Biodiversity of vagile arthropods and forest succession

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Abstract

Previous studies of forest succession have demonstrated that the diversity of plants and less mobile animals gradually increase through successional time, reach a maximum, and decline to a less diverse but stable climax community. In this study, we explored the applicability of this trend to very vagile arthropods, whose home ranges likely exceeded the size of the treated area. Vagile arthropods were collected in early June 1998 at Black Rock Forest, a temperate mixed hardwood forest in New York. Two replicate plots in each age class of 11, 41, 65, and 87 years since a clear-cutting event were sampled. Arthropods were sampled using pan traps and sorted to morphospecies. Species richness and individual abundance at each plot were assessed through raw numbers , Shannon and Simpson Diversity Indices and an evenness index. Chi-square tests were conducted to assess significant differences among all samples and samples within the same age classes, forest area, and taxonomic orders.

Results indicated that overall species diversity and abundance were high early after a clear-cut (11 years) and peaked at mid-succession (65 years). Diversity and abundance were low in the sites of the 41 year class, and they also declined at the oldest forest sites. Different processes may be responsible for the two peaks. Colonist and open-habitat specialists with great dispersal abilities and large cruising ranges likely accounted for the early peak, whereas the later peak was probably due to the actual increase in community diversity through the persistence of early forest succession

species. Overall trends in succession reflect the changes in the diversity and abundance of specific taxa.

While certain taxa did show no significant change in diversity and abundance through successional time, other vagile taxa sampled in large quantities seemed to follow natural community successional processes characterized by a peak in mid-succession. These patterns suggest that certain vagile arthropod taxa may be used as bioindicators of the successional status of forest ecosystem. However, factors other than successional age alone likely affected vagile arthropod distribution.

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Introduction

Succession and the state of ecology

Succession is an important concept that has been the subject of much study throughout the history of ecology (McIntosh 1985). Broadly, it refers the replacement of one kind of community by another (Stiling 1996). Principles of succession are still subject to debate, and other aspects have not received adequate attention. One area that has been left to many assumptions and has not been the focus of studies is the role of vagile organisms in community processes through succession.

Community relations and subjects of succesional studies

One reason for the lack of study in the succession of vagile organisms involves the notion of a community. A community may refer to a group of organisms generally of wide taxonomic affinities that occur together many of which will interact within a framework of horizontal and vertical linkages (Giller 1995). In turn, intraspecific and interspecific interactions within and between trophic levels define members of a local community. While communities imply interactions between populations, they are distinct from assemblages, which refer to groups of species of the same locality or on the same resources without the implication of species interaction (Price 1997). With organisms that are highly mobile, they may be assumed to be part of an assemblage of an area, but their mobility makes their distinction as members of a community may remain questionable.

Communities are often defined by spatial boundaries in which they exist (Magurran 1988). Plants and sessile organisms have often the subject of successional studies (Timoney 1996, Whittle et al. 1997). Without much dispersion, home ranges of these organisms are implicitly fixed, and they can be assumed to be members of a local community. As such, they would likely reflect the successional state of the community with accuracy.

On the other hand, a major problem associated with sampling any mobile organism in an ecosystem is that the organisms in the sample may not necessarily be a representative of the local community; a vagile organism may simply be traveling through the sample site (Niemela 1996). With increased vagility, the likelihood of species abundance and distribution not dependent on local interactions and processes and, hence, misrepresentation as local community members increases. Consequently, vagile taxa whose locomotive ranges exceed a defined local community area, such as aerial arthropods, are not often the focus of monitoring projects or are excluded from successional studies altogether.

Significance of this project- indicators of succession

Exclusion of vagile organisms from ecological monitoring programs neglects potentially the most taxonomically abundant and diverse animal taxa in an area. Aerial and other vagile arthropods can be easily sampled, are usually easy to identify, and are very abundant. As such, these organisms could be used as easily accessible bioindicators of the ecological status of a community if they demonstrate successional patterns. Such a demonstration would indicate that vagile arthropods are likely members of the local community.

This study explored the relationship between the biodiversity of vagile arthropods and time since a clear-cut. Unlike previous studies on succession, the subject of this study was highly mobile, focusing on those taxa that disperse aerially. If their diversity curves closely tracked patterns of taxa that are known forest community members, then moblie arthropodsmight also be less vagile than assumed. As likely members of the local forest community and could be used to reliably monitor forest successional processes. Based on the results and their pattern of diversity, the suitability of these animals for monitoring projects could be determined.

In general, insects have been found to reflect successional patterns as conditions of host population changes, which may be plants or other arthropods that are herbivorous (Price 1997). Studies on the effects of logging, loss of old-growth specialists did not result in a decrease in total number of species; regenerating sites have been found to carry more species than unlogged sites (Niemela 1996). Such results have also been found at Black Rock Forest, a temperate forest in the Hudson Highlands of New York (Danoff-Burg unpublished data). In turn, they have been useful indicator species for studying succession.

Mechanisms, patterns and theories of succession

The appropriate pattern of succession in the community should be recognized to determine whether an organism is a member of a successional community. Ecological succession often refers to the change in an ecosystem that is usually predictable and directional, such that a pattern of development is observable (Price 1997). In turn, progressive changes in vegetation and animal life that tend toward climax occur in succession (Stiling 1996). However, the causes, processes, and patterns of succession have long been full of convolution and subject to contention. In spite of extensive research done to this point, the mechanisms of succession and its direction and end have remained far from reaching a conclusion (McIntosh 1988). Based on the type of ecosystem, succession of a community can follow a variety of trends. This study explored autogenic succession in a temperate mixed deciduous forest following a clear-cut.

In autogenic succession, vegetation has been found to drive changes in the process of succession, as opposed to allogenic succession, in which the climax community depends on changes in abiotic factors , such as soil and climate conditions (McIntosh 1985). Clements (1905) provided one of the earliest theories of autogenic succession (McIntosh 1985). He divided succession into three functions. The first function is association, the state of the climax community. Another function is invasion, which involves the movement of plants toward successful recolonization of an area. The third function, succession , was explained as the series of invasions of sufficient magnitude and persistence to bring about a decrease or disappearance of original occupants.

Among various theories of autogenic succession, conventional ecological theory suggests that diversity should increases with time. Based on autogenic processes, Odum (1969) proposed that higher energy production than energy loss by vegetation in an ecosystem was thought to result in an accumulation of biomass that would allow for greater energy utilization (McIntosh 1985). However, various studies have challenged the conventional notion of increase to a climax community in autogenic succession.

Studies of temperate forest succession have provided much of the challenges to conventional theory (McIntosh 1985). Studies by Woodward and Whitaker (1968-1969) and Loucks (1970) of temperate oak forest communities following a fire did not find a culmination to a climax. Rather, they found that, following a period of initial increase, biodiversity of vegetation actually decreased from some successional stage before reaching a climax (Price 1997). Such a pre-climactic peak about 50 years into succession was attributed to the persistence of earlier successional vegetation (Price 1997). Terrestrial arthropods have also affirmed the successional process of a peak around mid to late-succession and decline to a stable climax community characteristic of forest succession (Niemela 1996, Cooper 1913). Further, contradicting notions of homogeneity, forest community should be considered as a mosaic of different ages (Magurran 1988). Therefore, similar patterns were expected in this study.

Fires are one example of a disturbance that causes succession in communities. Disturbances may be natural or anthropogenic. Measured by its intensity times its duration, period, or frequency they vary in their degree of effect. Studies have attributed reduced biodiversity of soil communities to human perturbations (Giller 1995). A clear-cut is an example of a human disturbance, and, based on this study, conclusions about its effect on biodiversity could be assessed.

Following a disturbance, recovery occurs through the recolonization by organisms. Simberloff and Wilson (1969, 1970) performed a well-known demonstration of recovery following a disturbance (Stiling 1999). Their study displayed the ability of a disturbed community to recover. It also suggested that multiple stable states may exist in an area undergoing succession. Studies have indicated that certain species were important in hastening recovery of a disturbed community. Local extinction or large-scale reduction of specialists of old-growth forests inhibits recolonization by these species (Niemela 1996). Such specialists of older forest stands may represent keystone species toward which conservation efforts should be directed. In turn, such keystone species may be identified within vagile arthropods.

Hypotheses

Based on the unique properties of aerial arthropods, several hypotheses about their pattern of succession were proposed in this study. The null hypothesis was that these arthropods were not members of any local community on this geographic scale and did not specialize on patches of specific ages. If this were the case, results would show that diversity and abundance were uniformly distributed among sites or in a manner dissimilar to other hypotheses, and plots within age classes would be no more similar than other comparisons.

If flying arthropods were members of the local communities, they would follow less vagile terrestrial arthropod and plant diversity curves characteristic of autogenic forest succession (Whitaker and Woodward 1968, Danoff-Burg, unpublished data). Therefore, diversity and abundance would increase to a maximum at mid succession and then decrease with time to the stable community size of the climax community. Also, plots within age classes would be most similar.

If aerial arthropods were principally colonizer species and members of disturbed patch plant communities, diversity and abundance would have a negative relationships with time. This has been found in previous studies of flying insects. Using flying carabid beetles, populations have been found to be highest early after a clear-cut (10 years or less) and followed by a decline from 20 to 60 years into climax succession (Niemela 1996, Butterfield 1996, Roff 1994, Barbosa 1989). In turn, early in succession, plots of the same age group would be most similar, and later age groups would have no relationship.

Methods

Site of collection

Aerial insects were collected in early June at Black Rock Forest in New York, a northeast temperate forest. Geographically, it is located in the Hudson Highlands at approximately 74° 01' W and 41°23' N. The forest had been classified by Raup (1938) as an oak-hickory type in which the white oak is most characteristic and, often, most abundant, and the soil has been found to be in a transition zone (Braun 1950). However, the undergrowth constituents may differ within this forest type (Braun 1950). Once owned by Harvard School of Forestry, the forest contains sites that have been clear-cut at various times in its history along with sites that have remained undisturbed.

A map at the forest recording the year of clear-cut treatment and consultation of the forest manager were used to determine the age of sample plots. Plots were sampled in age classes of 11, 41, 65, and 87 years since clear-cuts (Table 1). Age classes were determined by the arithmetic mean of plot ages. Each age class consisted of two plots. These plots also came from three different areas in the forest (Table 1).

Successional stage was determined by corresponding ages of successional stages in other studies and by observation of the vegetation development at the site. The 11-year class represented the early succession stage, where there was little canopy cover and much herbaceous flora. Both plots in the 11-year class were11 years old. The 41 and 65-year classes represented mid to late succession, in which both understory vegetation and climax forest trees coexisted. One of the plots in the 41-year-old class was 40 years old, while the other was 41. In the 65-year-old site, one plot was 61 years old and the other was 68 years old. The 87-year-old sites represented the climax forest communities, marked by the dominance of oak. One plot was 78 years since a clear-cut and the other had been left undisturbed for 96 years.

Trapping

Collection was done using pan traps, a technique for sampling aerial arthropod (Peng et al 1993). These traps were made by adding 1-2 in. of water to pans lined with yellow contact paper at the bottom. Ample dishwashing detergent was added to break surface tension, preventing arthropods with the ability to walk along water surface from doing so. Salt was added as a preservative for the trapped specimens.

The traps were set out from June 5-6, and they were harvested 5 days later on June 10-11. Six traps were set out in 3 pairs along a linear transect. The first pair was approximately 15 meters from the road and subsequent pairs were 20 meters apart. Traps in each pair were 10 meters apart from each other. The samples were strained from the traps with a fish net and then transferred into falcon tubes. The tubes were then filled with 80% ethanol solution, the standard concentration for arthropod preservation (Milne 1980).

The pan traps were set on the ground of the forest plots. Such positioning limited the range of aerial arthropods sampled to those under the canopy cover and flying within a few feet of the ground. While such a placement would sample arthropods that were not necessarily the most vagile, it also limited collection of those whose home ranges clearly exceeded that of the sample plot. In turn, the likelihood of sampling aerial arthropods that were more characteristic of the community was increased.

Figure 1. Map of sites used at Black Rock Forest. Plots from the same forest area are circled.

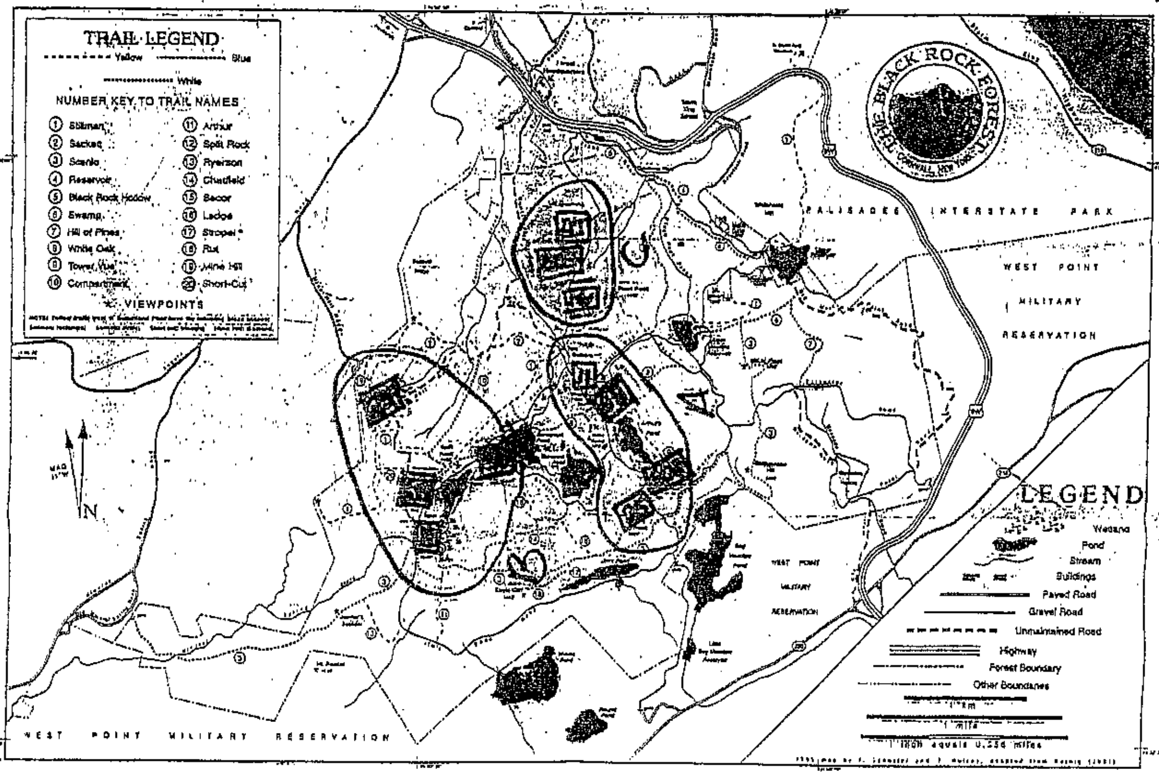


Table 1. Ages, Age Classes, and Areas of Sites.

Site No.	*4*	*6*	*10A*	*10B*	*16*	*20*	*21*	*22*
Age	11	68	61	11	41	96	78	40
Age Class	11	65	65	11	41	87	87	41
Area	A	A	B	B	C	C	A	B

The traps were also situated shading to prevent evaporation of the water. This may have introduced a bias in sampling toward aerial arthropods characteristic of the particular plant. Therefore, placement of traps under the shade of a variety of vegetation in the sampled community may have normalized this possible bias. Further, the likelihood of nonaerial and less vagile organisms falling from a leaf or branch into the pan trap was increased.

Sorting

In the lab, the collected arthropods were sorted to morphospecies. The taxomic orders in the study were large *Diptera* (flies), *Coleoptera* (beetles), and *Araneae* (mostly spiders)., *Homoptera* (plant bugs and aphids), *Collembola* (springtails), and miscellaneous arthropods. Separation of morphospecies in each order were based on wing venation, shape of antennae, color, and size. Excluded from this dataset were small *Diptera* (flies), *Hymenoptera* (parasitic wasps and ants), and immature individuals, which were often damaged or too difficult to identify.

Record and analysis of data

Data was recorded and analyzed to determine the changes in aerial arthropod populations in the succession of forest stands. Species diversity and abundance were recorded. Results were expressed in a variety of ways.

Overall diversity and abundance were each graphed against time on an X-Y scatter plot. Taxonomic composition of species and individuals was determined at each site and represented in a column graph as well as linearly over time. Mean values were calculated among the sites and between age classes, and Chi-square tests were conducted against the mean.

In addition to the raw numbers, both the Shannon and Simpson Diversity Indices were calculated (Shannon and Weaver 1949, Simpson 1949), as was Hill's Evenness Index (Hill 1973). The Shannon Diversity (H') provided a statistical analysis of species richness that accounted for evenness of species abundance Index (Magurran 1988). It was calculated by using the equation:

$$H' = -\sum p_I \ln p_i$$

where p_i is the proportion of individuals found in the ith species and ln is the natural logarithm.

The Simpson Diversity Index placed greater weight of abundance of individual species and, in turn, assessed dominance of species among the different plots (Magurran 1988). Simpson's Index (D_s) was calculated as:

$$D_s = \sum_{i=1}^{s} [(n_i (n_i - 1))]/[N(N-1))]$$

where n_I is the number of individuals in the ith species. Hill's Evenness was calculated to assess evenness of species distribution at each plot. The equation used was the inverse of the product of the Shannon and Simpson Diversity Indices:

$$E=1/(H' * D_I)$$

Significant variations in index values over all sites were assessed by an ANOVA.

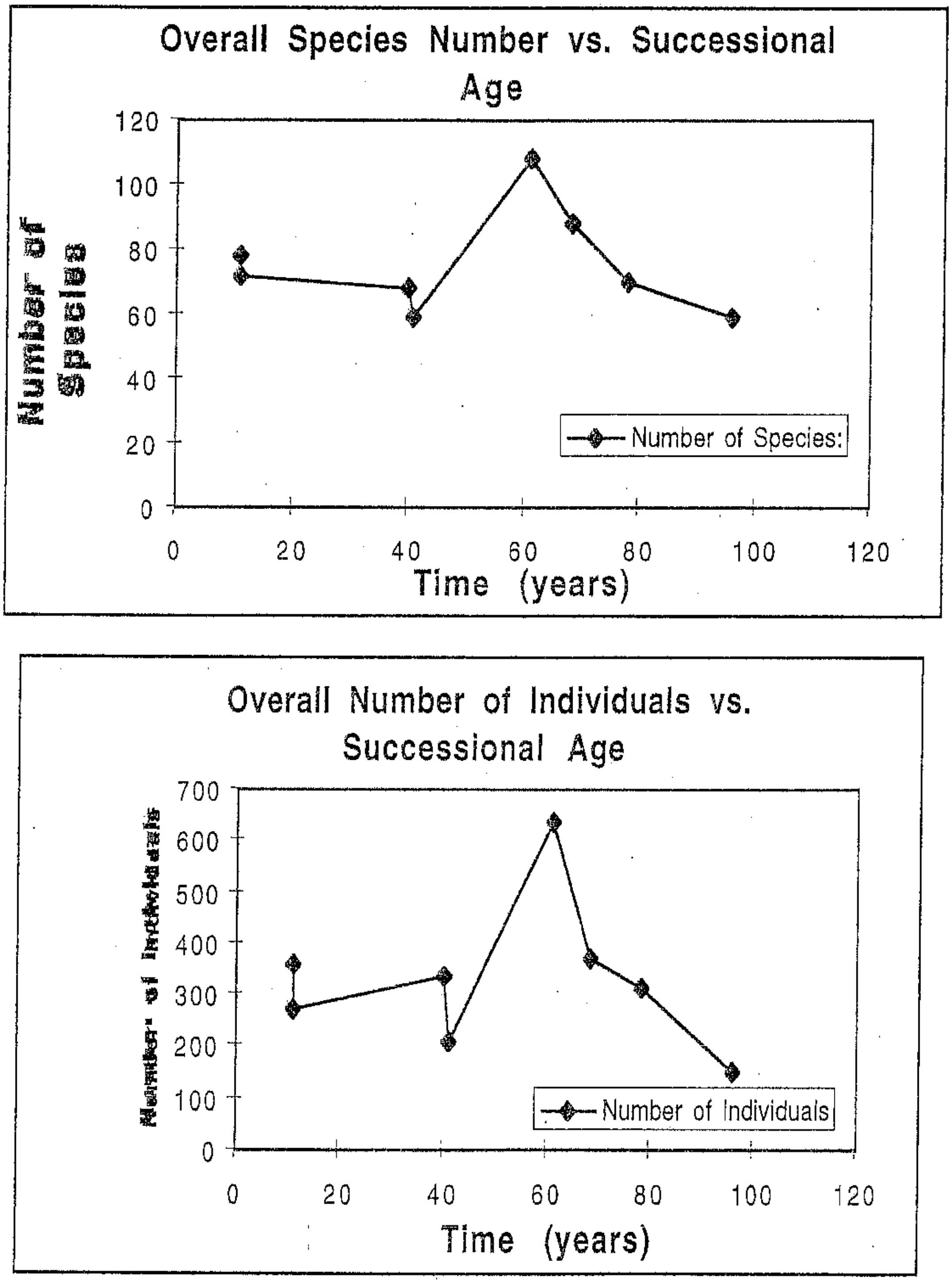
Chi-square were used to calculate significant difference in mean species richness and individual abundance within plots of the same age classes as well as in the same area in the forest. Tests of significance were conducted for the same variables within taxonomic orders. Microclimate data, including temperature, humidity, leaf litter depth, leaf litter composition, slope, percent canopy, percent rock cover, and plant species at and around each sample site, were also recorded to make site characterizations.

Results:

Overall diversity and abundance with time

Results of this study indicated an overall trend of initially high diversity and abundance declining slightly before peaking at mid to late succession and, subsequently, declining at the oldest sites. Total diversity (total number of species) and abundance (total number of individuals) was highest at 11 years and 65 years after a clear-cut and lowest in the 41 year old and 87 year classes (Fig. 2).

Figure 2. Graphs of overall species richness and individual abundance of sites versus time. The trend shows the peak in diversity prior to a decline to a climax community, characteristic of forest succession .



Using the mean as the expected value, chi-square tests of overall diversity and abundance at all sites indicated that the sites of different ages were significantly different from each other ($p \leq 0.05$) , while tests between sites of the same age class found no statistically significant difference in overall number of species (Table 4). Overall abundance was highly significant both among all sites and within sites of the same class (Table 4).

Diversity and abundance of taxonomic orders over time

Examination of diversity and abundance of taxonomic orders at each site consistently exhibited some form of peak diversity prior to the oldest sites. Taxonomic groups did reveal certain variations in successional patterns from each other. Diversity and abundance of large *Diptera* and *Homoptera* followed the same overall trend of an initially high species richness followed by a decline before a major mid-successional peak (Figs. 3 and 4). Diversity and abundance of *Coleoptera* followed a general trend of low diversity early in succession, peak at mid to late succession, and then steady decline at the oldest sites (Figs. 3 and 4). Diversity and abundance of *Aranea* was highest in early succession class and then declined close to linearly. (Figs. 3 and 4).

Results of chi-square tests of species richness and individual abundance found some trends in taxa to be statistically significant. In large *Diptera* and *Coleoptera*, variation from the mean was found to be signifiant across all ages, and comparisons within age classes found significant variation only at the 11-year age class in large *Diptera*. Differences in bundance were igure 3. Graphs of taxonomic orders of species and individuals in each plot age. *Coleoptera* is the most abundant and diverse taxon. Large *Diptera* is also highly abundant and diverse.

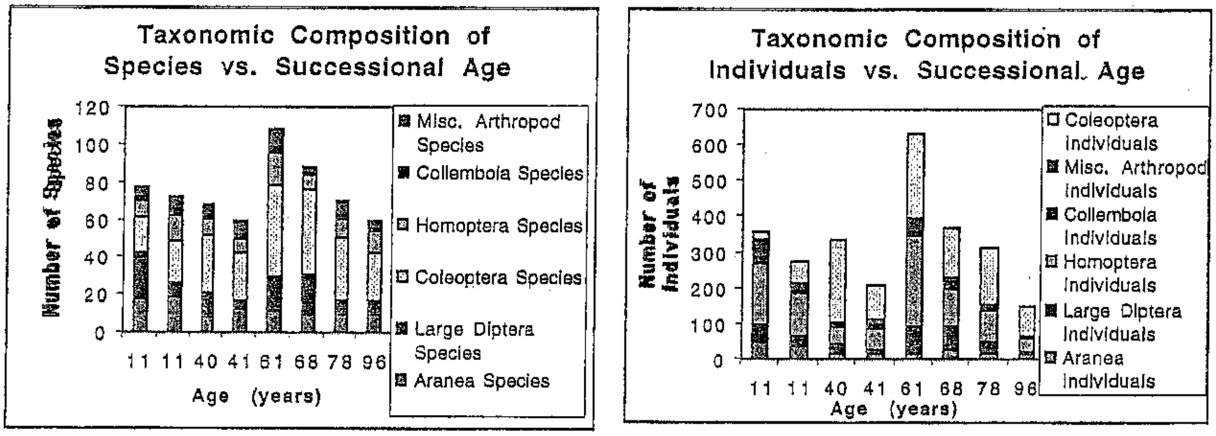
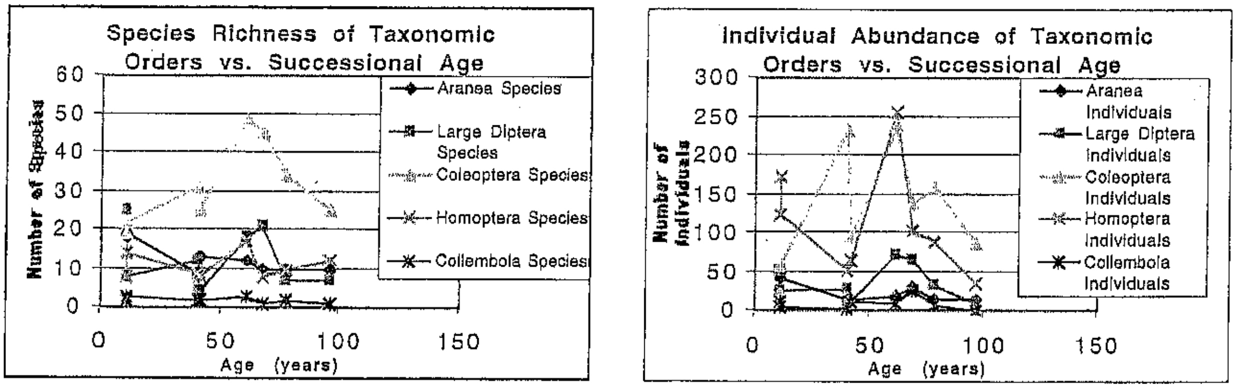


Figure 4. Graph of species richness and abundance at each taxonomic order versus time. *Coleoptera* most clearly exhibits trends characteristic to forest succession. In general, trends are similar to those observed in overall species richness and individual abundance.



generally significant among and between age classes except in *Araneae*, which had significant variations in abundance across plots but not between age classes. Trends in the species richness of *Araneae*, *Homoptera*, and *Collembola* were not statistically significant (Table 3).

Among the taxonomic orders that were sampled, *Coleoptera* was clearly the most species diverse and taxonomically abundant major group (Table 2). It averaged 32 species per site and 129 individuals per site and made up about 40% species and individuals per site (Table 2). While large *Diptera* was the second most species-rich order, averaging 13 species per site, it was the third most abundant taxa, averaging 37 individuals per site (Table 2). While averaging 11 species per plot, *Homopter*a was the second most abundant, averaging 112 individuals per site (Table 2). *Homoptera* also recorded the highest abundance at any site at 255 individuals in the 61-year plot (Table 2). *Araneae* averaged 13 species and 24 individuals per site. *Collembola* was both the least abundant and least diverse taxon, averaging 2 species and 9 individuals per site (Table 2).

Similarity Comparisons

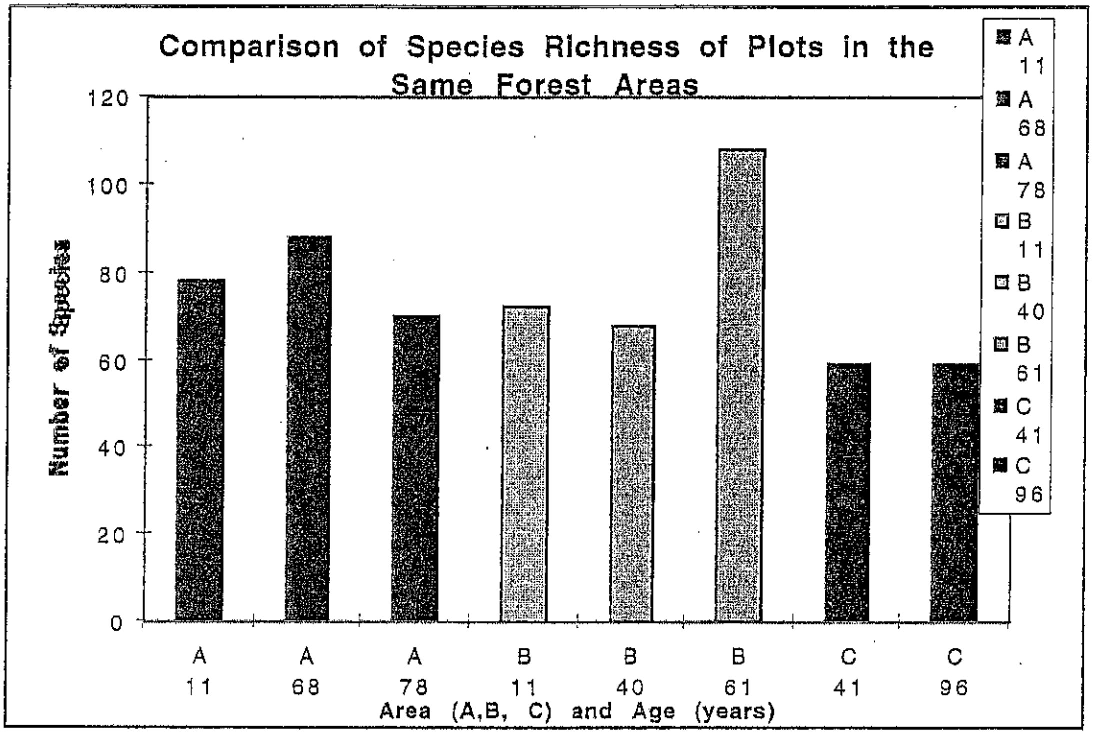
While similarity comparisons through chi-square tests suggested that sites of the same age class were generally similar to each other, they also indicated that sites in the same geographic area in the forest were similar to each other than sites from different areas (Table 3). Significant variation in sites in the same forest area was not found for overall species richness but for individual abundance, as was found in comparisons across ages (Table 3). However, in general, the graph of diversity and abundance of sites in the same area also indicated the same trend of succession occurs within an area as overall diversity and abundance independent of plot area (Fig. 5).

Within taxonomic orders, variation in species richness or individual abundance was significant at one or more areas (Table 3). However, species richness of *Aranea* and *Collembola* were not significant in plots in the same area.

Table 2. Summary of Results- Species Richness and Individual Abundance and Taxonomic Breakdown for Each Site. Mean abundance and species richness were calculated from this data.

Age:	11	11	40	41	61	68	78	96
Area:	A	B	B	C	B	A	A	C
Number of Species:	78	72	68	59	108	88	70	59
Number of Individuals	356	273	336	208	636	370	315	151
Aranea Species	18	19	9	13	12	10	10	10
Aranea Individuals	49	41	15	14	19	30	15	14
Large Diptera Species	25	8	12	4	18	21	7	7
Large Diptera Individuals	51	25	28	11	73	65	33	10
Coleoptera Species	19	22	31	25	49	45	34	25
Coleoptera Individuals	22	58	233	95	237	137	159	85
Homoptera Species	8	14	9	8	17	8	10	12
Homoptera Individuals	172	124	51	65	255	102	89	35
Collembola Species	2	3	2	2	3	1	2	1
Collembola Individuals	12	4	3	11	9	26	8	1
Misc. Arthropod Species	6	6	5	7	9	3	7	4
Misc. Arthropod Individuals	50	21	6	12	43	10	11	6

Figure 5. Graphs of Species Richness and Individual Abundance of sites grouped by forest area. Except for area B, richness and abundance seem to be similar in forest plots .in the same area.



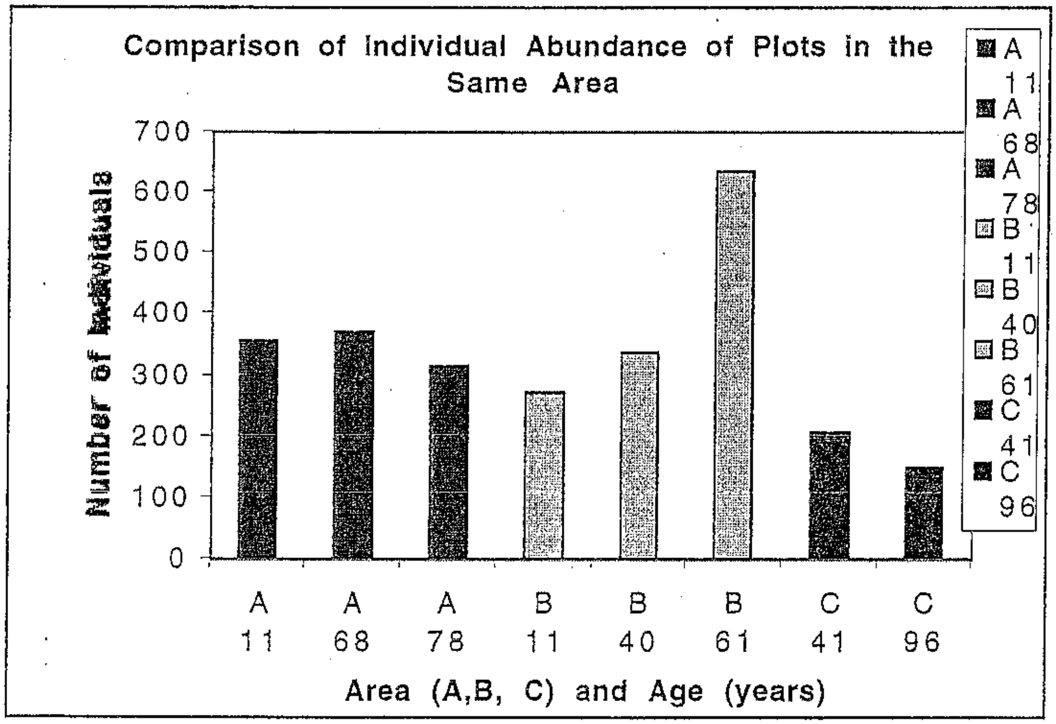


Table 3. Summary of Results of Chi-Square Tests (p≤ 0.05). Significance was marked by "Y" for yes, "N" for no. "Y" was followed by thesite age class or area if results were not significant for all conditions of a variable.

	All		**L. Dipt.**		**Ara.**		**Col.**		**Hom.**		**Clm.**	
Variable	*Rich*	*Abu*	*Rich*	*Abu*	*Rich*	*Abu*	*Rich*	*Abu*	*Rich*	*Abu*	*Rich*	*Abu*
Among Ages	Y	Y	Y	Y	N	Y	Y	Y	N	Y	N	Y
Within Age Classes	N	Y	Y- 11	Y- 11, 41, 87	N	N	N	Y	N	Y- 11, 65, 87	N	Y
Among Areas	Y- B	Y	Y- A	Y- A, B	N	Y- A, B	Y- A, B	Y- A, B	Y- C	Y	N	Y- A, C

Indices of diversity and evenness

The indices of diversity and evenness provided mixed results (Table 4). Shannon Diversity Index showed a trend toward increasing diversity that peaked at the 65-year class before decreasing at the climax sites. Variance of Shannon Diversity Index values was lowest in the youngest sites, peaked at the 65-year-old class sites, and, subsequently, declined (Fig. 6). Simpson Diversity Index indicated a rough trend of decreasing diversity (Fig. 6). Simpson values were highest in the 11-year-old and 65 year-old classes. Hill's Evenness values were exponentially low and varied (Table 4). The most even site was the 96-year-old plot (Table 4). A single-factor ANOVA of each of the diversity indices across age classes found significant variation only with the Shannon Index values (Table 4).

Figure 6. Graphs of Diversity Indices. Shannon Index values follow trends characteristic of forest succession. Simpson Index values are more variable but roughly follow the same. Hill's Evenness values were too small and variable to graph.

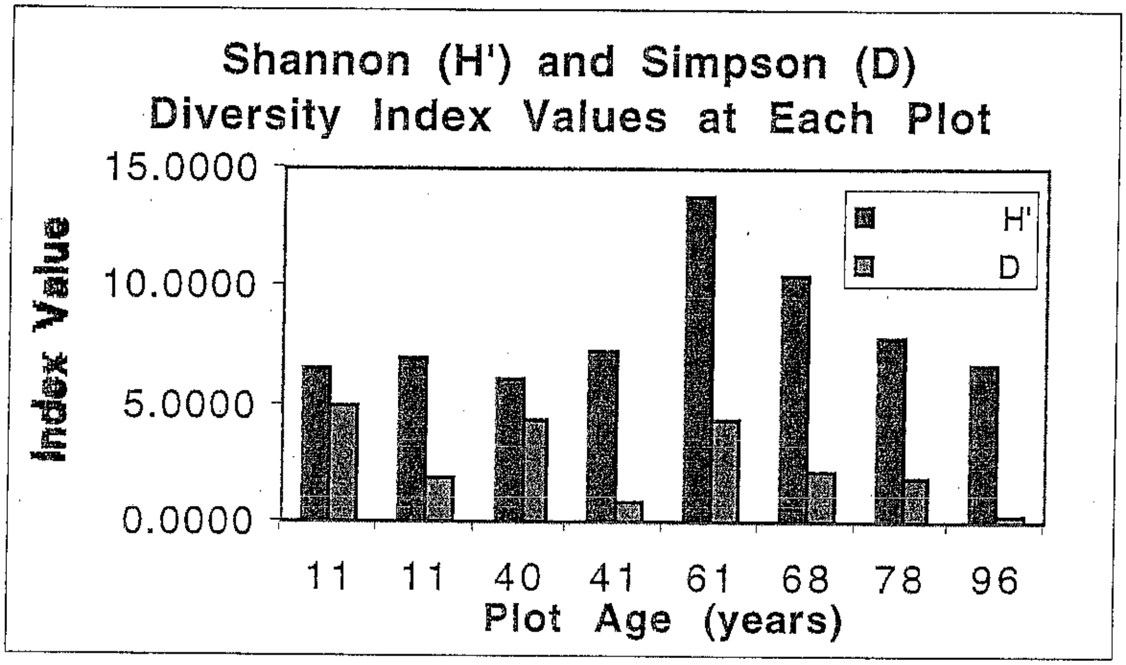


Table 4. Shannon Diversity (H'), Simpson Diversity (D), and Hill's Evenness (E) Index values. **Significance in variation among plots of different ages was found to be significant only in the Shannon values ($p \leq 0.05$).

Plot	4	10B	22	16	10A	6	21	20	ANOVE p-value
Age	11	11	40	41	61	68	78	96	-
N_0	78	72	68	59	109	88	68	59	-
N	356	273	336	208	636	370	315	151	-
H'	6.59979	6.92909	6.08735	7.21549	13.89966	10.44805	7.88545	6.75169	** 0.03886
D	4.99697	1.95390	4.42950	0.88883	4.31185	2.12154	1.93404	0.30537	0.64350
E	0.00027	0.00050	0.00051	0.00083	0.00000	0.00001	0.00019	0.00383	0.51109
VAR H'	-0.04661	-0.08822	-0.03899	-0.15053	-0.24355	-0.20868	-0.12177	-0.16350	-

Discussion

Explanation of overall trends

The results of overall diversity and abundance based on both actual numbers of individuals and species suggested the role of the factors expressed in both alternative hypotheses. In general, vagile arthropods appeared to include colonist, generalist, and mid-successional specialist species of the local community. While the Shannon Diversity Index supported the significance of the general trend found in overall diversity and abundance, the Simpson Diversity Index indicated that dominance in the sampled arthropods to be most evident in the 11-year-old and 65-year-old age classes. The trend of decreasing dominance at the oldest age class indicated that aerial arthropod taxa were possibly being excluded and, therefore, were not part of climax communities.

While species richness supported the trend of peak diversity prior to reaching a climax, high variation in individual abundance did not adequately support the trend found with species richness. While the same trend in species richness was found in individual abundance, variation in results was so high that variation within age classes was also significant. However, significant values may have been due to the large numbers involved in the chi-square analysis (Danoff-Burg, personal communication). Individual abundances may have affected Simpson's Diversity and Hill's Evenness values that incorported them into diversity calculations.

Various factors can affect the individual abundance of species, specifically, biases in sampling methods. Therefore, in this study, species richness rather than individual abundances may provide more informative and accurate results on diversity through succession. In turn, the diversity indices that place greater weight on abundance of individual species, such as the Simpson's Index, and Hill's Evenness of species distribution may not necessarily be appropriate measures for diversity in this study. Instead, Shannon Index values may have provided a more reliable assessment of diversity in this study.

Lack of significant variation in diversity and abundance at sites from the same area in the forest indicated that factors other than simply time since a clear-cut affected the results. Specifically, the general similarity in species distribution in the same areas indicated that regional characteristics affected the results that were obtained. Plots from the same areas in the forest were probably more similar in characteristics such as vegetation and microhabitat conditions.

Overall, the null hypothesis that successsion was not apparent in vagile arthropods could be rejected. Closer examination of specific taxonomic groups provided better indication of the successional roles played by arthropods of varying vagilities. No one hypothesis was supported by all the taxonomic orders. Within each taxonomic order, different hypotheses, including the null hypothesis, were supported.

Successional processes

Previous studies have found that open-habitat and generalist species with great dispersal abilities tend to colonize rapidly following a clear-cut and reach peak species richness after 10 years (Butterflield 1996, Niemela 1996). High diversity and abundance of aerial arthropods in the youngest sites supported their roles as colonists and open-habitat specialists.

As a forest regenerates, species characteristic to the forest community arrive and exclude colonists by outcompeting them for resources (Stiling 1992). Further, development of canopy cover reduce open space, resulting in the emigration of open habitat specialist species. As a result, decrease in overall diversity and abundance of vagile arthropods at forest stands of 41 years may have been due to exclusion of open-habitat specialist species., especially in large *Diptera* and to a less significant degree in overall trends of *Aranea*..

A mid-successional peak in diversity occurs among vagile organisms at the Black Rock Forest, which is characteristic of the successional pattern found in many temperate forest ecosystems (Niemela 1996, McIntosh 1985). This peak in diversity was largely due to an increase in beetle diversity. In late succession of a forest, slower rates of reproduction characteristic of forest community specialists prevent them from outnumbering and excluding less superior competitors for resources, such as generalist and colonist species that tend to reproduce at higher rates (McIntosh 1988). Therefore, persistence of generalists and any remaining colonists along with old growth specialists may have contributed to the peak in diversity at the 65 year class. The subsequent decrease in diversity at the climax forest stands reflected the dominance of old-growth specialists and exclusion of other species for resources (Niemela 1996). Trends of continued decline in aerial arthropod diversity and results of the Simpson Diversity Index that assessed dominance indicated that aerial arthropods were not necessary the dominant species in forest climax communities. The decrease in abundance reflected a decrease in resources available.

Statements about major/minor taxa

While overall diversity and abundance revealed particular trends through time following a clear-cut, successional trends occur within taxonomic orders that comprise the overall diversity and abundance of vagile arthropods. Trends in diversity and abundance vary within each taxonomic group. In fact, certain trends characteristic of particular roles in succession are more marked in some taxa than in others. Nevertheless, in general, even the most vagile taxa follow some pattern of diversity over time characteristic of forest succession.

Large Diptera

Large *Diptera* likely represented the most vagile of the major taxonomic orders sampled for this study. Such superior dispersal abilities would be conducive to colonization. Further, they may have been the most likely taxa to have home ranges exceeding the area of the sampled plot. However, based on their patterns of species richness, the null hypothesis was rejected. In turn, their trend of succession matched the overall trend of succession in aerial arthropods, which showed elements of both of the alternative hypotheses.

High diversity and abundance of large *Diptera* at the 11 year-old class site indicated that species in the order serve as colonists and open habitat specialists in an ecosystem. Yet, there was much variance in diversity and abundance of large *Diptera* within the two youngest sites. However, high variability in biodiversity is characteristic of early succession (McIntosh 1988). Therefore, such high variability may reflect variation in vegetation at the two different 11-year-old sites rather than random distribution of this vagile taxa.

Large *Diptera* was most abundant on average at the 65-year class site, following the diversity curve characteristic of members of local forest communities. Therefore, as an order, they may not be as vagile or they may not disperse as readily as often assumed. In turn, certain members of the order may be specialists of mid to late succession forest communities.

Individuals of large *Diptera* may played a variety of roles in succession. They exhibited characteristics of invader species as well as community members. In general, large *Diptera* are ubiquitous, prevalent in a variety of habitats. Also, they can provide a variety of functions in an ecosystem as pollinators of flowers, scavengers, parasites, predators, and even prey for wildlife (Milne 1980). Based on their wide distribution range and significant pattern of forest succession, individual species in this taxon could potentially serve as indicators for status of forest succession.

Aranea

Araneae, along with *Collembola*, represented the most terrestrial and, presumably, the least vagile, of the major taxa that was collected in the pan traps. Based on vagility alone, they might be expected to be specialists of a particular forest type rather than colonists. Nevertheless, they are ubiquitous predators that can be found in a variety of habitats, such as on the ground, under rocks, among grasses, on plants, and in trees (Milne 1980). In addition to their wide habitat range, their status as a predator would make them attractive as indicators, as they would likely reflect the ecological status of the trophic levels below them. However, lack of statistical significance in their patterns of diversity and abundance resulted in a failure to reject the null hypothesis, and evidence of succession was not clearly in this taxa.

Their omnipresence of these terrestrial organisms may have contributed to their sampling in the pan traps designed for primarily for aerial monitoring. The observed trends in diversity and abundance over time at the sites suggested that they were characteristic of open habitat and disturbed plant patch specialists. Their diversity and abundance were highest in early succession and declined linearly with time since a clear-cut. Their populations were likely affected by the herbaceous species of disturbed patches. Previous studies have indicated that populations of spiders may be most affected by the floral composition of the habitat rather than by time through succession (Hurd and Fagan 1992). Their low vagility would make their inculsion in this study questionable, and the sensitivity of *Araneae* to plant composition in a habitat may make this major taxa problematic for inclusion in any study on succession.

Coleoptera

Coleoptera was not only the most taxonomically diverse and abundant of all taxanomic orders, but their successional trend most closely matched the trend found in members of local forest communities. Throughout the different plots, beetles were collected in abundant quantities. Relatively, their abundance was initially low before peaking at mid to late-succession before declining to a stable climax.

Individuals in the order *Coleoptera* represent a great diversity of taxa and dispersal abilities. Beetles may disperse by both flight and travel on land. Certain families of beetles, such as the staphylinides, represent very active taxa that can fly swiftly as well as run rapidly on the ground (Milne 1980). Further, they tend to be predators of other insects. Therefore, species in this order and particularly, the staphylinide superfamily, may be the best candidates for bioindicators of ecosystem health.

Homoptera

Homoptera were most abundant early in succession at the youngest sites, numbering over 100 individuals. While their abundance declined with increasing age, the variability of species richness and variation of abundance within each age class prevented a rejection of the null hypothesis, and they do not appear to follow any clear patterns of succession.

Diversity and abundance of *Homoptera* could not be attributable to succession alone or even primarily to succession. For instance, many aphids of this order have been found to exhibit an attraction to yellow (Ahmad 1983). In turn, the contact paper on the pan traps may have drawn a disproportionately high number of aphids into traps in certain areas.

Individuals in the order *Homoptera* are known to specialize on particular plants, such as grasses, shrubs, and trees (Milne 1980). High abundances in certain areas may have reflectd an attraction to the disturbed plant habitats, characterized by herbaceous plants that grow close to the ground. Therefore, exclusion of such herbaceous plants at older sites by more competitive trees may have resulted in reduced abundances of *Homoptera* as in early succession.

However, aphids were exceptionally abundant at the 61 year old site and the 78 year old site. The heterogeneity of forest ecosystems and disperal tendencies of *Homoptera* individuals may account for patterns of distribution (McIntosh 1988). Both sites are situated in the same area as an 11-year-old sites that with high populations of *Homoptera*. One reason for flight in *Homoptera* is the dispersal to new plant host sites following crowding in an original site.

Herbaceous plants similar to those in the more open-canopied early succession may have persisted in these older sites. Therefore, they may have invaded these older sites, which would provide an application of the benefits of preserving a variety of forest stands to enhance recolonization of species with various functional roles in an ecosystem (Niemela 1996). Nevertheless, no clear succession patterns were exhibited in *Homoptera.*

Collembola

Low taxonomic diversity and difficulty in species identification of this order likely contributed to the low number of *Collembola* species found in this study (Milne 1980). Therefore, abundance may have served as a more appropriate indicator of successional patterns. High variability across sample sites and in age classes resulted in a failure to reject the null hypothesis in *Collembola*; no successional patterns could be adequately supported by the results. As an example of a less vagile and terrestrialtaxa, the sampling technique was probably not suited for obtaining adequate results about successional patterns in this taxa.

Conclusion

In general, the arthropods sampled by pan traps likely play a variety of roles in the succession of the forest, especially the more vagile and aerial arthropods. Therefore, it appears that organisms should not necessarily be excluded from successional studies based on vagility. In fact, of the three taxonomic orders that failed to reject the null hypothesis, only one

(Homoptera) was aerial. However, lack of significance in *Aranea* and *Collembola* was probably caused by the type of sampling, which was designed to attract aerial arthropods.

Specific taxonomic orders, such as large *Diptera* and *Coleoptera*, are likely to be functional in local communities and their successional processes. Some species of large *Diptera* may be members of early successional communities, while those of *Coleoptera* and large *Diptera* may also be a part of late successional processes. As such, they may be used to accurately monitor forest succession and local ecosystem health.

Because vagile species can be easily captured in large quantities, they may be preferable to litter-dwelling organisms. Vagile beetle taxa such as the *staphylinidae*, or rove beetles, which can actively disperse both terrestrially and aerially, may be particularly ideal for monitoring the successional status of a silvicultural community. Closer examination of species in each order would be necessary to find a particular species that clearly display succession of a forest. In turn, suhc a species could be used as a bioindicator.

However, various factors other than merely succession or time itself likely played a role in the distribution of arthropod diversity at Black Rock Forest. Areas near each other shared similarities in taxonomic composition. In turn, forest area may affect the distribution of orgainsims that take part in successional processes. Also, certain organisms were highly sensitive to plant composition in an area, such as *Aranea* and *Homoptera.* Habitat fragmentation may have produced the variability in distribution among forest areas and, in some taxa, within forest areas. Fragmentation may have also contributed to low diversity at the 40-year-old site. It was located at an intersection of two roads and likely subject to much edge effects. However, in a fragmentated and artificially perturbed, vagile taxa may actually be less inhibited in their dispersal and, therefore, serve as appropriate taxa for study.

Recommendations

Based on this study, forest management may be enhanced by using aerial arthropods for monitoring strategies. By understanding successional patterns and roles of particular taxa, aerial arthropods may be easily sampled to assess the status of a forest ecosystem. Their diversity and abundance may provide much information about the ecological health of a forest stand beyond the scope of this study. In addition to continuing research toward finding an appropriate bioindicator, the effects of other factors on arthropod diversity and abundance could also provide useful information. Though excluded from this study, parasitic *Hymenoptera* may also be an appropriate subject for future studies due to their species diversity and variety of functions in an ecosystem.

Future research could focus on continuing and refining this study. In addition to searching for a specific indicator taxa, more statistical analyses could be conducted on the data from the taxonomic orders. A logarithmic series could be applied to normalize the individual abundances and to apply them in more informatively (Peng et al. 1993, Magurran 1988). Further statistical tests and measures could quantify more rigorously the variables examined in this study.

Further research on the effects of other factors in vagile arthropod distribution is also necessary. Further, the nature and effects of disturbances, especially roads, should also be studied. Finally, to better assess forest heterogeneity, future successional studies could be conducted in particular areas of the forest or take more samples from such areas of similar vegetation composition.

One way to apply the results of this study may be to use aerial arthropods on measuring the effects of maintaining undisturbed sites on recolonization and recovery rates following a disturbance. Data from this study indicated that through dispersion and recolonization of species, heterogeneity of forest communities may be useful to maintain a diversity of species. Such a study could explore a more recent ecological concept of metapopulation dynamics.

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Appendix

Unpublished data from a previous study at Black Rock Forest (Danoff-Burg 1996)

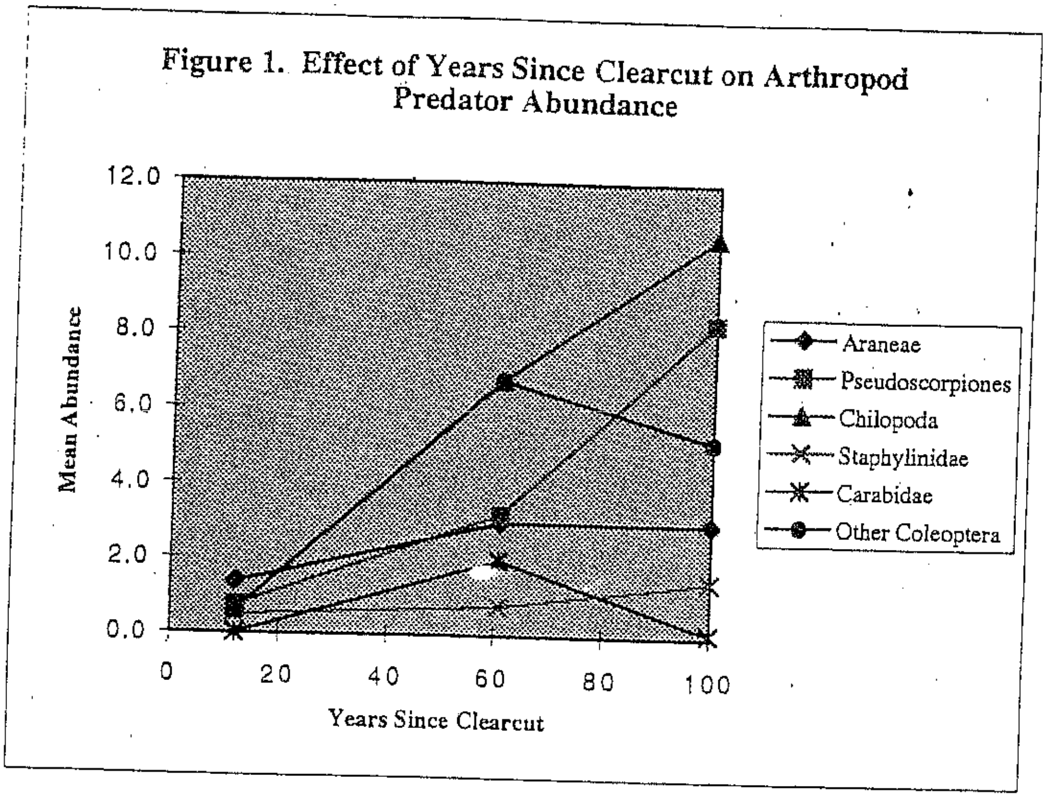

Figure 1. Effect of Years Since Clearcut on Arthropod Predator Abundance

Calculation of Chi-Square values using MS-Excel

Calculations of Chi-Square Tests:

Site Age	Number of Species	Overall Mean Number of Species	Standard Error	Within Age Class Mean	Standard Error	Chi-Square Value	p-value
11	78	75.25	0.10049834	75	0.12		
11	72	75.25	0.14036545	75	0.12	0.24	0.62420612
40	68	75.25	0.69850498	63.5	0.318897638		
41	59	75.25	3.50913621	63.5	0.318897638	0.63779528	0.25603405
61	108	75.25	14.2533223	98	1.020408163		
68	88	75.25	2.160299	98	1.020408163	2.04081633	0.15729926
78	70	75.25	0.36627907	64.5	0.468992248		
96	59	75.25	3.50913621	64.5	0.468992248	0.9379845	0.86671209
Mean:	75.25						

Overall Chi-square: 24.7375415

p-value: (using the "chidist" function) 0.00084451

Site Age	Number of Individuals	Overall Mean Number of Individuals	Standard Error	Within Age Class Mean	Standard Deviation	Chi-Square Value	p-value
11	356	330.625	1.94749527	314.5	5.476152623		
11	273	330.625	10.0435255	314.5	5.476152623	10.9523052	0.00093487
40	336	330.625	0.08738185	272	15.05882353		
41	208	330.625	45.4801985	272	15.05882353	30.1176471	4.0661E-08
61	636	330.625	282.053355	503	35.16699801		
68	370	330.625	4.68927221	503	35.16699801	70.333996	5.0067E-17
78	315	330.625	0.73842155	233	28.8583691		
96	151	330.625	97.588327	233	28.8583691	57.7167382	3.0272E-14
Mean:	330.625			476.75			

Overall Chi-square: 442.627977

p-value: (using the 1.6999E-91

"chidist"

function)

Site Age/Area	Number of Species	Within Area Mean	Standard Deviation	Chi-Square Value	p-value
11/A	78	78.6666667	0.00564972		
68/A	88	78.6666667	1.10734463		
78/A	70	78.6666667	0.95480226	2.06779661	0.355617948
11/B	72	82.6666667	1.37634409		
40/B	68	85.3333333	3.52083333		
61/B	108	85.3333333	6.02083333	10.9180108	0.004257789
41/C	59	59	0		
96/C	59	59	0	0	1

Site Age/Area	Number of Individuals	Within Area Mean	Standard Deviation	Chi-Square Value	p-value
11/A	356	253	41.9328063		
68/A	88	253	107.608696		
78/A	315	253	15.1936759	164.735178	1.69126E-36
11/B	273	415	48.5879518		
40/B	336	415	15.0385542		
61/B	636	415	117.689157	181.315663	4.24428E-40
41/C	315	233	28.8583691		
96/C	151	233	28.8583691	57.7167382	3.02716E-14

Large Diptera	Site Age	Number of Species	Overall Mean Number of Species	Standard Error	Within Age Class Mean	Standard Error	Chi-Square Value	p-value
	11	25	12.75	11.7696078	16.5	4.378787879		
	11	8	12.75	1.76960784	16.5	4.378787879	8.75757576	0.00308319
	40	12	12.75	0.04411765	8	2		
	41	4	12.75	6.00490196	8	2	4	0.25603405
	61	18	12.75	2.16176471	19.5	0.115384615		
	68	21	12.75	5.33823529	19.5	0.115384615	0.23076923	0.15729926
	78	7	12.75	2.59313725	7	0		
	96	7	12.75	2.59313725	7	0	0	0.86671209
	Mean:	12.75						

Overall Chi square: 32.2745098

p-value: (using the 3.6122E-05

"chidist"

function)

Site Age	Number of Individuals	Overall Mean Number of Individuals	Standard Error	Within Age Class Mean	Standard Deviation	Chi-Square Value	p-value
11	51	37	5.2972973	38	4.447368421		
11	25	37	3.89189189	38	4.447368421	8.89473684	0.00285994
40	28	37	2.18918919	19.5	3.705128205		
41	11	37	18.2702703	19.5	3.705128205	7.41025641	0.00648531
61	73	37	35.027027	69	0.231884058		
68	65	37	21.1891892	69	0.231884058	0.46376812	0.49586819
78	33	37	0.43243243	21.5	6.151162791		
96	10	37	19.7027027	21.5	6.151162791	12.3023256	0.00045239
	37			476.75			

Chi square 106

p-value (using the "chidist" function) 6.1956E-20

	Site Age	Number of Species	Overall Mean Number of Species	Standard Error	Within Age Class Mean	Standard Error	Chi-Square Value	p-value
Aranea	11	18	12.625	2.28836634	18.5	0.013513514		
	11	19	12.625	3.21905941	18.5	0.013513514	0.02702703	0.86941706
	40	9	12.625	1.04084158	11	0.363636364		
	41	13	12.625	0.01113861	11	0.363636364	0.72727273	0.25603405
	61	12	12.625	0.03094059	11	0.090909091		
	68	10	12.625	0.54579208	11	0.090909091	0.18181818	0.15729926
	78	10	12.625	0.54579208	10	0		
	96	10	12.625	0.54579208	10	0	0	0.86671209
	Mean:	12.625						

Overall Chi square: 8.22772277

p-value: (using the 0.31294263

"chidist"

function)

Site Age	Number of Individuals	Overall Mean Number of Individuals	Standard Error	Within Age Class Mean	Standard Deviation	Chi-Square Value	p-value
11	49	24.625	24.1275381	45	0.355555556		
11	41	24.625	10.8889594	45	0.355555556	0.71111111	0.3990752
40	15	24.625	3.76205584	14.5	0.017241379		
41	14	24.625	4.58439086	14.5	0.017241379	0.03448276	0.85268368
61	19	24.625	1.28489848	24.5	1.234693878		
68	30	24.625	1.17322335	24.5	1.234693878	2.46938776	0.11608317
78	15	24.625	3.76205584	14.5	0.017241379		
96	14	24.625	4.58439086	14.5	0.017241379	0.03448276	0.85268368
	24.625			476.75			

Chi square 54.1675127

p-value (using the "chidist" function) 2.1791E-09

Coleptera	Site Age	Number of Species	Overall Mean Number of Species	Standard Error	Within Age Class Mean	Standard Error	Chi-Square Value	p-value
	11	19	31.25	4.802	20.5	0.109756098		
	11	22	31.25	2.738	20.5	0.109756098	0.2195122	0.63941185
	40	31	31.25	0.002	28	0.321428571		
	41	25	31.25	1.25	28	0.321428571	0.64285714	0.25603405
	61	49	31.25	10.082	47	0.085106383		
	68	45	31.25	6.05	47	0.085106383	0.17021277	0.15729926
	78	34	31.25	0.242	29.5	0.686440678		
	96	25	31.25	1.25	29.5	0.686440678	1.37288136	0.86671209
	Mean:	31.25						

Overall Chi square: 26.416

p-value: (using the 0.00042433

"chidist"
function)

Site Age	Number of Individuals	Overall Mean Number of Individuals	Standard Error	Within Age Class Mean	Standard Deviation	Chi-Square Value	p-value
11	22	128.25	88.0238791	40	8.1		
11	58	128.25	38.4800195	40	8.1	16.2	5.6994E-05
40	233	128.25	85.5560429	164	29.0304878		
41	95	128.25	8.62037037	164	29.0304878	58.0609756	2.5412E-14
61	237	128.25	92.2149123	187	13.36898396		
68	137	128.25	0.59697856	187	13.36898396	26.7379679	2.33E-07
78	159	128.25	7.37280702	122	11.22131148		
96	85	128.25	14.5852827	122	11.22131148	22.442623	2.1652E-06
	128.25			476.75			

Chi square 335.450292

p-value (using the "chidist" function) 1.6007E-68

Homoptera

Site Age	Number of Species	Overall Mean Number of Species	Standard Error	Within Age Class Mean	Standard Error	Chi-Square Value	p-value
11	8	10.75	0.70348837	11	0.818181818		
11	14	10.75	0.98255814	11	0.818181818	1.63636364	0.20082521
40	9	10.75	0.28488372	8.5	0.029411765		
41	8	10.75	0.70348837	8.5	0.029411765	0.05882353	0.25603405
61	17	10.75	3.63372093	12.5	1.62		
68	8	10.75	0.70348837	12.5	1.62	3.24	0.15729926
78	10	10.75	0.05232558	11	0.090909091		
96	12	10.75	0.14534884	11	0.090909091	0.18181818	0.86671209
Mean:	10.75						

Overall Chi square: 7.20930233

p-value: (using the "chidist" function) 0.40741773

Site Age	Number of Individuals	Overall Mean Number of Individuals	Standard Error	Within Age Class Mean	Standard Deviation	Chi-Square Value	p-value
11	172	111.625	32.6552352	148	3.891891892		
11	124	111.625	1.37192049	148	3.891891892	7.78378378	0.00527173

40	51	111.625	32.9262318	58	0.844827586		
41	65	111.625	19.474944	58	0.844827586	1.68965517	0.19364653
61	255	111.625	184.155795	178.5	32.78571429		
68	102	111.625	0.82992721	178.5	32.78571429	65.5714286	5.6045E-16
78	89	111.625	4.58580627	62	11.75806452		
96	35	111.625	52.5992441	62	11.75806452	23.516129	-1.2387E-06
	111.625			476.75			

Chi square 328.599104

p-value (using the "chidist" function) 4.6746E-67

Collembola

Site Age	Number of Species	Overall Mean Number of Species	Standard Error	Within Age Class Mean	Standard Error	Chi-Square Value	p-value
11	2	2	0	2.5	0.1		
11	3	2	0.5	2.5	0.1	0.2	0.65472085
40	2	2	0	2	0		
41	2	2	0	2	0	0	0.25603405
61	3	2	0.5	2	0.5		
68	1	2	0.5	2	0.5	1	0.15729926
78	2	2	0	1.5	0.166666667		
96	1	2	0.5	1.5	0.166666667	0.33333333	0.86671209
Mean:	2						

Overall Chi square: 2

p-value: (using the "chidist" function) 0.95984037

Site Age	Number of Individuals	Overall Mean Number of Individuals	Standard Error	Within Age Class Mean	Standard Deviation	Chi-Square Value	p-value
11	12	9.25	0.81756757	8	2		
11	4	9.25	2.97972973	8	2	4	0.04550027
40	3	9.25	4.22297297	7	2.285714286		
41	11	9.25	0.33108108	7	2.285714286	4.57142857	0.03250945
61	9	9.25	0.00675676	17.5	4.128571429		
68	26	9.25	30.3310811	17.5	4.128571429	8.25714286	0.0040592
78	8	9.25	0.16891892	4.5	2.722222222		
96	1	9.25	7.35810811	4.5	2.722222222	5.44444444	0.01963066
	9.25						

Chi square 46.2162162

p-value (using the "chidist" function) 7.9346E-08

Large Diptera	Site Age/Area	Number of Species	Within Area Mean	Standard Deviation	Chi-Square Value	p-value
	11/A	25	17.6666667	3.04402516		
	68/A	21	17.6666667	0.62893082		
	78/A	7	17.6666667	6.44025157	10.1132075	0.006367147
	11/B	8	12.6666667	1.71929825		
	40/B	12	12.6666667	0.03508772		
	61/B	18	12.6666667	2.24561404	4	0.135335283
	41/C	4	5.5	0.40909091		
	96/C	7	5.5	0.40909091	0.81818182	0.365712299

Site Age/Area	Number of Individuals	Within Area Mean	Standard Deviation	Chi-Square Value	p-value
11/A	51	49.6666667	0.03579418		
68/A	65	49.6666667	4.73378076		
78/A	33	49.6666667	5.59284116	10.3624161	0.005621212
11/B	25	42	6.88095238		
40/B	28	42	4.66666667		
61/B	73	42	22.8809524	34.4285714	3.34142E-08
41/C	11	10.5	0.02380952		
96/C	10	10.5	0.02380952	0.04761905	0.827259347

Aranea	Site Age/Area	Number of Species	Within Area Mean	Standard Deviation	Chi-Square Value	p-value
	11/A	18	12.6666667	2.24561404		
	68/A	10	12.6666667	0.56140351		
	78/A	10	12.6666667	0.56140351	3.36842105	0.185590893
	11/B	19	13.3333333	2.40833333		
	40/B	9	13.3333333	1.40833333		
	61/B	12	13.3333333	0.13333333	3.95	0.138761312
	41/C	13	11.5	0.19565217		
	96/C	10	11.5	0.19565217	0.39130435	0.531614577

Site Age/Area	Number of Individuals	Within Area Mean	Standard Deviation	Chi-Square Value	p-value
11/A	49	31.3333333	9.96099291		
68/A	30	31.3333333	0.05673759		
78/A	15	31.3333333	8.5141844	18.5319149	9.45901E-05
11/B	41	25	10.24		
40/B	15	25	4		
61/B	19	25	1.44	15.68	0.000393669
41/C	14	14	0		
96/C	14	14	0	0	1

Coleoptera	Site Age/Area	Number of Species	Within Area Mean	Standard Deviation	Chi-Square Value	p-value
	11/A	19	32.6666667	5.71768707		
	68/A	45	32.6666667	4.65646259		
	78/A	34	32.6666667	0.05442177	10.4285714	0.005438317
	11/B	22	34	4.23529412		
	40/B	31	34	0.26470588		
	61/B	49	34	6.61764706	11.1176471	0.003853307
	41/C	25	25	0		
	96/C	25	25	0	0	1

	Site Age/Area	**Number of Individuals**	**Within Area Mean**	**Standard Deviation**	**Chi-Square Value**	**p-value**
	11/A	22	106	66.5660377		
	68/A	137	106	9.06603774		
	78/A	159	106	26.5	102.132075	6.64204E-23
	11/B	58	172.666667	76.1492921		
	40/B	223	172.666667	14.6724582		
	61/B	237	172.666667	23.9697555	114.791506	1.18397E-25
	41/C	95	90	0.27777778		
	96/C	85	90	0.27777778	0.55555556	0.456056544

Homoptera	**Site Age/Area**	**Number of Species**	**Within Area Mean**	**Standard Deviation**	**Chi-Square Value**	**p-value**
	11/A	8	8.66666667	0.05128205		
	68/A	8	8.66666667	0.05128205		
	78/A	10	8.66666667	0.20512821	0.30769231	0.85740392
	11/B	14	13.3333333	0.03333333		
	40/B	9	13.3333333	1.40833333		
	61/B	17	13.3333333	1.00833333	2.45	0.2937577
	41/C	8	4.5	2.72222222		
	96/C	1	4.5	2.72222222	5.44444444	0.019630659

	Site Age/Area	**Number of Individuals**	**Within Area Mean**	**Standard Deviation**	**Chi-Square Value**	**p-value**
	11/A	172	121	21.4958678		
	68/A	102	121	2.98347107		
	78/A	89	121	8.46280992	32.9421488	7.02592E-08
	11/B	124	143.333333	2.60775194		
	40/B	51	143.333333	59.479845		
	61/B	255	143.333333	86.996124	149.083721	4.23527E-33
	41/C	65	50	4.5		
	96/C	35	50	4.5	9	0.002699796

Collembola	**Site Age/Area**	**Number of Species**	**Within Area Mean**	**Standard Deviation**	**Chi-Square Value**	**p-value**
	11/A	2	1.66666667	0.06666667		
	68/A	1	1.66666667	0.26666667		
	78/A	2	1.66666667	0.06666667	0.4	0.818730753
	11/B	3	2.66666667	0.04166667		
	40/B	2	2.66666667	0.16666667		
	61/B	3	2.66666667	0.04166667	0.25	0.882496903
	41/C	2	1.5	0.16666667		
	96/C	1	1.5	0.16666667	0.33333333	0.846481725

	Site Age/Area	**Number of Individuals**	**Within Area Mean**	**Standard Deviation**	**Chi-Square Value**	**p-value**
	11/A	12	15.3333333	0.72463768		
	68/A	26	15.3333333	7.42028986		
	78/A	8	15.3333333	3.50724638	11.6521739	0.002949596
	11/B	4	5.33333333	0.33333333		
	40/B	3	5.33333333	1.02083333		
	61/B	9	5.33333333	2.52083333	3.875	0.144063659
	41/C	11	6	4.16666667		
	96/C	1	6	4.16666667	8.33333333	0.003892417

Sample Calculation of Diversity Indices (site 4)

Ni	p_i	$p_i.\ln(p_i)$	p_i^2	$N_0=$	78
147	2.161765	1.666558	4.673227	N =	356
16	0.235294	-0.340452	0.055363	H'=	6.5998
15	0.220588	-0.333410	0.048659	D =	4.9970
13	0.191176	-0.316313	0.036548		
13	0.191176	-0.316313	0.036548	$N_1=$	734.9398
13	0.191176	-0.316313	0.036548	$N_2=$	0.2001
9	0.132353	-0.267655	0.017517	E =	0.0003
8	0.117647	-0.251772	0.013841		
8	0.117647	-0.251772	0.013841		
8	0.117647	-0.251772	0.013841		
5	0.073529	-0.191917	0.005407	site 4	
4	0.058824	-0.166660	0.003460		
4	0.058824	-0.166660	0.003460		
4	0.058824	-0.166660	0.003460		
4	0.058824	-0.166660	0.003460		
4	0.058824	-0.166660	0.003460		
4	0.058824	-0.166660	0.003460		
3	0.044118	-0.137687	0.001946		
3	0.044118	-0.137687	0.001946		
3	0.044118	-0.137687	0.001946		
2	0.029412	-0.103716	0.000865		
2	0.029412	-0.103716	0.000865		
2	0.029412	-0.103716	0.000865		
2	0.029412	-0.103716	0.000865		
2	0.029412	-0.103716	0.000865		
2	0.029412	-0.103716	0.000865		
2	0.029412	-0.103716	0.000865		
2	0.029412	-0.103716	0.000865		
2	0.029412	-0.103716	0.000865		
2	0.029412	-0.103716	0.000865		
1	0.014706	-0.062052	0.000216		
1	0.014706	-0.062052	0.000216		
1	0.014706	-0.062052	0.000216		
1	0.014706	-0.062052	0.000216		
1	0.014706	-0.062052	0.000216		
1	0.014706	-0.062052	0.000216		
1	0.014706	-0.062052	0.000216		
1	0.014706	-0.062052	0.000216		
1	0.014706	-0.062052	0.000216		
1	0.014706	-0.062052	0.000216		
1	0.014706	-0.062052	0.000216		

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1	0.014706	-0.062052	0.000216
1	0.014706	-0.062052	0.000216
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1	0.014706	-0.062052	0.000216
1	0.014706	-0.062052	0.000216
1	0.014706	-0.062052	0.000216
1	0.014706	-0.062052	0.000216
1	0.014706	-0.062052	0.000216
1	0.014706	-0.062052	0.000216

Calculation of Single-Factor ANOVA for Diversity Indices

Anova: Single Factor

H'

SUMMARY

Groups	Count	Sum	Average	Variance
Column 1	2	13.528878	6.76443899	0.05421946
Column 2	2	13.3028391	6.65141957	0.63634865
Column 3	2	24.3477083	12.1738542	5.95682323
Column 4	2	14.637149	7.31857448	0.64270591

ANOVA

Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	42.0488661	3	14.0162887	7.69059079	0.038858824	6.591392321
Within Groups	7.29009725	4	1.82252431			
Total	49.3389633	7				

Anova: Single Factor

D

SUMMARY

Groups	Count	Sum	Average	Variance
Column 1	2	6.95086892	3.47543446	4.6301549
Column 2	2	5.31832332	2.65916166	6.26818342
Column 3	2	6.433391	3.2166955	2.39873206
Column 4	2	2.23941181	1.11970591	1.32627936

ANOVA

Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	6.68041877	3	2.22680626	0.60910976	0.643599743	6.591392321
Within Groups	14.6233497	4	3.65583743			
Total	21.3037685	7				