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Title of Thesis — Titre de la thèse

ON CERTAIN SPATIAL CHARACTERISTICS OF THE DISTRIBUTION
OF WOODLAND SPECIES IN FARMLAND

University — Université

Carleton University

Degree for which thesis was presented — Grade pour lequel cette thèse fut présentée

Doctor of Philosophy

Year this degree conferred — Année d'obtention de ce grade

1982

Name of Supervisor — Nom du directeur de thèse

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ON CERTAIN SPATIAL CHARACTERISTICS
of the
DISTRIBUTION of WOODLAND SPECIES
in FARMLAND

by

© JOHN DAVID MIDDLETON, B.Sc., M.Sc.

A thesis submitted to the Faculty of
Graduate Studies and Research in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy

Department of Biology

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Ottawa, Canada

May, 1982

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The undersigned hereby recommend to the Faculty of
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ABSTRACT

I compared the distribution of plants and animals in discontinuous forest in farmland, with the distribution of the same species in continuous forest. All taxa were recorded as present or absent at intervals of 25 m along 15 km of transects. From these data were calculated indices of frequency and aggregation. These indices were used to test whether the isolation of woods in farmland has caused the distribution of woodland organisms to be changed in the way predicted by the equilibrium theory of island biogeography. There was no consistent response of taxa to the fragmentation of forest. The pattern of distribution of fewer than 10% of taxa is consistent with the predictions of island theory, but additional data available for some of these taxa diminish the probability that insular processes have contributed to the present pattern. I conclude that farmland south of Ottawa is not perceived as a system of biogeographic islands, because woodland species have long since evolved efficient mechanisms for medium-distance movement in response to the ubiquitous spatial heterogeneity of intact, continuous forest.

A stand of virgin forest had the lowest number of species of any forest examined. The relationship of degree of disturbance to species richness among the forests of this study strongly suggests that frequent disturbance is an essential factor in producing the characteristics of forests in eastern Canada.

The impoverished vegetation of the virgin forest challenges the validity of two common rationalizations of the conservation ethic. I discuss the implications of this observation, and conclude that moral arguments form the only defensible foundation for conservation.

ACKNOWLEDGEMENTS

I am grateful for the help given by many people. Dr. Gray Merriam gave constant but unobtrusive guidance, which I greatly appreciated. Dr. D.A. Smith and Dr. G. Carmody gave excellent and complementary support throughout the process. John Wegner was particularly helpful with a multitude of details, practical and theoretical. Dr. P. Keddy made many thoughtful suggestions. Many other people also helped me to explore ideas. Financial support was given by the Natural Sciences and Engineering Research Council of Canada, Gulf Canada Limited, and Carleton University. I thank all of these for making important contributions to my work, and to my enjoyment of it.

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- is there anything in these absurd ideas - do they indicate mind & body retrograding to ancestral type of consciousness etc etc. -

Charles Darwin, 1838, 'N' notebook
(commenting on a now-obscure theory)

... might the theoretician's cardinal sin be, not to be wrong, but to be uninteresting?

C.F. Kennel 1982.

SECTION I

General Introduction

Ecological systems have various properties that can be studied scientifically. Among these properties are patterns of energy flow, material cycles, and trophic relationships. Ecological systems are also characterized by a distribution of components in space, and it is this property I have chosen to study. All aspects of the structure and function of an ecological system, without exception, are associated with one or more points in space. It seems reasonable to expect that the pattern in space will integrate and reveal properties of the system. This seems especially likely in any system that is marked by pronounced spatial heterogeneity.

My study was conducted in just such a system: forests near Ottawa where the impact of humans is widespread and obvious. Although pristine wilderness has a tremendous attraction, both scientific and metaphysical, it would be a mistake to restrict ecology to the study of it alone. It is a moot point whether there remains any place on this earth not significantly affected by human actions. Furthermore, it is philosophically objectionable to exclude a system from consideration because of the presence of a single species. The land around a city is no less an ecological system than was the pristine forest that once occupied the site. One need only recall such classical studies as those of Elton (1966) in England, Clements (1936) in North America, and

Braun-Blanquet (1932) in continental Europe to realize how much of our ecological understanding has been based on the examination of human-dominated ecosystems.

Ecologists from Carleton University have been studying farmland south of Ottawa for many years. Their studies have focused on its obvious spatial heterogeneity. Rural Ontario, and farmland in other parts of the world, is a mosaic of fields, forests, roads, and buildings. Basic natural history shows that the differences among patches in this mosaic are great enough to be perceived by organisms living there, and thus it is interesting to ask what effect this has on the system as a whole.

Historically, ecological ideas evolved on the assumption that local systems were essentially homogeneous and static. The subsequent evolution of these ideas has almost always involved the incorporation of more and more dynamic and heterogeneous elements (see for example the reviews by Egerton (1973) and McIntosh (1980).)

Watt (1947) made a significant contribution to this process by giving a powerful exposition of the idea that the pattern of vegetation is intimately related to its functioning. Andrewartha and Birch (1954) revolutionized ideas in animal population ecology by demonstrating how

spatial distribution and local abundance of a species are parts of the same continuum. Elton (1966) summarized one of the most thorough investigations of any ecological system, and concluded that movement of animals among dissimilar patches of habitat was one of the fundamental organizing principles of the system. Southwood (1977) made an elegant summary of the idea that habitat heterogeneous in space and time is a templet on which are shaped all ecological processes. Meanwhile, accumulation of empirical data gave massive support to the idea that most species are aggregated in space. This generalization is now accepted as one of the most thoroughly corroborated ideas in ecology (Harper 1977, Greig-Smith 1979). Many workers now realize that heterogeneity can sometimes be used as an explanatory axis in studies of ecological systems, and need not always be dismissed as unwanted variability or noise. Thus, the idea of spatial heterogeneity has become a recurring theme in the recent development of ecological theory.

One particular manifestation of this theme has been the theory of island biogeography (Preston 1962; MacArthur and Wilson 1963, 1967). This theory offered an appealing and conceptually elegant explanation for the observation that small oceanic islands far from mainland tend to have a small number of species. The interpretation of this theory is that the small populations of islands rather frequently die out

but are not immediately replaced, because movement to isolated islands is difficult and infrequent. The same reasoning has been applied to systems of isolated patches of habitat on continents in a great number of studies. (The abundant literature is reviewed by Simberloff (1974) and Gilbert (1980).)

The application of equilibrium theory to a system must involve the implicit assumption that movement among patches of habitat is infrequent. This is a significant claim about the importance of movement in organizing the ecological system in question. However, it is not obvious that this claim is well supported in most continental systems. All species have mechanisms for moving through space, and it is clear that the gross geographical range of a species is partly dependent on these mechanisms. It is less clear whether frequent movement through space is an important part of the local ecology of a system a few square kilometres in size. This question can be examined to advantage in the exaggerated pattern of farmland, where it simplifies to the question of whether patches in the mosaic are interconnected by the movement of organisms to any significant degree.

Previous studies in farmland suggested that movement among woods is frequent and important for at least some species (Wegner and Merriam 1979, Gottfried 1979, Gliwicz

1980, Gilbert 1980, Middleton and Merriam 1981, Henderson 1981). Unfortunately, these studies normally involve only a small set of species, especially small mammals and birds, and it is not always clear how to separate general principles from the idiosyncrasies of particular natural histories. It was the primary objective of the present study to determine whether movement among woods was of general importance for many different sorts of species (plants and animals) in this rural ecosystem, and by implication, whether similar medium-distance movements might also be important in a system of continuous forest. I intended this to be a contribution to the general question of the importance of spatial heterogeneity in the organization of ecological systems. This investigation is documented in the second section of this thesis.

As part of this study, I investigated several areas of continuous forest to establish a standard of comparison for evaluating the patterns in farmland. These forests included a rare example of virgin forest: the Shaw Woods Nature Reserve. It became clear during this investigation that the virgin forest showed certain properties of outstanding interest. These are reported in the third section of this thesis.

In the fourth section I discuss how the results from Shaw Woods have implications for questions of conservation, and in particular how they challenge some common ideas about the value of virgin forest.

In summary, this thesis documents an investigation of certain spatial characteristics of a large ecological system dominated by humans. These spatial characteristics are taken as evidence for aspects of the structure and function of this system. The results are extrapolated to make statements about a broader class of ecological systems, and about their conservation.

SECTION II

Agriculture as a Vivisection Experiment in Woodland

'Undisturbed, stable "natural" vegetation is probably the worst possible place in which to look for the processes by which its character is maintained. It is there that they are least likely to be seen. The nature of a balancing system is best explored by disturbing the balance' (Harper 1977).

INTRODUCTION

In eastern Canada, as in many other parts of the world, clearing of land for intensive agriculture has created a distinctive pattern in the rural landscape. Remnants of the original continuous forest remain as discontinuous clumps surrounded by large expanses of fields, roads, and other new and foreign environments. This agricultural clearing may be considered as a sort of massive perturbation experiment: in effect, the vivisection of a complex biological system. In the present study I examined the distribution of woodland organisms in farmland in order to evaluate the importance of certain factors affecting the spatial structure of a forested ecosystem. This was possible because there still exists extensive continuous forest that can act as a control for the vivisection experiment,

It has long been recognized that woods in farmland resemble islands, and many attempts have been made to understand their characteristics in terms of the equilibrium

theory of island biogeography (Preston 1962; MacArthur and Wilson 1963, 1967; Simberloff 1974; Gilbert 1980). This theory predicts that species will recognize two phases (such as woodland and non-woodland) in the system, and will show local extinctions and recolonizations in one of these phases. All of these have been demonstrated for at least a few woodland species in the farmland of southern Ontario (Taylor 1978, Wegner and Merriam 1979, Middleton and Merriam 1981, Henderson 1981), and elsewhere (Helliwell 1976, Gottfried 1979, Rey and McCoy 1979, Gliwicz 1980, Diamond 1981, Brown 1981). However, the theory also predicts that the rates of extinction will be accelerated and the rates of recolonization reduced such that the equilibrium species number is significantly depressed relative to an equal area of continuous forest. In other words, the theory predicts that some species will be locally extinct in some places at all times, even though the pattern of extinctions may be dynamic. This has been more difficult to demonstrate in farmland. Studies of individual species have tended to show that local extinctions are quickly eliminated by colonists (often within one season), so that the equilibrium number of species is likely to be only slightly reduced, if at all, by the constraints of insularity (Gottfried 1979, Middleton and Merriam 1981, Henderson 1981, with small mammals; Levenson 1981, with forest trees). Such results add to the doubt that is being expressed as to the applicability of the

equilibrium theory in general (Simberloff 1974, Gilbert 1980). In a recent review Gilbert (1980) concluded that 'quantitatively... it would seem that the model has little evidence to support its application to any situation'.

The question of whether or not the theory of island biogeography is a useful descriptor of woodland fragments in farmland is important for two reasons. First, this theory is invoked in many discussions of such fragments and is suggested as the basis for management decisions (Goeden 1979, Gilbert 1980, Diamond 1981). Second and more important, the theory involves predictions about the dynamic character of the distribution of woodland species in space and time. By testing these predictions in farmland, we can make an assessment of the dynamic character of the distribution of these same species in other forests not affected by artificial fragmentation. The equilibrium theory is based on the difference between two rates: local extinction and immigration. If either or both of these rates is extreme (0 or 1), the system either collapses or converges to the state of a continent. Thus, the theory applies in a non-trivial way only to those systems where both rates are away from their extreme values. As a corollary, if we can demonstrate that equilibrium insular processes have had a significant effect on the distribution of species among islands, it follows that movement among

islands must have been restricted. Thus, by assessing whether the theory applies to farmland, we can make conclusions about the ability of woodland organisms to move through space, by noting how this movement has been affected by discontinuities of the magnitude imposed by humans in farmland.

The equilibrium theory makes several predictions, the most obvious of which are that the number of species on islands will be lower than on mainland, and that the number of species will be related to island area and to distance from mainland. All of these are quantifiable in principle. However, in farmland and other systems of continental islands, the measurement of these parameters is difficult. Compilation of complete species lists is always a very time-consuming process, especially when more than one taxon is sampled simultaneously with different techniques. Calculation of area is relatively straightforward, although involves establishing a perimeter that is often much less distinct than that of a 'real' island. Calculation of distance is especially difficult, since the parameter is actually not geographic distance but rather biological isolation. The two are nearly equivalent in oceanic systems where the water among islands can be considered a homogeneous barrier as perceived by many terrestrial taxa. Distance and isolation are certainly not equivalent in

farmland. The character of land among woods can have a great effect on the movement of organisms (Wegner and Merriam 1979), depending on whether it includes wooded hedgerow or cultivated field or paved highway. There exists the option of measuring the rate of movement for each taxon across different sorts of land between woods. Such studies are again very time-consuming. Furthermore, there is no reason to expect that such studies would solve the problem at hand, for the rate of movement among woods could be almost zero over the several-year span of a field study, yet still be adequate, relative to the rate of local extinction, to prevent depression of the total species number in the woods.

A final problem is that no factor acts alone. Innumerable aspects of habitat, history, competitive interactions, and other ecological factors all affect the distribution and abundance of species, whether or not insular processes are in operation. Ecologists cannot document let alone control for these factors, except in broad outline. The solution is to control, however imperfectly, for as many factors as possible, and to compensate for the imprecision at this stage by using a large sample size of many woods and many different species. However, this option is not open in practice where the investigation of each individual wood or species is itself a major undertaking.

In the present study, I attempted to overcome all these problems by investigating a more abstract but more basic aspect of the equilibrium theory of island biogeography. The technique is based on the idea that presence or absence at a point (or within a small area) is an unambiguous and easily assessed property of many different sorts of organisms, and that ultimately, any operation of equilibrium insular processes must act by way of a changed distribution of these presences and absences in space. This study does not attempt to give an explanation for the distribution of any given species. Instead, it takes advantage of a simple technique to obtain data on a large number of very different species over a large extent of space. These data are analysed for certain statistical properties following from the equilibrium theory, to determine whether insular processes have made a detectable contribution to the present distribution of woodland species in farmland. The complicating effect of other factors is dealt with by the use of separate controls and treatments, the use of a large sample size, and the use of many different sorts of organisms, such that any important, systematic complicating factor is unlikely to come into play, or at least to go unnoticed. A particular strength of this technique is its taxonomic breadth. It can, in principle, aspire to make statements about large ecological systems, and not just about the autecology of individual species or groups of

species. I am unaware of any previous study of distribution of species among woods in a system resembling farmland that attempted to apply its methods over so broad a range of taxa.

The rationale is illustrated in Figure 1. Before clearing for agriculture began (say, 200 years ago), we could have collected certain data on the spatial distribution of species along a continuous transect in the forest, such as their presence or absence at evenly spaced points. If we assume that the forest was heterogeneous and that the degree of heterogeneity was broadly similar over the whole area, it follows that we could have collected statistically equivalent data by combining data from a number of small discontinuous transects instead. Thus, if clearing had had no effect on the distribution of the species within the remnants, the original pattern would still be obtained by sampling transects within the remnants (Figure 1b). Now suppose that the remnants respond to clearing by behaving as islands, such that there are certain empty islands for a given species at any given point in time. This will have at least two effects on the composite spatial pattern for that species, effects that we may use as criteria for detecting the operation of insular processes (Figure 1c):

Figure 1. Rationale of the method used in this study.
 a) forest of 200 years ago. b) after fragmentation.
 c) after local extinction without recolonization.
 d) continuous forest of past or present. e) comparison
 of spatial pattern to reveal operation of insular
 processes in farmland. ● - present ○ - absent.
 Details in text.

1) The gaps (runs of absences) will be larger in some parts of the record.

2) The remaining presences will be more clumped relative to the absences.

Note that these will be true even though the local biology and local pattern of distribution has not changed at all in those remnants where the species is still found. By now we no longer have direct access to the original pattern of the continuous forest. However, with certain assumptions, we may substitute the pattern obtained from an existing area of continuous forest as a surrogate for the original pattern in what is now farmland (Figure 1d). By comparing this pattern to that obtained from the forest remnants, the operation of the insular biogeographic processes will be revealed (Figure 1e).

The assumption that linking several discrete transects into one composite transect is equivalent to sampling a single transect, is robust for the procedures used in this study. (The following arguments follow Pielou (1964, 1969).) Consider a two-phase mosaic formed by placing randomly-oriented lines on a plane. For present purposes, the two phases may be considered as areas of presence and absence of some species. This mosaic serves as a useful

model of a random mingling of presences and absences. Within this mosaic, the probability that the species is present at a given point is dependent upon whether it is present at an adjacent point, for any given separation between the two points, and this probability is independent of the presence of the species at two, three, or more points away. That is, the mosaic is an example of a stationary Markov process. Thus, when sampling a real mosaic to test its deviation from the random model, we need ordered data on pairs of points, the pairs being taken from anywhere within the mosaic. Sampling along a continuous transect is an efficient way of accumulating such data, but it is not necessary. Any arrangement of the pairs is mathematically equivalent. Furthermore, we need not assume that the real mosaic conforms to the random model, for deviation from randomness gives us a measure of pattern in the real mosaic.

When linking separate transects into one composite transect we bring together as adjacent points the end points of the separate transects that are actually widely separated in space. This introduces a possible error, for these points are essentially independent of each other and not linked by the appropriate Markov transition probability. However, these illegitimate pairs constitute a small proportion of the pairs sampled (no more than 7% in any part of this study) and so contribute, at worst, a small error to the estimate.

The value of the probability that a given point is the same as its neighbour is dependent upon the spacing between the points, and will vary as the spacing varies, for any given mosaic. Thus, data collected at any given spacing of pairs of points give information on only one aspect of the pattern of the mosaic. In the present study, one particular spatial scale was identified as of particular interest. It is the scale of the size of woods in farmland and their mutual separation, a scale on the order of hundreds of metres. When sampling, I used a separation between points of 25 m and a total length of transect of over 6 km in both the continuous and discontinuous forests, so that the scale of interest was well bounded on either side. This has the possible disadvantage that processes acting at an intermediate spacing might combine to give a spurious response, mimicking but independent of the process of interest. For example, a perfectly regular sequence of presences and absences in groups of 100 m would be detected as a highly aggregated pattern when sampled at intervals of 25 m, even though this pattern has nothing to do with processes acting at the level of presence and absence in whole woods of several hundred metres in length. To guard against this problem, I measured a second aspect of the distribution of presences and absences, namely the length of strings of absences. This is a criterion that can be related directly to the feature of interest, namely empty woods.

Unfortunately, gap length is sensitive to absolute abundance of the species in question. That is, some process leading to a general reduction in abundance could lead to a distribution with gaps larger than whole woods even though mobility was not affected and equilibrium insular processes were not in operation. This is not a problem with the first criterion, in which absolute abundance is taken into account. Thus, since each of these criteria is sensitive to an error to which the other is not, the combination of the two gives a much more powerful and sensitive test than either alone.

There will be various other, more direct impacts on the distribution of species within the forest remnants. These may include cutting of trees, grazing by cattle, introduction of exotics, and increasing the ratio of edge to interior, among others. Any tendency to decrease the general abundance of a woodland species in the remnants will interfere with the first criterion mentioned above by increasing the length of gaps independently of the effects of insular processes. However, in most cases there is no reason to suppose that such general effects will change the pattern of clumping (although a contagious disease might do so). Thus, a measure of aggregation that abstracts out the effect of absolute abundance and looks at only the residual pattern will usually be unaffected, and will remain sensitive to the contribution of the insular processes.

Incomparability of treatment and control forests could lead to errors of two different sorts. First, the control forest could represent an underestimate of the heterogeneity of the original forest in farmland, as perceived by its inhabitants. This could come about if, for example, only those areas too rocky or steep for agriculture were left uncleared. To the extent that this is the case, the sample from woods in farmland does not represent all of the heterogeneity of the original intact forest, as it does not take into account all elements of the original landscape. In this case we could observe a pattern of restricted distribution in farmland with no counterpart in the existing continuous forest, and wrongly conclude that the human fragmentation has been responsible when in fact the difference in pattern existed even 200 years ago, before human impact. That is, errors of this type will tend to make us accept too many cases as showing local extinction without recolonization. This will affect conclusions only if there is, in fact, a difference in pattern between the continuous and discontinuous forest transects. Alternatively, if the control forest is actually more heterogeneous (as perceived by the organisms being studied) than was the original farmland forest, we may confound a changed pattern in farmland brought about by insular processes with a similar pattern in the existing continuous forest brought about by a quite unrelated situation. For example, this latter could be

a pattern of localized suitable habitat surrounded by only slightly inappropriate ~~habitat~~ through which movement is nevertheless easy and frequent. In this case we would fail to detect the very process for which we are searching. I guard against this possibility by using forests as similar as possible, by using a large sample in each forest, and by sampling a wide range of very different taxa, some of which would be expected to react to any cryptic disjunction of the sort mentioned above, and so give clues as to its existence.

The tests used here are asymmetric. The criteria described are minimal requirements for subscribing to the view that insular processes have made a significant contribution to the pattern as measured. A positive result to both does not demonstrate that this mechanism has been in operation, but merely that it remains a plausible hypothesis. However, a negative result for one or both of the criteria is much more compelling. By the argument outlined here, such a negative result entails that insular processes have not made a measurable contribution to the pattern observed.

By determining whether the distribution of woodland species has been significantly constrained by the fragmentation of forest in farmland, we can make conclusions about the ability of these species to persist in and move

among patches of suitable habitat, and thus indirectly about the importance of such persistence and movement in maintaining the spatial structure of the original intact, continuous forest.

METHODS

I examined the spatial distribution of various types of organism in four types of forest in the Great Lakes-St. Lawrence Forest Region of Canada (Rowe 1977):

1) extensive continuous forest (350 km²) of Gatineau Park, Quebec.

2) fifteen small (1- to 25-ha) remnants of forest in farmland south of Ottawa.

3) a small (50-ha) little-disturbed forest reserve (Burnham Provincial Park, Peterborough).

4) a 50-ha stand of virgin forest contiguous with a much larger area of forest (Shaw Woods).

Details of the sampling sites are given in Appendix 1.

All sampling was carried out in mesic mixed deciduous forest dominated by Acer saccharum. Open canopy, bare rock, standing water, saturated soil, discontinuous litter, and human artifacts were all rare, covering in total no more than 5% of any transect in any area. Canopy, shrub layer, herb layer, and furniture (fallen logs, boulders, etc.) were each assessed on a scale of 0 (absent) to 2 (abundant) as a measure of one aspect of the similarity of the forests. Relative distribution of taxa in the different areas was also used as a measure of their degree of similarity.

Farmland transects were sampled in farm woods within 30 km of Ottawa. Woods ranged in size from 1 to 25 ha. Each wood had a closed canopy of Acer saccharum with lesser and variable amounts of Fraxinus americana, Fagus grandifolia, Ostrya virginiana, Tilia americana, and other trees. Ground flora included species typical of mesic forests in eastern Ontario such as Trillium grandiflorum, Erythronium americanum, Caulophyllum thalictroides, and Allium tricoccum. No point in any wood was more than 200 m from the nearest edge. Transects were placed along the longest diagonal, to maximize the number of points taken in each, and ranged in length from 250 to 1000 m. Each wood was from 300 to 500 m away from its nearest neighbour, except for two pairs that were in fact contiguous but sampled separately because they appeared as two distinct pieces in shape and

orientation. Woods were on glacial drumlins or on the slopes of drainage valleys (above the level of flooding), and were on land rockier or steeper than adjacent cultivated fields. The land among woods included typical features of the rural mosaic including open fields, pastures, roads, and buildings. The degree of connection among woods by way of hedgerows and fencelines was variable. In no case were any connections comparable in character to the woods themselves. All woods showed obvious signs of human impact such as lanes, paths, evidence of grazing, and stumps.

Gatineau is a rolling irregular upland based on precambrian rocks. It is generally unsuitable for farming, although many scattered attempts have been made. Less than 10% of its area is now clear because of human activity, and almost none of this was included in the present study. Its climate is rather different from that of the adjacent farmland, with a growing season about 11 days (6%) shorter (Rowe 1977), even though the two areas are separated by only 30 km. I sampled a single continuous transect in the midst of an area of many thousands of hectares of continuous forest. Forests on the transect were similar in composition to those of woods in farmland, except for a larger (but always minor) representation of conifers such as Tsuga canadensis, Abies balsamea, and Pinus strobus.

Burnham and Shaw were sampled as rare examples of little-disturbed mesic forest, that might be closer to the original state of farmland than is Gatineau. Each is too small to act as an adequate control on its own, but can supply data to illuminate other parts of the study.

Burnham is a stand of mesic forest on a drumlin near Peterborough, Ontario, 250 km to the west of Ottawa (Peterborough Field Naturalists 1973). It is part of a stand of trees approximately 600 ha in size, which is in turn surrounded by roads and open fields. It has had light use as a source of firewood, but is now protected as a provincial park. I sampled it along two transects separated by about 200 m, one at the top of the drumlin, and one towards its base. Vegetation along the transects was dominated by Acer saccharum, Fagus grandifolia, and Tsuga canadensis, with an understory of Trillium spp., Erythronium americanum, Caulophyllum thalictroides, and others.

Shaw includes two main areas of mesic forest on gravelly glacial soils near Eganville, Ontario, 100 km northwest of Ottawa (Dugal 1980). One area has had a history like that of Burnham, while the other has been practically untouched by humans. Both areas were sampled with a single transect in each at a distance of about 400 m one from the other. These two stands are part of a 50-ha nature reserve continuous

with a band of forest extending many kilometres. The transects sampled forests with Acer saccharum, Fagus grandifolia, Tsuga canadensis, and a very sparse ground cover.

Humans have lived in this general area for thousands of years (Jenness 1977), but no large settlements or extensive clearings were made until after the establishment of European settlers in about 1800. The maximum extent of clearing was reached sometime before 1900, as was the case in other parts of southern Ontario (Scott 1979). Fire was an important factor, and caused extensive changes to forests adjacent to farmland as late as 1900, and to the forest of Gatineau Park in 1923 (Lopoukhine 1974). Thus, these forests are typical of temperate forests where the average interval between successive fires is on the order of a century or less (Lorimer 1977, Cwyner 1978, Forman and Boerner 1981, Johnson 1981). Shaw and Burnham are atypical in that they have been neither clear-cut nor burned within the approximately 200 years of recorded local history (Dugal 1980, Peterborough Field Naturalists 1973).

I determined the presence or absence of various types of organisms at points spaced 25 m apart along approximately 6 km of transect in Gatineau, 6.5 km in farmland woods, and 1.25 km in each of Burnham and Shaw. In practice, each point

was a small circular quadrat (after Pielou 1964, 1969). Distances were estimated by pacing. The sampling method differed according to taxon:

1) trees - any visible living part of a woody species normally capable of attaining a height of at least 3 m, within a quadrat of radius 5 m extending up through the canopy.

2) herbs - any visible living part of a non-woody angiosperm, excluding sedges and grasses, within a quadrat of radius 5 m.

3) ferns - any visible living part of a fern, within a quadrat of radius 5 m.

4) squirrels - four species of diurnal sciurids identified by sight or sound (or presence of burrows for Marmota monax), within a quadrat of radius approximately 25 m.

5) invertebrates - approximately 300 cm³ of leaf litter taken at each point was placed in a Tullgren funnel for 48 hours. Ten distinctive taxa were chosen, including collembolans, pseudoscorpions, and a hemipteran.

In most cases, the taxa used were species. In a few cases where field identification was difficult, two or three congeneric species were lumped, or a genus was used. For the invertebrates, identification was much less certain. Some of these taxa may be species mixtures of unknown composition. The taxonomic authorities used were Maynard 1951, Scott 1961, Marie-Victorin 1964, White and Hosie 1968, Cody 1978, Gillett and White 1978, and, for invertebrates, W.R. Richards (Biosystematics Research Institute, Agriculture Canada, Ottawa; personal communication).

Trees, ferns, squirrels, and invertebrates were sampled during the summer (June-August 1980 and 1981). Herbs were sampled during the period of maximum growth in the spring (May 1981).

The use of small quadrats instead of points has the potential to introduce certain errors. Use of quadrats is a practical necessity because, for many species, the 'outside' and 'inside' of its local distribution are not clearly defined (Pielou 1964, 1969). Quadrat size for a given taxon was the same in all forests, so comparisons among forests are not biased. There is a problem when comparing among taxa which were sampled with different sized quadrats. Squirrels and invertebrates were sampled with quadrats of a different size than those of the plants in this study.

However, I argue that a squirrel present at 20 m from a point is, in ecological fact, also present at that point, because his daily movements will take him across that point within a short period of time. By contrast, the much smaller quadrat size (several cm in diameter) used for invertebrates probably tended to give a bias towards underestimation of these taxa, as compared to the plants and squirrels. However, I repeat that comparison of any taxon among different forests is proper and unaffected by this potential error in every case.

There was a single continuous transect in Gatineau, two in each of Burnham and Shaw, and fifteen in woodland fragments in farmland. In analysis of the latter cases, the separate transects were linked end to end to form a single composite transect for each area.

All further analyses were conducted on the sequence of presences and absences for each taxon.

The mean, standard deviation, and maximum length of gaps (sequences of absences) was calculated for each taxon along the continuous transect in Gatineau as a standard to assess the significance of observed gaps in farmland. The length of the largest empty wood in farmland was compared with the maximum and upper-95% confidence limit for gap size in

Gatineau, and was considered as exceptional if it exceeded either of these numbers.

The degree of aggregation of presences along transects was determined in two ways. The blocks test examines the number of pairs of presences between which there are no absences, and compares this to the number that would be expected if the same number of presences and absences were randomly mingled. The runs test examines the number of uninterrupted sequences of absences or presences and compares this to the number that would be expected if the same number of presences and absences were randomly mingled. The probability generated by each test is inversely proportional to deviation from a random pattern and independent of absolute abundance (Pielou 1979). This probability was used as an index of aggregation. These tests do not involve the assumption that the real mosaic conforms to the random model. Instead, they take the difference between real and random mosaics as a measure of the patterned (that is, other-than-random) nature of the real mosaic.

The frequency of each taxon in each area was taken to be the proportion of points at which it was present.

The insular theory predicts that species will be lost from whole islands. Thus, the woods in this study constitute

natural units, and the distribution of taxa among woods is a parameter of interest. The incidence of each taxon was defined for each area separately as the number of segments in which that taxon was found at least once. In farmland, segments corresponded to individual woods, and ranged in size between 9 and 44 points according to the size of the woods. For comparison, the Gatineau transect was divided into 15 non-overlapping segments of almost equal size (13-15 points each), to match the number of transects in forest fragments in farmland. Burnham and Shaw were divided into four segments each. Average length of segments was between 12 and 15 points in the different areas. This provides a rough measure of distribution among units the size of woods. Frequency (proportion of points at which a species is present) can be precisely measured and compared, but will not necessarily indicate loss from whole woods because it also responds to change in abundance within woods. Incidence responds directly to loss from whole woods, but it is harder to interpret because there are no natural units in the control forest comparable to woods. Because of the difficulty of deciding on a completely adequate control, incidence was always used in conjunction with frequency, and no conclusion was based on the use of incidence alone. That is, either lower frequency or lower incidence was taken as evidence of restricted distribution.

Curves of cumulative number of taxa against number of points sampled were calculated as a measure of the relative species richness of each area. The calculations were made separately for each of 15 woods in farmland, 15 segments in Gatineau, and 4 segments in each of Burnham and Shaw. Composite curves were calculated for each area by taking the mean of all the segments. Composite curves were calculated for all taxa taken together, and for each type of organism (trees, herbs, ferns, squirrels, invertebrates) separately. Furthermore, each of these curves was calculated in two different ways: using all taxa, and using only those taxa found in both of Gatineau and farmland (excluding those unique to one or the other).

RESULTS

I collected 64 186 data, each being the presence or absence of a given taxon at a given point in a forest near Ottawa. A summary of the characteristics of those data relevant to the question at hand is given in Appendix 2. The complete set of data is available at a nominal charge from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa K1A 0S2, Canada.

Taxa accumulated less rapidly along transects in farmland than in the continuous forest of Gatineau.

Interestingly, accumulation was even slower in the virgin forest reserve Shaw Wood. This pattern was clear-cut for all taxa taken together (Figure 2), and for each of trees, herbs, and ferns taken separately (Figure 3). All patterns remained the same when taxa absent from one of Gatineau or farmland were omitted from the calculation.

Of the 111 taxa recorded, 25 were not found in farmland, and 28 were not found in Gatineau, which left 58 common to the two main areas, and 86 found at least once in farmland. Neither Burnham nor Shaw contributed a species not found elsewhere.

All the forests examined were broadly similar in their major characteristics (Figure 4). Sugar maple (Acer saccharum) was dominant everywhere, being found in every segment without exception, and at over 80% of points in all areas. White ash (Fraxinus americana) was also found in each segment of Gatineau and farmland. Beech (Fagus grandifolia), ironwood (Ostrya virginiana), and yellow birch (Betula alleghaniensis), were each found in at least half the segments of both Gatineau and farmland. The major differences in the gross characteristics of the forests were the greater incidence of basswood (Tilia americana) in farmland (13 of 15 segments in farmland against 7 of 15 segments in Gatineau), and the presence of some boreal

Figure 2. Accumulation of taxa with increased sampling effort.
 Mean $\pm$ S.D. O - Gatineau, ● - farmland,
 Δ - Burnham, ▲ - Shaw.

Figure 3. Taxa accumulated after sampling 12 points. Mean $\pm$ S.D.
 a - all taxa, s - subset excluding any taxon not found
 in both of Gatineau and farmland.

O - Gatineau, ● - farmland, Δ - Burnham, ▲ - Shaw.

Trees				Shrubs				Ground Cover				Furniture			
G	F	B	S	G	F	B	S	G	F	B	S	G	F	B	S
02	02	1	1	0	0	0	0	0	0	0	0	0	0	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2

Figure 4. Physiognomic structure of forests.
 G - Gatineau, F - farmland, B - Burnham, S - Shaw.
 2 - abundant, 1 - intermediate, 0 - absent.

species in Gatineau. These species occurred at fewer than 15% of points, and were never dominant at any one point (Appendix 2).

Various patterns of abundance were observed. There was a tendency for taxa to be more frequent (be present at a higher proportion of points; Table I) and have a higher incidence (be present in more wood-sized segments; Table II) in Gatineau than in farmland. An aggregated or clumped distribution was demonstrated for most taxa in the continuous forest of Gatineau, and in the discontinuous forest of farmland (Table III). Only a minority of taxa were more clumped in farmland, and neither this nor the preceding conclusion was dependent upon the order in which segments were linked together to form the composite farmland transect. All taxa had gaps in their distributions in the continuous forest of Gatineau, and for all but the most common, gaps were on the order of hundreds of metres to kilometres. Similar gaps were also observed in the virgin forests of Burnham and Shaw.

So far, each measure of the spatial distribution of taxa (frequency, incidence, aggregation, gap size) has been reported independently of all others. The various tests of restricted spatial pattern may also be applied sequentially to each taxon in turn, to ask how many taxa are

	All taxa	Taxa found in both areas only
More frequent in Gatineau	59 53.2%	34 58.6%
More frequent in farmland	51 45.9%	23 39.7%
Equally frequent	1 0.9%	1 1.7%
	N = 111	N = 58

Table I. Relative frequency of taxa in Gatineau and farmland.

	All taxa	Taxa found in both areas only
Higher incidence in Gatineau	66 59.5%	41 70.7%
Higher incidence in farmland	38 34.2%	10 17.2%
Equal incidence	7 6.3%	7 12.1%
	<hr/> N = 111	<hr/> N = 58

Table II. Relative incidence of taxa in Gatineau and farmland.

	by Blocks test	by Runs test	by Both tests
Aggregated in Gatineau ($p < .05$)	48 65.7%	50 68.4%	47 64.4%
Aggregated in farmland ($p < .05$)	44 58.7%	46 61.3%	44 58.7%
More aggregated in farmland than in Gatineau	23 46.0%	23 46.0%	23 46.0%

Table III. Aggregation of taxa in Gatineau and farmland

simultaneously more restricted in distribution, and more aggregated, and characterized by longer gaps in farmland. When this is done, it can be seen that very few taxa show a consistent response that might suggest the operation of insular processes in farmland (Table IV).

DISCUSSION

The continuous forest used in this study is not a perfect match to the original forest of what is now farmland, but is similar in many important ways, as described earlier. Its adequacy as a control in this study is further borne out by the results. The physiognomic structure of the forest as measured along the Gatineau and farmland transects was very similar (Figure 4). The

general abundance and mix of tree species, factors likely to be good indicators of the character of a system, were also very similar in the two areas. Furthermore, most of the analyses used here treat taxa found in both of farmland and Gatineau. None of the conclusions reached below was sensitive to the inclusion or exclusion of any taxon peculiar to one or the other of the main areas.

The result of each analysis taken separately is consistent with the idea that island-like processes may have had an impact on the distribution of woodland species in

Table IV. Simultaneous application of tests of restricted spatial distribution in farmland.

Total number of taxa recorded	111	
Taxa recorded in farmland	86	
Of above, lower incidence or frequency in farmland	42	
More aggregated in farmland	21	
Both of above	17	
Both of above, and with unexpectedly* long gaps in farmland	7	6.3%

* at least one empty wood in farmland with gap length greater than one of the maximum or upper-95% confidence limit for gap size in Gatineau.

farmland. A point in a forest remnant in farmland has fewer taxa than a point in the continuous forest of Gatineau (Figure 2). There is a mild tendency for taxa to be less frequent and have a lower incidence in farmland (Tables I and II). Some taxa are also more aggregated in farmland than in continuous forest, although this is true of only a minority (Table III). Most taxa were absent from at least a few entire woods in farmland (by the sampling procedure used here), although most also showed long gaps of comparable size in their distribution in Gatineau (Appendix 2).

However, a species whose distribution is restricted by the processes described by the equilibrium theory of island biogeography should be more restricted in distribution and more aggregated and characterized by longer gaps in farmland, as explained in the Introduction (Figure 1). When all criteria are required, the island hypothesis becomes untenable in the great majority of cases (Table IV). In only seven ~~of 86~~ taxa are minimal requirements met. This is so even though, when making the tests, any trend, no matter how small, was accepted, without any assessment of statistical significance.

The combination of results argues against the applicability of the equilibrium theory of island biogeography for each of the remaining 79 taxa. Either the

taxon is not more restricted in its distribution in farmland, or it is no more aggregated than in the control, or the gaps in its distribution are of an unremarkable size as compared to the continuous forest. This is not an artifact of the use of Gatineau as a standard of comparison. If the relatively undisturbed forests of Burnham and Shaw are used instead, the hypothesis of a significantly different pattern in farmland is rejected even more clearly. The great majority of species were more abundant in farmland than in the virgin forests, no taxon was found in the virgin forests but not in farmland, and species accumulated at a comparable or greater rate in farmland (Figure 2). The pattern of taxa in the virgin forests is discussed in more detail elsewhere (Section III).

The combination of local extinctions and restricted recolonization remains a possible explanation for seven taxa. This by no means demonstrates that the insular mechanism has been involved. This mechanism seems unlikely on the basis of subsidiary data available for some taxa.

First, it is interesting to note that the short list includes representatives from each of the five main groups of taxa: two trees (Fagus grandifolia, Betula alleghaniensis), two herbs (Trillium erectum, Smilacina racemosa), one fern (Athyrium filix-femina), one squirrel

(Tamias striatus), and one invertebrate (Isotoma sp.). That is, there seems to be no differential response of mobile vertebrate and wingless invertebrate, for example, as might be expected if it was really restricted mobility that was driving the observed pattern. Next, in five of the seven cases, the apparently empty woods represent runs of absences no longer than gaps seen elsewhere within a wood in farmland, or in Shaw or Burnham. That is, there are precedents for gaps of this size even when isolation by open areas is not a factor.

In two of the seven cases I have access to more detailed distributional data that suggest that the supposed significant pattern may be no more than sampling artifact. Yellow birch (Betula alleghaniensis) was absent from my transects in seven of fifteen segments in farmland. However, more thorough searching of these woods demonstrated that there are at most two truly empty woods, and in one of these the species was deliberately removed by selective cutting in the late 1970's (K. Wong, unpublished data). Similarly, chipmunks (Tamias striatus) were absent from transects in six of fifteen segments in farmland. However, data from more detailed studies (Gyug 1978, Middleton 1979) show that not more than two of these were really empty, at least at the time of those studies.

These extra data are not conclusive, but they further reduce the probability that insular processes have contributed to the pattern of distribution of taxa in farmland. Furthermore, recall that these seven candidates represent only about 8% of the taxa seen in farmland. Even if all were good illustrations of the insular process, they would constitute a small minority.

A number of alternative interpretations may be raised to account for these results. One view might be that all sensitive species have already become totally extinct in farmland because of its changed structure. There were 25 taxa found in Gatineau but not at all in farmland in this study (Table V). However, there were just as many showing the opposite pattern (28 taxa found in farmland but not in Gatineau). There were representatives from each of the five main groups of organisms examined in this study, and for the great majority of these taxa the number seen in either area was so small that sampling inefficiency seems to be the most parsimonious explanation for their absence in the other region. Nevertheless, in a few cases (such as A. pensylvanicum;

Table V) the pattern seems to be more than an artifact. That is, the taxon is relatively frequent in Gatineau and Shaw, but absent from farmland. In these few cases it is possible to suggest that island-like effects have been in operation, although I have no evidence to support this interpretation in preference to any other.

Table V. Taxa absent from Gatineau or farmland, with indication of where and how often they were recorded. G - Gatineau, f - farmland, B - Burnham, S - Shaw. Number following each letter indicates at how many points the taxon was found in that forest.

<u>Absent from Gatineau</u>	<u>Absent from farmland</u>
Acer negundo f5	Acer pensylvanicum G77 S8
Aesculus hippocastanum f1	Alnus rugosa G4
Carpinus caroliniana f7	Picea glauca G33
Carya cordiformis f3	Populus grandidentata G9
Crataegus spp. f9	Ulmus rubra G5
Malus sylvestris f1	Anemone sp. G1
Pinus resinosa f1	Clintonia borealis G36
Populus balsamifera f2	Coptis groenlandica G6
Populus tremuloides f1	Dentaria diphylla G4 B2
Quercus alba f5	Epifagus virginiana G1
Quercus macrocarpa f10	Hepatica sp. G1 B1
Rhus typhina f3	Medeola virginiana G14
Thuja occidentalis f5 B3	Mitchella repens G4
Ulmus americana f1	Panax trifolius G5
Ulmus thomasii f25 B1	Pedicularis canadensis G2
Xanthoxylum americanum f9	Streptopus roseus G57 B3
Aster sp. f1	Trifentalis borealis G49 S1
Geranium bicknellii f2	Trillium undulatum G13
Geranium robertianum f3	Phegopteris connectilis G1
Geum aleppicum f3	Botrychium multifidum G1
Impatiens capensis f5	Cystopteris fragilis G2
Potentilla sp. f1	Osmunda cinnamomea G3
Sanicula gregaria f13	Osmunda claytoniana G2
Cystopteris bulbifera f2 B2	Osmunda regalis G2
Polystichum acrostichoides f7	Thelypteris palustris G2
Thelypteris noveboracensis f3	
Sciurus carolinensis f2	
Orchesella ainsliei f6	

It would be difficult to explain by the insular interpretation why so few species show an intermediate degree of response (7; Table IV). The equilibrium theory does not predict total extinction but rather a depressed incidence for most species. The proposed mechanism of the equilibrium theory acts by way of two rates, of extinction and immigration, the causes of both of which are probabilistic in nature (MacArthur and Wilson 1967). Some species may be so prone to local extinction and so poor in moving that they may disappear altogether from the island system. Others may be so good at moving and so persistent that their distribution among islands is not depressed at all. However, if both types are found among the inhabitants of a system of islands, the theory predicts that many other species showing an intermediate response will also be found. That is, there will be many species for which the probability of extinction is somewhat increased and the probability of successful recolonization slightly depressed such that they are found on some but not all possible islands at any given point in time. There is no expectation of a simple distinction between island and non-island species. It is for this reason that the equilibrium theory can be reduced to a curvilinear relationship among species number, area, and distance, but not to a threshold between two states. In fact, it is the realization that this will lead to an ever-changing pattern of different assemblages of

species that makes the equilibrium theory more interesting and more subtle than a simple question of suitable or unsuitable habitat. If we try to interpret the data of this study in terms of the island theory we must conclude that over 90% of the 111 species are either totally excluded from islands (26; Table V) or are unaffected by the insularity (78), and that less than 10% of them (7; Table IV) show an intermediate response. This pattern is difficult to reconcile with the idea that equilibrium insular processes have had a major part in shaping the distribution of these species.

By contrast, there are many species common in farmland for which it is plausible to suggest that rates of local extinction and recolonization are too low to have yet reached an equilibrium appropriate to the new circumstances. That is, the farmland system may be oversaturated with species, having not had time to relax to a lower equilibrium as yet. Many forest herbs are clonal perennials with most of their biomass concentrated underground. Such species are very resistant to external perturbations and can reach great ages on the order of centuries. However, fertile seeds are rarely produced, so geographical expansion is very slow. For example, Holland (1980) concluded that trout lily (Erythronium americanum) is still expanding its gross geographic range in Nova Scotia in response to the retreat

of the glaciers, such is its restricted mobility. The combination of great persistence and slow movement may make a species very slow to respond to changes of potential significance to it. An herb of English forests, Mercurialis perennis, is still a rather good indicator of forest conditions of 400 years ago, having neither gained nor lost much ground since that time (Peterken and Game 1981). Many of the herbs, trees, and some of the ferns such as bracken (Pteridium aquilinum), may have a combination of natural history traits tending to make them respond at a similar slow rate, such that the time available since extensive clearing in farmland began (say, 150 years) has been insufficient for them to ~~come to~~ equilibrium. This idea is worthy of further study for it bears on the future state of the altered forest system in farmland.

This study did not involve all species found in forests, and it is always possible to imagine that a future study of other taxa might come to a different conclusion with respect to the importance of island processes in farmland. More interestingly, there may be whole groups of taxa that would show a contrary response. For example, the soil invertebrates, and members of the decomposition sub-system in general, were examined only superficially in this study. Such organisms have natural history traits quite different from those of most of the taxa looked at here, and have a

crucial role in an ecological system such that a change in their distribution or abundance might ramify through the whole system in a significant way. Thus, it seems important to collect better data on the woodland decomposers before conclusions are made firm about the importance of clearing in farmland.

Whatever the present status of woodland species in farmland it is easy to think of future changes that would tend to increase the isolation of forest remnants, decrease the rate of movement among remnants, and so precipitate or exacerbate the operation of island processes. The ongoing tendency to remove or reduce wooded fencelines and woods themselves can only increase the probability that the system of forest remnants in farmland will be endangered by the effects of reduced movement of species in the future. Thus, the possibility of such effects should be kept in mind by anyone concerned with questions of conservation in farmland.

However, notwithstanding the various points raised above, by far the most reasonable conclusion based on the evidence of the taxa canvassed here, is that the impact of agricultural clearing in farmland has not yet been perceived as a significant constraining factor to the distribution of the woodland species still living there. It is interesting to ask what this result has to say about the factors

affecting the spatial structure of continuous forest. The majority of species seen in Gatineau, the continuous forest control of this study, were distinctly aggregated in space (Table III). This is consistent with the common pattern for most ecological systems (Harper 1977, Greig-Smith 1979). It does not necessarily follow that this pattern has involved any long-distance movements by organisms. It is possible to think of a species spreading amoeba-like across the forest over many generations, periodically splitting into fragments that are separated in space but broadly continuous in the temporal dimension. However, recall that this forest was extensively damaged by fire in 1923. Much of the spatial structure as revealed by adult organisms at least has been reassembled within the last 50 years, although it is still possible to suggest that this is just the latest manifestation of a more ancient pattern preserved through the fire by resistant seeds or perennating organs.

However, when the results from farmland are taken into consideration, a different conclusion becomes likely. The spatial distribution of woodland organisms in farmland could not be distinguished from that in continuous forests by several indices. Here, there is no question of slow multi-generation movement across the areas between woods. Thus, unless the present pattern is a static relict of the pattern from the original continuous forest that has

remained essentially unchanged for 150 years, without a significant number of local extinctions for any of the 86 taxa examined in farm woods, then there must have been long-distance movements among woods. These are movements not only of large mobile vertebrates, but also of wingless collembolans, and trees, and herbs, and ferns. The most reasonable synthesis of the preceding ideas is to conclude that these species have always been faced with the problem of having populations discontinuous in space as measured on the scale of kilometres, and that they have evolved mechanisms of movement in association with this mode of dispersion that are still found adequate to deal with the landscape as it has recently been changed by humans in farmland.

This conclusion is very sensitive to the assumption that the spatial pattern of organisms in these forests is dynamic, and does not persist unchanging in any location for 150 years or more. As discussed above, it is plausible to consider that certain species might be able to live in a way that violates this assumption. However, the response seen here was common to all types of organisms examined, and it is very difficult to believe that all these species had a static pattern. It has been demonstrated that certain species at least have distributions that are very mobile in the rural mosaic of this study (Middleton and Merriam 1981,

Henderson 1981). There is also considerable evidence to support the generality that an ever-changing pattern in space is the norm for both plants and animals (see for example Elton 1966, Harper 1977, Taylor and Taylor 1979). Even the most sedentary organisms seen in this study have some biological structures appropriate to the task of spreading the species through space.

The assumption that the similarity in pattern between continuous and discontinuous forest is due to long-term stasis for all taxa is demonstrably untenable. The similarity could conceivably arise in a situation in which some species were very static, whereas others were very dynamic. This is unsatisfying because there is so little evidence of an intermediate response. In the absence of evidence for this 'dimorphic' suggestion, I conclude in favour of the third possibility, namely that the distribution of the great majority of woodland species has been unaffected by the existing degree of forest fragmentation in farmland because these species have long since evolved efficient mechanisms for medium-distance dispersal in response to the ubiquitous spatial heterogeneity of continuous forest. These results add further support to the conclusion of Gilbert (1980) 'that many, if not all, insular continental situations are at best badly described by the equilibrium model'.

Each application of the theory of island biogeography involves the implicit assumption that movement among islands is a difficult and infrequent process. The results of this study support the growing body of evidence that movement is easier and more frequent in continental areas affected by humans than is assumed by the island theory (Elton 1966, Harper 1977, Taylor and Taylor 1979, Gilbert 1980). This opens the door to the possibility that medium-distance movements play a more important role in determining the local structure of all ecological systems than is generally assumed. The ability to move easily among woods in farmland is easiest to understand if it is considered a special case of frequent movement among discontinuous populations in continuous forest. If this is a reasonable interpretation, it demands an answer to the question of what effect this regular flow of organisms has on the functioning of the intact, but also heterogeneous, continuous system. There are few data available to address this question in continuous forest, although there are now abundant data demonstrating that the heterogeneity exists, and that it is significant in the obviously patchy systems of farmland. I conclude that we have not yet come to grips with the implications of the ubiquitous spatial heterogeneity of ecological systems, and that both theoretical and practical understanding will benefit from study of the functional significance of this heterogeneity, as they have done so often in the past.

SECTION III

The Impoverished Vegetation of a
Virgin Forest:
Shaw Woods, Ontario

INTRODUCTION

Less than 200 years ago, extensive continuous forest covered much of what is now farmland in eastern Canada. A considerable proportion of the Great Lakes-St. Lawrence Forest Region (Rowe 1977) is still covered by trees. However, forests that have not felt considerable human influence are very rare indeed.

One such stand of virgin forest is in Shaw Woods, a 'natural treasure' (Dugal 1980) now maintained as a nature reserve by the Shaw family, the Nature Conservancy of Canada, and the National Museum of Natural Sciences. The existence of this rare example of undisturbed forest offers the opportunity of studying some of the factors that determine the characteristics of a forested ecosystem, and how these factors react to human impact.

There are two main schools of thought on how an ecosystem (of any kind) ought to react to a significant external perturbation. The classical succession model predicts that species diversity grows as the system matures, and as more and more biological specialists accumulate. By one version of this theory, the increasing complexity of a maturing system imparts stability to the system, much as extra struts and braces in a building frame increase its

stability (Elton 1966). By a second version, the increasing complexity accumulates only by grace of a stable external environment. By this version, the specialists thought to be characteristic of the mature system are more like fragile baroque ornamentations than structural girders (May 1974). There are two corollaries of this theory, in whatever version. First, the greatest number of species should be found late in the successional sequence. Second, any significant external perturbation sufficient to change the system should decrease the number of species by setting the system back to a less mature stage.

A very different idea of how a system responds to perturbation is the intermediate disturbance hypothesis (Huston 1979). This theory predicts that the maximum species diversity will be reached at some intermediate point in the successional process, and will decline thereafter. As the system matures, competitive pressures eliminate the many species adapted to disturbed states of the system and leave only a relatively small number able to thrive and monopolize the resources of the system after a long period free from disturbance. By this theory, the greatest number of species are neither structural beams nor fragile ornamentations on the completed edifice, but rather part of the confusion of the building site where the main elements of the final structure coexist with the scaffolding, tools, and rubbish heaps of the earlier stages of construction.

The question of which model is more useful is an important area of study, for two reasons. First, there is the obvious reason that we might want to know how systems react to shocks because we are so often the cause of such shocks, and by knowing more of the processes of reaction we may be able to avoid some of the worst results. Second, and more interesting, is the fact that the way a system responds to perturbation is one of the best indicators of the relative importance of the various factors that affect the structure of that system. Often a perturbation experiment is the only efficient way to gain insight into the factors responsible for essential properties of a system, for these factors may be almost invisible when the system is at rest (Harper 1977). Unfortunately, the time required for many interesting experiments in forest would be prohibitive if they were attempted in the conventional manner with continuous observation from beginning to end. However, equivalent results can sometimes be obtained by observing only the conclusion of fortuitous 'natural' experiments that were begun unintentionally many years ago. The changes made to forests in eastern Canada by European settlers may be considered 'experiments' of this type.

In the present study I compared certain characteristics of the virgin forest of Shaw Woods, undisturbed by major external perturbation for at least two hundred years, with

the equivalent characteristics of several other forests that have been affected by humans to very different degrees. The purpose of this study was to analyse the differences among these forests in such a way that some insight might be had into the factors of most importance in shaping the characteristics of these forests.

METHODS

The methods and sampling sites were the same as those described in the previous section. The transects in Shaw Woods were placed in the least disturbed areas of mesic forest (Sections E and J of Dugal 1980). Section E is essentially virgin forest, undisturbed by significant external perturbation for at least two hundred years, whereas Section J has been subject to some lumbering as recently as the 1950s.

RESULTS

The main results were outlined in the previous section. Data relevant to the present discussion are as follows.

For a given amount of sampling effort, fewer species are found in Shaw Woods than in any other area of forest examined in this study. This is true for all taxa taken

together, and for each of trees, herbs, and ferns taken separately (Figures 2, 3).

There were only four species of squirrels recorded in this study, and they showed no relationship to sampling effort. All but Sciurus carolinensis (grey squirrel) were seen in Shaw. This squirrel has only recently expanded its range northward in eastern Ontario (Rand 1945) and was found in only the two most southerly sites of this study (Burnham and farmland).

The soil invertebrates showed a pattern contrary to that of the plants. Shaw yielded a higher number of taxa per unit effort of sampling than any of the other areas. Recall, however, that I did not examine the whole species pool but only a very restricted set of ten taxa, so that this result is much less reliable than those for the plants and squirrels.

All of the trends reported above remained the same whether calculated on the basis of all taxa, or on the basis of a subset from which were omitted any taxa absent from either of the two largest areas (Gatineau and farmland).

The physical structure of the forests was similar except for ground cover which was much reduced in Shaw and, to a lesser extent, in Burnham (Figure 4).

All species seen in Shaw were also very common elsewhere. I recorded no species unique to the virgin forest, and in all but five cases, the species seen in Shaw were also seen in each of Burnham, Gatineau, and farmland. The complete list is given in Table VI .

DISCUSSION

One of the most obvious differences among the forests examined here is that some are continuous over large areas whereas others are in the form of small clumps more or less separate from other nearby woods. However, in the previous section I showed that this factor is of little or no significance to the distribution of woodland species in farmland, and cannot be used to explain the differences in the characteristics measured here.

All woods examined here are part of the Great Lakes-St. Lawrence Forest Region. However, they are found in three different sections of the region (Rowe 1977). The differences among sections are minor, and mainly concern the relative abundance of the less common species, especially conifers. The more common deciduous species are the same, with sugar maple (Acer saccharum) being dominant everywhere. Furthermore, all the results reported here are the same whether they are based on all taxa seen, or on only those

Table V. Plant taxa recorded from Shaw Woods.

Trees

Abies balsamea
Acer pensylvanicum and A. spicatum
Acer saccharum
Betula alleghaniensis
Fagus grandifolia
Fraxinus americana
Ostrya virginiana
Tilia americana
Tsuga canadensis

Herbs

Actaea pachypoda and A. rubra
Arisaema triphyllum
Caulophyllum thalictroides
Erythronium americanum
Maianthemum canadense
Polygonatum pubescens
Ranunculus abortivus
Smilacina racemosa
Trientalis borealis
Trillium erectum
Trillium grandiflorum

Fern

Dryopteris spinulosa

found in each of the two main areas (Gatineau and farmland). Thus, the conclusions reached below are not artifacts of an invalid comparison among incomparable forests.

It is difficult to quantify the degree of disturbance of an ecological system. The index of 'hemeroby' (on a scale of 1-6) is one method of integrating the intensity, range, and duration of all human effects (intentional or otherwise) that has proved useful in certain studies (Sukopp, Elvers, and Mattes, 1981). The common sense of a field-naturalist is another. Whatever method is used the relative intensity of disturbance is much easier to determine. In the present study there was a clear range in the degree of disturbance, from the heavily disturbed woods in farmland (hemeroby 3-4), through the moderately disturbed forests of Gatineau (2-3), to the relatively lightly disturbed forests of Burnham Park (1-2), and the virgin forest of Shaw Woods (1). There is an equally clear-cut difference among the species richness of these forests, with a pronounced maximum in Gatineau (Figure 2). These results argue strongly in favour of the intermediate disturbance hypothesis as the best descriptor of the dynamics of this forest system as it responds to significant external perturbation.

Other features of the data support this conclusion. Of the 98 plant taxa recorded in this study, only 21 were found

in Shaw Woods. Eighteen of these were also found in each of the other areas as well (farmland, Gatineau, Burnham), and no species was found only in Shaw. The list of taxa is composed entirely of very common species that could be found with little effort in most forests in the region (Table VII). There is no evidence of accumulation of rare species uniquely adapted to undisturbed forest. On the contrary, the main characteristic of these data is the absence of many taxa found in the more disturbed forests. Furthermore, although I did not record any measure of abundance, my clear impression while working in the virgin forest is that the absolute abundance of plants of any kind, especially ground vegetation, is noticeably lower than in other forests. The virgin forest has an impoverished vegetation.

This poverty is not due to any unsuitability of the general area. The more disturbed areas of Shaw Woods immediately adjacent to the virgin stand but still within the reserve proper are much richer in species (unpublished observations; Dugal 1980). The very low richness of the virgin forest is a true feature of the way it has developed.

The litter invertebrates did not show the same pattern. Although my sampling technique for these animals was rather inefficient compared to that for the plants, the indications are that the virgin forest is especially rich in species of

invertebrates (Figure IV). The leaf litter of this forest is noticeably thick, and samples of invertebrates extracted from it seem to be especially abundant in individuals as compared to samples from other forests, although I have no quantitative measure of this. A more detailed survey of invertebrates and other taxa not examined in this study might force modification of my statement that the number of taxa increases less rapidly with increased sampling effort in Shaw than in other, more disturbed forests.

This study was based mainly on numbers of taxa. However, this is not the only characteristic of a system that can change as the system recovers from a perturbation. Age distribution, growth form, and structural complexity may also change. A model of Derived Heterogeneity (Patterson 1972, Dwyer and Merriam 1981) predicts that the total heterogeneity of a system will increase as it recovers from perturbation, whether or not species diversity does the same. Investigation of other dimensions of the virgin forest system might allow retention of the idea that total complexity of some sort increases to a maximum late in the recovery process even though the species diversity of plants clearly declines. My technique was not designed to address this question, but the physiognomic data are obliquely relevant. These data fail to support the idea that the physical structure of virgin forest is much different from that of more disturbed forests (Figure 4).

I conclude that the relationship among the forests examined in this study is well described by the intermediate disturbance hypothesis. A corollary of this conclusion is that the impoverished vegetation of the virgin forest of Shaw Woods is due to the absence of many species adapted to a more disturbed regimen. These conclusions have implications for questions of conservation. These implications are discussed in the following section.

SECTION IV

Commentary on the Conservation of
Virgin Forest

The Shaw Woods Nature Reserve is a magnificent forest. It cannot fail to move any naturalist who visits it. It is undoubtedly worthy of the protected status it enjoys thanks to the Shaw family, the Nature Conservancy of Canada, and the National Museum of Natural Sciences. However, it is an interesting exercise to ask ourselves why we think it is worthy of protection. In this note I wish to point out that two of the standard rationalizations of the conservation ethic do a rather bad job of justifying our concern in this case.

Parts of Shaw Woods are virgin forest that has remained undisturbed by major catastrophes for at least 200 years, and perhaps for much longer. Undisturbed ecosystems of any kind are a very rare commodity in the more settled parts of Canada these days. The impact of humans on almost all parts of the landscape is very easy to see. Would we not then be justified in arguing that Shaw Woods should be conserved as a remnant of what we have destroyed elsewhere?

On consideration of all the facts, I think we are forced to answer no. Human impacts on the natural world are unquestionably very severe and widespread. However, to a large extent the human impacts have merely replaced equally severe impacts of other sorts. A growing body of evidence demonstrates that frequent disturbance is an integral factor

in most ecological systems, and that areas left undisturbed for two centuries or more have always been rare. Thus I disagree with Dugal (1980) when he suggests that Shaw Woods offers a glimpse of what Ottawa Valley forest used to be like. Shaw Woods is probably not representative of any widespread ecosystem of the past, and an appeal for its conservation on this basis is ill-founded.

Perhaps the most common plea of conservationists is for the protection of the natural diversity of the world, and especially for the protection of species. It is commonly assumed that virgin ecosystems are particularly rich in rare species. Thus, can we not justify the protection of Shaw Woods on the basis of the protection of natural diversity?

Once again the answer must be no. Shaw Woods is downright boring for a list-ticking naturalist, at least so far as vascular plants are concerned. The poverty of the vegetation in its least disturbed sections is outstanding. Almost any other piece of forest in southern Ontario would be more suitable as a reserve if richness and rarity of species were the criteria.

Among the other areas I examined in this study was a small wood just south of Ottawa, less than a hectare in size. It is a miserable tangle of prickly ash, poison ivy,

and dead elms, thoroughly trampled by cattle. I would not go so far as to say I would want it cleared, but it would be at the bottom of my list of priorities for conservation. I am confident most naturalists would agree with my assessment. Nevertheless, I found more species of plants in this wood, with less than a quarter the sampling effort, than in the virgin forest of Shaw Woods. Furthermore, this wood had the highest proportion of rarities (although some of them were exotics) of all the woods I examined in my study. Shaw Woods had the lowest. I find this comparison a powerful reminder of the fact that the protection of diversity is not our main goal in preserving virgin forest.

Let me state that I approve wholeheartedly of the protection of Shaw Woods, and of all nature reserves. I hope their number increases by leaps and bounds in the future. I realize that this will not come about without a series of battles in which good public relations and propaganda will be the main weapons. There need be nothing dishonourable or dishonest about this. For example, I could quite truthfully point out in this case that Shaw Woods is a rare and irreplaceable bit of the natural world, and that it has been of great value to my own scientific research at least. My point is simply that this sort of argument must be used with care.

A justification for conservation that has the ring of objectivity and 'scientific truth' can be particularly valuable in public discussions. However, it is very dangerous to forget that such 'scientific' justifications are neither the whole nor the most important parts of the conservation ethic. Such 'truths' can be falsified, perhaps more easily than is generally realized, as I hope I have shown.

Other factors are also of importance in justifying conservation of virgin forest, as an honest examination of motives will reveal. For example, the massive size and broad spacing of trees in Shaw Woods are aesthetically very satisfying, quite aside from any scientific significance they may have. But there is no reason to insist that all natural systems worthy of conservation will be of special aesthetic appeal - consider virgin grassland of Saskatchewan as compared to adjacent rangeland for example, or a shield lake before and after acidification. Our motives for conservation seem to be rooted at a deeper level, where they are to a certain extent isolated from the utilitarian demands of economic or scientific or aesthetic value.

There is no shortage of attempts to justify conservation with arguments using the concepts of moral philosophy (see for example Worster 1977, Livingston 1981). It is probably true that such moral arguments are messy, and poor sellers in public discussion. Nevertheless, they should be pursued by all conservationists for ultimately they alone are the justification of our concern for the protection of the natural world.

SECTION V

Summary and General Conclusions

This study was designed to investigate a forested ecosystem in terms of certain of its spatial characteristics. One hundred eleven taxa of plants and animals were recorded as present or absent at points 25 m apart along 15 km of transects in woods in farmland and in nearby continuous forest. From these data were calculated indices of frequency and aggregation. These indices were used to test whether the isolation of woods in farmland has caused the distribution of woodland organisms to be changed in the way predicted by the equilibrium theory of island biogeography. This study led to the following conclusions:

- 1) The majority of taxa are significantly aggregated in both continuous forest and farmland.

- 2) There is no consistent response of all taxa to the fragmentation of forest in farmland. All possible combinations of increased or decreased abundance with increased or decreased aggregation are exhibited by some taxa.

- 3) Only a small minority (less than 10%) of woodland organisms in farmland show a change in spatial distribution that might be caused by the processes described by the equilibrium theory of island biogeography. The possible

candidates include representatives of each type of organism examined in this study (trees, herbs, ferns, squirrels, invertebrates).

4) More detailed distributional data available for a few taxa further diminish the plausibility of the insular hypothesis.

5) Farmland as it exists today near Ottawa is not perceived by woodland species as a system of biogeographic islands. This is probably because these species have long since evolved efficient mechanisms for medium-distance movements in response to the ubiquitous spatial heterogeneity of intact, continuous forest.

In the course of the preceding investigation, I recorded data on a rare stand of virgin forest that has been free of major disturbance for at least 200 years. These data were given a separate analysis, from which were derived the following conclusions:

6) The virgin forest is characterized by an outstanding poverty of vegetation. Both species and individuals are less common than in any other forest examined in this study. I recorded no species of plant unique to the virgin forest. All species seen were also widespread and common in other types of forest examined.

7) The pattern of species richness in the forests of this study is well described by the intermediate disturbance hypothesis. The impoverishment of the vegetation of the virgin forest is due to the absence of the many species adapted to a more disturbed regimen.

The results from the virgin forest raised some interesting questions about conservation. Exploration of these questions led to the following conclusions:

8) Two common rationalizations of the conservation ethic do a very poor job of justifying conservation of virgin forest in eastern Ontario.

9) Apparently 'objective' and 'scientific' rationalizations of the conservation ethic are effective tools for public debate, but can be dangerous and counter-productive if pursued uncritically.

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APPENDICES

Appendix I

Details of Sampling Sites

Map references refer to starting points and directions of transects.

Gatineau - a single continuous transect parallel to Ridge Road trail, NW from junction with Fortune Lake trail, to edge of clearing beyond Champlain; map sheet 31G/12W Wakefield, 230388 NW to 287407.

farmland - 15 separate transects

map sheet 31G/5 Ottawa
Barrhaven Creek 435153 NE
Nepean Wood 438135 SE
Nepean Satellite 440137 SW
Nepean Creek 448138 W
Nepean Triangle 445138 SW
Heart's Desire 443119 NW

Wegner and Merriam 1979
Wegner and Merriam 1979
Wegner and Merriam 1979

map sheet 31G/4 Kemptville
Waterson Corners 462066 NW
Carsonby 460010 SE
Low Wood 422992 S
Central Wood 426994 SW
Large Wood 424996 NW
Divided Ungrazed 432996 W
Divided Grazed 433996 SE
North Gower Large 454976 NW
Dalmeny A 584987 N

Gyug 1978

Middleton and Merriam 1981
Middleton and Merriam 1981
Middleton and Merriam 1981
Middleton and Merriam 1981
Middleton and Merriam 1981
Gyug 1978
Henderson 1981

Burnham - two transects parallel to two main arms of trail in Mark S. Burnham Provincial Park, Peterborough, north from parking area.

Shaw - two transects in Shaw Woods Nature Preserve, in Sections E (heading SE) and J (heading NW) of Dugal (1980).

G - Gatineau
 f - farmland
 B - Burnham
 S - Shaw

● wood
 — transect

APPENDIX II

Summary of Data

G - Gatineau
f - farmland
B - Burnham
S - Shaw

BLOCKS, RUNS - degree of aggregation, expressed as $-\log p$
where p is probability observed pattern or one
more aggregated could have arisen from random
mingling of presences and absences
- higher numbers indicate greater aggregation

GAPS -

$\bar{x}$, SD, max - mean, standard deviation, and maximum observed
gap length in Gatineau
maxf - longest empty wood in farmland

Trees	FREQUENCY			INCIDENCE			BLOCKS			RUNS			GAPS		
	G	f	B	S	G	f	B	S	G	f	B	S	X	SD	max
<i>Abies balsamea</i>	59	7	1	2	13	2	1	2	4	0	0	0	5	8	43
<i>Acer negundo</i>	0	5	0	0	0	2	0	0	-	1	-	-	-	-	44
<i>Acer pensylvanicum</i>	77	0	0	8	14	0	0	3	8	-	-	-	6	5	20
and <i>A. spicatum</i>	26	15	0	0	9	3	0	0	2	6	-	-	11	13	50
<i>Acer rubrum</i>	210	221	48	48	15	15	4	4	3	6	-	-	2	1	3
<i>Acer saccharum</i>	0	1	0	0	0	1	0	0	-	-	-	-	-	-	-
<i>Aesculus hippocastanum</i>	4	0	0	0	3	0	0	0	2	-	-	-	44	59	146
<i>Alnus rugosa</i>	94	90	4	2	15	8	2	1	0	14	0	0	44	4	13
<i>Betula alleghaniensis</i>	38	8	0	0	12	3	0	0	5	0	-	-	4	4	37
<i>Betula papyrifera</i>	0	7	0	0	0	4	0	0	-	1	-	-	-	-	24
<i>Carpinus caroliniana</i>	0	3	0	0	0	3	0	0	-	1	-	-	-	-	44
<i>Carya cordiformis</i>	6	1	4	0	5	1	2	0	0	1	0	-	31	40	117
<i>Cornus spp.</i>	0	9	0	0	0	1	0	0	-	9	-	-	-	1	-
<i>Crataegus spp.</i>	93	49	21	39	14	10	4	4	4	4	0	0	4	4	17
<i>Fagus grandifolia</i>	66	96	15	1	15	15	3	1	4	5	0	-	5	4	14
<i>Fraxinus americana</i>	1	1	0	0	1	1	0	0	-	-	-	-	112	62	156
<i>Juglans cinerea</i>	0	1	0	0	0	1	0	0	-	-	-	-	-	-	44
<i>Malus sylvestris</i>	34	43	1	2	12	11	1	2	1	1	-	-	8	13	57
<i>Ostrya virginiana</i>	33	0	0	0	8	0	0	0	5	-	-	-	10	14	43
<i>Picea glauca</i>	0	1	0	0	0	1	0	0	-	2	-	-	-	-	44
<i>Pinus resinosa</i>	43	5	0	0	10	3	0	0	4	2	-	-	7	12	55
<i>Pinus strobus</i>	0	2	0	0	0	1	0	0	-	1	-	-	-	-	31
<i>Populus balsamifera</i>	9	0	0	0	4	0	0	0	3	-	-	-	-	-	44
<i>Populus grandidentata</i>	0	1	0	0	0	1	0	0	-	1	-	-	36	39	108
<i>Populus tremuloides</i>	0	1	0	0	0	1	0	0	-	-	-	-	-	-	44

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OF / DE

	FREQUENCY			INCIDENCE			BLOCKS			RUNS			GAPS		
	G	f	B	S	G	f	B	S	G	f	B	S	X	SD	max
Prunus spp.	26	11	1	0	12	7	1	0	0	0	0	-	8	9	26
Quercus alba	0	5	0	0	0	3	0	0	-	1	-	-	-	-	-
Quercus macrocarpa	0	10	0	0	0	7	0	0	-	0	-	-	-	-	-
Quercus rubra	30	4	0	0	8	2	0	0	7	0	-	-	13	17	55
Rhus typhina	0	3	0	0	0	1	0	0	-	1	-	-	-	-	-
Thuja occidentalis	0	5	3	0	0	2	2	0	-	1	0	-	-	-	-
Tilia americana	18	117	13	11	7	14	3	3	0	7	1	0	13	21	51
Tsuga canadensis	31	15	25	27	11	4	3	4	7	2	3	0	1	12	60
Ulmus americana	0	1	0	0	0	1	0	0	-	-	-	-	-	-	-
Ulmus rubra	5	0	0	0	4	0	0	0	0	-	-	-	-	-	89
Ulmus thomasi	0	25	1	0	0	10	1	0	-	0	-	-	-	-	31
Xanthoxylum americanum	0	9	0	0	0	2	0	0	-	8	-	-	-	-	44

Herbs

Actaea pachypoda	71	26	5	6	13	8	2	2	11	1	0	-	7	6	7	30	17
and A. rubra	1	66	22	0	1	8	3	0	-	21	6	-	115	130	207	44	44
Allium tricoccum	1	0	0	0	1	0	0	0	-	-	-	-	115	146	218	44	44
Anenome sp.	56	11	0	0	13	3	0	0	4	3	-	-	6	7	34	23	23
Aralia nudicaulis	5	9	2	2	4	4	2	1	0	1	0	0	1	38	45	125	44
Arisaema triphyllum	5	34	2	0	4	9	1	0	0	5	0	-	45	61	151	13	13
Asarum canadense	0	1	0	0	0	1	0	0	-	-	-	-	-	-	-	44	44
Aster sp.	19	101	38	1	7	10	4	1	4	27	0	-	18	23	76	14	14
Caulophyllum thalictroides	5	6	0	0	5	2	0	0	0	1	-	-	45	42	102	44	44
Claytonia caroliniana	36	0	0	0	7	0	0	0	20	-	-	-	22	21	65	44	44
Clintonia borealis	6	0	0	0	1	0	0	0	5	-	-	-	75	76	155	44	44
Coptis groenlandica	4	0	2	0	2	0	1	0	2	-	0	-	72	102	190	44	44
Dentaria diphylla																	
Dicentra canadensis																	
and D. cucullaria	63	21	1	0	9	6	1	0	14	8	-	-	15	21	59	14	14

	FREQUENCY			INCIDENCE			BLOCKS			RUNS			GAPS		
	G	F	B	S	G	F	B	S	G	F	B	S	X	SD	max
<i>Epifagus virginiana</i>	1	0	0	0	1	0	0	0	0	1	0	0	1	165	44
<i>Erythronium americanum</i>	148	181	44	28	13	13	4	3	3	8	1	7	3	6	26
<i>Fragaria vesca</i>	1	16	0	0	1	5	0	0	0	5	1	1	115	24	132
<i>Galium</i> spp.	25	4	0	0	9	2	0	0	1	1	0	0	10	17	60
<i>Geranium bicknellii</i>	0	2	0	0	0	2	0	0	0	0	0	0	+	+	+
<i>Geranium robertianum</i>	0	3	0	0	0	1	0	0	0	0	0	0	+	+	+
<i>Geum aleppicum</i>	0	3	0	0	0	2	0	0	0	0	0	0	+	+	+
<i>Hepatica</i> sp.	1	0	1	0	1	0	1	0	0	0	0	0	115	45	147
<i>Impatiens capensis</i>	0	5	0	0	0	1	0	0	0	1	0	0	+	+	+
<i>Malanthemum canadense</i>	127	31	6	11	15	3	1	3	13	8	1	1	4	4	14
<i>Medeola virginiana</i>	14	0	0	0	5	0	0	0	2	0	0	0	26	30	92
<i>Mitchella repens</i>	4	0	0	0	4	0	0	0	0	0	0	0	45	47	107
<i>Mitella diphylla</i>	1	13	0	0	1	4	0	0	0	8	0	0	45	89	178
<i>Panax trifolius</i>	5	0	0	0	4	0	0	0	0	0	0	0	38	42	109
<i>Pedicularis canadensis</i>	2	0	0	0	1	0	0	0	1	0	0	0	115	57	155
<i>Polygonatum pubescens</i>	133	17	7	10	15	5	3	3	4	1	0	0	2	2	9
<i>Potentilla</i> sp.	0	1	0	0	0	1	0	0	0	0	0	0	+	+	+
<i>Ranunculus abortivus</i>	3	47	0	2	3	8	0	1	0	6	0	1	57	86	185
<i>Sanguinaria canadensis</i>	17	44	0	0	4	7	0	0	5	11	0	0	21	41	121
<i>Sanicula gregaria</i>	0	13	0	0	0	1	0	0	0	18	0	0	+	+	+
<i>Smilacina racemosa</i>	53	62	44	5	13	11	4	3	3	10	0	0	6	6	22
<i>Streptopus roseus</i>	57	0	3	0	12	0	1	0	7	0	0	0	6	8	31
<i>Thalictrum dioicum</i>	16	15	2	0	10	4	1	0	0	1	0	0	13	15	53
<i>Tiarella cordifolia</i>	8	2	0	0	6	1	0	0	1	0	0	0	32	31	89
<i>Trientalis borealis</i>	49	0	0	0	11	0	0	1	7	1	0	0	8	10	41
<i>Trillium erectum</i>	68	30	13	14	14	5	3	4	3	5	0	0	5	6	32
<i>Trillium grandiflorum</i>	54	103	31	36	12	12	4	4	6	18	0	2	7	10	111
<i>Trillium undulatum</i>	13	0	0	0	3	0	0	0	3	0	0	0	24	27	64
<i>Uvularia grandiflora</i>	55	7	2	0	10	3	2	0	10	1	0	0	7	14	66
<i>Viola</i> spp.	81	77	3	0	14	14	3	0	3	0	0	0	4	4	23

	FREQUENCY			INCIDENCE			BLOCKS			RUNS			GAPS							
	G	f	S	G	f	S	G	f	S	G	f	S	G	f	S					
Tamiasciurus hudsonicus	27	22	10	9	7	5	3	3	6	5	0	0	4	2	1	0	14	34	132	44
Invertebrates																				
Collembola; Isotomidae	48	55	2	13	13	7	2	4	1	14	0	0	0	10	0	1	6	7	29	23
Isotoma sp.	45	74	13	11	13	11	4	4	3	2	0	0	4	1	0	0	6	7	30	12
Collembola; Entomobryidae	0	6	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	31
Lepidocyrtus sp.	86	20	3	35	15	9	3	4	4	0	0	0	2	0	0	0	4	3	12	31
Orchesella ainsliei	62	11	11	17	12	8	3	4	1	0	1	0	0	0	0	0	4	10	58	31
Orchesella hexfasciata	157	48	8	33	15	12	4	4	9	0	0	1	6	0	0	1	2	4	23	31
Orchesella pallens																				
Tomocerus sp.																				
Collembola; Poduridae	86	25	2	22	15	10	1	4	6	0	0	0	0	0	0	0	3	3	13	31
Neanura muscorum	13	2	1	0	8	2	1	0	0	0	0	0	0	0	0	0	16	13	39	44
Hemiptera; Lygaeidae	71	18	8	13	15	9	4	4	0	0	0	0	0	0	0	0	3	3	14	31
Pseudoscorpionida																				

END

1	0	4	1	0	9	1	8	4
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FIN