Diversity of Surface-Active Terrestrial Invertebrates in Forested Landscape Ecosystems, Lincoln and Bristol, Vermont 1999-2002

A Report to the Colby Hill Ecological Project

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Introduction

Invertebrates dominate the earth's biota. The number of described species approximates 2 million, but some estimates of invertebrate species richness are as high as 80 million (New 1998). Despite their important contribution to biological diversity, however, terrestrial invertebrates have generally received little attention in conservation planning.

The development of state endangered species lists in the mid-1980's was one of the first actions with clear implications for the conservation of invertebrates in New England (McCollough 1997). It resulted in some conservation efforts focused on rare and endangered species. Unfortunately the breadth of invertebrate taxa represented on state lists is extremely limited and reflects an inter-state disparity of invertebrate expertise at academic institutions that influences status and listing (McCollough 1997).

In addition to their contribution to biodiversity, invertebrates have begun to receive attention from conservationists and ecological planners for their potential usefulness in biomonitoring (Kremen et al. 1993). Invertebrates can provide an attractive alternative to larger animals in ecosystem monitoring for several reasons including their wide distribution relative to vertebrates, their rapid population turnover, and the ease with which they can be sampled in statistically significant numbers (Kremen et al. 1993). Terrestrial invertebrates are low on the food chain and thus respond more rapidly to subtle environmental changes than vertebrates. In small preserves, invertebrates offer a way of monitoring ecological integrity that may not be feasible with relatively small vertebrate populations.

One of the challenges of working with invertebrates is that conducting a thorough inventory is both time-consuming and costly. The dedication of numerous taxonomic specialists is required to achieve species level identification for many groups. To address this problem, some efforts have been made by ecologists (Oliver and Beattie 1996; Colwell and Coddington 1994; Hammond 1994) to establish time- and cost-effective shortcut methods for the estimation of invertebrate species richness and diversity. The current study employs two of these methods by using extrapolation (Colwell and Coddington 1994) to estimate taxa richness and focal groups (Hammond 1994) as surrogates for larger invertebrate assemblages.

The Colby Hill Ecological Project is a local effort to describe the biological diversity in a mid-elevation landscape of the Green Mountains in Lincoln and Bristol, Vermont. One of the goals of the project is to provide baseline data on the taxa present. As part of the Colby Hill Ecological Project, we examined the surface-active terrestrial invertebrate diversity in three forested landscape ecosystems at the Guthrie-Bancroft Farm in Lincoln and Bristol, Vermont. We used sampling methods designed to capture those species primarily active on the ground surface or within the forest litter. Lapin (2000) has classified, described, and numbered these landscape ecosystems. The ecosystems targeted were: a rich, moderately well drained, seepy, northern hardwood forest (RFW) on ablation till deposits that are shallow to bedrock (ES6 in Lapin 2000) ; a well drained, beech-red maple-red oak-sweet birch transition hardwood forest (THF) on deep ablation till deposits (ES1 in Lapin 2000); and a somewhat poorly drained, red spruce-balsam fir-hemlock-yellow birch forest (SF) on deep, dense, compact basal till deposits (ES14 in Lapin 2000). The ecosystems lie at elevations between approximately 1200-1400 ft (365-425 m) and are situated in close proximity to one another (within approximately 1km of one another), but belong to different

landform-level ecosystems (Lapin 2000).

Two important criteria used to assess the conservation value of an ecosystem are diversity and rarity of resident species (Magurran 1988). We analyzed the diversity and rarity of invertebrates at two taxonomic levels—family-level and species-level. Within each forest type, we calculated the α-diversity of invertebrate families and estimated the family richness. We also estimated the overall family richness of the three ecosystems pooled. We compared the ecosystems to assess their similarity (β-diversity) to one another at the family level. Additionally, we selected three focal groups for identification to the species level: ground beetles (Family: Carabidae), ants (Family: Formicidae), and spiders (Order: Areneida). According to Danks (1997), it is generally better to have species-level information on a few carefully chosen groups than family-level information on many. Species are the functioning entities of nature and each species has a different tolerance for conditions, therefore species-level identification offers the opportunity to examine ecosystem interactions in a way that family-level information generally does not (Danks 1997). The focal groups were chosen because they are diverse, abundant, believed to be sensitive to environmental changes, able to be sampled by standardized techniques, and, perhaps most importantly, taxonomically well-known. These focal groups have been chosen as taxa to identify to the species-level by other researchers as well (Oliver and Beattie 1996).

Methods

In each of three forested ecosystems RFW (44°09.537′ N, 73°01.719′ W), THF (44°09.197′ N, 73°01.837′ W), and SF (44°08.994′ N, 73°01.134′ W) on the Guthrie-Bancroft parcel (Figure 1), pitfall and litter samples were collected twice each year (once in May or June and once in July or August) from 1999-2002 (Table 1). Pitfall traps were set approximately 5 m apart in a linear transect and left open for one week. Traps consisted of a small plastic cup containing a dilute formalin solution. A piece of bark was carefully placed above each trap to keep out rain, but loosely enough so that there was room for invertebrates to move beneath and enter the trap. When the traps were recovered, three 4-L samples of forest litter were collected near the pitfall traps. The litter samples were placed into Berlese funnels to extract the litter-dwelling invertebrates. Collection dates were May 13 & July 25, 1999 and May 27 & July 15, 2000, June 8 & August 4, 2001, and June 22 & August 17, 2002.

The number of pitfall traps placed in each ecosystem varied from year to year. Six pitfall traps were placed at each site in each season in 1999, ten were placed in 2000 and 2001, and eight were placed in 2002. The variation in pitfall trap numbers was, in part, a result of the discovery that during the July 1999 collection, several of the traps were disturbed (probably by a bird or a mammal). In July 1999, the disturbed pitfall traps were reset and collected on August 1, 1999 (with the exception of one pitfall trap from RFW that was not reset). In subsequent years, larger numbers of traps were set at each location so that traps would not need to be reset and at least six intact pitfall traps would be obtained from each site.

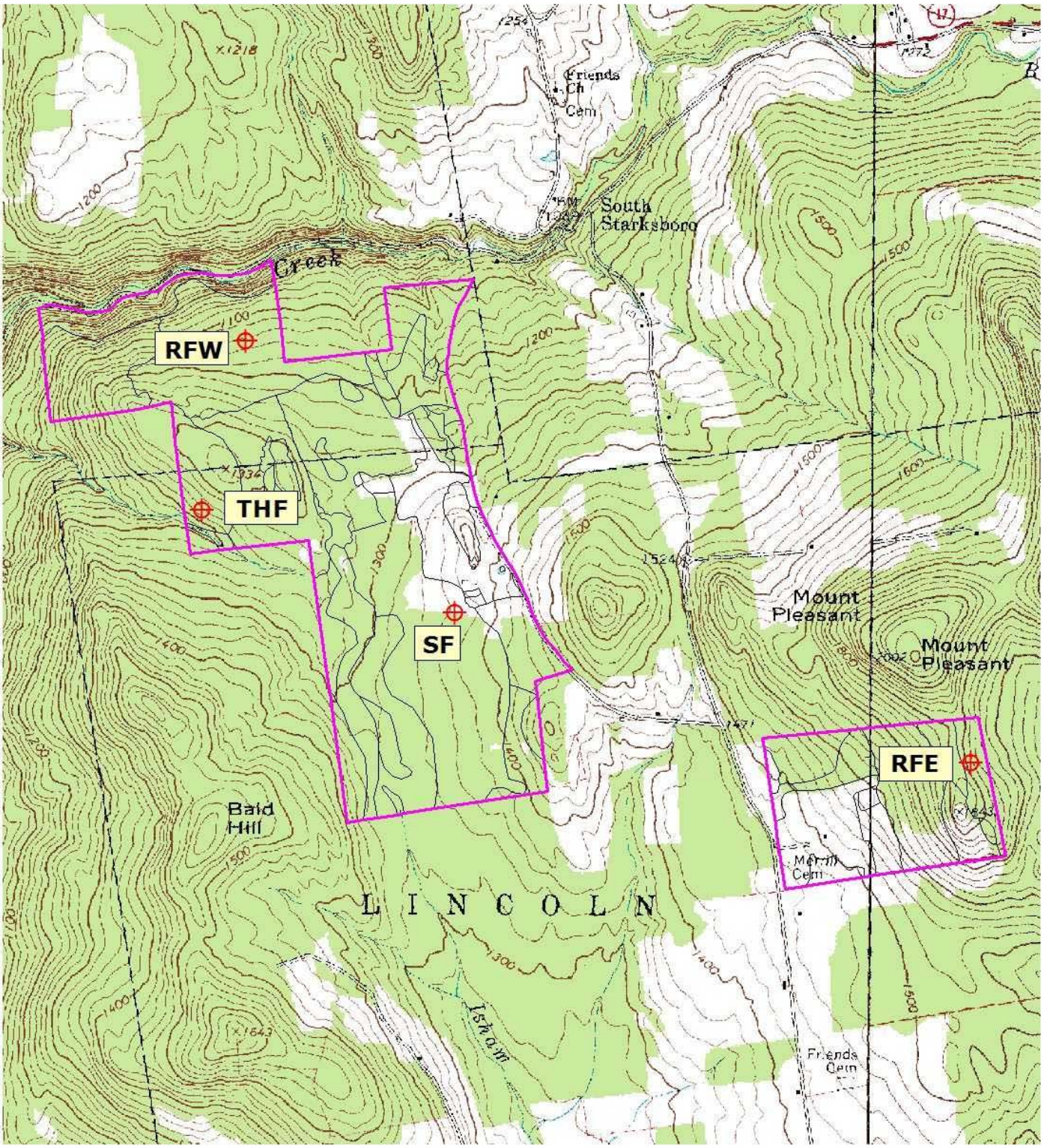


Figure 1. Sample site locations of surface-active invertebrates for the Colby Hill Ecological Project, Bristol and Lincoln, Vermont, 1999-2002. RFW = Rich hardwood forest west, THF = Transition hardwood forest, SF = Spruce-fir forest, RFE = Rich hardwood forest east. Base map is USGS Bristol and Mt. Ellen quads.

Though litter samples were collected in June 2002, they were not processed quickly enough in Berlese funnels to yield specimens and no results were obtained. In addition to the collections made at the three forest ecosystems, pitfall and litter samples were also collected on the same dates in 2000 from a rich hardwood forest (RFE), floristically similar to RFW, but without active groundwater seepage and on a different aspect; its location was east of the other three (44°08.700′ N, 72°59.692′ W) on the Wells parcel (Figure 1).

All adult specimens recovered from pitfall traps and litter samples in 1999 and 2000 were identified to the family level, except for three problematic orders (Acarina, Pseudoscorpionida, and Psocoptera). The Acarina are an extremely difficult group to identify to the family level and are typically lumped by order in data analyses. Similar difficulties with the Pseudoscorpionida and the Psocoptera forced us to treat them at the order level. All adult specimens belonging to the three focal groups (ground beetles (Family: Carabidae), ants (Family: Formicidae), and spiders (Order: Areneida)) that were recovered from pitfall traps and litter samples in 1999, 2000, 2001, and 2002 were identified to species-level (except specimens that were immature or damaged in a way that prevented species-level identification). In the case of the spiders, species-level identification was not possible for all specimens belonging to the family Linyphiidae. The Linyphiidae is a family of spiders comprised of tiny specimens that are quite difficult to identify and are here treated as a group, a common practice given the difficulty with the systematics of the taxon (Miller 1999). Expert assistance was obtained to identify Linyphiid specimens collected in 1999, but was not available in subsequent years.

Table 1. Summary of pitfall trap and litter sampling effort in the Colby Hill Ecological Project, Lincoln and Bristol, VT, 1999-2002.

Month-Year	Number of pitfall traps set per site	Total number of pitfall traps set (all sites)	Sites at which traps were set	Disturbed pitfall traps	Total number of undisturbed pitfall traps collected (all sites)	Number of litter samples processed per site	Total number of litter samples processed
May 1999	6	18	RFW, THF, SF		18	3	9
July/August 1999	6	18	RFW, THF, SF	RFW3	17	3	9
May 2000	10	40	RFW, THF, SF, RFE	THF2, THF6, SF2, SF3, SF7, SF10	34	3	12
July 2000	10	40	RFW, THF, SF, RFE	THF2	39	3	12
June 2001	10	30	RFW, THF, SF	SF10	29	3	9
August 2001	10	30	RFW, THF, SF	SF2, SF4, SF6	27	3	9
June 2002	8	24	RFW, THF, SF	SF1	23	0	0
August 2002	8	24	RFW, THF, SF		24	3	9
Totals		**224**			**211**		**69**

Calculations and Data Analysis for Family-Level Data

Family Richness Estimates

In order to standardize the number of samples collected from each ecosystem over the first two years for analyses, we used only the first six numbered pitfall traps from each site in each season in the numerical analyses of family data that follow. We pooled the 1999 and 2000 data for each ecosystem type and tallied the observed number of families in each ecosystem. We then used non-parametric methods for the estimation of taxa richness from small samples (Colwell and Coddington 1994) to obtain family richness estimates. Of several estimators reviewed by Colwell and Coddington (1994), we chose three measures to estimate family richness, in order to compare the results and test their efficacy. They were:

$$F_1^* = F_{obs} + (a^2/2b), \quad (1)$$

$$F_2^* = F_{obs} + (L^2/2M), \quad (2)$$

$$F_3^* = F_{obs} + L\,(n\text{-}1/n), \quad (3)$$

where:

F_1^*, F_2^*, and F_3^* are estimates of the family richness in an assemblage;

F_{obs} is the observed number of families in the sample;

a is the number of families represented by a single individual;

b is the number of families represented by exactly two individuals;

L is the number of families that occur in only one subsample;

M is the number of families that occur in exactly two subsamples;

and n is the number of subsamples (a subsample corresponded to a pitfall trap or litter collection).

Two of these formulas, (1) and (2), were first employed by Chao (1984) and are referred to as Chao 1 and Chao 2. The third formula (3) was developed by Burnham & Overton (1979) and is referred to as the jackknife estimator (or Jack 1).

Family Level Diversity

The Shannon index of diversity (Magurran 1988) was calculated for families in each ecosystem. The widely used Shannon index takes into account both richness and evenness and is calculated from the equation:

$$H' = - \Sigma p_i \ln p_i \quad (4)$$

where p_i is the proportion of individuals belonging to the i^{th} family (Magurran 1988). The diversity values were tested for significant differences between ecosystems (Magurran 1988) by pairwise t-tests using the formula:

$$t = H_1' - H_2' / (\text{Var } H_1' + \text{Var } H_2')^{1/2} \quad (5)$$

where Var H_1' and Var H_2' are the variances in ecosystem 1 and 2 respectively.

Family Level Similarity (β-diversity)

We calculated several measures of β-diversity (or differentiation diversity) to examine the degree of similarity in family diversity between ecosystems. We used three different similarity indices to compare the ecosystems—Sorenson qualitative, Sorenson quantitative, and Morisita quantitative—because each had its unique limitations. The Sorenson qualitative index is a simple calculation, but it takes no account of relative taxa abundance or identity (Magurran 1988). It is calculated from the equation:

$$C_s = 2j/(a + b) \qquad (6)$$

where j = the number of families found in both sites and a = the number of families in Site A with b the number of families in Site B. The Sorenson quantitative index takes into account relative taxa abundance:

$$C_N = 2\,\Sigma N_j / (N_a + N_b) \qquad (7)$$

where N_a = the total number of individuals in site A, N_b = the total number of individuals in site B, and N_j is the lower of the two abundances recorded for the j^{th} family found in both sites. Thus if 12 individuals of a family were found in Site A and 29 individuals of the same family were found in Site B the value 12 would be included in the summation of N_j. The Sorenson quantitative index, like many quantitative similarity indices, is strongly influenced by family richness and sample size (Magurran 1988). Unlike the Sorenson quantitative index, the Morisita-Horn quantitative index is not influenced by family richness or sample size, but it is highly sensitive to the abundance of the most abundant family (Magurran 1988). The Morisita-Horn index is:

$$C_M = 2\,\Sigma\, x_i\, y_i / (L_a + L_b)\, N_a\, N_b \qquad (8)$$

where x_i is the number of individuals of the i^{th} family in site A, y_i is the number of individuals of the i^{th} family in site B, N_a and N_b are the total number of individuals in site A and site B, $L_a = x_i\,(x_i - 1)/ N_a\,(N_a - 1)$ which is the probability that two randomly selected individuals from site A will belong to the same family and $L_b = y_i\,(y_i - 1)/ N_b\,(N_b - 1)$ which is the same probability in site B.

Calculations and Data Analysis for Species-Level Data on Focal Groups

The focal group data from 1999-2002 were qualitatively analyzed to determine the total number of species collected, the number of species found in only one forest ecosystem, and the number of species that were collected by only one of the sampling techniques. This qualitative analysis included all mature specimens in the focal groups that were collected over the four sampling seasons.

Focal group data from specimens collected only in pitfall traps was quantitatively analyzed utilizing the EstimateS© software program developed by Colwell (1997). The EstimateS© software program was used to assess the efficiency of pitfall trapping by generating species abundance curves. This software program was also used to calculate a variety of indices that measure species richness and species diversity. In addition to Chao 1, Chao 2, and Jack 1, the EstimateS© program calculates several other measures of species richness such as the Abundance-based Coverage Estimator (ACE) and the Incidence-based Coverage Estimator (ICE). Measures of species richness and species diversity were calculated using data from six pitfall traps per site per collection cycle in order to standardize the data set for each forest

ecosystem type and for each year. For this reason, the observed number of species used in the quantitative calculations were in some cases smaller than the number of species used for qualitative analyses (because some species were collected only in litter samples or else were only collected in one of the additional pitfall traps in years 2000-2002).

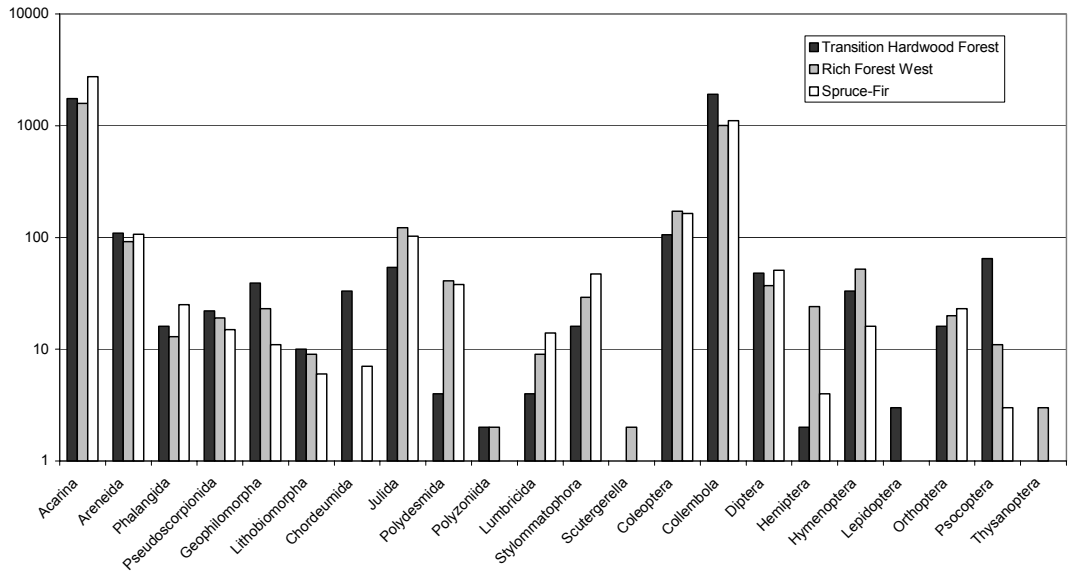
Results & Discussion

Family Diversity

Overall Family Richness

From the three ecosystems that were sampled in 1999 and 2000, we collected 11,990 specimens in 107 subsamples (71 pitfall traps and 36 litter samples). The specimens represented seven classes and 22 orders (Figure 2). The order with the largest number of specimens was the mites (Order: Acarina); the 6,073 mite specimens comprised more than 50% of all specimens. The orders with next highest number of specimens were the springtails (Collembola) and the beetles (Coleoptera). The order Coleoptera was represented by the largest number of families (22).

Figure 2. The relative abundances of surface-active invertebrate orders in three ecosystems at Guthrie-Bancroft Farm, Lincoln/Bristol, Vermont, 1999 and 2000.



We identified 5,761 specimens to the family level and sorted them into 101 invertebrate families. The three problematic orders were each treated as a single family for a minimum of 104 observed families. We calculated estimates of overall family richness for the site by pooling the data from the three ecosystems sampled (Table 2). The overall family richness values measured by three estimators were within a quite narrow range (134-139) suggesting that the estimates from the pooled data may be zeroing in on the actual family richness value. In general, however, extrapolation techniques tend to underestimate

actual richness values (Colwell and Coddington 1994) and this effect is compounded by treating the problematic orders (Acarina, Pseudoscorpionida, and Psocoptera) as single families.

Ecosystem Family Richness and Shannon Diversity

The number of observed families within an ecosystem did not differ greatly between ecosystems and ranged from 63-70 families (Table 2). The ecosystem family richness estimates (Table 2) ranged from 86-97 families for RFW, from 89-115 families for SF and from 85-116 families for THF.

Table 2. The family richness estimates of surface-active invertebrates for three forest ecosystems at the Guthrie-Bancroft Farm, Lincoln/Bristol Vermont, 1999 and 2000. RFW = Rich hardwood forest west; SF = Spruce-fir forest; THF = Transition hardwood forest; F_1^*, F_2^*, and F_3^* = family richness estimators; F_{obs} = number of observed families; a=number of families represented by a single individual b = number of families represented by exactly two individuals; L = number of families in only one subsample; M = number of families in only two subsamples; N = number of subsamples.

	RFW 99-00	**SF 99-00**	**THF 99-00**	**Pooled data 99-00**
$F_1^* = F_{obs} + (a^2/2b)$	86	115	93	134
$F_2^* = F_{obs} + (L^2/2M)$	97	91	116	138
$F_3^* = F_{obs} + L\ (n\text{-}1/n)$,	91	89	85	139
N	35	36	36	107
a	17	22	19	30
b	9	5	6	15
L	22	23	23	35
M	9	11	5	18
F_{obs}	70	67	63	104

Each forest ecosystem had several families that were not found in the other two forest types.

The Shannon Diversity Index values for the three ecosystems were numerically close and ranged from 1.71 - 1.84 (Table 3) with RFW having the highest value. Pairwise t-tests of the three ecosystems showed no significant difference in the Shannon diversity values of SF and THF, but did show a statistically significant difference between the diversities of RFW and each of the other two ecosystems.

Table 3. Shannon family diversity index values for surface-active invertebrates from three forest ecosystems at the Guthrie-Bancroft Farm, Lincoln/Bristol Vermont, 1999 and 2000. RFW = Rich hardwood forest west; SF = Spruce-fir forest; THF = Transition hardwood forest; H′ = Shannon diversity index; Var H′= variance.

	RFW 99-00	**SF 99-00**	**THF 99-00**
H′	1.84	1.71	1.74
Var H′	6.73	6.10	5.75

Neither the observed number of families nor the family richness estimates offered compelling evidence that any ecosystem had appreciably higher family richness than the others. The Shannon diversity index, which takes into account evenness as well as richness, indicated that RFW is more diverse than THF and SF at the family level due more to greater evenness than a greater number of families.

Ecosystem Similarity (β-Diversity)

The three indices of ecosystem similarity yielded no clear trends in similarity across ecosystems at the family level. The Sorenson qualitative index values were very similar for all pairwise comparisons. Both of the quantitative indices yielded results which suggest that SF and RFW were most similar and THF and RFW were least similar. Spatially, RFW and THF were adjacent ecosystem types, whereas SF was approximately 1 km south of RFW.

Table 4. Ecosystem similarity values for three forest ecosystems at the Guthrie-Bancroft Farm, Lincoln/Bristol Vermont, 1999 and 2000.
RFW = Rich hardwood forest west; SF = Spruce-fir forest; THF = Transition hardwood forest.

	RFW vs. THF	SF vs. RFW	THF vs. SF
Sorenson Qualitative Index C_s	65.7%	66.2%	68.1%
Sorenson Quantitative Index C_N	71.2%	72.6%	59.8%
Morisita-Horn Index C_M	88.3%	96.0%	78.7%

Species Diversity

Species Accumulation Curves

One of the challenges of using sampling techniques to assess biodiversity is having confidence in the level of sampling. Sampling needs to be sufficient to offer the opportunity for most targeted species to be captured. However, sampling should not be overly prohibitive with regard to time or expense. One way to assess the effectiveness of sampling is the construction of species accumulation curves.

The effectiveness of pitfall trapping for focal group species was examined by tallying average species accumulation for eight pitfall traps at each site (for each collection cycle in which eight pitfall traps were collected). The results of this analysis (Figure 3) show that species accumulation did not seem to level off with 8 traps at any of the forest ecosystems, suggesting that a single collection cycle was not adequate to estimate species diversity for the focal groups. However, when the overall species accumulation for four years of pitfall trapping data were examined (Figure 4), the curves for both SF and THF began to level off after 3 years of sampling (36 traps) whereas the curve for RFW appeared to be gradually climbing even after four years (48 traps). These data suggest that most species within the focal groups have been captured in both THF and SF, but that further effort might yield new species within the focal groups in RFW (though from the slope of the curve the number of new species might prove rather small).

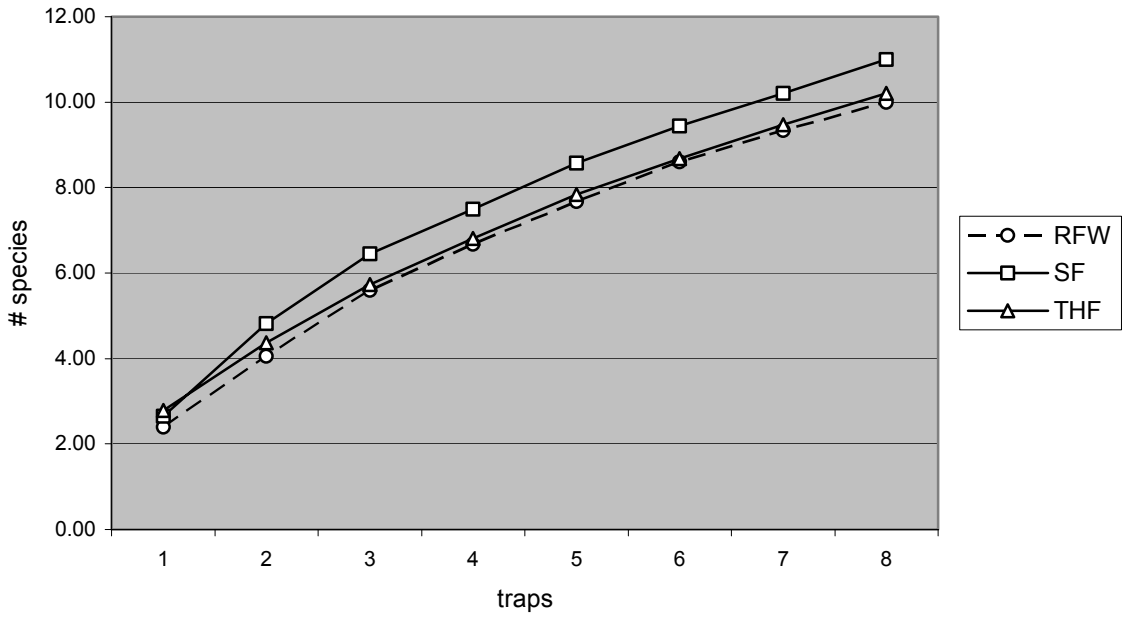


Figure 3. The species accumulation curves for focal group species (ground beetles, ants, and spiders) by number of traps in three forested ecosystems averaged over multiple collection cycles and years where 8 traps were available (RFW n=6, SF n=3, THF n=5) at the Guthrie-Bancroft Farm, Lincoln/Bristol Vermont, 1999-2002. *RFW = Rich hardwood forest west; SF = Spruce-fir forest; THF = Transition hardwood forest.*

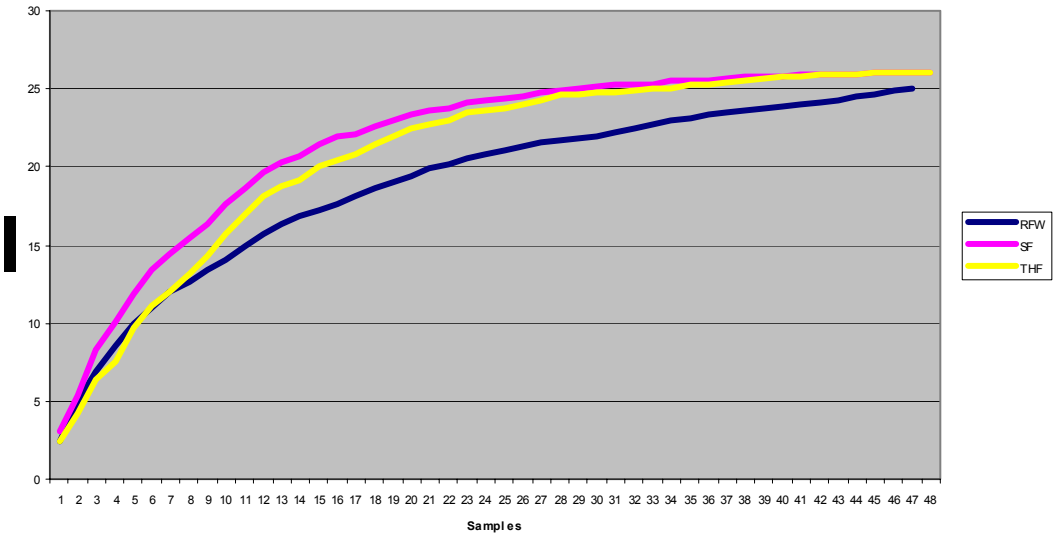


Figure 4. The species accumulation curves for focal group species (ground beetles, ants, and spiders) over four years (using 6 traps per site) in three forested ecosystems at the Guthrie-Bancroft Farm, Lincoln/Bristol Vermont, 1999-2002. *RFW = Rich hardwood forest; SF = Spruce-fir forest; THF = Transition hardwood forest.*

Ants

A total of 174 ant specimens were collected and identified to the species level from the three ecosystem types over the four years (Table 5). The sample was comprised of 5 species. The two most commonly collected species (*Aphaenogaster rudis, Stenamma diecki*) accounted for more than eighty percent of all ant specimens. Two species were collected from only one forest type. The abundance of ants collected in the spruce-fir forest was markedly lower than either of the other two forest ecosystem types, and the most commonly collected species (*Aphaenogaster rudis*) was not found there at all. However, one of the species, *Camponotus herculeanus*, was found only in the spruce-fir forest. The two least commonly collected species (*Leptothorax acervorum, Camponotus herculeanus*) were collected only in pitfall traps. None of the species was collected only in litter samples, but one of the commonly collected species (*Stenamma diecki*) was collected abundantly in litter samples and only infrequently in pitfall traps.

Table 5. Species presence and abundance of ants collected from three forest ecosystems in Lincoln and Bristol, Vermont 1999-2002. P=total number of pitfall traps, L= total number of litter samples, [1]=found in only one of the three forest ecosystems, [3]=found only in pitfall traps. *RFW = Rich hardwood forest; SF = Spruce-fir forest; THF = Transition hardwood forest.*

Family	*Species Name & Authority*	RFW P=67 L=21	THF P=65 L=21	SF P=59 L=21	Total
Formicidae	*Aphaenogaster rudis* Buckley	30	42		72
Formicidae	*Camponotus herculeanus* Linnaeus [1,3]			9	9
Formicidae	*Lasius alienus* Foerster	13	8	1	22
Formicidae	*Leptothorax acervorum* Fabricius [1,3]		2		2
Formicidae	*Stenamma diecki* Emery	27	38	4	69
		70	**90**	**14**	**174**

The estimators of species richness for ants from all sites were equal to the number of observed species (Table 6) suggesting that it is unlikely that future pitfall trapping effort would have yielded new ant species from the study site.

Table 6. The species richness estimates of ants for three forest ecosystems at the Guthrie-Bancroft Farm, Lincoln/Bristol Vermont, 1999-2002. *RFW = Rich hardwood forest west; SF = Spruce-fir forest; THF = Transition hardwood forest; S_{obs} = number of observed species N = number of samples.*

Ants	RFW 99-02	SF 99-02	THF 99-02	Pooled data 99-02
N	47	48	48	143
S_{obs}	3	2	3	4
Chao 1; $S_1^* = S_{obs} + (a^2/2b)$	3.2	1	3	4
Chao 2; $S_2^* = S_{obs} + (L^2/2M)$	3.2	1	3	4
Jack 1; $S_3^* = S_{obs} + L\ (n-1/n)$,	3.98	2.98	3	4
ACE	3.93	3.09	3	4
ICE	3.72	3.11	3	4

Ground Beetles

A total of 621 ground beetle specimens were collected and identified to the species level from the three ecosystem types over the four years (Table 7). The sample was comprised of 26 species. The most commonly collected species (*Synuchus impunctatus*) accounted for more than forty percent of all ground beetle specimens. Thirteen species were collected from only one forest ecosystem type (though four of these were also collected from RFE when it was sampled in 2000) and eight species were represented by a single specimen. Seventeen species were found only in pitfall traps, and three species were found only in litter samples. This suggests that pitfall trapping is a good method for collecting a diversity of carabid species, but that litter samples offer the potential to capture a few species that may be less commonly collected in pitfall traps. Some species were relatively abundant in two ecosystems, but completely absent from the third; for example, *Platynus decentis* was absent from THF despite its relatively high abundances in SF & RFW (Table 7).

Table 7. Species presence and abundance of ground beetles collected from three forest ecosystems in Lincoln and Bristol, Vermont 1999-2002. P=total number of pitfall traps, L= total number of litter samples, [1]=found in only one of the three forest ecosystems, [2]=found only in litter samples, [3]=found only in pitfall traps, [4]=despite being found in only one of the three forest ecosystems, species was also collected in RFE. *RFW = Rich hardwood forest; SF = Spruce-fir forest; THF = Transition hardwood forest.*

Family	***Species Name & Authority***	**RFW P=67 L=21**	**THF P=65 L=21**	**SF P=59 L=21**	**Total**
Carabidae	*Agonum fidele* Casey. [1,2]	1			1
Carabidae	*Agonum mutatum* Gemminger & Harold [1,3]	1			1
Carabidae	*Agonum retractum* Leconte	34	11	7	52
Carabidae	*Agonum trigeminum* Lindroth [1,3]	1			1
Carabidae	*Calathus ingratus* Dejean[1,3,4]			10	10
Carabidae	*Calosoma frigidum* Kirby[3]	3		4	7
Carabidae	*Cymindis cribricollis* Dejean	2	8		10
Carabidae	*Cymindis neglecta* Haldeman [1,3]		1		1
Carabidae	*Gastrellarius honestus* Say [1,2,4]			2	2
Carabidae	*Notiophilus aeneus* Herbst [1,3]			9	9
Carabidae	*Olisthopus parmatus* Say [1,3]	1			1
Carabidae	*Platynus decentis* Say	29		32	61
Carabidae	*Platynus hypolithos* Say [1,3]		1		1
Carabidae	*Pterostichus adoxus* Say [1,3,4]		1		1
Carabidae	*Pterostichus adstrictus* Eschscholtz[1,3]			12	12
Carabidae	*Pterostichus coracinus* Newman	50	1	15	66
Carabidae	*Pterostichus diligendus* Chaudoir[3]	6		7	13
Carabidae	*Pterostichus lachrymosus* Newman[3]	12		1	13
Carabidae	*Pterostichus pensylvanicus* Leconte[3]		6	2	8
Carabidae	*Pterostichus rostratus* Newman	2	17	3	22
Carabidae	*Pterostichus stygicus* Say	13	1	17	31
Carabidae	*Pterostichus tristis* Dejean [1,3,4]		8		8
Carabidae	*Sphaeroderus canadensis* Chaudoir[3]	8	4	2	14
Carabidae	*Sphaeroderus lecontei* Chaudoir[3]	14	3	4	21
Carabidae	*Synuchus impunctatus* Say[3]	43	183	28	254
Carabidae	*Trechus apicalis* Motschulsky [1,2]			1	1
		220	**245**	**156**	**621**

The estimators of species richness for ground beetles (Table 8) seem to suggest that the most potential for capturing new species in future pitfall trapping is in the transitional hardwood forest where the observed number of species was 10 but species richness estimates ranged from 11.95-14.5. The numbers seem to suggest that future effort in the other ecosystems would not be expected to yield many new species and that the overall number of new species from all sites combined would be low.

Table 8. Species richness estimates of ground beetles for three forest ecosystems at the Guthrie-Bancroft Farm, Lincoln/Bristol Vermont, 1999-2002. *RFW = Rich hardwood forest west; SF = Spruce-fir forest; THF = Transition hardwood forest; S_{obs} = number of observed species N = number of samples.*

Ground Beetles	RFW 99-02	SF 99-02	THF 99-02	Pooled data 99-02
N	47	48	48	143
S_{obs}	12	14	10	18
Chao 1; $S_1^* = S_{obs} + (a^2/2b)$	12.25	14	14.5	20
Chao 2; $S_2^* = S_{obs} + (L^2/2M)$	13	14	14.5	19
Jack 1; $S_3^* = S_{obs} + L\ (n-1/n)$,	13.96	13.98	12.94	20
ACE	12.39	14	12.37	18.72
ICE	13.23	14.49	11.95	18.89

Spiders

A total of 252 spider specimens were collected and identified to the species level from the three ecosystem types over the four years (Table 9). The sample was comprised of 36 species belonging to 12 different families. The family Linyphiidae had the highest number of species (11) despite being identified to the species level in only one year. The four most commonly collected species (*Neoantistea magna, Wadotes hybridus, Wadotes calcaratus, Pirata montanus*) accounted for sixty-five percent of spider specimens. Interestingly, 25 of the species were collected from only one of the sampled ecosystems. Fourteen species were represented by a single specimen. Fifteen species were found only in pitfall traps and eleven species were found only in litter samples suggesting that both collection techniques were useful in estimating the richness of spiders. One species (*Cryphoeca montana*) was found only in the rich hardwood forest (RFE) that was sampled in 2000.

The estimators of species richness for spiders (Table 10) seem to suggest that each of the ecosystems offers the potential for successfully finding new species from future pitfall-trapping effort and that the number of species overall could be increased significantly with greater effort. Spiders differ from the other two focal groups in this regard in that both the ground beetle and ant species estimates were very close to the number of observed species. One possible explanation for this difference was the inclusion of species-level identifications of Linyphiidae species from only one of the collection years. If it had been possible to identify the Linyphiids from all four years, the species richness estimates may have been much closer to the observed number of spider species for the individual ecosystems and for the three sites taken as whole.

Table 9. Species presence and abundance of spiders collected from three forest ecosystems in Lincoln and Bristol, Vermont 1999-2002. P=total number of pitfall traps, L= total number of litter samples, [1]=found in only one of the three forest ecosystems, [2]=found only in litter samples, [3]=found only in pitfall traps, [4]=despite being found in only one of the three forest ecosystems, species was also collected in RFE, * denotes species that was found only in RFE. *RFW = Rich hardwood forest; SF = Spruce-fir forest; THF = Transition hardwood forest.*

Family	Species Name & Authority	RFW P=67 L=21	THF P=65 L=21	SF P=59 L=21	Total
Liocranidae	*Agroeca ornate* Banks [1,3]		2		2
Amaurobiidae	*Amaurobius borealis* Emerton	2	1	1	4
Linyphiidae	*Bathyphantes pallidus* Banks [1,3]			1	1
Linyphiidae	*Bathyphantes* sp. A (nr. Yukon)[1,3]	1			1
Linyphiidae	*Centromerus persolutus*	4	4	2	10
Linyphiidae	*Ceraticelus* sp. A [1,2]	1			1
Linyphiidae	*Ceratinella brunnea* Emerton[1]	2			2
Dictynidae	*Cicurina arcuata* Keyserling[3]	1	3		4
Dictynidae	*Cicurina brevis* Emerton	2	4	4	10
Dictynidae	*Cicurina pallida* Keyserling[3]	3	13	3	19
Dictynidae	*Cicurina placida* Banks[1,3]	1			1
Clubionidae	*Clubiona canadensis* Emerton [1,3]		1		1
Agelenidae	*Cryphoeca montana* Emerton*				
Linyphiidae	*Eperigone maculata* Banks [1,2]			2	2
Linyphiidae	*Lepthyphantes zebra* Emerton [1,3]	1			1
Salticidae	*Metaphidippus canadensis* (Banks)[1,2]	1			1
Thomisidae	*Misumena vatia* Clerck [1,3]			1	1
Hahniidae	*Neoantistea magna* Keyserling[3]	17	19	14	50
Hahniidae	*Neoantistea* cf. *radula* Emerton [1,2]		1		1
Salticidae	*Neon nellii* Peckham & Peckham [2]	1	1		2
Thomisidae	*Ozyptila americana* Banks [1,2]			1	1
Thomisidae	*Ozyptila beaufortensis* Strand [1,3]			2	2
Thomisidae	*Ozyptila distans* sp. N Dondale and Redner [1,3]		2		2
Liocranidae	*Phurotimpus alarius* Hentz	1	2		3
Lycosidae	*Pirata insularis* Emerton [1]			2	2
Lycosidae	*Pirata montanus* Emerton	13	2	21	36
Theridiidae	*Robertus riparius* Keyserling [1,2]		1		1
Linyphiidae	*Sisicottus montanus* Emerton[1,3]			1	1
Linyphiidae	*Tapinocyba simplex* Emerton		1	2	3
Lycosidae	*Trochosa pratensis* Emerton [1]			3	3
Lycosidae	*Trochosa terricola* Thorell[1,4]			2	2
Linyphiidae	*Tunagyna debilis* Banks[1]			2	2
Amaurobiidae	*Wadotes calcaratus* Keyserling [3]	9	7	20	36
Amaurobiidae	*Wadotes hybridus* Emerton	9	22	11	42
Linyphiidae	*Walckenaeria directa* O. Pickard-Cambridge[1,3]	1			1
Gnaphosidae	*Zelotes fratris* Chamberlin [1,2]			1	1
		70	**86**	**96**	**252**

Table 10. The species richness estimates of spiders for three forest ecosystems at the Guthrie-Bancroft Farm, Lincoln/Bristol Vermont, 1999-2002. *RFW = Rich hardwood forest west; SF = Spruce-fir forest; THF = Transition hardwood forest; S_{obs} = number of observed species N = number of samples.*

Spiders	RFW 99-02	SF 99-02	THF 99-02	Pooled data 99-02
N	47	48	48	143
S_{obs}	9	10	12	16
Chao 1; $S_1^* = S_{obs} + (a^2/2b)$	12.33	11	14.67	25
Chao 2; $S_2^* = S_{obs} + (L^2/2M)$	13.5	14.5	14.67	40.5
Jack 1; $S_3^* = S_{obs} + L\ (n\text{-}1/n)$,	11.94	12.94	15.92	22.95
ACE	12.63	12.32	16.59	25.34
ICE	11.29	11.81	15.79	30.94

Focal Group Diversity

The Shannon diversity values for each of the three focal groups was calculated using the EstimateS© software program (Table 11). The Shannon diversity values for ants were very low at each of the three ecosystems and overall, which should not come as a surprise given that so few ant species were collected over the four years of sampling. The Shannon diversity values for ground beetles were fairly high from both RFW and SF, but were noticeably lower at THF (despite this site yielding the highest number of individuals). The very low Shannon diversity values for ground beetles at THF may be attributable to the overwhelming abundance of one species (*Synuchus impunctatus*) at THF (Table 7). The Shannon diversity values for spiders were fairly similar from ecosystem to ecosystem and overall.

Table 11. Shannon diversity index values for spiders, ants, and ground beetles from three forest ecosystems at the Guthrie-Bancroft Farm, Lincoln/Bristol Vermont, 1999-2002.
RFW = Rich hardwood forest west; SF = Spruce-fir forest; THF = Transition hardwood forest.

	RFW	SF	THF	Pooled data 1999-2002
Ants	0.79	0.33	0.98	1.27
Ground Beetles	2.01	2.28	1.01	2.06
Spiders	1.84	1.99	2.07	2.13

Ecosystem Similarity (β-Diversity)

Three indices were used to compare the similarity of ecosystems for both ground beetles and spiders (Table 12). There were not enough species of ants found to make such a comparison useful for that focal group. The similarity values indicate that for ground beetles RFW and SF were most similar, whereas for spiders RFW had approximately the same similarity to SF as to THF. Additionally, the similarity values strongly suggest that THF and SF were most different from one another for both ground beetles and spiders. This was especially true for ground beetles where there were very low similarity values for both quantitative indices. Moreover, the similarity values for ground beetles between RFW and THF were also fairly low suggesting that THF was an important contributor to the overall diversity of the ground beetle fauna at Guthrie-Bancroft farm. The transitional hardwood forest yielded the highest number of ground

beetle individuals of any of the three ecosystems (245), but had the lowest species richness of any of the three (13 species) and the lowest Shannon diversity value. Despite having a low ground beetle species count, four of the thirteen species found there were not found in either of the two other ecosystems which may in part account for the low similarity values.

Table 12. Similarity index values for ground beetle and spider species at three forest ecosystems at the Guthrie-Bancroft Farm, Lincoln/Bristol Vermont, 1999-2002.
RFW = Rich hardwood forest west; SF = Spruce-fir forest; THF = Transition hardwood forest.

Focal Group	Index	RFW vs. THF	SF vs. RFW	THF vs. SF
Ground beetles	Sorenson Qualitative Index	55%	61%	53%
	Sorenson Quantitative Index	29%	57%	23%
	Morisita-Horn Quantitative Index	53%	84%	36%
Spiders	Sorenson Qualitative Index	63%	42%	49%
	Sorenson Quantitative Index	62%	64%	49%
	Morisita-Horn Quantitative Index	81%	84%	70%

Ground Beetle Diversity: A Comparison with Similar Studies

It can be difficult to interpret the species-level diversity findings in this study without reference to a suitable comparison at locations outside of the Guthrie-Bancroft Farm. Fortunately, several ground beetle studies have been conducted in the mountains of Vermont (Rykken 1995, Boone 2000, Dickert 2001) that offer an opportunity for comparison within that focal group. All three previous ground beetle researchers used pitfall trapping. Boone also collected insects using light traps and malaise traps, but it is unclear from his study whether ground beetles were collected using these techniques (it is likely that light traps would attract some species of ground beetle). His study seems to indicate that the numbers of species and individuals were tallied based on pitfall trap data alone. Both Rykken and Dickert collected ground beetles from study sites in the Green Mountain National Forest, and Boone collected from three sites at Mount Mansfield.

Rykken (1997) collected at elevations between 1,100 ft (336 m) and 2300 ft (702 m) from three different Ecological Land Types (ELT) in the northern section of the Green Mountain National Forest (GMNF) in central Vermont, but found no significant differences between carabid distributions at the ELT level. She found that most of the carabid fauna of the mid-elevation western Green Mountains was comprised of forest generalists, with some specialist species responding to a moisture gradient at the site scale. She suggested that her results might indicate that carabid assemblages vary more at a higher scale (such as the Land Type Association) or at a lower scale (such as the Ecological Land Type Phase).

Dickert (2001) examined the hypothesis that carabid assemblages vary at the Land Type Association (LTA) level by sampling across eight Land Type Associations in the GMNF. Dickert found that carabid species assemblages showed no significant differences at the LTA level when using Shannon's measure of diversity, but she found that one of the eight LTAs (LTA 0) was significantly different from the

others when using cluster analysis and pairwise comparisons of Morisita similarity values. Interestingly, LTA 0 represented the highest elevations (above 2,500 ft (762 m)) in Dickert's study and included spruce-fir and non-forested alpine habitat, which suggests that the difference may have been more attributable to elevation changes than the general landscape characteristics that differentiated the other LTAs. Dickert therefore concluded that carabid assemblages did not differ appreciably at the LTA level, and instead suggested that many of the differences in relative abundance and diversity detected in carabid communities by Rykken at the site level could best be explained at a finer scale of land classification such as the Ecological Land Type Phase.

In the third study, Boone (2000) examined carabid distribution in three different forest types at different elevations at Mt. Mansfield: Site 1 – subalpine balsam fir forest (3,840 ft (1,170 m)), Site 2 – mixed hardwood forest (2,000 ft (610 m)), and Site 3 – sugar maple forest (1,360 ft (414 m)). Similar to Dickert, Boone found that carabid beetle assemblages differed significantly between the high elevation habitat and the deciduous habitats at lower elevations. There were differences in mean number of species and individuals between the high elevation site and the other two sites, but the lower elevation sugar maple and mixed hardwood sites were similar to one another. One model, however, consistently showed that site 2 – the mixed hardwood forest – was more diverse than the other two sites. Species composition of the mixed hardwood forest was compared to Rykken's list of species from GMNF ELTs (1997). More species were trapped in the mixed hardwood forest by Boone (45) than in the three ELTs studied by Rykken combined (Table 13).

Table 13. Comparison of carabid species counts from four studies conducted in Vermont.

	Number of individuals	**Number of species**	**Number of species occurring in all sites***	**Number of species occurring in only one site***	**Number of species represented by only one individual**
Rykken (1995)	9041	35	18	12	7
Dickert (2001)	1316	46	4 (1998 data only)	12 (1998 data only)	18
Boone (2000)	8793	67	21	30	17
Colby Hill Project	621	26	7	13	8

*The term "site" refers respectively to the ELT (Rykken), the LTA (Dickert), the site (Boone), and the ecosystem (Colby Hill).

The number of individuals and the number of species of ground beetles collected in the Colby Hill Project were smaller than in any of the previous studies (Table 13), but the amount of trapping effort was also lower. Of the 28 species collected by all three of the previous researchers, 20 were collected in this study as well (Table 14). One species, *Platynus hypolithos*, was not collected by any of the other researchers, but was found in this study. According to Bell (1992), *P. hypolithos* is a species that is rapidly advancing northward in Vermont after a rather recent crossing of the Hudson River.

Table 14. Carabid species and number of individuals collected in four studies in Vermont.

Species name	Rykken	Dickert	Boone	Colby Hill
Agonum fidele	0	7	6	1
Agonum harrisii	0	2	1	0
Agonum melanarium	0	1	1	0
Agonum mutatum	28	1	34	1
Agonum octopunctatum	0	0	1	0
Agonum palustre	0	0	5	0
Agonum retractum	2458	185	1479	52
Agonum sordens	0	0	1	0
Agonum superioris	0	0	1	0
Agonum trigeminum	0	1	0	1
Amara lunicollis	0	0	1	0
Anisodactylus sanctaecrucis	0	1	0	0
Bembidion obstusum	0	1	0	0
Bembidion wingatei	5	9	4	0
Bembidion semicinctum	22	1	2	0
Bembidion versicolor	0	0	1	0
Bradycellus lugubris	0	0	6	0
Bradycellus nigrinus	0	3	0	0
Calasoma frigidum	7	0	2	7
Calathus gregarious	0	0	1	0
Calathus ingrates	180	37	346	10
Carabus goryi	35	1	0	0
Carabus nemoralis	0	0	2	0
Carabus serratus	0	0	35	0
Clivina fossor	1	1	2	0
Cymindis cribricollis	10	11	466	10
Cymindis neglecta	0	8	0	1
Dicaelus politus	1	2	3	0
Dromius piceus	0	0	1	0
Dyschirius integer	0	1	0	0
Elaphrus clairvillei	0	0	2	0
Gastrellarius honestus	42	1	29	2
Harpalus caliginosus	0	0	1	0
Harpalus fulvilabrus	2	0	0	0
Harpalus pleuriticus	0	0	2	0
Harpalus somnulentus	0	1	1	0
Loricera pilicornis	0	0	1	0
Metabletus americanus	0	0	2	0
Myas cyanescens	2	2	119	0
Nebria lacustris	0	0	1	0
Nebria pallipies	0	0	3	0
Notiobia (Anisotarsus) terminate	0	0	1	0
Notiophilus aeneus	8	6	16	9
Notiophilus nemoralis	0	1	101	0
Olisthopus parmatus	2	3	6	1
Patrobus longicornis	0	0	8	0
Patrobus foveocollis	0	0	28	0

Platynus decentis	533	11	329	61
Platynus hypolithos	0	0	0	1
Platynus mannerheimi	17	0	67	0
Platynus tenuicollis	0	0	4	0
Poecilus (Pterostichus) lucublandus	0	0	16	0
Pseudamara arenaria	3	1	4	0
Pterostichus adoxus	63	15	34	1
Pterostichus adstrictus	684	4	227	12
Pterostichus brevicornus	0	11	328	0
Pterostichus commutabilis	0	0	1	0
Pterostichus coracinus	1221	105	332	66
Pterostichus diligendus	92	3	132	13
Pterostichus lachrymosus	0	1	90	13
Pterostichus luctuosus	1	4	0	0
Pterostichus melanarius	1	0	6	0
Pterostichus mutus	1	0	8	0
Pterostichus patruelis	0	1	1	0
Pterostichus pensylvanicus	1032	32	970	8
Pterostichus punctatissimus	1	1	28	0
Pterostichus rostratus	872	62	393	22
Pterostichus stygicus	1	15	248	31
Pterostichus tenuis	0	2	0	0
Pterostichus tristis	549	83	177	8
Scaphinotus viduus	10	3	43	0
Sphaeroderus Canadensis	423	45	475	14
Sphaeroderus lecontei	503	24	570	21
Sphaeroderus nitidicollis	0	0	6	0
Stenolophus (Agonoderus) comma	0	0	1	0
Synuchus impunctatus	228	627	1537	254
Trechus apicalis	2	1	23	1
Trechus crassiscapus	0	1	21	0
Total Count	**9041**	**1316**	**8793**	**621**

At the site level, the ranges of values for individuals and species observed in the Colby Hill Project were most similar to those found by Dickert (Table 15). This is most likely a function of trapping effort since these two studies had the least intensive trapping regimes. A comparison of statistical measures across studies is somewhat difficult to do because not all values are available from all studies; nevertheless the values that are available offer some insight. Shannon diversity values at Colby Hill were generally higher than those found by Dickert and with the exception of one ecosystem (THF) compared favorably with those found by Rykken. Boone used the EstimateS© software program (Colwell 1997) to calculate a variety of indices that estimate species richness. Boone's estimated values for species richness were consistently higher than those estimated at the site level in the Colby Hill Project (Table 15). Presumably the difference is a function of the larger numbers of observed species at each of Boone's sites as compared with the ecosystems at Colby Hill. Whether increased effort would have generated the numbers of observed species at Colby Hill that were found in Boone's study is somewhat doubtful given the flattening out of the species accumulation curves for focal groups in the Colby Hill Project (Figure 4).

Finally, the relatively large differences between Shannon diversity values at the three Colby Hill ecosystems (Table 11) and the relatively low similarity values for ground beetles across the three ecosystems (especially between THF and the other two ecosystems) appear to support Rykken's second hypothesis that carabid assemblages vary at a finer scale than the Ecological Land Type. The three ecosystems at Colby Hill all lie within close proximity to one another and do not appear to offer much geographic isolation, which suggests that the observed differences in carabid assemblages are a result of responses to site-scale factors such as moisture and/or nutrient regimes.

Table 15. Statistical ranges of values at the site level for carabid diversity in four studies in Vermont. *Blank spaces indicate statistical values that were not available from some studies.*

Ranges of values at the site level	Rykken	Boone	Colby Hill	Dickert
Number of individuals	2720-3518	970-4296	156-220	47-140
Species observed		39-45	10-14	9-16
Shannon diversity H´	2.18-2.28		1.01-2.28	0.56-1.29
ACE		41-60	12-14.5	
ICE		41-60	12-14.5	
Chao 1		41-112	12-14	
Jacknife 2		41-60	12-15	
Michaelis-Menten		41-45	11.5-18	

Conclusions

There were significant differences in family level diversity between ecosystems, but family richness did not differ significantly. Therefore, the difference must be in the evenness component of diversity. There were no clear trends in family level similarity between ecosystems. At the species level, ground beetles were much less diverse in the transition hardwood forest ecosystem than in the other forest ecosystem types, but this trend did not hold true for the other focal groups.

Sampling effort over the four seasons seemed to be adequate based on both the richness estimators and the species accumulation curves generated for focal group species. Estimator values for family richness, ant richness, and ground beetle richness were very close to the number of observed values. This was not necessarily true for spider richness estimates, which seemed to suggest that a few new species in each ecosystem and several species overall remained as yet undetected. This may, however, be a result of species-level identifications of Linyphiidae species having been included from only one of the collection years.

Litter samples served as an important tool in supplementing the number of observed species for ground beetles, but were especially important for spiders. Nearly one third of spider species were found only in litter samples.

Each of the ecosystems includes families and species that were not found in the other sampled ecosystems. All of the focal groups had species that were found in only one of the sampled ecosystems. Two species of ants were found in only one ecosystem, even though ants were not particularly diverse in this study overall (only five observed species). Also, more than two-thirds of the spider species observed

were found in only one ecosystem. These findings suggest that the overall biodiversity of surface-active invertebrates, and likely of other organisms as well, is enhanced by the preservation of the three forest ecosystems that were examined. The loss of any one ecosystem could easily result in the local extinction of species from the property.

Finally, the results of the ground beetle data in this study appear to support Rykken's second hypothesis that carabid assemblages vary at a finer scale than the Ecological Land Type. The three ecosystems at Colby Hill all lie within close proximity to one another and do not appear to offer much geographic isolation, which suggests that the observed differences in carabid assemblages are a result of responses to site scale factors such as moisture and/or nutrient regimes.

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