Vertically stratified arthropod diversity in a Florida upland hardwood forest

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Abstract

Species diversity is typically higher in tropical forest canopies than in ground layers, but this pattern is absent in temperate forests. However, hardwood forests of Florida are typified by the intermingling of temperate and tropical species. It is thus unclear how diversity in Florida forests might be vertically stratified. This project is one of the first investigations to compare arthropod communities at varying layers (strata) of a Florida hardwood forest, from ground to canopy habitats. We installed terrestrial and arboreal pitfall traps to survey the arthropod community along a vertical gradient from the forest ground to upper canopy. We collected 830 arthropods from the 34 traps, amounting to 103 morphospecies across 15 orders. Coleoptera was the most morphospecious order, followed by Diptera, Araneae, and Hymenoptera. Species alpha diversity, richness, and abundance all decreased with height from the ground and horizontal distance from the tree. We discuss the vertical stratification of orders in addition to diversity metrics. This study is the first to reveal canopy strata effects on arthropod diversity in a Florida forest, and shows how diversity and composition changes along within site gradients.

Key Words: canopy; Florida; hardwood hammock; insect; vertical stratification

Resumen

La diversidad de especies suele ser mayor en las copas de los bosques tropicales que en las capas de tierra, pero este patrón está ausente en los bosques templados. Sin embargo, los bosques de madera dura de la Florida, se caracterizan por la entremezclada de especies templadas y tropicales. Por lo tanto, no está claro cómo se puede estratificar verticalmente la diversidad en los bosques de la Florida. Este proyecto es una de las primeras investigaciones para comparar comunidades de artrópodos en diferentes capas (estratos) de un bosque de madera dura de la Florida, desde el suelo hasta los hábitats del dosel. Instalamos trampas de caída terrestres y arbóreas para estudiar la comunidad de artrópodos a lo largo de un gradiente vertical desde el suelo del bosque hasta el dosel superior. Recolectamos 830 artrópodos de las 34 trampas, que consistia de 103 morfoespecies en 15 órdenes. Coleópteros fue el orden más morfospecioso seguido por Diptera, Araneae e Hymenoptera. La diversidad alfa, la riqueza y la abundancia de las especies disminuyeron con la altura desde el suelo y la distancia horizontal desde el árbol. Discutimos la estratificación vertical de órdenes además de las métricas de diversidad. Este estudio es el primero en revelar los efectos de los estratos del dosel sobre la diversidad de artrópodos en un bosque de Florida y muestra cómo la diversidad y la composición cambian junto con los gradientes del sitio.

Palabras Clave: dosel; Florida; hamaca de bosque de madera dura; insecto; estratificación vertical; diversidad

Canopies house a major portion, perhaps the majority, of forest biodiversity (Erwin 1982; Lowman & Wittman 1996), but this assertion has been met with criticism (Hammond 1990; Hammond et al. 1997; Walter et al. 1998; Stork & Grimbacher 2006.). Advances in canopy access enabled the discovery of vertical stratification in forests, i.e., clear delineations in communities across the ground-overstory vertical height (Basset et al. 2003a). In general, tropical forests are thought to increase in species diversity with vertical height (Basset et al. 2003a), but this pattern has been disputed recently (Ulyshen 2011). In particular, there is debate regarding how temperate and tropical forests might vary in patterns of diversity with vertical height (Parker & Brown 2000; Basset 2001; Basset et al. 2003a).

Diversity generally was thought to increase with vertical height in tropical forests, but this hypothesis is still under debate (Basset et al. 2003a; Ulyshen 2011). For example, fruit-eating nymphalid butterfly communities in Ecuador, and beetle assemblages in Australia, showed that canopy and ground species diversity was about equal (DeVries et al. 1997), and small mammal diversity decreased with height in a Brazilian Atlantic rain forest (Vieira & Monteiro-Filho 2003). Collembola communities were stratified in tropical rainforests, but diversity did not vary between the ground and canopy (Rogers & Kitching 1998). Flying insects in rainforests in Panama, Papua New Guinea, and Brunei stratified vertically and, in some cases, were more abundant in the canopy (Sutton et al. 1983). Still, a family of moths in a Costa Rican rain forest showed an increase in species diversity with vertical height, but the pattern reversed in a different family of moths (Brehm 2006). Researchers point to tree architecture or resource variation to explain deviations from the general patterns, especially among smaller taxonomic groups (Basset 2001; Basset et al. 2003a, b).

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In general, it is expected that tropical, but not temperate, forests show increasing diversity with vertical height (Basset 2001; Basset et al. 2003a). However, Florida biodiversity is largely driven by the confluence of temperate and tropical species commingling on the peninsula (Webb 1990; Kautz & Cox 2001). In fact, Florida forests are classified as temperate or tropical only by tree species composition (Greller 1980). Thus, it remains unclear what pattern of stratification, if any, might be structured in Florida forests (Su & Woods 2000). To further this endeavor, we examined how richness and diversity of arthropods in an upland hardwood forest in south-central Florida changed with vertical structure.

Materials and Methods

St. Sebastian River Preserve State Park encompasses about 8,800 ha in Brevard and Indian River counties, Florida (Florida Division of Recreation and Parks 2005). We delimited a 120 × 90 m (1.08 ha) plot in a 6.5 ha patch of mesic upland hardwood forest at the confluence of the North and South Prongs of the St. Sebastian River within St. Sebastian River Preserve State Park in Indian River County, Florida (generally located at 27.831400°N, 80.509100°W). The specific study site is characterized by sandy clay soils and upland hardwood forest, a rare habitat in the park (less than 0.04% of land area) (Florida Division of Recreation and Parks 2005). Upland hardwood forest is a type of mesic upland habitat that includes a high diversity of plants and animals, including the overstory trees Florida maple (*Acer saccharum floridanum* (Chapm.) Small & A.Heller) (Sapindaceae), pignut hickory (*Carya glabra* (Mill.) Sweet) (Juglandaceae), southern hackberry (*Celtis occidentalis* L.) (Cannabaceae), white ash (*Fraxinus americana* L.) (Oleaceae), sweetgum (*Liquidambar styraciflua* L.) (Altingaiceae), southern magnolia (*Magnolia grandiflora* L.) (Magnoliaceae), loblolly pine (*Pinus taeda* Blanco) (Pinaceae), white oak (*Quercus alba* L.) (Fagaceae), live oak (*Q. virginiana* Mill.) (Fagaceae), and laurel oak (*Q. hemisphaerica* W. Bartram ex Willd.) (Fagaceae) forming a closed canopy (Florida Natural Areas Inventory 2010).

All hardwood trees > 150 cm diam at breast height were included as candidates for sampling. Trees judged unsafe to climb (e.g., major signs of damage, lack of suitable anchor sites) were excluded, and 7 trees were randomly selected for sampling from the 22 that met the above criteria. Bole height, crown height, and diam at breast height were recorded. Additionally, drip line diameter at each cardinal direction and overstory density via convex spherical densitometer were recorded (Jennings et al 1999; Fiala et al. 2006).

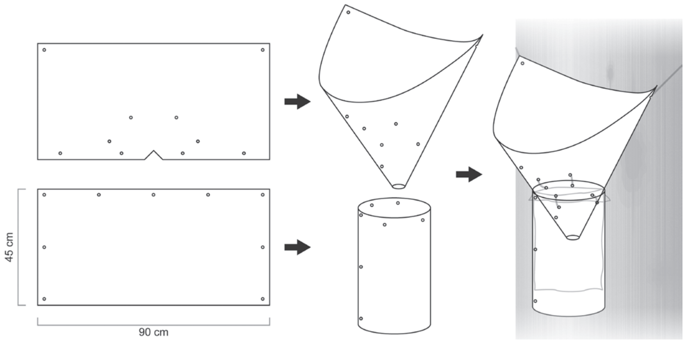

Fig. 1. Arboreal pitfall tap design. Two sheets of metal flashing are cut to length and punched with holes. Next, a cylinder and funnel are formed and secured with pop rivets or similar fastener. A plastic bag is inserted into the cylinder, and the cylinder and funnel are attached with tie straps. The bag is then filled with about 100 mL of 98% propylene glycol and secured to a tree trunk of branch such that arthropods slide down the funnel and into the collection fluid.

Each tree was fitted with 5 traps: 2 at the soil line and 3 arboreally. Two pitfall traps were installed by burying commercially available polystyrene drinking cups with a 9 cm diam flush with the soil surface. Both pitfall traps were positioned in random directions relative to the tree (determined by randomly selecting a compass azimuth with 2° resolution); one at 1 m from the tree base, and the other equidistant to the tree base and the drip line. The remaining 3 traps, of a new design inspired by Pinzón & Spence (2008), were placed aboveground in the tree (Fig. 1). These arboreal pitfall traps were constructed from two 40 cm lengths of 25 cm wide aluminum flashing measuring less than 0.01 cm thick. One length was used to form a funnel and the other a collector. The traps were tightened against trunks or branches of trees with string. Trap locations were in part determined by individual tree structure, such that the flexible funnel could bend to the contours of the tree. This formed a smooth transition zone across which arthropods may fall into a 6 mL plastic bag placed within the collector and secured with plastic tie straps (Fig. 1). About 100 mL of 98% propylene glycol was used as a preservative in all traps instead of the more typical 50% solution because of the probable dilution by rainwater (Hall 2006). We opted against using ethylene glycol to avoid poisoning non-target animals (Hall 2006; Jud & Schmidt-Entling 2008).

Arboreal traps were placed using a canopy access method, termed single rope technique (SRT) (Moffett et al. 1995; Lowman 2009). A line was placed over a crotch in the tree's upper crown. One end of the line was anchored to the base of another tree, and ascended the other end by use of a harness and typical rock-climbing and caving equipment. This allows for maximum maneuverability within the tree, and was far less disruptive than spike climbing or the use of heavy machinery (e.g., cherry picker, crane).

Thirty-four traps were installed in the 7 trees from 1 to 12 m aboveground (1 tree had suitable sites for only 2 arboreal traps). Traps caught arthropods for 10 to 22 d. We removed all traps at the project's end, filtered trap contents through filter paper, and preserved filtered contents in 70% isopropyl. All arthropods collected in the traps were identified to morphospecies using a Leica M80 stereomicroscope (Leica Microsystems, Buffalo Grove, Illinois, USA).

The number of morphospecies in each order were tallied in 2 m height increments. Alpha diversity using Shannon-Weaver and Simpson diversity indices and pairwise β diversity with the Sørensen-Dice index were calculated (Dice 1945; Sørensen 1948; Hill 1973). The Chao1 index and the abundance-based coverage estimator (ACE) were used to extrapolate species richness from our data (Chao 1984, 1987; Palmer 1990; Colwell & Coddington 1994; O'Hara 2005; Chiu et al. 2014). Rarefied species richness was calculated at 2 m height increments to predict total species richness in the habitat (Hurlbert 1971; Heck et al. 1975). Ground traps near or far from the tree base were tested to determine if they captured distinct arthropod communities using an analysis of similarity (ANOSIM) with the Bray-Curtis index and 10,000 permutations. Polynomial regression was used to test if arboreal trap height predicted morphospecies richness. Lastly, rarefaction curves were used to understand the level of sampling in the environment.

Results

We collected a total of 830 arthropods from the 34 traps, amounting to 103 morphospecies across 15 orders. Coleoptera was the most morphospecious order (31 morphospecies), followed by Diptera (21 morphospecies), Araneae (13 morphospecies), and Hymenoptera

(10 morphospecies). Several other orders contained less than 10 morphospecies. We identified only a single morphospecies for 3 orders: Decapoda, Diplopoda, and Phthiraptera. Morphospecies richness negatively correlated with trap height ($b = -2.21, 0.11$; $R^2 = 0.93$; $F_{2,9} = 76.17$; $P < 0.0001$) (Fig. 2). Araneae, Collembola, and Lepidoptera all showed higher morphospecies richness on the ground than associated with trees (Fig. 3). Indeed, overall pairwise β diversity was highest between the ground and vertical classes (Table 1). Among ground-level pitfall traps, arthropod communities captured 1 m from the tree base had different compositions than those positioned equidistant to the tree and drip line (ANOSIM $P < 0.001$; 10,000 permutations). The tree base has higher species richness (64 vs 49 species) and individual abundance (448 vs 214), but equivalent diversity (Shannon: 2.96 vs 3.01; Simpson: 0.903 vs 0.906) (Table 2). The number of traps deployed was not predictive of trap morphospecies richness, but rarefaction curves by height class indicated that our survey is a conservative estimate of total species diversity in the habitat (Fig. 4).

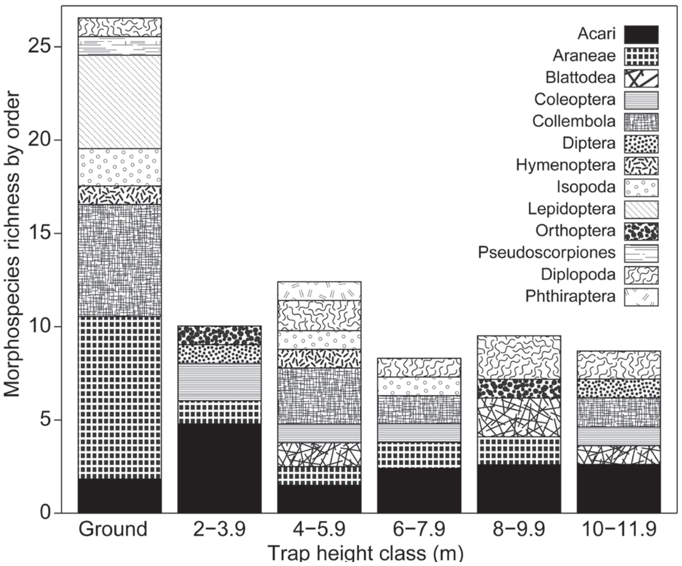

Fig. 3. Mean morphospecies richness categorized by order across 2 m height classes in an upland hardwood hammock in Florida, USA.

Discussion

Tropical forests are expected to have increased diversity with vertical height, whereas temperate forests are expected to have equivalent diversity levels within the ground and canopy layers (Bassett 2001; Basset et al. 2003a, b). However, our study in Florida forests found that species diversity and richness decrease with height (Fig. 2). Alpha diversity was higher on the ground than the canopy. Arboreal traps decreased in diversity with height, and ground traps decreased in diversity with distance from the tree (Table 2). Species richness and individual abundance also followed these patterns (Table 2). Beta diversity was highest between the ground and arboreal traps, and more similar height classes had more similar beta diversities (Table 1). Although this pattern was unexpected, it is not unique among studies of diversity with vertical height. For example, neotropical litter-dwelling ants were more common on the ground than the canopy (Longino & Nadkarni 1990). Lepidoptera in Borneo showed a decrease in abundance in the forest canopy relative to lower levels, which might be due to variation in resources (Schulze et al. 2001).

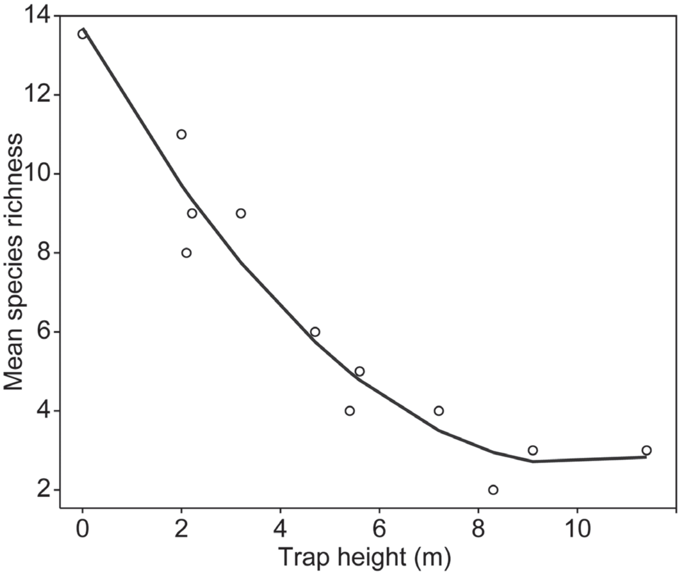

Fig. 2. Polynomial ($b = -2.21, 0.11$; $R^2 = 0.93$; $F_{2,9} = 76.17$; $P < 0.0001$) regressions of trap height and mean species richness for arthropods collected in an upland hardwood forest in Florida, USA. Species richness declines with vertical height.

Most orders in our study were widely dispersed across the ground-canopy gradient (Fig. 3). For example, Acari were found in equivalent species richness at all levels (Fig. 3). Araneae were found on all but the highest areas of tree canopies, but the majority of Araneae morphospecies were collected on the ground. This likely reflects the location of prey abundance. Orthopterans seemed to be limited to the lower trunk and canopy but were never found on the ground, likely because they could evade terrestrial traps, though it also may reflect the location of food sources for Orthopterans. Collembola richness was highest on the ground, but at least 1 morphospecies was detected at nearly every height class (Fig. 3). Because Collembola commonly live in soil layers, surveys of canopy soils likely would reveal more species. Several orders normally associated with the terrestrial level, including Blattodea and Coleoptera, were found only higher up on trees. The reverse pattern was found for Lepidoptera, which were found only on the ground (Fig. 3). This is likely an effect of seasonality and trapping methodology, both of which resulted in more larval Lepidoptera than adults. These differences in stratification across orders might be indicative of the different microhabitats that primary and secondary consumers occupy or use differently. However, some of the differences we detected might change seasonally and interannually, as has been suggested elsewhere (Longino & Nadkarni 1990; Schulze et al. 2001).

In this sense, our study is spatially and temporally limited; multi-yr research along a latitudinal gradient would reveal how stratified

Table 1. Pairwise β diversity using the Sørensen-Dice index ($\bar{x} = 3.5$) for collections of arthropods at different height classes (m above soil) in an upland hardwood forest in Florida, USA.

	Ground	2–3.9	4–5.9	6–7.9	8–9.9
2–3.9	0.94				
4–5.9	0.97	0.72			
6–7.9	0.99	0.91	0.75		
8–9.9	0.98	0.93	0.84	0.65	
10–11.9	0.95	0.75	0.90	0.95	0.90

Table 2. Diversity and richness statistics for arthropods in an upland hardwood hammock in Florida, USA. Arthropods were sampled on the ground at 2 distances from the tree trunk, or at 5 heights (m) above the soil on tree trunks. *H* is Shannon diversity index; Simp is Simpson index; Rich is the mean species richness per trap; Ind is the mean number of individuals per trap; Chao1 and ACE (abundance-based coverage estimators) are species richness estimates.

Class	*H*	Simp	Rich	Ind	Chao1	ACE
All	3.59	0.94	4.88	32.08	198.96 ± 26.92	228.60 ± 9.88
Ground	3.35	0.93	7.31	47.23	202.07 ± 41.05	236.05 ± 10.79
Far	3.01	0.91	8.17	35.67	68.46 ± 10.73	87.33 ± 6.28
Close	2.96	0.90	9.14	64.00	147.25 ± 40.13	164.62 ± 8.26
Arboreal	3.44	0.95	7.00	20.00	74.00 ± 13.30	8.03 ± 5.33
2–3.9	2.23	0.81	7.00	96.76	49.00 ± 13.49	58.71 ± 4.56
4-5.9	1.26	0.50	4.00	31.67	27.00 ± 13.13	26.25 ± 2.59
6–7.9	0.77	0.38	4.00	68.00	5.5 ± 1.26	6.59 ± 1.08
8–9.9	1.38	0.70	2.50	6.50	16.00 ± 10.07	28.67 ± 2.14
10–11.9	2.02	0.81	7.00	91.50	18.50 ± 3.65	22.39 ± 2.46

diversity varies with seasons, yr, and as the tree community shifts from tropical to temperate. Further, rarefaction curves showed that many more morphospecies would be identified with increased sampling across all height classes. Further study could better resolve how taxa are stratified. Such studies also could reveal the extent to which invasive species may impact canopy diversity (Kaspari 2000). Ours and future investigations will contribute toward resolving the debate regarding the pattern of vertical stratification in temperate vs tropical forests. Our study revealed an unexpected pattern of vertical stratification in diversity at the confluence of temperate and tropical assemblages.

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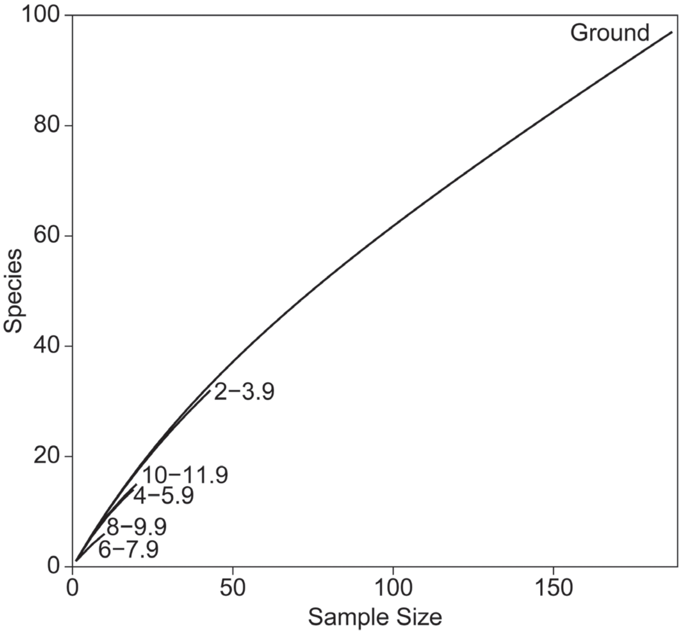

Fig. 4. Rarefaction curves for size height classes of arboreal and ground pitfall traps collecting arthropods in an upland hardwood forest in Florida, USA. Steep curves indicate that further sampling would reveal additional morphospecies.

References Cited

Basset Y. 2001. Invertebrates in the canopy of tropical rain forests: how much do we really know? Plant Ecology 153: 87–107.

Basset Y, Aberlenc H-P, Barrios H, Curletti G, Bérenger J-M, Vesco J-P, Caussem P, Huag A, Hennion A-S, Lesobre L, Marquès F, O'Meara R. 2001. Stratification and diel activity of arthropods in a lowland rainforest in Gabon. Biological Journal of the Linnean Society 72: 585–607.

Basset Y, Hammond PM, Barrios H, Holloway JD, Miller SE. 2003a. Vertical stratification of arthropod assemblages, pp. 17–27 *In* Basset Y [ed.], Arthropods of Tropical Forests: Spatio-temporal Dynamics and Resource Use in the Canopy. Cambridge University Press, Cambridge, United Kingdom.

Basset Y, Novotny V, Miller SE, Hitching RL. 2003b. Canopy entomology, an expanding field of natural science, pp. 4–6 *In* Basset Y [ed.], Arthropods of Tropical Forests: Spatio-temporal Dynamics and Resource Use in the Canopy. Cambridge University Press, Cambridge, United Kingdom.

Brehm G, Axmacher JC. 2006. A comparison of manual and automatic moth sampling methods (Lepidoptera: Arctiidae, Geometridae) in a rain forest in Costa Rica. Environmental Entomology 35: 757–764.

Chao A. 1984. Nonparametric estimation of the number of classes in a population. Scandinavian Journal of Statistics 11: 265–270.

Chao A. 1987. Estimating the population size for capture-recapture data with unequal catchability. Biometrics 43: 783–791.

Chiu CH, Wang YT, Walther BA, Chao A. 2014. Improved nonparametric lower bound of species richness via a modified Good-Turing frequency formula. Biometrics 70: 671–682.

Colwell RK, Coddington JA. 1994. Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society London B 345: 101–118.

DeVries PJ, Murray D, Lande R. 1997. Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. Biological Journal of the Linnean Society 62: 343–364.

Dice LR. 1945. Measures of the amount of ecologic association between species. Ecology 26: 297–302.

Erwin TL. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. The Coleopterists Bulletin 63: 74–75.

Fiala A, Garman SL, Gray AN. 2006. Comparison of five canopy cover estimation techniques in the western Oregon Cascades. Forest Ecology and Management 232: 188–197.

Florida Division of Recreation and Parks. 2005. St. Sebastian River Preserve State Park Unit Management Plan. Department of Environmental Protection, Tallahassee, Florida, USA.

Florida Natural Areas Inventory. 2010. Upland Hardwood Forest. Guide to the Natural Communities of Florida. Florida Natural Areas Inventory, Tallahassee, Florida, USA.

Greller AM. 1980. Correlation of some climate statistics with distribution of broadleaved forest zones in Florida, USA. Bulletin of the Torrey Botanical Club 107: 189–219.

Hall DW. 2006. The environmental hazard of ethylene glycol in insect pit-fall traps. The Coleopterists Bulletin 45: 193–194.

Hammond PM. 1990. Insect abundance and diversity in the Dumoga-Bone National Park, N. Sulawesi, with special reference to the beetle fauna of lowland rain forest in the Toraut region, pp. 197–254 *In* Knight WJ, Holloway JD [eds.] Insects and the Rain Forests of South East Asia (Wallacea). Royal Entomological Society, St. Albans, United Kingdom.

Hammond PM, Stork NE, Brendell MJD. 1997. Tree-crown beetles in context: a comparison if canopy and other ecotone assemblages in a lowland tropical forest in Sulawesi, pp. 184–223 *In* Stork NE, Adis J, Didham RK [eds.] Canopy Arthropods. Chapman & Hall, New York, USA.

Heck KL, van Belle G, Simberloff D. 1975. Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. Ecology 56: 1459–1461.

Hill MO. 1973. Diversity and evenness, a unifying notation and its consequences. Ecology 54: 427–432.

Hurlbert SH. 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52: 577–586.

Jennings SB, Brown ND, Sheil D. 1999. Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. Forestry 72: 59–74.

Jud P, Schmidt-Entling MH. 2008. Fluid type, dilution, and bitter agent influence spider preservation in pitfall traps. Entomologia Experimentalis et Applicata 129: 356–359.

Kaspari M. 2000. Do imported fire ants impact canopy arthropods? Evidence from simple arboreal pitfall traps. The Southwestern Naturalist 45: 118–122.

Kautz RS, Cox JA. 2001. Strategic habitats for biodiversity conservation in Florida. Conservation Biology 15: 55–77.

Longino JT, Nadkarni NM. 1990. A comparison of ground and canopy leaf litter ants (Hymenoptera: Formicidae) in a neotropical montane forest. Psyche 97: 81–89.

Lowman MD. 2009. Canopy research in the twenty-first century: a review of arboreal ecology. Tropical Ecology 50: 125–136.

Lowman MD, Wittman PK. 1996. Forest canopies: methods, hypotheses, and future directions. Annual Review of Ecology and Systematics 27: 55–81.

Moffett MW, Lowman MD, Nadkarni NM. 1995. Canopy access techniques, pp. 3–26 *In* Lowman MD, Nadkirni NM [eds.] Forest Canopies. Academic Press, Burlington, Massachusetts, USA.

O'Hara RB. 2005. Species richness estimators: how many species can dance on the head of a pin? Journal of Animal Ecology 74: 375–386.

Palmer MW. 1990. The estimation of species richness by extrapolation. Ecology 71: 1195–1198.

Parker GG, Brown MJ. 2000. Forest canopy stratification—is it useful? American Naturalist 155: 493–484.

Pinzón J, Spence J. 2008. Performance of two arboreal pitfall trap designs in sampling cursorial spiders from tree trunks. Journal of Arachnology 36: 280–286.

Rogers DJ, Kitching RL. 1998. Vertical stratification of rainforest collembola (Collembola: Insecta) assemblages: description of ecological patterns and hypotheses concerning their generation. Ecography 21: 392–400.

Schulze CH, Linsenmair KE, Riedler K. 2001. Understory versus canopy: patterns of vertical stratification and diversity among Lepidoptera in a Bornean rain forest. Plant Ecology 153: 133–152.

Sørensen T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species and its application to analyses of the vegetation on Danish commons. Kongelige Danske Videnskabernes Selskab 5: 1–34.

Stork NE, Grimbacher PS. 2006. Beetle assemblages from an Australian tropical rainforest show that the canopy and the ground strata contribute equally to biodiversity. Proceedings of the Royal Society of London B 273: 1969–1975.

Su JC, Woods SA. 2000. Importance of sampling along a vertical gradient to compare the insect fauna in managed forests. Environmental Entomology 30: 400–408.

Sutton SL, Ash CPJ, Grundy A. 1983. The vertical stratification of flying insects in lowland rain forests of Panama, Papua New-Guinea and Brunei. Zoological Journal of the Linnean Society 78: 287–297.

Ulyshen MD. 2011. Arthropod vertical stratification in temperate deciduous forests: implications for conservation-oriented management. Forest Ecology and Management 261: 1479–1489.

Vieira EM, Monteiro-Filho ELA. 2003. Vertical stratification of small mammals in the Atlantic rain forest of south-eastern Brazil. Journal of Tropical Ecology 19: 501–507.

Walter DE, Seeman O, Rodgers D, Kitching RL. 1998. Mites in the mist: how unique is a rainforest canopy-knockdown fauna? Austral Ecology 23: 501–508.

Webb DS. 1990. Historical Biogeography, pp. 70–100 *In* Myers RL, Ewel JJ [eds.] Ecosystems of Florida. University of Central Florida Press, Orlando, Florida, USA.