identical community structures diverging due to the random and varying dispersal abilities. In contrast, deterministic niche theory would predict that communities would converge at a singular endpoint, which would vary only due to changing environmental conditions. If only dispersal, of either individuals or species, is allowed to vary stochastically, then the resultant community composition is essentially random, determined by priority effects. The sequence of arrival would be a factor in the eventual composition of a community. The historical contingency of a community would ultimately dictate its composition. However, recent studies suggest the effect of historical contingency is temporary, and that, depending upon the rate of change in any given community, more deterministic processes begin to assert themselves upon community structure over the course of time (Collinge & Ray 2009).

Null Models in Community Analysis

To determine if patterns in community structure, and thus community assembly prior to that, are stochastic or deterministic, an analysis is required that can distinguish between the two. One of the most powerful analytical tools available to test for randomness is the null model. A null model is a statistical technique that allows for patterns to be compared against randomizations of the same data, whereby it is possible to see if the observed pattern differs significantly from patterns created by chance alone (Gotelli & Graves 1996). Null models use randomizations of real data to approximate stochastic processes. The iterations of the randomization of the data are used to create a distribution. This distribution serves as a proxy for stochastic processes, creating a pattern that could arise by chance alone. A particular index must be chosen as a test statistic, and when the mean of the indices generated by the simulations is compared against the index generated by the real data, the probabilities resulting from the distribution allow one to say whether or not the observed pattern could happen as a result of stochastic processes, or if, in the case of community assembly, if species interactions structure the assemblage.

Since Connor & Simberloff (1979) used a primitive form of the null model to reanalyze Diamond's data sets, null models have gained popularity, being used for tests of biogeographical patterns (Colwell & Lees 2000), species co-occurrence (Gotelli 2000, Gotelli & McCabe 2002, Meyer & Kalko 2008), and community assembly (Gotelli & Graves 1993, Gotelli & Ellison 2002, Rugiero & Luiselli 2007). At the most basic level null models are created by the randomizations of presence-absence matrices. Certain elements of a matrix can vary stochastically, while others are (sometimes) held fixed, mimicking an ecological constraint found in the real data set (Gotelli & Graves 1996). This is most often achieved by preserving either the row or the column totals of a matrix. However, the model is sensitive to the degree of constraint. If the model is not constrained enough, then there is a risk that the model will be overly prone to type II statistical error. On the other hand, if the model is constrained too much, then it becomes overly prone to a type I statistical error (Gotelli 2000).

Despite their statistical power, null models are not tests for mechanistic processes (Gotelli & Graves 1996, Gotelli & McGill 2006). Only the patterns that emerge from ecological mechanisms can be observed (Gotelli 2001). A pattern may appear to be random relative to the mechanism being tested. Thus, a random pattern is indicative of a situation where there is no obvious mechanism or mechanisms structuring an assemblage. On the other hand, a non-random pattern can be seen to inform of a mechanism. That is, an “ecological constraint” or multiple constraints can be seen to be acting on the assemblage. If species interactions (a form of ecological constraint) structure a community, the pattern that emerges will be non-random. The null model itself, though, will not be able to detect what constraints might be acting to structure the assemblage.

One important aspect of null model analysis is the use of a valid regional source pool to construct presence-absence or abundance matrices. The regional species pool is the “reservoir of species that are potentially able to exist in this community” (Dupre 2000). The construction of these source pools relies heavily on past sampling efforts and accurate taxonomic knowledge of the species that exist in a given area (Gotelli & Graves 1996). Scale is also an important consideration, as changes in scale can radically affect how a species pool is defined (Swenson et al. 2006). In order to test for patterns of assembly it is necessary to have a valid assessment of the number and diversity of species that have the potential to create the assemblage (Magurran 2004).

One of the criticisms of null models is that they cannot differentiate between patterns that are due to current processes or to historical processes that can no longer be detected (Drake 1990). However, this can be avoided, at least in model or semi-controlled systems, by the sterilization of all materials. This ensures that there is a “clean slate” from which the study can start, and thus removes any possibility of undetectable historical processes confounding the interpretation of current patterns of assembly.

The Study System: Arthropods in Bird Nests

Arthropods are a dominant component of the Earth’s fauna, and thus knowledge of the processes that structure their assemblages is useful, if not integral, to understanding how these communities function. The fauna associated with bird nests is dominated by arthropods (Hicks 1959, Riley 2000). Although much study has been devoted to arthropods associated with bird nests, most has focused on parasitic species of Diptera or Acarina that have an impact upon avian fitness (Dawson & Bortolotti 1997, Whitworth 2003, Puchala 2004, Proudfoot et al. 2006). The little work has been done on non-parasitic species has focused almost exclusively on inventories of species (e.g., McAtee 1927, Hicks 1959, Iwasa et al. 1995, Riley 2000) and taxonomic descriptions and revisions (e.g., Grimaldi 1997, Gilbert & Wheeler 2007) with only a few studies examining the arthropod fauna from an ecological perspective (e.g. Bajerlein et al. 2006). Previous studies of arthropods occurring in bird nests have documented diverse assemblages. Iwasa et al. (1995) reared 4623 specimens representing 23 species of Diptera from nest material in Japan. These included specimens from the families Anthomyiidae, Fannidae, Muscidae, Calliphoridae, Heleomyzidae, Sphaeroceridae, Sepsidae, and Stratiomyidae, among others. In a two year study conducted at the same sites used in this study, Riley (2000) catalogued over 90 000 specimens representing 71 species from 13 insect orders. The highest abundance was recorded for the mite species *Dermanyssus hirundinis* Hermann (Acarina, Dermanyssidae) which was directly linked to the presence of the birds in the nest. Additionally, Siphonaptera (two species, 893 individuals), Coleoptera (162 individuals from 13 families), and Diptera were present in high numbers. Of the dipterans, notable dominant species included *Neossos* *marylandicus* Malloch (Heleomyzidae) and *Carnus hemapterus* Nitzsch (Carnidae), both of which are bird nest specialists, rarely collected outside of bird nests, and which have at least one life stage that is saprophagous.

The determinants of arthropod community structure in bird nests have not been researched and are poorly understood. Three distinct possibilities exist as to the organization of the arthropod community structure. It could be completely random, where any species that arrives at a nest and finds it a suitable habitat will colonize it. It could also be a "strong" assemblage, where the same group of species is consistently found in all nests and whose individual components are necessary for the community to function as a whole. The third possibility is that certain species exclude other species (Diamond's "forbidden species combinations"), and that primary colonization by one of the competing species automatically excludes the other from the nest. However, it is important to note that any particular assemblage will not remain static in time. The pattern of assemblages will change over a given period of time, and the changes that occur in the species composition of the nests will allow for an elucidation of the differences between "colonizers" (the species that arrive at a nest), and the "establishers" (the species who remain in a nest) (Drake 1991).

For the purpose of this study, the term community refers only to the organisms (in this case, arthropods) that live inside the bird nest box. This definition conveniently avoids the pitfalls associated with varying definitions of communities that are often phylogenetically too narrow or broad, or operate on wildly different levels of scale (Drake 1990).

Bird nest boxes provide ideal study sites in which to test hypotheses related to arthropod community ecology. They represent semi-closed systems in which it is possible to minimize “noise” that could interfere with the interpretation of results. For the purpose of this study the nest box represents a discrete habitat patch, with each nest box acting as a replicate. Nest boxes can also be completely sampled for arthropod fauna. Every individual within the nest box can be accounted for, provided that the specimen is in good condition and that adequate taxonomic knowledge exists for the species. Groups of bird nest boxes also provide micro-scale geographical and spatial variation in which it should be possible to test for the randomness of colonization patterns, specifically regarding saprophagous species in which phoresy or ectoparasitism have not been documented. Bird nest boxes are also easily sterilized between breeding seasons, which removes any of the potential for historical processes to impact upon the interpretation of observed patterns.

For the purpose of this study, I use the term “arrival” and “colonization” as synonymous. The term “establishment” reflects those species that have arrived or colonized a nest box and then remained for a period of time.

Objectives, Questions and Hypotheses

The primary objective is to determine if the patterns of community assembly of saprophagous arthropods in bird nest boxes are random or non-random. If the pattern is seen to be non-random, then it is apparent that some ecological constraint is functioning to structure the community. This can be broken down into two components. The first is the determination of which species arrive at the next box (the pattern of colonization), and the second is the determination of; which species remain in the nest box after a specified period of time (the pattern of establishment).

The Pattern of Colonization

The first question is whether or not the pattern formed by the initial species colonizing the nest box is random or non-random. The null hypothesis is that the saprophagous arthropod species found in bird nest boxes form a random pattern. The alternative hypothesis is that the saprophagous arthropod species found in bird nest boxes form a non-random pattern.

The Pattern of Establishment

The second question asks if the assembly of saprophagous arthropods that remain in the bird nest boxes after a set period of time forms a random or non-random pattern. The null hypothesis is that the pattern of remaining saprophagous arthropods is a random pattern. The alternative hypothesis is that the saprophagous arthropods that remain in the bird nest box form a non-random pattern. If the pattern is a non-random pattern, then does the assemblage of remaining saprophagous arthropods form a nested subset when compared to the initial colonizers of the nest box? The null hypothesis is that the assemblage does not form a nested subset. The alternative hypothesis is that the assemblage of remaining saprophagous arthropods in the bird nest box form a nest subset of the initial colonizers. For all of the questions the null hypotheses and the alternative hypotheses are equally informative. They both have the ability to demonstrate pattern, and, in the case of the nested subsets, might infer a possible mechanism for the pattern.

MATERIALS AND METHODS

Study Sites

The project was conducted at two sites on the western end of the Island of Montreal, Quebec, Canada: the Macdonald Campus Farm of McGill University, and Stoneycroft Wildlife Area, a small wildlife refuge. The study took place during the spring, summer, and autumn of 2007.

The Macdonald Campus Farm (108 ha, 45°24’43” N, 73°56’28” W, elev. 32 m) is used primarily as an agricultural teaching farm, with the land use consisting of fields of corn or clover, some grazing pasture for cattle, and grassed areas surrounding human structures. This site contained 23 nest boxes that have, in the past, been primarily used by House Sparrows (*Passer domesticus L.*) although there has been some documented nesting by Tree Swallows (*Tachycineta bicolour Vieillot*) (Riley 2000). Three of these original nest boxes were inaccessible and thus excluded from the study. An additional 22 nest boxes were erected on the farm during early April 2007 to bring the total number of nest boxes to 42. The nest boxes were mounted on telephone poles or metal stakes erected specifically to support the nest boxes, and all were between 2.5 m and 4 m from the ground. The majority of the nest boxes were situated so that there was a 15 m interval between individual boxes.

The Stoneycroft Wildlife Area (22 ha, 45°25’46” N, 73°56’18” W, elev. 43 m) is approximately 1 km north of the Macdonald Campus Farm. It contains numerous habitat types, but mainly consists of abandoned agricultural fields, semi-permanent wetlands, mature beech-maple forest, and hawthorn scrub. The 28 next boxes in the Wildlife area are all at the edge of the wetland area, in the abandoned agricultural fields, or at the edge of the hawthorn. In previous years the nest boxes were used by House Sparrows and Tree Swallows (Riley 2000, Pers. Observ.). Fourteen additional nest boxes were built and erected during early April 2007 to bring the total at the site to 42. The nest boxes at the Stoneycroft site were mounted on metal poles between 2 m and 3m from the ground. There were two exceptions; one nest box was attached to a small building while the other was located on the top of a fence post. The nest boxes were placed so that the minimum distance between any two boxes was 10 m. All nest boxes at both study sites were wooden, and were approximately 25 cm high, 10 cm deep, and 10 cm wide, with an entrance hole diameter of 35 mm. Prior to the breeding season, the nest boxes that had been erected in previous years were emptied and thoroughly cleaned, sterilized with a bleach solution, and then rinsed several times with water to flush any remaining bleach solution. This removed any arthropods that might have been present in the nest box from the previous year.

Nest Box Monitoring

Nest boxes were monitored every two to three days beginning in early April as soon as the new nest boxes were erected. Monitoring was conducted by observing the nest box from a distance through binoculars; nest boxes were not approached during the duration of occupancy by birds. The species using the nest, nest-building and feeding activity of adult birds at the nest box, territorial behaviour, and the presence of young (based on cries from the nest box) were all recorded. Once a nest box was determined to be occupied and active, observations were made every second day. When no more activity was seen at the nest box after two consecutive observations, the young were considered to have fledged and the contents of the nest box were ready for sampling.

If adults were seen bringing nest material to a box, but were no longer observed during the time period for incubation and fledging, the nest was considered to have been abandoned and was excluded from the study because of the difficulty in determining the precise time of abandonment. Furthermore, abandoned nests were not active for the same length of time as nests from which young fledged, and thus would have had less time for potential colonization by arthropods. Additionally, nests that showed obvious signs of predation by Red Squirrels

(*Tamiasciurus hudsonicus* Erxleben) were also considered abandoned and excluded from the study.

Sample Collection

Once a nest box had been classified as having successfully fledged young, two samples of the nest material, of roughly equal volume and mass, were removed from the nest box. Before being removed from the nest boxes, the nest material was divided using a garden trowel to bisect the nest material along the vertical axis, and then separated with the trowel and a chemist's spatula for the finer material. The sample was then scraped or lifted into a plastic zip-lock bag for transport back to the lab. The first sample (T) was taken to extract the saprophagous arthropod species that had arrived, or colonized the nest box initially. The second sample (T+60) was taken 60 days after the initial sample was obtained. This second sample was used to determine the saprophagous arthropod species that had remained, or established themselves in the nest box, or additional species that had arrived in the interim.

Once in the laboratory the samples of nest material were placed in emergence traps, designed so that there was one elevated exit and one exit on the floor of the trap. A small jar containing propylene glycol as a preservative was affixed to each exit. The emergence trap was used to collect adults emerging from larvae, pupa, or puparia. Emergence traps were chosen over other systems (i.e. berlese funnels) of collecting arthropods from the nest box material as it allowed for the collection of both emerging adult individuals as well as larvae. For most holometabolous insects, adults are more easily identified than immature stages. The elevated exit was used to primarily collect dipterans, which tend to fly upwards as adults while the floor exit was used for coleopterans or other arthropods that primarily walk. The nest material remained in the emergence trap until no further arthropods were observed to have entered the attached jars. The jars were then removed, and the specimens were transferred to 70% ethanol. After the emerged specimens were removed, the nest material inside the emergence trap was also placed in 70% ethanol.

The preserved nest material was examined after removal from the emergence trap in order to retrieve any remaining larvae or pupae. Small portions of nest material were placed in a large Petri dish filled with water, causing the majority of the specimens to float to the top. All specimens obtained from the nest material in this manner were placed in 70% ethanol.

Small specimens of Diptera were chemically dried using hexamethyldisilazane (HMDS), and large flies were dried using ethyl acetate. Coleoptera were air-dried. Dried specimens were then pinned or pointed. Specimens of other orders were kept in 70% ethanol. Specimens were identified initially to the family level and at this point specimens belonging to families in which there are no documented records of saprophagy were removed. The remaining specimens were identified to genus, or morphospecies. Psocoptera were identified using Mockford (1993). Coleoptera were identified using Marshall (2006) and Downie and Arnett (1996). Diptera were identified using McAlpine et al. (1981, 1987) and Ferrar (1987) for the immature stages. Specimens identified in this study are deposited at the Lyman Entomological Museum, McGill University (Ste-Anne-de-Bellevue, QC).

Statistical Analyses

To determine if the saprophagous arthropods from the nest boxes of the two species of birds could be pooled for subsequent analyses, faunal similarity was calculated using the Morisita-Horn index. This index is considered less sensitive to species richness and sample size than other biodiversity indices (Wolda 1981). However, it is highly sensitive to the most abundant species, and thus the raw abundance data were square-root transformed prior to analysis, as suggested by Clarke & Warwick (2001). EstimateS Version 8.2 (Colwell 2009) was used to calculate the Morisita-Horn index. To test for differences in the raw abundance between the nests of the two bird species, a two-tailed t-test was used.

Null Model Analysis

Two null model analyses were used to determine if the pattern of assembly of the saprophagous nest box arthropods appeared random or non-random. Species data from the nest box contents, with singletons removed, were entered into a presence-absence matrix and analyzed using a co-occurrence null model in EcoSim version 7.72 (Gotelli & Entsminger 2010).

The first analysis was conducted using a sequential swap algorithm with fixed row totals and equiprobable column totals and was run for 5000 iterations. Setting the column totals to equiprobable in the randomizations is based on the assumption that every species has an equal opportunity to colonize each nest box. This ensures that, in the randomizations, the nest boxes in which no species were observed have just as much chance of containing individuals.

The second analysis was performed in the same manner as the first, but keeping the column totals fixed. Several nest boxes yielded no specimens, and thus fixed column totals preserve these zero sums for these nests in the randomizations. This approximates a scenario where the likelihood of every individual colonizing a site is not equal. The probability of a co-occurrence happening by chance alone was determined using the C-score index (Stone & Roberts 1990) as this score is less prone to Type I and Type II errors than other indexes (Gotelli 2000). Based upon Diamond’s (1975) assembly rules, the C-score index measures the checkerboard pairs that are present in a presence/absence matrix. The higher the C-score index value, the higher the number of checkerboard pairs. The C-score index serves as an indicator of species interactions. In a community that is structured by species interactions, the C-score would be higher than in a community that is not (Gotelli & Entsminger 2010). The standardized effect size (SES) was also calculated for the analyses. As it is measured in terms of standard deviations, the SES allows comparisons between studies (Gotelli & McCabe 2002, Gotelli & Entsminger 2010). The SES is calculated by:

Observed index - mean(simulated indices)/standard deviation(simulated indices)

If the SES is > 2.0 or < -2.0, generally, it is statistically significant (Gotelli 2000). The null model analysis of species co-occurrence patterns for the saprophagous arthropods of the nest box T+60 samples was performed in the same manner as with the first (T) samples.

Cluster Analysis

To ascertain how the nest boxes grouped together in relation to the community composition of saprophagous arthropods at time T and time T+60 a cluster analysis was performed using JMP version 8.0 (SAS Institute 2010). The analysis was performed using hierarchical clustering with Ward's method, which calculates distances based on similarities. Due to the magnitude of difference that existed between the number of individuals in the samples, the data were square-root transformed prior to analysis.

RESULTS

Nest Box Samples

Of the 84 nest boxes erected, 26 were deemed to be active. Twelve of the active nests were at the Stoneycroft site, the remaining 14 were at the Macdonald Farm site.

Only five nest boxes from the Stoneycroft site were used in analyses, all of which were used by Tree Swallows. Of the other seven active nests, two were predated by red squirrels, one was abandoned for unknown reasons and one successfully reared young House Sparrows, but in the one day interval between fledging and the collection attempt, the nest contents were cleared by unknown means. Two nest boxes were used by House Wrens (*Troglodytes aedon Viellot*) and one by Great Crested Flycatchers (*Myiarchus crinitus L.*). Although the nest material was collected from these nest boxes, they were excluded from analyses because including additional species of birds would introduce extra variables that could obscure patterns.

At the Macdonald Farm site, 13 of the 14 active nest boxes produced young that successfully fledged, three Tree Swallow Nests and ten House Sparrow nests. The remaining box, containing a Tree Swallow nest, was abandoned .

One nest box at Macdonald Farm was left uncollected during the first round of nest collections. The House Sparrows that occupied the box remained in the box immediately after the first set of juveniles fledged, and subsequently produced a second clutch. Excluding that nest box, a total of eight Tree Swallow Nests and ten House Sparrow nests were used for the study. The earliest collection date was 2 July 2007, while the latest collection date was 2 August 2007. The mean collection date was 14 July 2007.

Patterns in Early Samples (Time T)

Arthropod diversity

The distribution of saprophagous arthropods among the initial collections of nest box samples was characterized by large variance. Some nest boxes contained no saprophagous arthropods while others produced large numbers (Table 1). A total of 5366 specimens, representing 14 species or morphospecies, were collected from the initial nest box samples (mean number of specimens per nest = 298.1 ± 611.3). The most abundant species overall was the carnid fly *Carnus hemapterus*, collected from 13 of 18 nests. While the adults are thought to feed on oily secretions from feathers or blood from bird hosts, the larvae of *C. hemapterus* are saprophagous (Grimaldi 1997). The mean abundance of these larvae in all of the nests was 193.6 ± 369.9 (Table 1), giving an indication of the variance in the abundance of *C. hemapterus* larvae in the nest boxes.

Faunal similarity between host species

The Morisita-Horn index score was 5.29, indicating that over half of the saprophagous arthropod species found in the nest boxes of Tree Swallows were also found in the nest boxes of House Sparrows. This value was sufficiently high to allow for the samples from both bird species to be pooled in analyses.

Null model analysis of assembly pattern

A presence/absence matrix with singletons removed was used to test for the assembly pattern at time T. For the null model analysis with equiprobable column totals, the C-score for the observed index was 2.71429, while the C-score for the mean of the simulated indices was 8.19779. The variance of the simulated indices was 1.24345. If the observed C-score index is higher than the mean of the simulated indices, then the observed pattern is thought to be the result of negative species interactions (Gotelli and McCabe 2002). In this analysis, p(observed ≤ expected) = 0.00000, while p(observed ≥ expected) = 1.00000. For a pattern to be viewed as random the probabilities should lie within accepted confidence intervals such that p (observed ≤ expected) = 0.05, while p(observed ≥ expected) = 0.95. For this analysis the standardized effect size (SES) was -4.91750.

In the null model analysis using fixed column totals, the C-score for the observed index was 2.71429, while the mean of the simulated indices was 2.79050. The variance of the simulated indices was 0.03425. The p (observed ≤ expected) = 0.43660, while p(observed ≥ expected) = 0.65320. These probabilities indicate that in the fixed column total analysis, the observed index falls well within the range of probabilities that could occur by chance alone. The SES was -0.41181.

Patterns in Late Samples (Time T+60)

Arthropod diversity

The remaining half of the nest material, collected 60 days after the initial half of the nest material was collected, yielded 3794 saprophagous arthropods, representing ten species (mean number of specimens per nest = 199.7 ± 253.8) (Table 2). As with the first set, *C. hemapterus* was the most abundant species (Table 2).

Faunal similarity between host species

Faunal similarity between the saprophagous arthropods in the nest material of the two nesting species of birds was calculated in the same manner as with the initial (T) samples. The Morisita-Horn index value for the second set of nest samples was 0.875. This value is once again considered to be high enough to allow for the pooling of the saprophagous arthropods in the nests of the two bird species. The two-tailed t-test revealed significant differences in saprophagous arthropod abundance between the nest boxes of the two bird species ($p = 0.013192$).

Null model analysis of assembly pattern

The null model analysis with equiprobable column totals yielded an observed C-score index of 5.71429, while the mean of the simulated indices was 8.55426, and the variance of the simulated indices was 1.34926. The higher value of the observed C-score relative to that of the first sample period reflects an increased level of species interactions. In the T+60 analysis $p(\text{observed} \leq \text{expected}) = 0.01200$ and $p(\text{observed} \geq \text{expected}) = 0.98820$. As with the samples taken at time (T), the probabilities indicate that the observed index occurs more frequently than by chance alone. The SES for this analysis was -2.44493.

In the fixed column total null model algorithm, the observed C-score index was 5.71429, while the mean of the simulated indices was 5.77638, and the variance of the simulated indices was 0.08717. The $p(\text{observed} \leq \text{expected}) = 0.49660$, while $p(\text{observed} \geq \text{expected}) = 0.56180$. These are similar to results of the fixed column analysis run for the data from time (T) and demonstrate that the probability of the observed pattern occurring by chance alone lies well within the

95% confidence interval. The SES for the T+60 fixed column total analysis was -0.21031.

Cluster Analysis

The cluster analysis revealed clear groupings based on nest box site (Macdonald Farm and Stoneycroft) and sample times T and T+60, although most individual nest boxes did not form pairwise clusters for times T and T+60 (Figure 1). While the nest boxes of the same site generally tended to form clusters, often these were nested within clusters formed by nest boxes of the other site. Two nest boxes from Macdonald Farm, F13 and F25, formed distinct groups for T and T+60. This is not surprising as these nest boxes contained the highest relative abundance of all the nest boxes in both sample periods.

DISCUSSION

The results of this study both accept and reject the null hypotheses that the community structure of saprophagous arthropods in bird nest boxes is random, depending upon the type of null model analysis performed. Although seemingly contradictory, these results allow for an investigation of possible stochastic and deterministic processes that could account for the differences observed.

Null Model Analysis: Colonization of Nest Boxes

The results of the equiprobable column total null model analysis of the nest box samples at time (T) do not support the null hypothesis that the initial community structure of saprophagous arthropods is random. The low observed C-score index relative to the simulations suggests that the initial community was structured and it appears that species aggregate together within certain nest boxes.

Although an aggregate pattern, where species coexist more than by chance alone, has not been as commonly documented as a negative co-occurrence patterns, positive species co-occurrence has been demonstrated in many communities (Bascompte et al. 2006, Guimaraes et al. 2006). One well documented mechanism that could lead to this pattern is facilitation (Bruno et al. 2003), in which one species modifies an environment so that it is more suitable for subsequent species that colonize the area (Stachowicz 2001). In the case of saprophagous arthropods that feed on decaying organic matter, this could also be true. Certain species could potentially alter the substrate so that the habitat is more suitable for other saprophagous species. Additionally, the presence of certain species could act to control predators of other species in the nest box. The European earwig, (*Forficula auricularia L.*) is omnivorous. This species was deemed part of the saprophagous guild as it will feed on decaying matter (Marshall 2006), although it has also been documented as a predator upon certain arthropods and might act to reduce numbers of other predators, or reduce densities of arthropods such as mites that might compete for resources in the nest box (Weiss and MacDonald, 1993).

In this scenario, priority effects would play a large part in the organization of the structure of the community. The first species or several species to occupy the nest box would mediate the environment such that it would allow for colonization of the nest box by the remaining species. Based on the observed pattern of species distribution, where some nest boxes contained no saprophagous arthropods, it could be inferred that the facilitator species only colonized specific nest boxes, and that unless these species were present, colonization by the remaining saprophagous arthropods did not occur.

While the initial colonization of facilitator species might in fact be a random pattern, the arrival at the nest box of other saprophagous species would generate a community that appears highly structured and non-random. The initial random pattern of colonization would be obscured by subsequent colonization events. The subtleties of the structuring of the community would be impossible to detect unless micro-scale time sampling was done. Although the nest material was collected immediately after the birds fledged, the arrival of the colonizing saprophagous arthropods possibly began much earlier, as soon as the birds began to modify the nest box.

Neutral Theory would argue that colonization by individuals can be seen as a stochastic process, where individuals have equal chance at arriving at any particular site (Hubbell 2001, Bell 2005). However, it is difficult to reconcile this with the concept of priority effects. This is partly because colonization operates on a continuum. It is an ongoing process, and every subsequent colonization event is mediated by those individuals that colonized before. In the case of nest boxes, colonization by any individual of any species can be viewed as a stochastic event. Neutral Theory would argue that local extinction of individuals is equally the result of stochastic factors. However, if the order of arrival of the individuals (and thus species) dictates the species that follow, then clearly it is not a stochastic process.

An alternate hypothesis to explain the observed pattern of the equiprobable column total null model analysis is the nature of the samples. Because of the preservation methods, it was impossible to measure the dry weight of the nest box contents. Previous studies though, have shown that House Sparrow and Tree Swallow nests differ dramatically in both their architecture and the mass of nest material. Riley (2000) documented that the nest material of House Sparrows contained almost twice the volume of Tree Swallow nests. The raw abundance data also indicates that there are significant differences between numbers of saprophagous arthropods that inhabit the nests of the two bird species. The detection of a strong coexistence pattern of saprophagous arthropods in the nest boxes could be a sampling artefact. Some of this difference in nest architecture is corrected for as the null model input matrices are structured as presence/absence data, rather than abundance-based measures. Nonetheless, three of a total of eight Tree Swallow nests produced no saprophagous arthropods, and thus, even in the structure of a presence/absence matrix, there was a bias towards House Sparrow nests which could lead to detection of a co-occurrence pattern based on nest architecture alone.

The results of the fixed column total null model analysis of the nest boxes samples at time (T) are quite different from that of the equiprobable column total analysis. Whereas the equiprobable column total analysis demonstrated a structured community with strong positive co-occurrence, the fixed column total analysis points to a community that is randomly assembled and, as such, the null hypothesis that the community of saprophagous arthropods forms a random pattern must be accepted based on this analysis.

Considering that the fixed column total null model analysis creates “islands” in the randomization matrices, where no cells will be filled at certain sites because no individuals were present in the observed matrix, the overall random structure of the community is not surprising. If the null model is constrained, as in the case of the fixed column total analysis, and fewer sites (nest boxes) are able to be filled by the sequential swap algorithm, then intuitively one would expect that the randomizations would create data matrices that are more structured than if the randomizations were allowed to vary stochastically throughout the entire matrix. Thus, when comparing the observed index to the mean of the simulated indices, the null model would not be able to reject the null hypothesis.

This also explains the lower mean of the simulated indices for the fixed column total analysis (2.79050) compared to that of the equiprobable column total analysis (8.19779). Fewer checkerboard pairs would be possible in the randomizations because certain cells, the ones located within sites that had no observed individuals, would be unavailable to fill. Checkerboard pairs would not occur in these sites, nor would they occur in the matrix space immediately adjacent to these sites, so that the C-score indices for the randomizations would be lower than if all of the matrix space was available to all possible combinations of checkerboard pairs.

If the random pattern evident in the fixed column total analysis is the true pattern, then by default it must be assumed that every nest box does not have an equal chance of colonization. This could be the result of limited dispersal abilities of saprophagous species, proximity to source pools, or a combination of both of these factors. One of the central tenets of Neutral Theory is that dispersal ability is a stochastic process that serves as a limit to an individual’s ability to colonize the optimal habitat or “niche” sensu Hutchison (Hubbell 2001). Dispersal ability is viewed as stochastic because it is seen as varying randomly between individuals. Competition rarely structures communities because the limiting dispersal ability of individuals precludes the arrival of all possible competitors in this habitat (Bell 2005, Hubbell 2005). In the absence of competition, a deterministic structuring process, the structuring of a community would be dependent on the dispersal ability, a stochastic process according to Neutral Theory. The limiting dispersal ability of saprophagous arthropods thus would result in an observed random pattern of community assembly.

Neutral theory can at least partially explain the random pattern of saprophagous arthropod community structure in bird nest boxes. However, even if individual dispersal ability is limited, the observed pattern of “patchiness”, where some nest boxes contain no saprophagous arthropods, empirically suggests that Neutral Theory cannot explain all of the observed pattern. If dispersal ability is stochastic, and varies among individuals, then at least some saprophagous arthropods should, by chance alone, arrive at all of the nest boxes. Invoking Neutral Theory to explain the random structure of the community does not extend to explaining why saprophagous arthropods were excluded from certain sites. The caveat is that in particular circumstances, the abundance of individuals in the source pool, the potential colonizers, might be low enough as render it impossible for individuals to colonize all suitable habitat types (Hurtt & Pacala 1995). Alternately, or in conjunction with the above factor, individuals tend to aggregate spatially, such that propagules cluster closer to their parents (Hubbell 2001). In this case, limited dispersal ability, low source pool abundance, and/or proximity to the source pool could result in a pattern of abundance where not all sites are colonized. Many of the saprophagous arthropods found in bird nest boxes are rarely, if ever, collected outside of this habitat (see discussion below). As such, it can be inferred that the source pools for these species, and individuals, are limited and their abundance is relatively low.

Other explanations for the observed pattern of nest box occupancy by saprophagous arthropods are based on biotic and abiotic factors. Although the nest boxes in which no saprophagous arthropods were present did not share similar attributes such as site location, height from the ground, or directionality, micro-environmental variables could have played a role in excluding saprophagous arthropods from these locations. Riley (2000) documented high mite abundance in certain nest boxes. Although mites were not retained for the purposes of this study, the initial sorting of nest material revealed hyper-abundances of mites in particular nests. In a semi-closed environment such as a nest box, this might translate to a strong actual limitation of space and/or resources for any other species who might potentially colonize. Highly efficient predators, such as carabid or staphylinid larvae (Coleoptera), might have also served to remove any saprophagous arthropods, but could have left the nest box long before the sample was taken, and thus would be undetectable. Although they are not saprophagous, and thus not included in the analysis, carabid and staphylinid larvae were found in several nest boxes.

The results of the two null model analyses differ in their detection of the type of pattern, but they are not necessarily incompatible with one another. Both could be informative of the processes acting to structure of saprophagous arthropod community of bird nest boxes, although these processes might be working on different levels of scale. Scale-dependency has been widely observed to affect the observed patterns of communities and is often used to explain how deterministic and stochastic processes can operate together (Swenson et al. 2006, Ellwood et al. 2009, Chase 2010, Pinto & Macdougall 2010). In a study that examined arthropod decomposers in tropical epiphytes, a similar system to nest boxes, Ellwood et al. (2006) found that stochastic processes accounted for the community structure at the same canopy level, but deterministic processes were evident when multiple canopy levels were added to the analysis. The results from the two null model analyses of time (T) of this study suggest the same pattern. Although the input matrix was the same for both the equiprobable and fixed column total null model analyses, the sequestering of randomizations in the fixed column total analysis does create a difference in scale between the two methods. The equiprobable column total analysis can be viewed as operating on a larger scale, albeit only slightly larger, than the fixed column total analysis. The "exclusion" of the nest boxes that returned observed zero sums for individuals in the fixed column totals create a difference of scale, in both real and matrix space. This "exclusion" results in the fixed column total analysis operating at a finer scale than the equiprobable analysis. This finer scale could account for the observed differences in pattern between the two methods.

Whether the differences in patterns are attributable to a statistical artefact or whether these differences are real is a matter of debate, and should be investigated more thoroughly. Gotelli (2000) observes that a “compromise algorithm” that has attributes of both the equiprobable and fixed column total algorithms might be a potential solution. However, this in itself is problematic, as constraining the null model to fit real observations and data no longer allows it to vary stochastically, and the simulated indices will not return values that are based on chance alone (Gotelli & Graves 1996).

When comparing the two methods of null model analysis, one statistic is interesting to note. The SES for the equiprobable column total analysis was -4.91750, while the SES for the fixed column total analysis was -0.41181. Gotelli & McCabe (2002) performed a meta-analysis of data across taxa and discovered that the SES differed significantly dependent upon the taxon. When compared to the SES results of Gotelli & McCabe’s meta-analysis, the SES result from the fixed column total is far closer to the values obtained by Gotelli & McCabe for invertebrate taxa. Gotelli & Entsminger (2010) caution that the SES is based on the assumption of normally distributed data within the null model, however they also assert that it nonetheless serves as a rough guide to compare studies. The one magnitude of difference between the equiprobable column total SES and the fixed column total SES accentuate the differences between the two null model analysis methods. Not considering other factors described above, and noting that more investigation is necessary to elucidate a truer picture, the SES value returned by the fixed column total analysis when compared to Gotelli & McCabe's value suggests that the fixed column total analysis might be a more reliable predictor of pattern than the equiprobable column total null model.

Null Model Analyses: Establishment in Nest Boxes

The results for the null model analyses at time T+60 demonstrate the same general patterns that were exhibited in the analyses at time T. The differences between patterns of the equiprobable and fixed column total analyses were retained. The equiprobable column total analysis rejected the null hypothesis that the observed pattern of community structure was random, while the fixed column total analysis accepted it. The potential statistical and biological reasons for these differences have been discussed in the previous section. However, there are some notable differences between the T and the T+60 analyses. The T+60 equiprobable column total analysis yielded a much higher observed C-score index compared to the same analysis at time T. This is indicative of more checkerboard pairs, and thus also indicative of a higher level of ecological constraints in the structure of the community at time T+60. Although the level of constraint is not statistically significant in that it does not alter the pattern of significant positive co-occurrence when the observed index is compared to the mean of the simulated indices, it is an indication that the mechanisms that operate to structure the community have changed from time T to time T+60.

Comparing Community Structure: Colonization and Establishment

The organization of community structure over a particular time interval has received considerable attention. Classical niche theory and island biogeographic theory would predict that, in the absence of disturbance, communities would arrive at a singular endpoint (Hutchinson 1957, MacArthur & Wilson 1963, 1967). Some studies of priority effects and historical contingency (Connell & Slayter 1977, Shulman et al. 1983, Almany 2003) share a similar viewpoint although others (Diamond 1975, Drake 1990, Chase 2003) have noted that stochastic processes can lead to multiple stable endpoints. The arrival of the best competitor of the colonizers serves to structure and regulate the community to the exclusion of potential new colonizers. The differences in the patterns elucidated from the equiprobable column total null model analysis between T and T+60 do demonstrate this, although not to a level of statistical significance.

Ecological constraints were more evident in the T+60 community than they were in the T community.

In contrast, Neutral Theory would predict that the stable endpoint would never be reached, or that the deterministic processes (competitive exclusion) that act on a community occur at such a slow rate that they are hardly deemed relevant (Hubbell 2001). The similarities between the T and the T+60 fixed column total analyses, which both supported the null hypotheses that the structure of the community is random, can be taken as an assertion of Neutral Theory. However, other methods of analyses do not support this view. The Morisita-Horn index indicates that the faunal similarity between the nest boxes of House Sparrows and Tree Swallows increased in the interval between T and T+60, suggesting either that species, and thus individuals, were undergoing rapid local extinction (competitive exclusion) or new species were colonizing a nest box environment that was predisposed to their arrival (facilitation and priority effects). The actual number of species of saprophagous arthropods, and their relative abundance, declined from T to T+60, which could suggest that competitive exclusion was at least one of the processes at work. It must be noted, however, that many of the individual specimens collected from the nest boxes were first instar larvae, which have a high natural mortality rate, which could also account for decreased overall abundance in the absence of deterministic processes.

The cluster analysis also provides evidence that the patterns in the null model analyses are also present relative to species abundance because they are grouped by nest box location and time interval. The depauperate nest boxes clustered together, as did the nest boxes that contained the highest abundance, but there is a distinct intermediate clustering that is not defined by either time or nest box location. The clustering of the high abundance and depauperate nest boxes is analogous to the equiprobable column total null model analyses, in that the high or low abundance of these nest boxes and relative high or low species richness played a major role in the formulation of the pattern of positive species co-occurrence. The intermediate clustering is more analogous to the fixed column total null model analysis. Despite some nestedness based on the site at which the nest boxes were located and sample period, there is a lack of obvious groupings amongst these clusters. This can be seen as the stochastic pattern evoked by the fixed column total analyses. However, if a truly neutral pattern, as seen throughout the entire dendrogram, was to be observed, then there would be no nestedness in the clustering at all. The cluster analysis clarifies the relationships between the nest boxes, but only accentuates the difficulties in assessing how the equiprobable and fixed column total null model analyses can be reconciled.

Life History and Ecology of Abundant Saprophagous Arthropods

The saprophagous arthropods that inhabit bird nests are rarely collected, and little is known of their life history and ecology. In this study, three bird nest specialists were identified; *Leptometopa latipes* Meigen (Diptera; Milichiidae), *Neossos marylandicus* (Diptera; Heleomyzidae), and *Carnus hemapterus* (Diptera; Carnidae). Despite the high abundance of these species in the nests, there is a paucity of collection records for them from general arthropod biodiversity and abundance surveys. *Neossos marylandicus* has never been collected outside of bird nests, while *C. hemapterus* and *L. latipes* are infrequently collected. This testifies to the degree of habitat specialization that these species exhibit, but does not explain how such high local abundance can escape detection at a larger scale.

The case of *C. hemapterus* is perhaps the most easily understood. This species is the most frequently collected of the three species with collection records dating back more than a century (Grimaldi 1997). While the larvae of this species are saprophagous, it is thought that adults feed on secretions or blood from birds inhabiting nests. This close association between the adult stage of the fly and the bird hosts may in part explain why they are so infrequently found outside of nests.

The presence of *C. hemapterus* larvae in the T+60 nest box samples is noteworthy, and provides additional information on the ecology of the species. First instar larvae were collected in the nest boxes 60 days after the birds had fledged from the nest. Although it is somewhat dependent upon temperature and microhabitat conditions, the rearing times of larvae in the nest box indicates that adults of *C. hemapterus* must have been present well after the birds had departed from the nest box. Either *C. hemapterus* recolonized the nest boxes after the initial sample was taken, or *C. hemapterus* remained in the nest box after the birds had left. In the latter scenario, larvae that remained in the nest after the first sample (T) was taken matured into adults. However, if this is the case, and mating between recently emerged *C. hemapterus* adults resulted females laying eggs which in turn developed into the larvae, they would have had to do so without feeding on the birds themselves. Unless individuals recolonized the nest boxes, it appears that the adults of *C. hemapterus* are able to feed on material left behind by the birds rather than the birds themselves, and females are able to produce eggs or larvae in the absence of avian hosts.

There is almost no documentation on the life history or ecology of *Neossos marylandicus* and *L. latipes*. McAtee (1927) noted that N. marylandicus larvae most likely feed in the detritus of nest boxes, while Whitaker et. al. (1991) observed *L. latipes* in bat guano. These species do not seem to have an association with the birds themselves. This partly explains why little is known about their life histories and ecology, as most studies that describe arthropod nest inhabitants do so in reference to those arthropods that impact avian fitness. More intensive sampling of non-parasitic bird nest specialists is necessary to understand the life history traits and ecology, and develop a more thorough knowledge of their distributions. Only through extensive sampling will the questions relating to the source pools of these species and their relative dispersal abilities be answered.

Concluding Remarks

The temporal scale at which this study was conducted might not be large enough to accurately detect differences between stochastic and deterministic processes that might be working to structure the community of saprophagous arthropods in bird nest boxes. The patterns that emerged from both forms of null model analyses, while unique and informative as they relate to the community at given points in time, are nonetheless relatively narrow in terms of macro-organism community assembly. A study conducted over multiple years might be required to tease apart the true nature of the processes that influence and patterns that result from community assembly of saprophagous arthropods in bird nest boxes. Even with this, disturbance, in the form of environmental variables such as temperature, precipitation, different host species, or years in which the nest is not occupied, might act to wipe clean or reset any possible endpoint that would allow for the elucidation of the patterns.

The spatial scale at which this study took place might not be sufficient to assess community structure patterns that are dependent upon an accurate knowledge of the true dispersal ability of individuals and species and the nature of the local and regional source pools. An analysis of nests of multiple bird species, spread over a wide set of environmental gradients, would prove useful to help understand the processes that structure the arthropod community in bird nests and bird nest boxes. As noted by Ellwood et al. (2009), the interpretation of the processes that act on structuring communities is largely a matter of estimating the correct scale at which to conduct a study; too narrow a scope will lead to the detection of one type of pattern, and too broad a scope, without taking into account finer scale patterns, will lead to the detection of another type of pattern. The reality is that both of these patterns probably exist, but it is necessary to account for all levels of scale before they become apparent.

The knowledge of life history traits and ecology of many arthropods, and especially saprophagous bird nest specialists, is poorly understood. A truer understanding of the saprophagous arthropod communities associated with bird nests necessitates a more thorough understanding of the roles that they play within these nests, their dispersal ability and their relative abundance in the regional source pools that serve as starting points for potential colonists.

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Table 1. Species of saprophagous arthropods identified in nest boxes. Species codes are used in Tables 2 and 3.

Taxon			**Species Code**
Order	**Family**	**Genus/Species**	
Psocoptera			
	Liposcelidae	*Liposcelis corrodens*	LIPCOR
	Lachesillidae	Lachesilla spp.	LACHSP
Dermaptera			
	Forficulidae	*Forficula auricularia*	FORAUR
Coleoptera			
	Scarabaeidae	species 1	SCASP1
	Scarabaeidae	species 2	SCASP2
	Dermestidae	*Dermestes sp.*	DERMSP
Diptera			
	Sphaeroceridae	*Leptocera* sp.	LEPTSP
	Carnidae	*Carnus hemapterus* (larvae)	CARHEL
		Carnus hemapterus (puparia)	CARHEP
	Milichiidae	*Leptometopa latipes* (larvae)	LEPLAT
	Sepsidae	species 1	SEPSP1
	Heleomyzidae	*Neossos marylandicus*	NEOMAR
	Muscidae	*Musca* species 1	MUSSP1
	Unknown	Diptera larvae species 1	DPLSP1
		Diptera larvae species 2	DPLSP2
		Diptera larvae species 3	DPLSP3
		Diptera larvae species 4	DPLSP4
		Diptera larvae species 5	DPLSP5

Table 2. Saprophagous arthropods collected in nests of Tree Swallows (TRES) and House Sparrows (HOSP) at time T

Nest Box

Bird Host Species

	S7	S14	S21	S40	S41	F1	F3	F10	F11	F13	F15	F17	F19	F20	F22	F23	F25	F41			
Species Code	**TRES**	**TRES**	**TRES**	**TRES**	**TRES**	**TRES**	**TRES**	**HOSP**	**HOSP**	**HOSP**	**HOSP**	**HOSP**	**HOSP**	**HOSP**	**HOSP**	**HOSP**	**HOSP**	**TRES**	**Total**	**Mean**	**SD**
LIPCOR	0	0	0	0	0	1	0	2	4	74	0	0	94	0	0	320	0	0	**495**	27.50	77.88
FORAUR	0	0	0	0	0	0	0	0	3	0	1	0	4	0	0	3	0	0	**11**	0.61	1.29
SCASP1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0.06	0.24
SCASP2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0.06	0.24
DERMSP	0	2	0	54		0	0	9	18	5	3	0	8	9	2	2	8	0	**120**	7.06	12.78
LEPTSP	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	**2**	0.11	0.47
CARHEL	0	0	1	7	25	1	166	798	57	1392	0	0	29	0	59	347	512	91	**3485**	193.61	369.93
CARHEP	0	0	0	0	0	0	0	0	0	451	19	0	0	0	0	0	74	0	**544**	30.22	106.49
LEPLAT	0	0	0	0	0	0	0	0	0	581	0	0	0	0	9	0	0	0	**590**	32.78	136.83
SEPSP1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0.06	0.24
NEOMAR	0	0	0	0	1	1	2	2	0	4	1	0	1	0	0	9	8	0	**29**	1.61	2.73
MUSSP1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	**3**	0.17	0.38
DPLSP1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	79	0	**82**	4.56	18.59
DPLSP2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	**1**	0.06	0.24
DPLSP3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	**1**	0.06	0.24
Total	**0**	**2**	**1**	**61**	**27**	**6**	**170**	**811**	**82**	**2508**	**25**	**0**	**138**	**9**	**70**	**684**	**681**	**91**	**5366**	**298.11**	**611.30**

Table 3. Saprophagous arthropods collected in nests of Tree Swallows (TRES) and House Sparrows (HOSP) at time T+60

Nest Box	S7X	S14X	S21X	S40X	S41X	F1X	F3X	F10X	F11X	F13X	F15X	F17X	F19X	F20X	F21X	F22X	F23X	F25X	F41X			
Bird Host Species																						
Species Code	**TRES**	**TRES**	**TRES**	**TRES**	**TRES**	**TRES**	**TRES**	**HOSP**	**HOSP**	**HOSP**	**HOSP**	**HOSP**	**HOSP**	**HOSP**	**HOSP**	**HOSP**	**HOSP**	**HOSP**	**TRES**	**Total**	**MEAN**	**SD**
LIPCOR	0	0	1	0	1	1	0	20	0	599	13	8	66	0	1	1	1	307	3	**1022**	53.79	14.964
LACHSP	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	3	**9**	0.47	1.50
FORAUR	17	0	0	1	0	0	1	37	3		0	3	1	56	0		7	0	5	**131**	7.71	14.88
DERMSP	0	1	1	2	3	1	0	13	12	25	11	0	13	3	0	0	1	0	3	**89**	4.68	6.86
CARHEL	99	0	0	0	43	0	0	329	276	266	645	20	99	10	168	2	486	0	81	**2524**	132.84	186.91
CARHEP	0	0	0	0	7	0	0	0	0	109	38	0	0	0	0	1	0	0	0	**155**	8.16	25.94
LEPLAT	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	**5**	0.26	1.15
NEOMAR	0	0	0	0	5	0	0	0	0	0	0	5	0	0	0	0	0	0	0	**10**	0.53	1.58
DPLSP1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**2**	0.11	0.46
DPLSP4	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	**1**	0.05	0.23
DPLSP5	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	**1**	0.05	0.23
Total	**116**	**3**	**2**	**3**	**59**	**8**	**1**	**399**	**291**	**999**	**708**	**41**	**180**	**69**	**169**	**4**	**495**	**307**	**95**	**3949**	**207.84**	**274.38**

Table 4. Presence-absence matrix with singletons removed used for null model analysis at time T

Species	**Nest Box**																	
	S7	**S14**	**S21**	**S40**	**S41**	**F1**	**F3**	**F10**	**F11**	**F13**	**F15**	**F17**	**F19**	**F20**	**F22**	**F23**	**F25**	**F41**
LIPCOR	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	1	0	0
FORAUR	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0
DERMSP (larvae)	0	1	0	1	0	0	0	1	1	1	1	0	1	1	1	1	1	0
LEPTSP	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
CARHEM	0	0	0	1	1	0	1	1	1	1	1	0	1	0	1	1	1	1
LEPLAT (larvae)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
NEOMAR	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	1	0
DPLSP1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0

Table 5. Presence-absence matrix with singletons removed used for null model analysis at time T + 60

Species	**Nest Box**																		
	S7	**S14**	**S21**	**S40**	**S41**	**F1**	**F3**	**F10**	**F11**	**F13**	**F15**	**F17**	**F19**	**F20**	**F21**	**F22**	**F23**	**F25**	**F41**
LIPCOR	0	0	0	0	0	0	0	1	0	1	1	1	1	0	0	0	0	1	1
LACHSP	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
FORAUR	1	0	0	0	0	0	0	1	1	0	0	1	1	1	0	0	1	0	1
DERMSP (larvae)	0	0	0	1	1	0	0	1	1	1	1	0	0	1	0	0	0	0	1
CARHEM	1	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1	1	0	1
LEPLAT (larvae)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
NEOMAR	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
DIPLSP1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

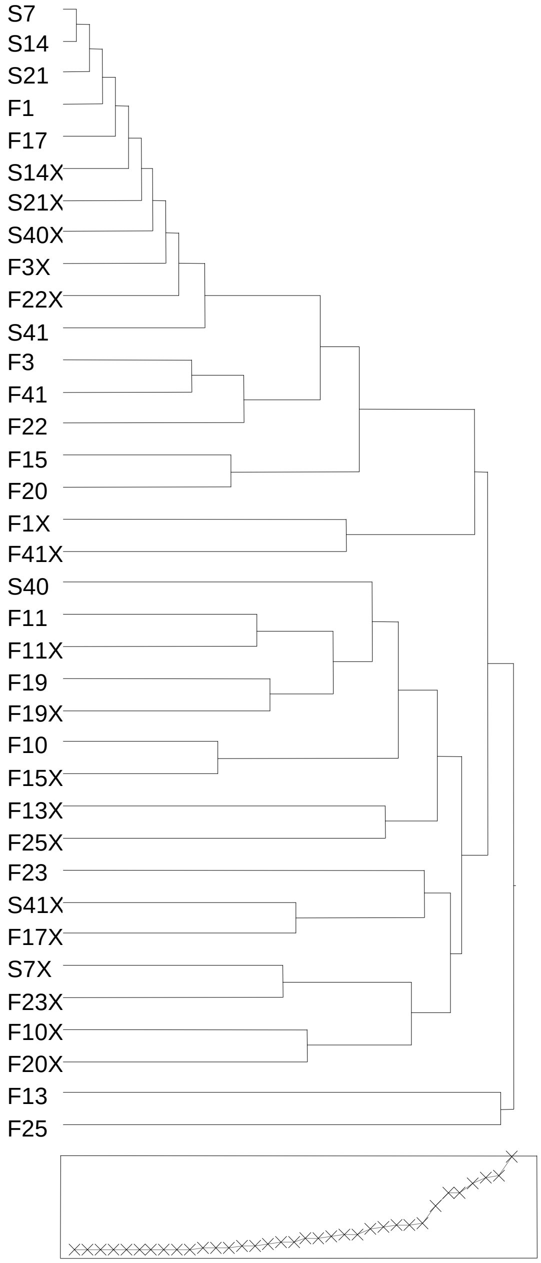

Figure 1. Cluster analysis of nest boxes relative to time T and T+60 and species abundance. Nest boxes from Stoneycroft are prefixed by "S"; nest boxes from Macdonald Farm are prefixed by "F". X after a nest box number denotes a sample taken at T+60. The lower panel represents the sequencing of clusters.