J.-L. DesGranges

Avian community structure of six forest stands in La Mauricie National Park, Quebec

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Abstract

A qualitative and quantitative study of bird communities was made in forest stands of six different types. Censuses were made by the spot-mapping technique. The precision of the results was tested by drawing a cumulative variety curve and by applying the performance test to the results compiled in each of the six quadrats.

The influence of species composition of the vegetation on avifauna within a given habitat is only indirect. The species composition affects the physiognomy of the vegetation which, in turn, influences the composition of the avian community. In the initial stands, which are open, most of the avifauna is found at ground level and in the shrubs, whereas in the denser growth of the older stands the majority is found in the canopy. The distribution of birds, therefore, follows the development of plant strata and the abundance of birds depends on the physiognomy of the forest, that is, on the number of growth-forms and distribution of trees.

The number of permanent resident species (mostly omnivorous) tends to increase during succession. This is probably attributable to the greater permanence of the climax forest, and its wider and more regular distribution which has permitted species to adapt their feeding habits to exploit a seasonally changing food supply, thus permitting them to remain resident throughout the year.

The diversity of an avian community, as calculated by the Shannon–Wiener formula, is influenced more by species variety than by equitability of abundance. Equitability (and indirectly diversity) of avian communities seems to depend mostly on the physiognomic diversity of the plant community. Thus, the more complex the physiognomy is, the greater the equitability value of the avian community tends to be.

Résumé

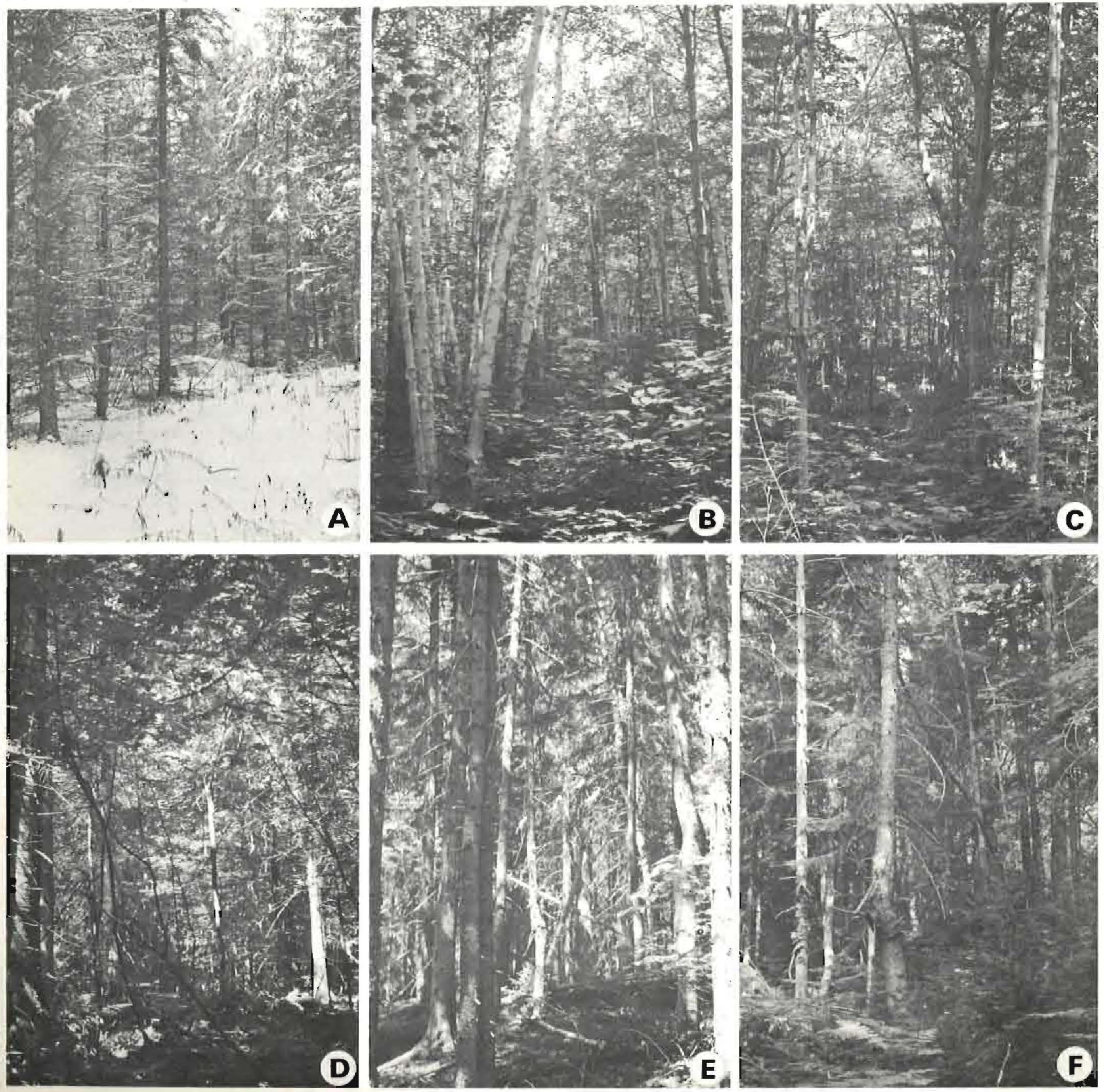
Une étude qualitative et quantitative des communautés d'oiseaux a été effectuée dans six peuplements forestiers différents en utilisant la technique des plans quadrillés. La précision des résultats a été contrôlée en traçant une courbe de variété cumulée et en appliquant le test de rendement aux données compilées dans chacun des six quadrats.

La composition végétale d'un habitat n'a qu'une influence indirecte sur la composition de l'avifaune. C'est par l'intermédiaire de la physionomie végétale qu'elle affecte, que la composition spécifique de la végétation influence la composition des communautés aviennes. Dans les formations claires des peuplements initiaux, la plus grande partie de l'avifaune se situe au niveau du parterre et des buissons, alors que dans les formations plus denses des peuplements plus âgés, elle se trouve au niveau de la strate supérieure. La distribution de l'avifaune suit donc l'étagement de la végétation et son abondance dépend de l'état physionomique de la végétation forestière, c'est-à-dire du degré de développement et de l'arrangement des arbres dans l'espace.

Le nombre d'espèces sédentaires (omnivores pour la plupart) a tendance à s'accroître dans la succession. Ceci semble attribuable à la plus grande permanence de la forêt climacique, ainsi qu'à sa répartition plus vaste et plus régulière. Ces espèces peuvent donc plus facilement adopter un mode d'alimentation qui leur permet de demeurer en ces lieux l'année durant.

La diversité des communautés aviennes, calculée à partir de la formule de Shannon-Wiener, varie davantage en fonction de la variété des espèces qu'en fonction de leur équitabilité d'abondance. L'équitabilité (et indirectement la diversité) des communautés aviennes semble dépendre en majeure partie de la diversité physionomique des peuplements forestiers. Ainsi, plus un peuplement présente une physionomie végétale complexe, plus la valeur d'équitabilité de sa communauté avienne tend à être élevée.

Plate 1
(A) white spruce plantation; (B) white birch stand; (C) sugar maple–yellow birch stand; (D) mixed stand; (E) red spruce stand; (F) fir stand



Introduction

In the last few years, ecologists have become aware of the close ties between the complexity of vegetation in forest stands and the structure of the bird communities they shelter. Thanks to the work of MacArthur and MacArthur (1961), MacArthur (1964), Recher (1969) and Karr and Roth (1971), among others, we now have a better understanding of the factors that govern the spatial and temporal distribution of birds in a community. However, these new theories have rarely been put to the test. I intend to verify them in this study.

From 7 May to 19 August 1972, and from 30 April to 10 August 1973, avian communities in six habitats at various successional stages were studied in detail (Plate 1). I considered such aspects of an ecological community structure as similarity, feeding niches, dominance, equitability and diversity. A study of these aspects was to help clarify the stability and ecological succession of avian communities in this part of the temperate cold forest zone (Grandtner 1966).

The study area

Located 10 km north of the town of Shawinigan (46°51'N; 72°43'W), La Mauricie National Park covers an area of approximately 500 km^2, bounded on the east by the St. Maurice river valley. The park lies in the southern part of the Canadian Shield and acts as a link between the Laurentian plateau and the lowlands of the St. Lawrence River. The highest peaks barely exceed 450 m.

Twenty-three forest species have been counted in La Mauricie National Park, the most common of which are: balsam fir (*Abies balsamea*, 23%), yellow birch (*Betula alleghaniensis*, 23%), red spruce (*Picea rubens*, 11%), and red maple (*Acer rubrum*, 10.5%) (Darveau 1971).

These various species form a series of distinct forest associations, irregularly distributed according to altitude, topography and soil composition. Sugar maple–yellow birch stands predominate in the southern section of the park. It is an association of deciduous mesophilic forest in acid and heavily podzolized moraine soils (Grandtner 1966). This association forms a climax in places that are well drained, well lit and of medium altitude. It is, therefore, often very abundant on steep slopes. In these locations, associations of resinous trees such as balsam fir and red spruce, occupy the lower, more humid areas.

At the northern end of the park, the higher altitude has produced an inversion, with the balsam fir stands occupying the summits and a few sugar maple–yellow birch stands located on mountain slopes that face south (Dansereau 1944, 1959, Grandtner 1966). The regenerative action of forest fires, woodcutting and insect infestations has resulted in the emergence here and there of some stands of white birch and trembling aspen (*Populus tremuloides*), which later become mostly fir stands.

Methods

1. Avian synecology[1]

Forests stands in various stages of succession were selected according to their extent, topography, homogeneity and accessibility. During the summer of 1972, two forest stands, one of white birch and one of balsam fir were selected and studied in detail. In 1973, I made an inventory of four stands: sugar maple–yellow birch, mixed, red spruce, and a white spruce plantation.

A quadrat measuring 305 m (1000 ft) on each side was delimited in each stand. The area thus defined was 9.3 ha (23 a). In a forest environment, an area of approximately 10 ha (25 a) makes an acceptable compromise between smaller quadrats, in which the perimeter–area ratio is too high, and larger-sized quadrats that would take too much time to cover. Thus a greater percentage of birds' territories is contained entirely within the quadrat and it is possible to cover the whole quadrat while the birds are most active (Blondel 1969*b*).

In addition to being as homogeneous as possible, the chosen locations should be enclosed (as much as possible) on all sides by an identical environment so as to avoid a fringe effect that could modify the nature and density of bird populations. With the help of a compass and a metal measuring-tape, I marked out paths at an equal distance of 61 m (200 ft) apart in each quadrat, which would allow me to pass within 30.5 m (100 ft) of any point in the quadrat. Control points were set up all along the paths with red marker tape and yellow paint.

Sampling was done by the spot-mapping technique described notably by Pough (1950) and reviewed by Blondel (1969*b*). This technique allows us to determine the number of males occupying a territory within a quadrat.

During the month of June and at the beginning of July, I covered each quadrat 10 times, that is to say, eight times in the morning and twice in the evening, taking care to record graphically all sightings of birds and all other signs of the presence of a pair, such as a nest, on a copy of the quadrat map, using a new copy for each visit.

Each quadrat was inventoried in turn, and I tried to complete each series of 10 censuses in as short a time as possible. This was necessary because territories change during the breeding season because of predation, competition and desertion of nests (Enemar 1959; Hall 1964).

Visits to the quadrats took place in the morning soon after sunrise and in the evening shortly before sundown, when weather conditions were favourable. I chose days when the sky was clear and there was little or no wind for the visits, since rain, high winds and extreme temperatures reduce the intensity and length of bird song (Armstrong 1954). Needless to say, sampling done under such conditions would result in under-estimation of the number of breeders.

I always did two consecutive censuses to cover the song period of birds that are active at dawn, as well as those that become active once the day has definitely begun. The evening censuses proved useful in clarifying the status of the more common species. I thereby departed from the conventional method based on a study of the daily activity of birds (see DesGranges 1974, DesGranges *et al.* 1977).

I tried to maintain as steady a walking pace as possible during each visit. On the average I walked through the quadrat paths at an approximate speed of 21.3 m (70 ft) per minute, which makes comparisons between the different visits easier.

If the exact location of all contacts with the various individuals of each species is indicated on a different map for each species, each couple's territory appears as a cloud of contacts. The number of clouds corresponds closely to the number of territories, or, in other words, to the number of pairs present within the quadrat's perimeter. When the limits of a certain territory reach outside the quadrat, the fraction of territory within the quadrat has been evaluated and included in the total of the other territories.

The sampling method described above is by far the surest. Properly applied, the margin of error is 10% at most (Blondel 1969*b*).

2. Forest synecology

The results of a systematic sampling of breeding bird populations on a designated plot of land would make very little sense, and would be difficult to interpret if the environment was not carefully chosen and described.

I therefore chose quadrats that were as homogeneous as possible and typical of a stage of succession. In each of the stands studied, I chose 11 environments that were representative of the vegetation. These environments were all at 30.5-m (100-ft) intervals and lined up along a transect passing perpendicularly through the quadrat. In each of these locations I marked out a quadrat of 9.1 m (30 ft) each way and identified the plant species within the quadrats. The cover index of each species of the three plant strata (trees, shrubs and herbs) (Smith 1973) was then evaluated by a method derived from Braun–Blanquet (1932).

The average height of the various species was noted along with information on the location, date, topography, exposure, drainage and soil conditions, as suggested by Emlen (1956) and Dansereau *et al.* (1966).

In addition, a system of quadrants was drawn around each of the 11 central points (represented by a tree). In each quadrant, I identified the tree closest to the centre and measured its distance from the centre. I also measured its diameter at chest height, and the height of its lowest branches. This technique was developed by Cottam *et al.* (1953) and has been described in detail by Shimwell (1972).

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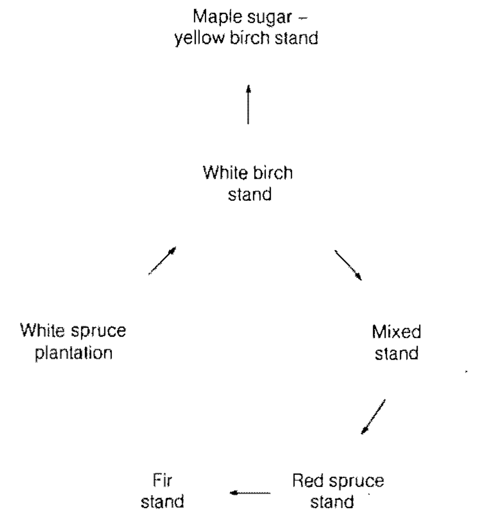
[1] Synecology is the study of the ecology of a group of organisms associated together as a unit.

The forest stands

I intend to follow the probable order of succession in presenting botanical descriptions, so as to bring out more clearly the relationships between each of the stands studied. The initial stage associations are described first, followed by the transitional stands and the climax associations. Figure 1 shows the order of succession chosen. The spruce plantation is not an initial association but an artificial stand. It is very unstable and has already begun to be replaced by an initial association. The polygonal layout used (Fig. 1) has the advantage of grouping together stands of a similar physiognomic type.

Figure 1
Ecological succession of forest stands studied. Arrows indicate successional trends (G. LeRoy, pers. comm.)



1. White spruce plantation

Although the trees had been planted in a line some 2 m apart in about 1930, the plantation's layout is not as neat today. The average distance between the trees has increased slightly and shows a large standard deviation (2.4 ± 1.3 m).

White spruce is dominant in the tree stratum as a whole, while trembling aspen and occasionally white birch are found where the plantation was deliberately cleared, and also beside the two forest paths passing through the stand. This stratum rises to 10 m above the ground.

The shrub stratum is very sparse. Conifers form a dense plant biomass from tree crown to ground level and leave little space for the growth of new shoots. However, a secondary felling in the eastern sector of the quadrat during 1968 and 1969 has allowed young trembling aspen and white birch to become established. Helped by such disturbances, they could eventually supplant the white spruce as dominant species in the stand and re-establish the normal ecological succession. The shrub stratum rises to approximately 6 m above ground level.

While several trembling aspen, white birch, red maple and balsam fir seedlings occur in the herbaceous stratum, white spruce are virtually absent. To those species are added such plants in the undergrowth as bunchberry *(Cornus canadensis)* and wild lily-of-the-valley *(Maianthemum canadense)*. Since the herbaceous stratum is of little significance, the moss cover, in contrast, is uninterrupted.

2. White birch stand

This stand covers the western slope of a mountain with fairly good exposure to the sun and good drainage, although the soil is wetter in some depressions.

White birch predominates in the tree stratum on the whole, but trembling aspen is more abundant in the wetter spots. Red maple is quite plentiful at the foot of the mountain. South of the quadrat, balsam fir displaces the white birch's dominance. The tree stratum rises to about 15 m above the ground.

These species are also found in the shrub stratum, which also includes striped maple *(Acer pensylvanicum)*, mountain maple *(Acer spicatum)* and beaked hazelnut *(Corylus cornuta)*. Balsam fir is also very abundant in this stratum and will probably eventually replace white birch as the dominant species in the tree stratum. The shrub stratum reaches 7 m above ground level.

The herbaceous stratum is greatly varied. It includes, among others, American bracken *(Pteridium aquilinum)*, wild sarsaparilla *(Aralia nudicaulis)* and large-leaved aster *(Aster macrophyllus)*. On the ground are found rocks covered with moss and lichens, rotten tree trunks and a large accumulation of dead leaves. Traces of the fire that ravaged this sector in 1923 are still present.

Dansereau (1959) classified stands of this type under the term BETULETUM PAPYRIFEREA. It is a variable and very wide-spread sub-climax. In the northern part of the St. Lawrence valley, and particularly in Mauricie, it seems to be evolving mainly towards ABIETUM BALSAMEAE, although it can very often lead to ACERETUM SACCHAROPHORI BETULOSUM.

3. Sugar maple–yellow birch stand

This stand is located on the eastern slope of a mountain. The quadrat's drainage is good, and a system of springs runs through it.

Sugar maple dominate the tree stratum, but beech and yellow birch are nonetheless very abundant. At the centre of the stand, a steep slope is covered with white cedar *(Thuja occidentalis)* and balsam fir. Black ash *(Fraxinus nigra)* and wild red cherry *(Prunus pensylvanica)* grow near the springs and along the road that crosses the quadrat. The tree stratum rises about 18 m above the ground.

In addition to the above-mentioned species, striped maple and mountain maple occur in the shrub stratum. Sugar maple and beech dominate in this stratum too, which reaches approximately 9 m above ground level.

The herbaceous species are greatly varied. Shining club-moss *(Lycopodium lucidulum)*, spinulose shield-fern *(Dryopteris spinulosa)*, wild sarsaparilla, large-leaved aster, acuminate aster *(Aster acuminatus)*, yellow clintonia *(Clintonia borealis)* and wild lily-of-the-valley are found in great quantity. A deep carpet of dead leaves covers the ground, and the wetter depressions are filled with moss. The lack of rotting trunks and branches on the ground suggests that this stand has not been exploited by forestry for many years.

According to Dansereau (1959), this stand forms an ACERETUM SACCHAROPHORI BETULOSUM association. It is considered to be a climax in the area under study.

4. Mixed stand

This stand takes up the whole eastern slope of a mountain. The quadrat's drainage becomes more and more rapid as the altitude increases and this encourages the growth of a great variety of trees.

At the foot of the slope, where drainage is only average and the till is deeper, balsam fir and yellow birch are most common in the tree stratum. Higher up, the more rapid drainage and shallower till favour the growth of red spruce, beech and sugar maple. This stratum rises to about 15 m above the ground.

The shrub stratum is also varied. In addition to the trees of the canopy, it includes the mountain maple, which is dominant. This stratum reaches about 7 m above the ground.

Most common in the herbaceous stratum are the spinulose shield-fern, wood-sorrel *(Oxalis montana)*, yellow clintonia and wild lily-of-the-valley. Mosses are not plentiful, but the ground is littered with dead leaves, branches and bare rocks.

Forest exploitation, added to considerable variation in moisture levels, accounts for the heterogeneity of this stand and the surrounding forest. Until recently (1952–1954), periodical cutting was done in these forests, alternating from softwood to hardwood. According to Heimburger (1941), the variety of species and age classes so characteristic of local forests was due to that constant exploitation.

5. Red spruce stand

Situated at the top of a mountain, this stand has a slight northeasterly exposure. The soil is well drained, but has some wet depressions.

Although red spruce is common in the tree stratum, it is only dominant in the middle of the quadrat. In the northern section, balsam fir is just as common and, in the southern part, the presence of a spring has led to the growth of yellow birch and red maple. This stratum reaches a height of 12 m above the ground.

The two coniferous species also take precedence in the shrub stratum. Here balsam fir is even more common than it is in the canopy. In the southern end of the quadrat, mountain maple makes up most of the middle stratum, which is generally less developed and reaches about 6 m above ground level.

The great range of herbaceous plants, in addition to balsam fir and red spruce seedlings, includes such shrubs as glabrous shadbush *(Amelanchier laevis)* and mooseberry *(Viburnum alnifolium)*. The most common underbrush plants are Clayton's fern *(Osmunda claytoniana)*, American bracken, yellow clintonia and wild lily-of-the-valley. The wet depressions contain moss along with dead leaves and branches strewn on the ground.

This association corresponds to the PICEETUM RUBENTIS of Dansereau (1959). As evidence of a past in which the climate was warmer and dryer, it is now an unstable pre-climax. The fire in 1923 and felling in 1939–40 have certainly helped to establish balsam fir in this stand and its gradual evolution towards an ABIETUM BALSAMEAE association.

6. Fir stand

This stand is located near the top of a mountain and has a slight easterly exposure. The ground is quite well drained and has a few slight depressions.

Most common in the tree stratum is the balsam fir. Some red spruce, white birch, red maple, yellow birch and cedars mingle with balsam fir, especially in places cleared during the selective cutting of red spruce in 1939 and 1940. The tree stratum rises about 12 m above the ground.

The shrub stratum is poorly developed and contains the same species. Here, too, the balsam fir predominates; the stratum reaches about 6 m above ground level.

The herbaceous stratum is relatively under-developed and is made up of balsam fir seedlings mixed mostly with bracken, yellow clintonia and wild lily-of-the-valley. The ground is almost completely covered with moss and with scattered branches left by felling and old fires.

According to Dansereau (1959) this stand is of the ABIETUM BALSAMEAE association. He considers it a near-climax that will never arrive at the climax stage because of continued inhibition by, perhaps, topographical, edaphic or microclimatic factors. This association is found all along the lower slopes of the Laurentians.

Assessing the data obtained with spot mapping

To assess the accuracy of data obtained with the spot-mapping technique, I have plotted cumulative variety curves and applied the performance test to the data collected from each quadrat.

1. Cumulative variety

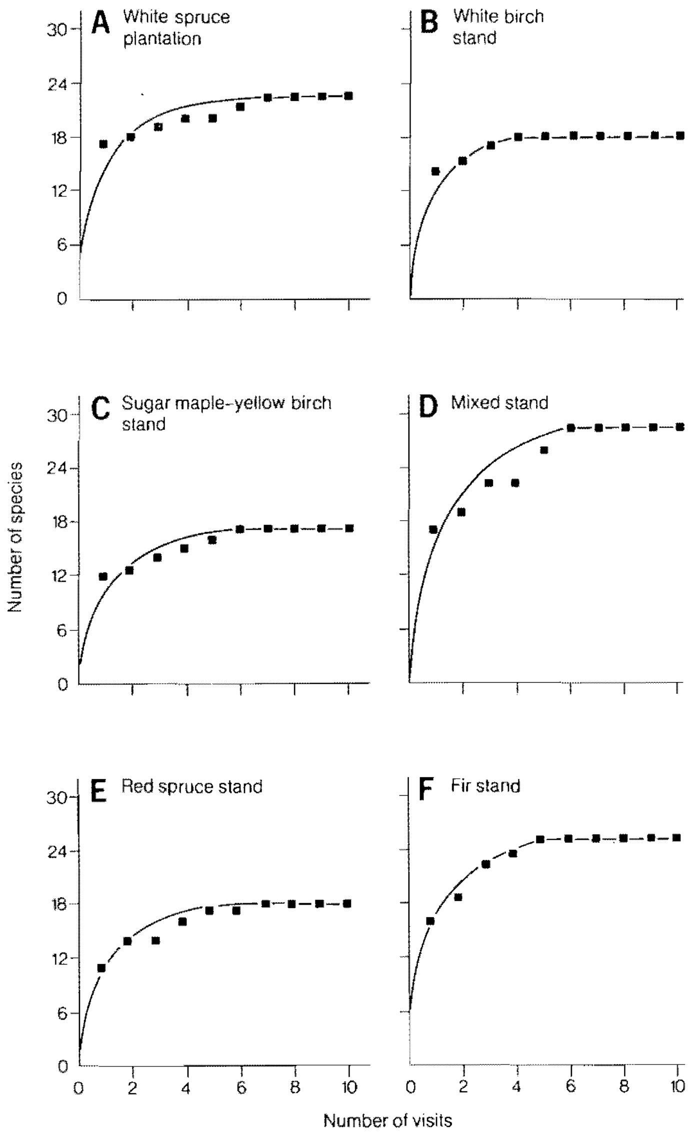
The first count done within a quadrat shows only a limited number of species. The second survey shows a certain number of new species in relation to the preceding visit. The cumulative variety of the second visit is the total number of different species contacted during the two visits, and so on. As the cumulative variety increases with the number of counts, it gets closer and closer to the actual variety. This can be shown by a cumulative curve. The cumulative variety curves obtained in each of the quadrats studied are collected in Figure 2.

As we can see, the increase in the number of new species is only significant during the first visits, and rapidly slows down to less than one species per visit. Thus, the observer encounters new species in proportion to the logarithm of the number of counts when the number is low; on the other hand, for a greater number of visits (six or more) the increase in the number of new species is further reduced, showing that the cumulative variety is probably closer to the actual variety (Frochot 1971).

For a more representative curve, the effects of aleatory fluctuations affecting the observed variety should be eliminated. One should combine the 10 counts several times at random and retain only the average values of the cumulative variety at the second and subsequent counts. This is all the more important since, in our case, counts taken in the evening yielded fewer species.

Unfortunately this technique requires a lot of time. I therefore plotted an approximate curve for each series of counts based on the different cumulative variety points obtained by considering the counts in the order in which they were made. Ordinarily, these curves would be close to those obtained otherwise and could be used to show that the measured variety is certainly close to the actual variety.

Figure 2
Cumulative variety curves for each quadrat. The lines were set by eye



2. Performance test

Performance (Enemar 1959, Blondel 1969*b*) expresses the observer's chance of noting a pair by some kind of contact each time he passes near its territory. It gives a percentage of the number of times the observer made contact in relation to the possible number of cases.

I considered a pair's performance to be the percentage of visits during which I recorded it. Only those whose territory was completely enclosed by the quadrat boundaries were taken into account.

A satisfactory performance calculation requires considerable uniformity in the counting technique. To be representative, the counts should be made by the same observer. In addition, the time of day and weather conditions should be similar. Finally, the walking pace should not be too rapid and be as constant as possible during all the counts.

I tried to follow these requirements as best I could. However, I decided to make some visits in the evening. Also weather conditions were not always similar from one count to another. Nevertheless, I did not think it necessary to take these irregularities into account in calculating the performance.

Not having established the difference on the data sheets between short-term contacts near a pair's territory and those made away from the territory, I took a maximum of only one contact per pair into consideration for each visit. This has led to under-estimation of the pair's performance; in fact, on some days I had no contact with a pair, while on other days I made contact several times in locations that were some distance from their territory.
The species performance is the average performance of all pairs of the same species nesting in a certain quadrat.
The overall performance of the community, or performance for the environment, is the average performance of the total reproductive avifauna of a certain quadrat.
The specific performances and overall performances of the quadrats studied have been published elsewhere (see DesGranges 1974).

In the six quadrats studied, the overall performance values lie between 38.3% (mixed stand) and 57.8% (sugar maple–yellow birch stand). The average is 47.6 ± 6.8%.

One can use overall performance to assess the minimum number of visits needed in a quadrat to ensure counts of at least 90% of the population. Seeing that the average performance in the environments studied is 47.6%, one can draw the following conclusions: on the first visit to a quadrat, the observer should note about 47.6% of the population and, according to the laws of probability, on the second visit, should record 72.5% of the population. By continuing in this manner, the observer will have noted 92.5% of the population by the fourth visit, and 99.8% by the tenth.

3. Conclusions

In view of the results of the cumulative variety curves and performance tests, I consider the data gathered through the spot-mapping technique to be significant.

Although the results of the cumulative variety curve and the performance test have been successfully monitored, a warning should be given about their real significance.

These results refer to a particular situation and apply to specific quadrats during a single nesting season.
It would be unwise to apply these values to the whole of the forest associations studied. In addition, annual fluctuations must be expected even within the quadrats studied (Brewer 1963).

Similarity of communities

Bird counts have been the subject of a considerable number of works. We need only look at bibliographical lists (Lack 1937, Kendeigh 1944, Blondel 1969 *b*, Erskine 1977) to see this. The authors of many of these works have described bird communities based on the presence of distinct species groups (Adams 1908, Pitelka 1941, Kendeigh 1945, 1946, Johnston 1947, Snyder 1950, Odum 1950, Johnston and Odum 1956, Bond 1957, Martin 1960, Haapanen 1965, 1966, etc.). Kendeigh (1948) even went so far as to propose a system of community nomenclature based on the dominant bird species and type of vegetation. Unfortunately, in general, the parts of habitats studied have often been chosen under the impression that they contained a particular bird community. This subjective selection assumes *a priori* the existence of types of bird communities and tends to demonstrate this. If parts of the habitats had been chosen at random, the authors would perhaps have found atypical or mixed bird communities (Krebs 1972).

I do not want to stir up an old debate (Gleason 1926, Clements 1936). Suffice it to say, as did Whittaker (1970), types of associations and communities are concepts created by man. They make excellent abstractions of the complex species groupings found in nature. In reality, communities comprise species with similar ecological requirements. Each one has its own particular ecotope (Whittaker *et al.* 1977), which is kept appreciably different from those of other species by a state of partial competition (Svärdson 1949, MacArthur 1958, Cody 1968, Fretwell 1969, Terborgh and Diamond 1970, Brown and Orians 1970, Diamond 1973). The result is a well structured bird community (Hairston 1959) that reappears whenever the appropriate ecological conditions are met. Communities do exist. Their classification in intermittent groups along a continuous gradient (Bond 1957, Terborgh 1971) may prove useful in the search for a better understanding of community structure. It was with this in mind that I undertook this study of avian communities, while recognizing that each community forms a well organized ecological whole and, by the same token, that each has definite characteristics suited to itself.

The first aspect I will deal with is the similarity between each of the communities. I will compare in turn the avian communities and plant communities (physiognomic and taxonomic) and will draw conclusions by making an overall comparison of the three groups of communities I have studied.

Several measures of similarity and many graphic layout techniques are available for this kind of study (Bond 1957, Beals 1960, Kikkawa 1968, Vernon 1970, James 1971, Power 1971).

I have chosen a taxometric method, *Taxmap classification program* (Carmichael 1970). This program includes notably the calculation of relative similarity between each of the communities, as shown by values for a certain number of variables. In my case, the variables are the specific abundance of birds (Table 1), the measurements of the physiognomic characteristics of the vegetation (Table 2) and the specific tree and shrub covers (Table 3). Before calculating the similarities, one transforms each variable to a value between 0 and 1. Then, if the operator wishes, the variables can be weighted in relation to the importance of the information they contain. To do this, we take the logarithm to the base of 2 of the number of classes (confidence interval of 95%) plus 1 included in the range of variation of each variable. The coefficients obtained are then multiplied by the similarity values obtained from the comparison between each variable of the different communities. This restores the relative importance of the different variables during the overall calculation of similarities between each of the communities.

I thought it best to make use of differential weighting in the specific case of avian communities because the presence (or absence) of a common species probably differentiates two communities more than the presence (or absence) of a rare species. In the case of plant communities (physiognomic and taxonomic) I considered each variable uniformly, since none seems more important than the others.

The calculation of similarity, or rather dissimilarity (i.e., 1 – similarity value) is done in the following manner. The relative dissimilarity between the values (V) of the i^{th} and j^{th} communities for a single variable (d_{ij}) is obtained by using the formula:

$$d_{ij} = | V_i - V_j | / (V_{\max} - V_{\min})$$

In other words, it is the difference between the values observed divided by the value of the maximum interval obtained for the communities as a whole.

The relative dissimilarity between the i^{th} and j^{th} communities, based on a large number of variables (d_{ij}), is obtained through the weighted arithmetical average (W) of their relative dissimilarities for each variable (d_{ij}). Thus, for n variables, we have:

$$\begin{aligned} D_{ij} &= \Sigma(d_{ij})_k \bullet W_k / \Sigma W_k \\ k &= 1 - n \end{aligned}$$

If we use equal weighting the formula is reduced to:

$$D_{ij} = \Sigma(d_{ij})/n$$

The dissimilarity values obtained for the different community groups are shown in Table 4. They have been converted into Cartesian co-ordinates by the *M-D-Scal* (Kruskal and Carmone 1969) for use in preparing the stereographic models of Figure 3.

This program, while transforming multi-dimensional co-ordinates into a space with reduced dimensions, includes the calculation of a stress value. This value allows us to judge the quality of the configuration obtained, since it represents the extent of the gap between the original dissimilarities and those obtained with the new configuration. The stress values calculated are: 0.0255 for the stereogram of avian communities, 0.0092 for the physiognomic plant communities and 0.0080 for the taxonometric plant communities. These values all correspond to a "perfect" configuration (Kruskal and Carmone 1969).

If we study these stereograms, we see that both the avian communities and the physiognomic plant communities divide into two large groups. At the bottom of the configuration one finds the communities of stands that are predominantly deciduous, while at the top of the models we find communities that are predominantly coniferous stands. In addition, in these two examples, the red spruce and fir communities proved to be combined. However, the taxonomic plant communities are more scattered; it is difficult to detect their associations. There seems to be a correlation between the avian communities and physiognomic plant communities. To ascertain this, I ranked the dissimilarity values of each of the community groups and applied the Spearman correlation test (Sokal and Rohlf 1969).

This test has shown that there is no significant correlation between the avian communities and the taxonomic plant communities. On the other hand, there is a statistically significant correlation ($r_s = 0.55$, $P < 0.05$) between the physiognomic and taxonomic plant communities, and an almost significant correlation ($r_s = 0.51$, $P < 0.10$) between the avian communities and physiognomic plant communities.

From two very different perspectives, one allowing for the numbers of birds of different species in certain forest stands, and the other using the plant physiognomy characteristics of these stands, such as the cover indexes of various strata, the type of underbrush and linear measurements (average distance between trees, average diameter of trees and average height of lowest branches) I made two similar classifications of the communities. With numerical variables, which I hoped described the three types of communities adequately, I showed that the plant composition of a habitat had only an indirect effect on the composition of the avifauna. It is by means of the plant physiognomy it affects that the species composition of the vegetation influences the composition of avian communities.

Some ornithologists have pointed out previously that plant physiognomy is one of the most important factors of those influencing birds in their choice of nesting habitat, and that floral criteria are only of secondary importance (Lack 1933, Svärdson 1949, Bond 1957, Hilden 1965). In showing that a connection exists between bird variety and stratum diversity, a number of authors have reached the same conclusion (MacArthur and MacArthur 1961, MacArthur *et al.* 1962, Recher 1969, Cody 1970, Karr and Roth 1971, Blondel *et al.* 1973, Morse 1976, Terborgh 1977).

Table 1
Population density of bird species present in quadrats studied

Species*	White spruce plantation	White birch stand	Sugar maple–yellow birch stand	Mixed stand	Red spruce stand	Fir stand
Broad-winged Hawk	—	—	P**	—	—	P
Ruffed Grouse	—	1	1	—	—	1
American Woodcock	2	—	—	—	—	—
Spotted Sandpiper	—	—	—	P	—	—
Black-billed Cuckoo	—	—	—	2	—	—
Barred Owl	—	—	—	1	—	—
Chimney Swift	—	—	P	—	—	—
Common Flicker	P	1	—	—	—	—
Pileated Woodpecker	—	—	1	1	—	—
Yellow-bellied Sapsucker	—	—	1	2	—	—
Downy Woodpecker	—	—	—	—	—	1
Crested Flycatcher	P	—	2	—	—	—
Least Flycatcher	—	7	2	1	—	—
Eastern Wood Pewee	—	—	2	2	—	—
Olive-sided Flycatcher	—	—	—	P	—	—
Barn Swallow	—	—	—	P	—	—
Gray Jay	—	—	—	—	2	—
Blue Jay	—	—	P	2	—	2
Black-capped Chickadee	—	7	—	2	—	2
Boreal Chickadee	2	—	—	—	—	—
White-breasted Nuthatch	—	4	—	—	—	—
Red-breasted Nuthatch	3	—	P	2	2	2
Brown Creeper	—	—	—	2	2	—
Winter Wren	—	—	7	4	3	3
American Robin	5	2	—	P	—	—
Hermit Thrush	—	14	9	4	—	6
Swainson's Thrush	13	—	—	—	7	7
Veery	—	16	6	12	—	—
Golden-crowned Kinglet	14	—	—	1	15	12
Ruby-crowned Kinglet	6	P	—	P	—	1
Cedar Waxwing	P	P	—	—	—	—
Solitary Vireo	3	—	—	P	—	3
Red-eyed Vireo	1	11	18	15	5	3
Black and White Warbler	—	2	2	—	—	—
Tennessee Warbler	2	—	—	—	—	—
Nashville Warbler	10	6	P	—	4	5
Northern Warbler	—	P	—	5	—	7
Magnolia Warbler	P	P	—	—	2	9
Cape May Warbler	12	—	—	2	2	—
Black-throated Blue Warbler	—	12	20	10	3	4
Yellow-rumped Warbler	6	—	—	6	2	6
Black-throated Green Warbler	—	P	—	—	—	9
Blackburnian Warbler	6	P	—	5	10	9
Chestnut-sided Warbler	1	—	—	—	—	—
Bay-breasted Warbler	6	—	—	—	6	15
Ovenbird	5	25	8	17	7	19
Northern Waterthrush	—	—	—	4	—	—
Mourning Warbler	—	P	—	—	—	—
Canada Warbler	—	P	2	4	—	—
American Redstart	—	2	12	6	—	—
Redwinged Blackbird	P	—	—	4	—	—
Common Grackle	P	—	—	—	P	—
Brown-headed Cowbird	P	—	—	P	—	—
Scarlet Tanager	1	—	6	2	—	—
Rose-breasted Grosbeak	—	2	4	4	P	2
Evening Grosbeak	P	P	—	P	P	P
Purple Finch	4	1	—	2	2	5
American Goldfinch	—	—	P	—	—	—
Dark-eyed Junco	5	6	P	P	5	7
Chipping Sparrow	9	—	—	—	—	—
White-throated Sparrow	7	6	—	—	2	6
Total species (9.3 ha)	30	27	24	37	21	27
Total species censused (9.3 ha)	22	18	17	28	18	25
Total individuals (9.3 ha)	123	125	103	124	81	146
Total individuals (100 ha)	1324	1344	1108	1334	872	1570
Males (100 ha)	662	672	554	667	436	785

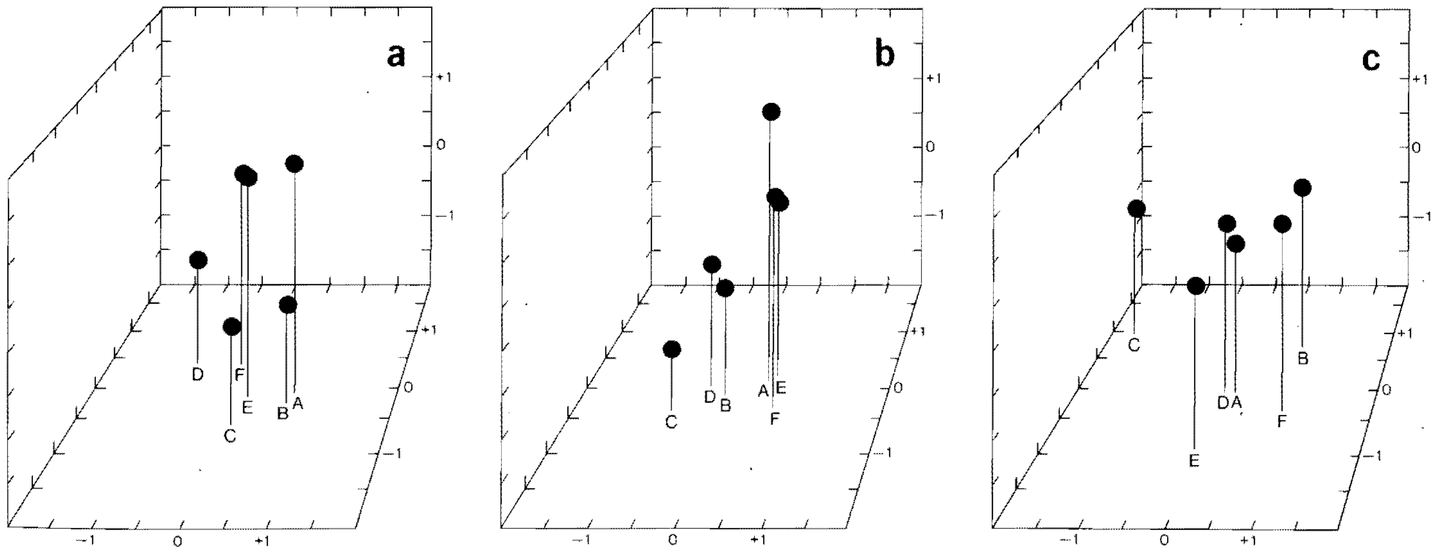
* List of bird names in Latin and English given in Appendix 1.
** P = Present

Table 2
Measurements of some physiognomic characteristics of vegetation in quadrats studied

Physiognomic characteristics	White spruce plantation	White birch stand	Sugar maple–yellow birch stand	Mixed stand	Red spruce stand	Fir stand
Cover index*						
Deciduous (tree stratum)	0.4	5.7	7.8	4.2	3.8	2.3
Coniferous (tree stratum)	3.4	0.5	0.0	2.2	4.2	4.1
Deciduous (shrub stratum)	0.0	4.0	4.8	4.6	1.6	1.6
Coniferous (shrub stratum)	1.5	1.2	0.2	1.3	3.5	3.0
Deciduous (herb stratum)	0.5	2.8	6.6	2.3	1.8	0.1
Coniferous (herb stratum)	0.0	0.1	0.8	0.4	2.4	2.6
Extent**						
Herb stratum	1	3	3	3	3	2
Moss stratum	3	1	2	1	2	2
Dead leaf cover	1	3	3	3	3	2
Dead branch litter	2	2	1	3	3	3
Bare soil and rocks	1	3	3	3	1	2
Humidity in soil	2	1	2	1	2	1
Dimensions†						
Av. dist. between trees (m)	2.4(1.3)	2.6(1.0)	4.2(2.1)	3.2(1.4)	2.7(1.3)	2.2(0.9)
Av. diam. of trees at breast height (cm)	12.2(3.6)	13.7(7.6)	17.0(9.4)	18.8(16.3)	15.0(8.9)	14.0(73.7)
Av. ht. of lowest branch (m)	0.2(0.9)	5.6(2.9)	4.2(2.9)	3.5(2.1)	3.3(2.7)	3.4(2.4)

* These cover indexes represent the totals of average indexes for the various species of the type considered. Species indexes have been allocated in the following manner: 5 – 100% to 81% covered, 4 – 80% to 61%, 3 – 60% to 41%, 2 – 40% to 21%, 1 – 20% to 1%, 0 – 0%.
** 1 – light, 2 – average, 3 – extensive.
† Standard deviations shown in parentheses.

Figure 3
Stereographic models of the similarity of avian communities (A), physiognomic plant communities (B), and taxonomic plant communities (C). The symbols are given in Figure 2. The similarity coefficient used takes positive as well as negative correlations into account (e.g., simultaneous presence as well as absence of a species). These stereograms are three-dimensional representations of the many similarities and dissimilarities among forest stands whose bird and plant communities have been described by numerical variables. This taxometric technique makes it possible to determine visually the stands which resemble each other because the points representing those stands are closely grouped in such figures



A White spruce plantation
B White birch stand
C Sugar maple–yellow birch stand
D Mixed stand
E Red spruce stand
F Fir stand

Table 3
Average species cover indexes* of trees and shrubs present in botanical quadrats studied

Species	White spruce plantation	White birch stand	Yellow birch stand	Mixed stand	Red spruce stand	Fir stand
Tree stratum						
Betula alleghaniensis	—	—	1.0	2.2	1.2	—
Abies balsamea	—	0.5	—	1.5	2.3	2.2
Picea rubens	—	—	—	0.6	1.9	1.4
Betula papyrifera	—	2.9	0.2	—	1.0	1.0
Acer rubrum	—	0.7	0.5	0.4	1.1	1.3
Populus tremuloides	0.4	1.4	—	—	—	—
Populus grandidentata	—	0.3	—	—	—	—
Acer saccharum	—	0.3	3.0	1.6	—	—
Fagus grandifolia	—	—	2.5	—	0.2	—
Thuja occidentalis	—	—	—	0.1	—	0.4
Pinus strobus	—	—	—	—	—	0.1
Picea glauca	3.4	—	—	—	—	—
Fraxinus nigra	—	0.1	0.3	—	—	—
Prunus pensylvanica	—	—	0.3	—	—	—
Acer spicatum	—	—	—	—	0.3	—
Total	3.8	6.2	7.8	6.4	8.0	6.4
Shrub stratum						
Betula alleghaniensis	—	—	0.2	0.7	0.5	—
Abies balsamea	—	1.2	0.2	1.1	2.3	2.4
Picea rubens	—	—	—	0.2	1.2	0.5
Betula papyrifera	—	0.9	—	—	—	0.5
Acer rubrum	—	0.6	0.7	0.3	0.5	0.9
Populus tremuloides	—	0.3	—	—	—	—
Acer saccharum	—	0.4	1.5	1.0	—	—
Fagus grandifolia	—	—	1.4	—	—	—
Thuja occidentalis	—	—	—	—	—	0.1
Picea glauca	1.5	—	—	—	—	—
Fraxinus nigra	—	—	0.1	—	—	0.2
Prunus pensylvanica	—	—	0.1	—	—	—
Acer spicatum	—	1.2	0.5	2.6	0.5	—
Acer pensylvanicum	—	0.5	0.3	—	—	—
Corylus cornuta	—	0.1	—	—	—	—
Cornus stolonifera	—	—	—	—	0.1	—
Total	1.5	5.2	5.0	5.9	5.1	4.6
Herb stratum						
Betula alleghaniensis	—	—	0.4	—	—	—
Abies balsamea	—	0.1	—	0.4	1.4	2.5
Picea rubens	—	—	—	—	0.9	0.1
Acer rubrum	—	0.2	0.5	0.2	0.5	0.1
Acer saccharum	—	0.2	2.7	0.5	—	—
Fagus grandifolia	—	—	0.4	—	—	—
Fraxinus nigra	—	—	0.1	—	—	—
Acer spicatum	—	1.2	1.0	1.3	0.3	—
Acer pensylvanicum	—	—	0.7	—	—	—
Corylus cornuta	—	1.1	—	0.3	0.1	—
Cornus stolonifera	0.4	—	—	—	0.1	—
Amelanchier laevis	—	—	—	—	0.4	—
Viburnum alnifolium	—	—	0.8	—	0.3	—
Sambucus canadensis	—	—	—	—	0.1	—
Taxus canadensis	—	—	0.8	—	0.1	—
Diervilla lonicera	—	0.1	—	—	—	—
Kalmia angustifolia	0.1	—	—	—	—	—
Total	0.5	2.9	7.4	2.7	4.2	2.7

* These cover indexes represent the totals of average indexes for the various species of the type considered. Species indexes have been allocated in the following manner: 5 – 100% to 81% covered, 4 – 80% to 61%, 3 – 60% to 41%, 2 – 40% to 21%, 1 – 20% to 1%, 0 – 0%.

Table 4
Dissimilarity values from comparison of avian, physiognomic plant and taxonomic plant communities

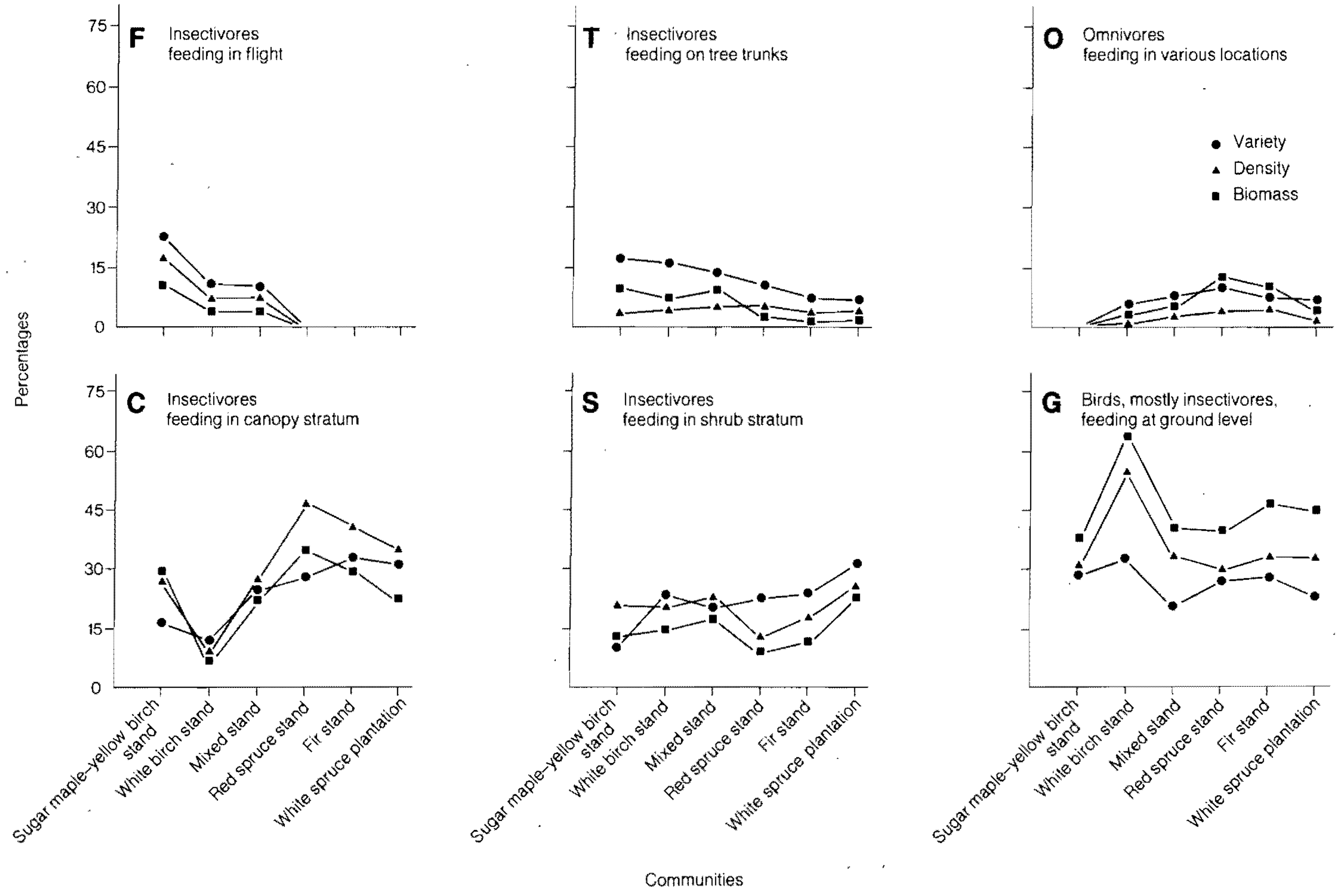
Avian communities						Physiognomic plant communities						Taxonomic plant communities					
1*						**1**						**1**					
.552	**2**					.604	**2**					.359	**2**				
.634	.349	**3**				.720	.351	**3**				.487	.515	**3**			
.612	.448	.317	**4**			.648	.193	.374	**4**			.270	.302	.404	**4**		
.301	.412	.427	.409	**5**		.457	.469	.517	.399	**5**		.388	.461	.548	.300	**5**	
.397	.457	.562	.471	.279	**6**	.449	.460	.668	.417	.244	**6**	.325	.389	.550	.298	.308	**6**

* 1 – white spruce plantation, 2 – white birch stand, 3 – sugar maple–yellow birch stand, 4 – mixed stand, 5 – red spruce stand, 6 – fir stand.

Stratigraphic feeding niches

As we have seen, the make-up of avian communities can vary considerably from one forest stand to another. The ecological requirements of certain species are sometimes so restrictive that some of them frequent only one stand. According to Hilden (1965), the distinctive feeding niche and nesting niche of each species are among the most important factors in the differential selection of habitat. In fact, we can predict that a certain species will frequent a particular habitat according to whether it feeds in flight or at ground level, or whether it nests in the bushes or the tops of trees. Dunlavy (1935) and Colquhoun and Morley (1943) were the first to note the vertical zonation of birds within forest stands. During the same period, Adams (1941) showed the existence of an identical stratification in certain forest invertebrates.

Figure 4
Comparison of the relative importance of the variety, density and consuming biomass of bird species of each stratigraphic feeding niche of the quadrats studied. The symbols are given in Figure 2 and in Table 5. The stands are arranged in order from the most deciduous to the most coniferous stand



To gain a better understanding of variations in the number of birds of a species in each stand, I decided to study the stratigraphic feeding niches.

From my own observations, as well as data provided by Cruikshank (1956), Bond (1957), MacArthur (1958), Godfrey (1967), Morse (1967, 1968) and Power (1971), I allocated a main stratigraphic feeding niche to each of the species identified, and a second niche to some species when they fed there regularly (Table 5). The table also gives the average individual weight for each species. With a few exceptions, they make up the arithmetical average of the weighted measurements of six specimens of the species (three males and three females). To the measurements provided by my specimens, I added those resulting from specimens collected during the nesting period from various locations in southern Quebec by researchers from the National Museum of Natural Sciences and the University of Montreal. In cases where I did not have sufficient data, I calculated the average individual weight for each sex and then determined the average individual weight for the species. The low values for the standard deviations indicate that the measurements obtained are probably fair approximations of the average individual weight for each species. The consuming biomass of each species, calculated according to the formula: $B = W^{.7}$ (Blondel 1969*a*) is also given in Table 5. This measurement takes into account the difference in metabolism due to the difference in the size of birds. It is directly proportional to the amount of energy taken from the environment (Blondel 1969*a*).

In Figure 4, I show the proportional distribution of variety, density and consuming biomass of bird species of each of the main stratigraphic feeding niches in the quadrats studied. The latter ranged from the most deciduous to the

Table 5
Stratigraphic feeding niche*, average weight and consuming biomass** of species found in quadrats studied

Species†	Stratigraphic feeding niche	Average weight (g)	Consuming biomass
Ruffed Grouse	G	533.33 ± 33.07	81.08
American Woodcock	G	160.20 ± 8.62	34.94
Black-billed Cuckoo	S	54.25 ± 1.96	16.37
Barred Owl	G	715.82 ± 23.38	99.62
Common Flicker	T, G	139.00 ± 3.45	31.63
Pileated Woodpecker	T	318.38 ± 15.75	56.50
Yellow-bellied Sapsucker	T	47.00 ± 1.44	14.81
Downy Woodpecker	T	26.70 ± 0.67	9.97
Crested Flycatcher	F	36.39 ± 1.88	12.38
Least Flycatcher	F	10.00 ± 0.28	5.01
Eastern Wood Pewee	F	14.90 ± 0.50	6.63
Gray Jay	O	74.12 ± 0.98	20.37
Blue Jay	O	90.92 ± 2.01	23.50
Black-capped Chickadee	S	10.70 ± 0.29	5.25
Boreal Chickadee	S	10.50 ± 0.23	5.19
White-breasted Nuthatch	T	22.00 ± 0.70	8.70
Red-breasted Nuthatch	T, C	10.53 ± 0.14	5.20
Brown Creeper	T	8.00 ± 0.32	4.29
Winter Wren	S	9.27 ± 0.35	4.75
American Robin	S, G	84.55 ± 3.91	22.33
Hermit Thrush	G	28.22 ± 1.05	10.36
Swainson's Thrush	G	32.55 ± 2.24	11.45
Veery	G	31.03 ± 0.77	11.07
Golden-crowned Kinglet	C	6.15 ± 0.24	3.57
Ruby-crowned Kinglet	S, C	6.67 ± 0.17	3.77
Solitary Vireo	C	15.07 ± 0.73	6.68
Red-eyed Vireo	C	17.02 ± 0.78	7.27
Black and White Warbler	T	10.10 ± 0.16	5.05
Tennessee Warbler	S	10.30 ± 0.52	5.12
Nashville Warbler	S	8.10 ± 0.19	4.32
Northern Parula	C	7.85 ± 0.05	4.23
Magnolia Warbler	S	8.23 ± 0.21	4.37
Cape May Warbler	C	10.90 ± 0.53	5.32
Black-throated Blue Warbler	S	9.64 ± 0.03	4.88
Yellow-rumped Warbler	S	12.02 ± 0.52	5.70
Black-throated Geen Warbler	C	9.67 ± 0.45	4.90
Blackburnian Warbler	C	9.78 ± 0.24	4.93
Chestnut-sided Warbler	S	9.82 ± 0.37	4.95
Bay-breasted Warbler	C	12.28 ± 0.52	5.79
Ovenbird	G	18.83 ± 0.81	7.81
Northern Waterthrush	S	17.38 ± 0.18	7.38
Canada Warbler	S	10.20 ± 0.21	5.08
American Redstart	F, S	8.25 ± 0.30	4.38
Red-winged Blackbird	S	55.70 ± 5.56	16.68
Scarlet Tanager	C	28.20 ± 0.80	10.36
Rose-breasted Grosbeak	C, S	47.62 ± 1.23	14.94
Purple Finch	O	25.75 ± 1.73	9.72
Dark-eyed Junco	G	17.77 ± 0.46	7.50
Chipping Sparrow	G	13.02 ± 0.69	6.03
White-throated Sparrow	G	24.52 ± 0.77	9.39

* F – insectivorous birds that feed in flight, T – insectivorous birds that feed on tree trunks, O – omnivorous birds which feed in different locations, C – insectivorous birds feeding at the canopy level, S – insectivorous birds feeding at the shrub stratum level, G – species (most of them insectivorous) feeding at ground level.

** $B = W^{.7}$

† Scientific names are given in Appendix 1.

Figure 5
Comparison of the relative importance of the variety, density and consuming biomass of bird species of the quadrats studied, in relation to the stratigraphic feeding niches. The symbols are given in Figure 2 and Table 5

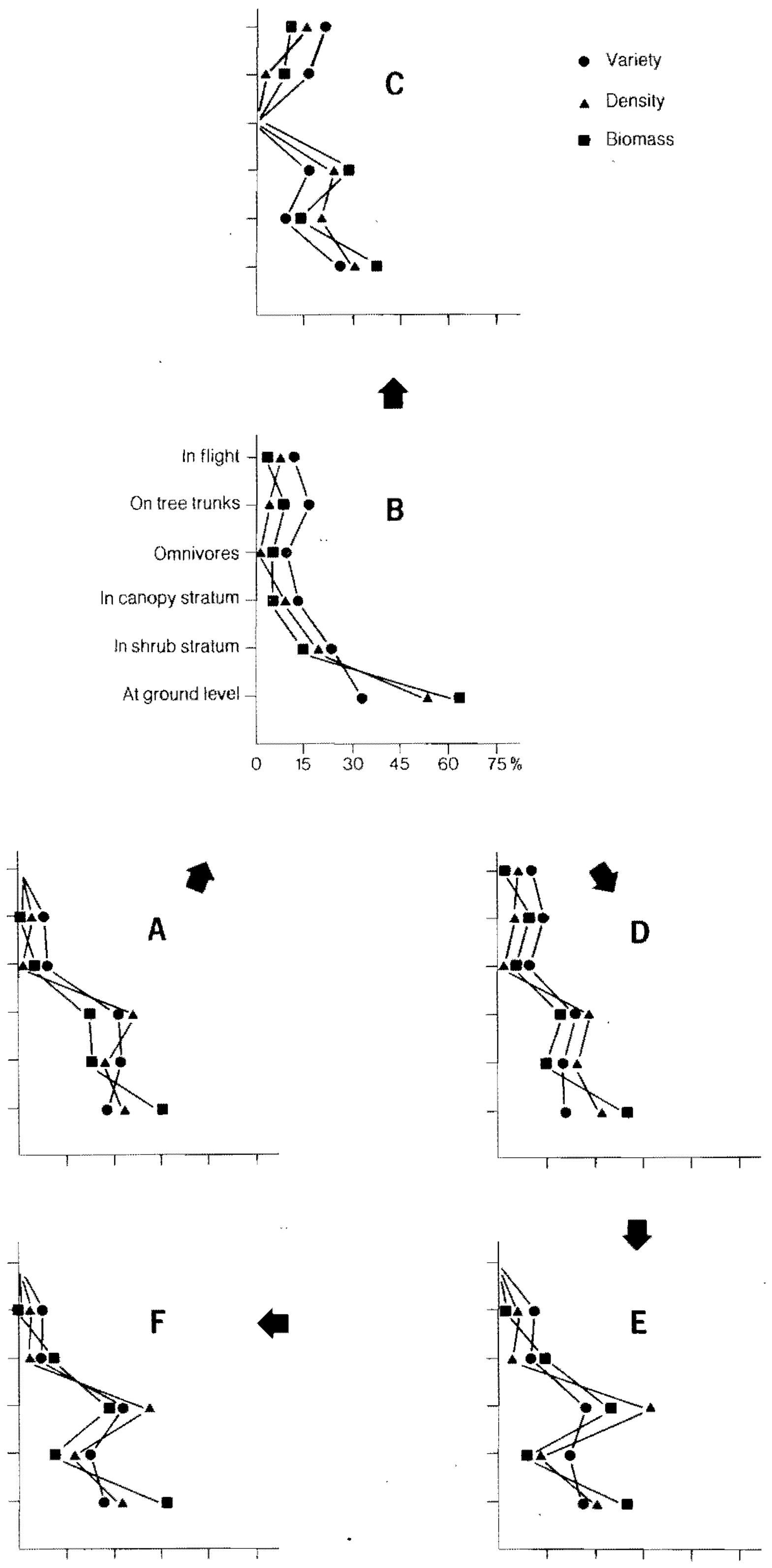


Table 6
Relative percentages of variety, density and consuming biomass of bird species in each stratigraphic feeding niche of quadrats studied

Stand	F*	T	O	C	S	G
			Variety			
Sugar maple–yellow birch	23.50	17.60	0.00	17.60	11.80	29.40
White birch	11.10	16.70	5.60	11.10	22.20	33.30
Mixed	10.70	14.30	7.10	25.00	21.40	21.40
Red spruce	0.00	11.10	11.10	27.80	22.20	27.80
Fir	0.00	8.00	8.00	32.00	24.00	28.00
White spruce plantation	0.00	4.50	4.50	31.80	31.80	27.30
			Population density			
Sugar maple–yellow birch	17.48	3.88	0.00	27.18	21.36	30.10
White birch	7.20	5.60	0.80	10.40	21.60	54.40
Mixed	7.26	5.65	3.23	27.42	22.58	33.87
Red spruce	0.00	4.94	4.93	46.91	13.58	29.63
Fir	0.00	2.05	4.79	41.10	18.49	33.56
White spruce plantation	0.00	2.44	3.25	34.96	26.02	33.33
			Consuming biomass			
Sugar maple–yellow birch	11.44	9.26	0.00	28.76	12.26	38.28
White birch	3.96	6.92	0.88	9.94	15.00	63.30
Mixed	3.93	9.27	5.86	22.00	18.81	40.14
Red spruce	0.00	3.64	11.55	35.42	9.99	39.40
Fir	0.00	1.92	9.03	30.16	12.17	46.72
White spruce plantation	0.00	1.69	4.20	23.32	25.65	45.15

* F – insectivorous birds that feed in flight, T – insectivorous birds that feed on tree trunks, O – omnivorous birds which feed in different locations, C – insectivorous birds feeding at the canopy level, S – insectivorous birds feeding at the shrub stratum level, G – species (most of them insectivorous) feeding at ground level.

most coniferous stand. In Figure 5, I show the proportional distribution of variety, density and consuming biomass of the bird species of each quadrat studied in relation to the stratigraphic feeding niches. The graphs are set out according to the order of succession adopted in Figure 1. The values used to draw the curves are given in Table 6.

Examination of these figures reveals the following trends in the stands studied:

- The insectivores feeding in flight (e.g., *Tyrannidae*) only frequent the predominantly deciduous stands. These forests, generally composed of tall and well spaced trees, are sparse enough to provide room for birds feeding in flight.

- Insectivores feeding on tree trunks (e.g., *Picidae, Sittidae, Certhiidae)* mainly frequent deciduous stands, probably because the trunks are bigger and easier to explore. In fact, unlike the evergreens, which frequently have closely packed branches, most of the branches of hardwood trees are usually concentrated near the top of the trunk. The lower trunk is usually quite open and easily exploited by climbing birds.

- Omnivores that feed in various locations (e.g. *Corvidae, Fringillidae)* are particularly common in coniferous stands. Although they eat a lot of insects during the reproduction period, these species are mostly sedentary granivores which, when winter comes, feed on conifer seeds. Since they probably evolved in the conifer forest (May 1946, Snyder 1950) it is natural that these species should be more varied and that they nest there in larger numbers. Ferry (1960) has noted a similar correlation between this generalized way of feeding and the sedentary character of the species in question. He also mentioned that bird populations become more sedentary as the forests approach the climax stage, since within a stable environment, species could more easily adapt their feeding habits to all seasons of the year. The lesser importance of these birds in artificial stands, such as the white spruce plantation, bears out this theory.

- Insectivores that feed at the canopy level (e.g., *Vireonidae, Parulidae)* tend to be more common in coniferous stands. This tendency is shown less in the number of species than of individuals: the latter reach up to 46.9% of all birds in red spruce. This population density, greater in the upper stratum of coniferous stands, coincides perfectly with the heavier mass of vegetation found at this level, which must surely contain a larger number of insects, at least during periods of infestation (Odum 1971, Krebs 1972). In fact, while hardwood stands are generally sparse enough to allow abundant second growth, the tree stratum of softwood stands forms an opaque screen that hinders the growth of new seedlings. The only noticeable growth of shrubs is found in places cleared by cutting or the death of old trees (e.g., the white spruce plantation). The small number of these birds within the white birch stand is also notable. This is a young stand in which the tree stratum is not yet fully developed and the shrubs, enjoying plenty of light, make up most of the vegetal biomass.

- Most insectivores seeking food in the shrub stratum (e.g., *Paridae, Parulidae)* are found in initial and disturbed stands. They generally avoid softwood stands. This tendency accords with the preceding category and the same explanation applies. Although I have attributed this niche to species that usually concentrate at the base of trees (in addition to shrubs), the population is very poorly represented in the middle stratum of coniferous stands, because the low branches of the conifers are usually stunted and often dead.

- The species (mostly insectivores) that feed on the ground (e.g., *Troglodytidae, Turdidae, Fringillidae)* predominate in the white birch stand. The tree and shrub strata of this young stand are still developing and are of only minor importance in the energy balance of the stand. In contrast, recent disruptions (fire, cutting) and the annual deposit of dead leaves have turned the ground into a very rich environment in which a myriad of small invertebrates recycle energy (Wallwork 1970). They form an invaluable source of food at ground level and explain the concentration of birds there.

- Only a few species, generally rare, feed in flight, on tree trunks or omnivorously. On the other hand, several generally common species feed in the tree or shrub strata or on the ground. Food sources and exploitation methods are probably more limited within the first three niches. They can only be shared among a small number of species, while the last three niches probably offer a greater variety of food sources and exploitation techniques. The small number of sedentary omnivores can be attributed to the severe climate of the Laurentian winter.

- A positive and statistically significant correlation exists between the relative importance of the variety, density and consuming biomass of the first three niches (F, T, O), but there is no such correlation between the relative importance of density and consuming biomass for the last three niches (C, S, G). Several species found at the shrub level (S) add little to the density and consuming biomass, while the species at the tree (C) and ground (G) levels are less varied, but more common and often larger.

The vegetation of the shrub stratum is very intermittent. Where it exists, it is made up of clumps of shrubs and isolated trees. Because it is heterogeneous, it provides a great variety of niches scattered sporadically throughout the stands. It can therefore support a varied but not numerous avifauna. I should mention that most "endemic" species of the various stands consist of species that feed within this stratum.

In contrast, the tree stratum and ground level are much more uniform. The canopy rarely lacking, usually forms a vegetal screen with trees of similar height and physiognomy. As with the ground level, its niches are less varied but greater in number. The firmness of the ground and the greater strength of the tree branches probably explain the presence of heavier birds at these two levels. The branches also hide the bigger prey hunted by larger birds (Schoener 1969, 1971).

The preceding factors clearly show that the division of the plant biomass, and therefore of the invertebrate biomass (Adams 1941) causes the differential division of the variety, density and consuming biomass of birds within a stand. The greater the relative density of the foliage of a stratum, the greater the proportion of birds in this stratum as a whole.

In initial stands, the vegetation is denser near the ground and becomes sparser as it approaches the crowns of the trees. On the other hand, coniferous stands have a very dense canopy with thinner foliage near the ground. Therefore, initial stands have a high bird density near ground level and low populations at the tree stratum level, while deciduous stands usually have the opposite distribution, with a high density in the upper stratum and a lower one near the ground.

Ferry (1960), Bock and Lynch (1970), Pearson (1971) and Karr (1971) obtained comparable results. This can be explained by the greater carrying capacity of the denser plant environments. In fact, the greater their productivity, the more insects they contain (Murdoch *et al.* 1972); they can therefore support a greater density of birds.

Dominance and diversity

Calculation of the dominance and diversity ratings of a community takes into account both the variety of species in the community and their respective densities.

The taxonomic variety, or if you prefer, the total number of species, varies according to the habitat, geographical location and abundance of avifauna (MacArthur 1972). It is an important element in the community structure and may sometimes indicate a difference between bird communities living in two stands with similar physiognomies. Just recently it was used as a measurement of the diversity of a community by Ferry and Frochot (1970), while for Whittaker (1972) it is the "alpha" diversity of a community.

While the variety values (Table 7) may be fair approximations of the real variety (cf. p. 12), these values are nonetheless under-estimated. It is not only that all of the species observed were not included in the calculation of variety (I left out the species not censused), but I also omitted some that may have nested in the stands without having a territory inside my quadrats.

However, I believe their number to be relatively low judging by the remarkable agreement with the results obtained by Martin (1960) in comparable habitats of Algonquin Park in Ontario.

Even if the calculations of variety prove rather similar in some of my stands, we must not forget that the species composition of each is different, as shown by the study of similarities.

The total density (Table 7) comes from the sum of the species densities. This scale of abundance varies according to the environment and goes as high as the amount of food and the number of available nesting sites will permit. In this way, it depends mostly on the variety of species that can nest there. Thus, the forest environment can support that many more birds when they belong to a large number of different species, probably because species with different needs complement each other rather than compete (Ferry and Frochot 1970).

A study of Table 1 shows that the importance of the number of bird species in different quadrats varies greatly. A certain percentage of these species, comprising the most common ones, are said to be dominant. They have a greater effect within the community since they take up most of the nesting sites and consume a large part of the food resources. Besides these species, a still greater percentage of the whole consists of rare species. Although they do not have as much impact within the community as the dominant species, they should not be overlooked. In fact, they add to the diversity of species, another important aspect of community structure.

In order to find out the extent of dominance among a greater or smaller number of species, I calculated the dominance index *(C)* (Table 7) of each community. This index, developed by Simpson (1949), is found by adding the relative importance index of each species belonging to a community. This can be formulated as follows:

$$C = \Sigma(n_i/N)^2$$

Where n_i = population density of i^{th} species,
N = total number of individuals

The dominance index values for each community are given in Table 7. While the bird communities of the sugar maple–yellow birch and white birch stands are made up mostly of common or rare species, those of the red spruce stand, white spruce plantation, mixed stand and fir stand contain a greater number of species with average populations. The general tendency is for dominance to be shared among more species as the environment becomes more stable (Odum 1971). Initial environments have an evolving plant physiognomy that causes some instability, attracting species with generalized niches at the expense of those with specialized niches. We therefore arrive at two groups: the first made up of common species and the second of rare ones. However, as succession progresses, the plant physiognomy stabilizes and the species divide into niches of more equal size through interspecific competition (Orians and Willson 1964, Slobodkin and Sanders 1969).

Table 7
Values for the variety *(S)*, density *(N)*, dominance *(C)* equitability *(E)*, Simpson diversity *(D)* and Shannon diversity *(H^1)* of avian communities in quadrats studied

Stand	S	N	C	E	D	H^1
White spruce plantation	22	123	0.067	0.926	0.933	2.861
White birch	18	125	0.101	0.872	0.899	2.520
Sugar maple–yellow birch	17	103	0.111	0.862	0.889	2.443
Mixed	28	124	0.063	0.899	0.934	2.995
Red spruce	18	81	0.088	0.918	0.912	2.654
Fir	25	148	0.063	0.919	0.937	2.957

The avian communities of the sugar maple–yellow birch stand and the white spruce plantation do not seem to follow the same trends. In fact, the sugar maple–yellow birch forms a climax and should normally act as a stable stand, while the white spruce plantation is a monoculture and should behave as an unstable stand because of its great vulnerability to insect infestations.

We should remember, however, that La Mauricie National Park is at the northern limit of distribution of sugar maple–yellow birch stands. It is therefore possible that the stand under study is more unstable than other stands of the same association farther south. The effect of this instability on the composition of the avifauna would be all the more pronounced, with the sugar maple–yellow birch stand as the only climax plant association, predominantly deciduous, to establish itself so far north in this part of North America.

Conditions in the white spruce plantation are probably temporary. The infestation of the spruce budworm created a surplus of food and lessened competition between the various bird species (Pianka 1971). Because of the greater overlap of niches, species that would otherwise have been rare within the plantation have been able to increase their numbers and reduce the dominance of usually common species. However, the situation was different in 1972, when the infestation was not so widespread, and it is reasonable to believe that dominance will reassert itself once the insect infestation has passed.

While the dominance index shows the degree to which the majority of individuals of a community are concentrated within a few very common species, the equitability index shows the degree to which individuals of a community divide into equal proportions for each species (Lloyd and Ghelardi 1964). Although these two notions are complementary, they are not reciprocal. The equitability index *(E)* can be calculated with the following formula:

$$E = H'/H_{\max} = -\Sigma(p_i)\,(\log_e p_i)/\log_e S,$$
where H' = Shannon and Wiener diversity index,
S = variety,
$p_i = n_i/N$ (cf. dominance index)

The equitability index for each community appears in Table 7. As might be expected, there is greater equitability within the white spruce plantation, fir, red spruce and mixed stands, but less within the sugar maple–yellow birch and white birch stands.

It is well known that communities differ considerably in the number of species they contain. For example, the taxonomic variety is generally greater in a tropical environment than in a temperate one, at the foot of a high mountain than at the summit, on a large island than on a smaller one, and on an island near a continent than on one isolated from continental masses. Also, in some communities, the species are about equally common, while in others most species are either very common or very rare.

This is not a coincidence; the variety and equitability of species in a community are based on certain ecological principles, and it was in order to facilitate their study that ecologists introduced the principle of community diversity.

There are several indexes for calculating the diversity of a community (Simpson 1949, Shannon and Weaver 1949, McIntosh 1967). I chose those of Simpson *(D)* and Shannon–Weiner *(H')*. The former is influenced to a greater degree by the more common species, while the latter fluctuates on the basis of the number of species and the equitability of their populations. In mathematical form, it is expressed as follows:

$$D = 1 - C$$
and $$H' = E \bullet H_{\max}$$

The diversity index values for each community are given in Table 7. Except for avian communities of the mixed and fir stands, the two indexes lead to diversity values that group communities in a comparable order. In fact, most diversity indexes are linked to each other by very precise correlations (DeBenedictis 1973, Hill 1973). In the case under study, a significant positive correlation exists between the two diversity indexes (with a threshold of probability of 99%). If the order of the avian communities of the fir stand and the mixed stand is inverted, it is because the Shannon–Weiner diversity index differentiates between two stands with comparable dominance values but with significantly different variety values, while the Simpson index does not. In the following discussions, only the Shannon–Weiner diversity index values are taken into consideration.

Use of a formula to calculate the diversity of a number of bird communities does not give us much. It is only when we compare the resulting values with each other, and with those derived from studying other aspects of the structure of ecosystems, that we can reach interesting conclusions.

I decided, therefore, to calculate the diversity values for the taxonomic and physiognomic plant communities of each stand. I applied the Shannon–Wiener index to the species cover indexes of the trees and shrubs of each quadrat (Table 3) to obtain the diversity values of taxonomic plant communities. However, the data concerning plant physiognomy do not lend themselves to such a formula; I had to develop my own diversity index for the study of physiognomic plant communities.

I began by grouping the data from Tables 2 and 5 into seven classes: cover factors of the three forest strata, complexity of underbrush, average distance between trees, average diameter of trees and average height of first branches. Then, in each class, I assigned a value of 1 to the most heterogeneous stands and a value of 0 to the other stands. Finally I gave each stand a diversity index equal to the sum of the values obtained by that stand for each of the classes considered.

The heterogeneity was measured in three different ways. For the cover factors, I gave a value of 1 to stands in which deciduous trees and conifers each formed at least one-third of the vegetation of the stratum studied. The complexity of the underbrush takes into account the herbaceous and moss strata, the layers of dead leaves and branches, and the extent of bare earth and rocks. I added up the indexes allotted to each stand according to these characteristics (Table 2), and calculated their averages, as well as the standard deviations. A value of 1 was assigned to stands with the less significant standard deviations –

$$Sx/\overline{X} \leq (Sx/\overline{X})_{\min} + [\,(Sx/\overline{X})_{\max} - (Sx/\overline{X})_{\min}\,]/2$$

— since it is in these stands that the characteristics under consideration are most equitably represented (see Roth 1976). Finally, in the last three classes, I assigned a value of 1 to the stand with the larger standard deviation –

$$Sx/\overline{X} \geq (Sx/\overline{X})_{\min} + [\,(Sx/\overline{X})_{\max} - (Sx/\overline{X})_{\min}\,]/2$$

— since it is in the latter that one finds the greatest heterogeneity among these characteristics. The values assigned and

Table 8
Measurements of heterogeneity of forest stands and diversity ratings of the plant physiognomy of each

Physiognomic characteristics	White spruce plantation	White birch stand	Sugar maple–yellow birch stand	Mixed stand	Red spruce stand	Fir stand
Cover factor (tree stratum)*	0	0	0	1	1	1
Cover factor (shrub stratum)	0	0	0	0	1	1
Cover factor (herb stratum)	0	0	0	0	1	0
Heterogeneity of underbrush**	0	1	1	1	1	1
Dist. between trees†	1	0	1	1	1	0
Diam. of trees	0	0	0	1	1	0
Ht. of first branches	1	0	0	0	0	0
Physiognomic diversity	2	1	2	4	6	3

* Cover factor = cover index of coniferous or deciduous trees/
0 – $0 <$ cover factor $< .5$ or cover factor > 2;
1 – $.5 \leq$ cover factor ≤ 2.

** $0,\ S_x/\bar{X} > (S_x/\bar{X})_{min} + |\,(S_x/\bar{X})_{max} - (S_x/\bar{X})_{min}\,|/2$;
$1,\ S_x/\bar{X} \leq (S_x/\bar{X})_{min} + |\,(S_x/\bar{X})_{max} - (S_x/\bar{X})_{min}\,|/2$.

† $0,\ S_x/\bar{X} < (S_x/\bar{X})_{min} + |\,(S_x/\bar{X})_{max} - (S_x/\bar{X})_{min}\,|/2$;
$1,\ S_x/\bar{X} \geq (S_x/\bar{X})_{min} + |\,(S_x/\bar{X})_{max} - (S_x/\bar{X})_{min}\,|/2$.

Table 9
Values for physiognomic plant community diversity ("H") and taxonomic plant community diversity (H^1) of quadrats studied

Stand	"H"	H^1
White spruce plantation	2	1.102
White birch	1	2.663
Yellow birch	2	2.809
Mixed	4	2.523
Red spruce	6	2.755
Fir	3	2.286

Table 10
Spearman correlation coefficients (r_s)* for comparison of values of various aspects of the structure of communities studied. **Avian communities:** population density (1), variety (2), Shannon diversity index (3), equitability (4), dominance (5). **Plant communities:** ecological succession (6), physiognomic "diversity" (7), Shannon taxonomic diversity (8). **Homogeneity of distribution of various stratigraphic feeding niches:** variety (9), density (10), consuming biomass (11). **Percentage of insectivorous birds feeding in flight:** variety, density and consuming biomass (12). **Percentage of insectivorous birds feeding on tree trunks:** variety, density and consuming biomass (13). **Percentage of omnivorous birds feeding in various locations:** variety, density and consuming biomass (14). **Percentage of insectivorous birds feeding at the canopy level:** variety (15), density (16), consuming biomass (17). **Percentage of insectivorous birds feeding at the shrub level:** variety (18), density (19), consuming biomass (20). **Percentage of species (mostly insectivorous) feeding at ground level:** variety (21), density (22), consuming biomass (23). **"Endemism"** (24)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
2	.714																						
3	.672	.929																					
4	—	—	.658																				
5	—	-.700	-.900	-.600																			
6	—	—	—	—	—																		
7	—	—	—	.615	—	.672																	
8	-.657	-.600	-.729	—	.843	—	—																
9	—	—	—	-.600	—	—	—	.557															
10	—	—	—	—	—	—	—	—	—														
11	—	—	—	—	—	—	.557	—	—	—													
12	—	—	—	—	.748	—	—	.648	.796	—	—												
13	—	—	—	—	.624	—	—	.648	.863	—	—	.943											
14	—	—	.596	.772	-.562	.643	.796	—	—	—	—	—	—										
15	—	—	—	.943	-.757	—	—	-.671	-.742	—	—	—	—	—									
16	—	—	—	.900	—	.600	.729	—	-.585	—	—	—	—	.710	.829								
17	—	—	.672	.643	—	.729	.643	—	—	-.742	—	—	—	—	.600	.829							
18	—	—	—	—	-.600	—	—	-.785	-.814	—	-.642	—	—	—	—	—	—						
19	—	—	—	—	—	-.757	—	—	—	—	—	—	—	—	—	—	—	—					
20	—	—	—	—	—	-.728	—	-.642	—	.686	—	—	—	—	—	—	—	—	.958				
21	—	—	—	—	.686	—	—	.557	—	—	—	—	—	—	—	—	—	—	—	—			
22	—	—	—	—	—	—	—	—	—	.829	—	—	—	—	—	—	—	—	—	—	—		
23	—	—	—	—	—	—	-.792	-.635	—	—	-.592	—	—	—	—	—	—	—	—	—	—	.886	
24	—	—	—	—	—	-.671	—	—	—	.772	—	—	—	—	—	—	-.600	—	.900	.958	—	.615	—

*Note: $r_s \geq |\,0.557\,|$ P: 0.01, $r_s = 0.917$; P: 0.05, $r_s = 0.811$

the diversity index computed for each quadrat are given in Table 8. Table 9 shows the diversity values of the physiognomic and taxonomic plant communities in the quadrats studied.

Application of the Spearman correlation test to the diversity values of the three types of communities (Table 10) does not provide any statistically significant correlations. However, it does allow us to confirm that the diversity of bird communities varies more according to the physiognomic than the taxonomic diversity of a stand. We may suppose that with more extensive community samples we would probably have obtained a significant correlation between the diversity of birds and the physiognomic diversity of the stands. Moreover, as I said before, several authors have already demonstrated that a correlation exists between avian diversity and the diversity of plant stratification.

Discussion and conclusions

Since the first studies of MacArthur (1955, 1957, 1960) and Hutchinson (1959), research on the biology of communities has dealt mainly with the extent of the diversity of organisms forming these communities. The interdependence of the diversity, stability and productivity of communities, in particular, has been the subject of much speculation and even a few generalizations. These subjects were discussed in detail during a recent symposium (Woodwell and Smith 1969).

Margalef (1968), Whittaker (1969) and Odum (1971) have suggested that the diversity increases during ecological succession, and often stabilizes or even diminishes slightly near the end of the succession. Whittaker (1965) and Pielou (1966) have shown that, in some cases, the diversity may even diminish during an ecological succession.

The work done by MacArthur (1955) and the study of stable environments (Connell and Orias 1964) suggest that greater stability is associated with greater diversity. However, we do not know the relation of cause and effect between the two. On the other hand, some works have led to different conclusions. Hurd *et al.* (1971) found an increase in diversity during a succession, but a simultaneous reduction in stability, while Futuyma (1973) showed that a negative correlation could exist between diversity and stability.

According to Margelef (1968), the higher the annual primary productivity of communities, the greater their diversity. Whittaker (1965), Odum (1971) and Krebs (1972) recognize this connection, but suggest that there could be some exceptions.

Figure 6 is a graphical layout in which correlations between certain aspects of the communities studied served to combine or divide the latter into groups with positive or negative correlations between them. The aspects studied can be divided into five types. In the first group, we consider the variety, density, dominance, equitability and diversity of bird communities. In the second, the taxonomic and physiognomic diversity of forest stands come into play. The third covers the variety, density and consuming biomass of bird species in each stratigraphic feeding niche. Lastly, I have studied the number of endemic species and the ecological succession of the various stands.

For each of the aspects studied, I arranged the resulting values in order and assigned a corresponding ranking of values to the appropriate stands. The values I matched were either rough measurements, index values, significance ratings (%) or homogeneity values *(Sx)*. I then applied the Spearman correlation test, only retaining the most significant values (positive or negative) of the correlation coefficients (r_s) (Table 10). For each of the aspects studied, I used the

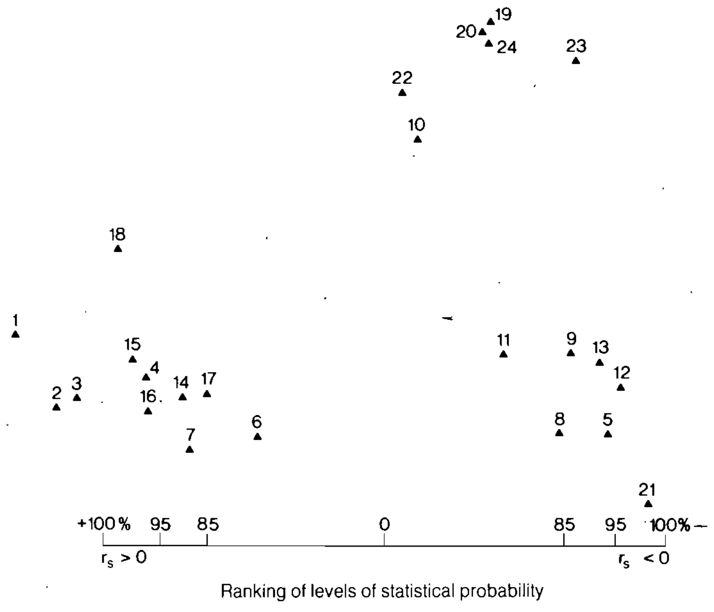


Figure 6
Graphical layout of the Spearman correlations of various structural aspects of the communities studied. The symbols are given in Table 10. This taxometric map is a two-dimensional representation placing aspects of the communities studied in relation to each other by using the two most significant values of their correlation coefficients as measures of similarity between the aspects considered. This taxometric technique makes it possible to determine visually the variables displaying the closest correlation as well as the strongest correspondence to all other aspects, because the points representing those variables are closely grouped in such figures. See text for more details

two most significant values of the correlation coefficient as measurements of similarity between the aspects under consideration. These similarity measurements were converted into dissimilarity measurements *(d)* with the following formula:

$$d = 1 - r_s$$

to be used in preparing Figure 6. In this way, a dissimilarity value of 0 is assigned for a perfect positive correlation, and a value of 2 for a perfect negative correlation. Thus I obtained two measurements of the interval (between 0 and 2) for each aspect studied, which allowed me to place each of the aspects studied on the figure by simple triangulation.

In this way, I defined the three principal groups of aspects with positive correlations between them. The first group includes the aspects that seem to be mainly governed by the physiognomic diversity of stands (lower left). The second group is made up of aspects associated with the dominance of avian communities (lower right). The third group comprises the aspects that show an important negative correlation concerning the ecological succession of the stands (upper right).

By analyzing this figure, I deduced the following points:

■ The diversity of avian communities, calculated with the Shannon–Weiner formula, depends more on the variety of species than on the equitability of their numbers. Tramer (1969) and Kricher (1972) arrived at the same conclusion.

■ The equitability (and indirectly diversity) of avian communities seems to depend mainly on the physiognomic diversity of forest stands. Therefore, the more complex the plant physiognomy of a stand, the greater the equitability of its avian community. The stand then provides a large variety of niches, which, for the most part, are comparable with one another. The bird species are distributed in roughly equal proportions, and so the stand has a high equitability index (and indirectly a high diversity index).

■ The homogeneity of the distribution of variety in bird species and their density and consuming biomass between each of the stratigraphic feeding niches do not seem to have significant effects. This situation could be foreseen, as some niches are more limited than others and cannot shelter as many species and individuals (cf. p. 23).

■ The physiognomic diversity of forest stands tends to increase with ecological succession. The tree stratum becomes more complex and the stand moves progressively towards a definitive plant physiognomy. This permanence of climax forests, as well as the size of their upper stratum, explains the increase in omnivorous species and species which feed in the tree stratum during the ecological succession leading to climax (cf. p. 22)

■ A negative correlation exists between the dominance and diversity of avian communities. However, a positive correlation has been established between the taxonomic dominance and diversity of forest stands (threshold of statistical probability of 95%). Vuilleumier (1972) found similar results in South America. I studied forests of two very different physiognomic types, as he did. Whereas he studied mesic and hydrophic forests, I compared coniferous with deciduous stands. Although he gave an ecological explanation for his observations, I do not believe that the taxonomic diversity of the stands I have studied would have a direct influence on avian diversity. The number of deciduous species is much greater than that of conifers. However, we know that the bird is a poor botanist, whatever the plant species in question; it is only interested in the physiognomy. Therefore, even if the deciduous forest is more varied than the coniferous, in the eyes of the bird it offers a comparable number of physiognomic forms. The lower diversity of bird communities in deciduous stands arises from other reasons (cf. pp. 24–25).

■ The most dominant avian communities are those with the most species that feed in flight and on tree trunks. As with the previous characteristics, I think this is a coincidence. Earlier (cf. p. 22) we saw that these niches were more numerous in deciduous stands. But I also pointed out that deciduous stands contained avian communities with the highest dominance because these stands were unstable (cf. pp. 24–25) It is therefore logical that a correlation should exist between these two feeding niches and the dominance of avian communities.

■ Species that feed in the shrubs (most of which are endemic species), as well as those that feed at ground level, are well represented in the initial stands, but their numbers diminish during the ecological succession leading to climax. I have already discussed this phenomenon in detail (cf. pp. 22–23).

In conclusion, it seems that the structure of avian communities depends largely on the plant physiognomy of the forest stands sheltering them. Very often the plant physiognomy becomes more complex during ecological succession until it reaches an almost definitive state. The result is a greater stability and diversification of feeding niches. In conjunction with this increase in stability (permanence of vegetation), the equitability of the population and the variety of species increase (Kricher 1972) and produce the greater diversity of older and more stable stands.

Appendix

Appendix 1
Scientific and English names of bird species mentioned in the text

Scientific name	English name
ACCIPITRIDAE	
Buteo platypterus	Broad-winged Hawk
TETRAONIDAE	
Bonasa umbellus	Ruffed Grouse
SCOLOPACIDAE	
Philohela minor	American Woodcock
Actitis macularia	Spotted Sandpiper
CUCULIDAE	
Coccyzus erythropthalmus	Black-billed Cuckoo
STRIGIDAE	
Strix varia	Barred Owl
APODIDAE	
Chaetura pelagica	Chimney Swift
PICIDAE	
Colaptes auratus	Common Flicker
Dryocopus pileatus	Pileated Woodpecker
Sphyrapicus varius	Yellow-bellied Sapsucker
Picoides pubescens	Downy Woodpecker
TYRANNIDAE	
Myiarchus crinitus	Crested Flycatcher
Empidonax minimus	Least Flycatcher
Contopus virens	Eastern Wood Pewee
Nuttallornis borealis	Olive-sided Flycatcher
HIRUNDINIDAE	
Hirundo rustica	Barn Swallow
CORVIDAE	
Perisoreus canadensis	Gray Jay
Cyanocitta cristata	Blue Jay
PARIDAE	
Parus atricapillus	Black-capped Chickadee
Parus hudsonicus	Boreal Chickadee
SITTIDAE	
Sitta carolinensis	White-breasted Nuthatch
Sitta canadensis	Red-breasted Nuthatch
CERTHIIDAE	
Certhia familiaris	Brown Creeper
TROGLODYTIDAE	
Troglodytes troglodytes	Winter Wren
TURDIDAE	
Turdus migratorius	American Robin
Catharus guttatus	Hermit Thrush
Catharus ustulatus	Swainson's Thrush
Catharus fuscencens	Veery
SYLVIIDAE	
Regulus satrapa	Golden-crowned Kinglet
Regulus calendula	Ruby-crowned Kinglet
BOMBYCILLIDAE	
Bombycilla cedrorum	Cedar Waxwing
VIREONIDAE	
Vireo solitarius	Solitary Vireo
Vireo olivaceus	Red-eyed Vireo
PARULIDAE	
Mniotilta varia	Black and White Warbler
Vermivora peregrina	Tennessee Warbler
Vermivora ruficapilla	Nashville Warbler
Parula americana	Northern Warbler
Dendroica magnolia	Magnolia Warbler
Dendroica tigrina	Cape May Warbler
Dendroica caerulescens	Black-throated Blue Warbler
Dendroica coronata	Yellow-rumped Warbler
Dendroica virens	Black-throated Green Warbler
Dendroica fusca	Blackburnian Warbler
Dendroica pensylvanica	Chestnut-sided Warbler
Dendroica castanea	Bay-breasted Warbler
Seiurus aurocapillus	Ovenbird
Seiurus noveboracensis	Northern Waterthrush
Oporornis philadelphia	Mourning Warbler
Wilsonia canadensis	Canada Warbler
Setophaga ruticilla	American Redstart
ICTERIDAE	
Agelaius phoeniceus	Red-winged Blackbird
Quiscalus quiscula	Common Grackle
Molothrus ater	Brown-headed Cowbird
THRAUPIDAE	
Piranga olivacea	Scarlet Tanager
FRINGILLIDAE	
Pheucticus ludovicianus	Rose-breasted Grosbeak
Hesperiphona vespertina	Evening Grosbeak
Carpodacus purpureus	Purple Finch
Carduelis tristis	American Goldfinch
Junco hyemalis	Dark-eyed Junco
Spizella passerina	Chipping Sparrow
Zonotrichia albicollis	White-throated Sparrow

References

Adams, C.C. 1908. The ecological succession of birds. Auk 25:109–153.

Adams, R.H. 1941. Stratification, diurnal and seasonal migration of animals in a deciduous forest. Ecol. Monogr. 11:190–227.

Armstrong, E.A. 1954. The behaviour of birds in continuous daylight. Ibis 96:1–30.

Beals, E. 1960. Forest bird communities in the Apostle Islands of Wisconsin. Wilson Bull. 72:156–181.

Blondel, J. 1969*a*. Synécologie des Passereaux résidents et migrateurs dans un échantillon de la région méditerranéenne française. Centre régional de Documentation pédagogique. Marseille. 239 pp.

Blondel, J. 1969*b*. Méthodes de dénombrement des populations d'oiseaux. *In* Lamothe, M.; Bourlière, F. *(réd.)*. Problèmes d'écologie: l'échantillonnage des peuplements animaux des milieux terrestres. pp. 97–151. Masson, Paris.

Blondel, J.; Ferry, C.; Frochot, B. 1973. Avifaune et végétation; essai d'analyse de la diversité. Alauda 41:63–84.

Bock, C.E.; Lynch, J.F. 1970. Breeding bird populations of burned and unburned conifer forest in the Sierra Nevada. Condor 72:182–189.

Bond, R.R. 1957. Ecological distribution of breeding birds in the upland forests of Southern Wisconsin. Ecol. Monogr. 27:351–384.

Braun-Blanquet, J. 1932. Plant sociology: the study of plant communities. McGraw-Hill, New York.

Brewer, R. 1963, Stability in bird populations. C.C. Adams, Occas. Pap. Cent. Ecol. Stud. West. Mich. Univ. No. 7. 12 pp.

Brown, J.L.; Orians, G.H. 1970. Spacing patterns in mobile animals. Annu. Rev. Ecol. Syst. 1:239–262.

Carmichael, J.W. 1970. The taxmap classification program. Univ. of Alberta. Mimeographed. 9 pp.

Clements, F.E. 1936. Nature and structure of the climax. J. Ecol. 24:252–284.

Cody, M.L. 1968. On the methods of resource division in grassland bird communities. Am. Nat. 102:107–147.

Cody, M.L. 1970. Chilean bird distribution. Ecology 51:455–464.

Colquhoun, M.K.; Morley, A. 1943. Vertical zonation in woodland bird communities. J. Anim. Ecol. 12:75–81.

Connell, J.H.; Orias, E. 1964. The ecological regulation of species diversity. Am. Nat. 98:399–414.

Cottam, G.; Curtis, J.T.; Hale, B.W. 1953. Some sampling characteristics of a population of randomly dispersed individuals. Ecology 34:741–757.

Cruickshank, A.D. 1956. Nesting heights of some woodland warblers in Maine. Wilson Bull. 68:157.

Dansereau, P. 1944. Interpenetrating climaxes in Quebec. Science 99:426–427.

Dansereau, P. 1959. Phytogeographia laurentiana II. The principal plant associations of the Saint-Lawrence Valley. Contrib. Inst. Bot. Univ. Montréal 75:1–147.

Dansereau, P.; Buell, P.F.; Dagon, R. 1966. A universal system for recording vegetation. Sarracenia 10:1–64.

Darveau, R.C. 1971. Parc national de la Mauricie. Description générale du couvert forestier. Parcs Canada. 65 pp.

DeBenedictis, P.A. 1973. On the correlations between certain diversity indices. Am. Nat. 107:295–302.

DesGranges, J.L. 1974. Étude de quelques communautés aviennes du Parc national de la Mauricie, Québec. Mémoire de maîtrise. Université de l'Alberta. xxi + 138 pp + annexes.

DesGranges, J.L.; Lane, P.; Colpron-DesGranges, L. 1977. Étude de l'activité journalière des oiseaux. Bulletin ornithologique 22:27–30.

Diamond, J.M. 1973. Distributional ecology of New Guinea birds. Science 179:759–769.

Dunlavy, J.C. 1935. Studies of the phyto-vertical distribution of birds. Auk 52:425–431.

Emlen, J.T. 1956. A method for describing and comparing avian habitats. Ibis 98:565–576.

Enemar, A. 1959. On the determination of the size and composition of a passerine bird population during the breeding season. Var Fagelvärld, suppl. 2:1–114.

Erskine, A.J. 1977. Birds in boreal Canada: Communities, densities and adaptations. Canadian Wildlife Service Report Series Number 41. 71 pp.

Ferry, C. 1960. Recherches sur l'écologie des oiseaux forestiers en Bourgogne. I: l'avifaune nidificatrice d'un taillis sous futaie de *Querceto-carpinetum scilletosum*. Alauda 28:93–123.

Ferry, C.; Froehot, B., 1970. L'avifaune nidificatrice d'une forêt de chênes pédonculés en Bourgogne: étude de deux successions écologiques. Terre Vie 24:153–250.

Fretwell, S.D. 1969. On territorial hehavior and other factors influencing habitat distribution in birds I – III. Acta Biotheor. 19:16–52.

Frochot, B. 1971. Ecologie des oiseaux forestiers de Bourgogne et du Jura. Thèse de doctorat. Univ. de Dijon. 144 pp.

Futuyma, D.J. 1973. Community structure and stability in constant environments. Am. Nat. 107:443–446.

Gleason, H.A. 1926. The individualistic concept of the plant association. Bull. Torey Bot. Club 53:7–26.

Godfrey, W.E. 1966. Birds of Canada. Nat. Mus. Can. Bull. No. 203. 428 pp.

Grandtner, M.M. 1966. La végétation forestière du Québec méridional. Presses de l'Univ. Laval. 216 pp.

Haapanen, A. 1965. Bird fauna of the Finnish forests in relation to forest succession I. Ann. Zool. Fenn. 2:153–196.

Haapanen, A. 1966. Bird fauna of the Finnish forests in relation to forest succession II. Ann. Zool. Feen. 3:176–200.

Hairston, N.G. 1959. Species abundance and community organization. Ecology 40:404–416.

Hall, G.A. 1964. Breeding bird census – why and how. Audubon Field Notes 18:413–416.

Heimburger, C.C. 1941. Forest-site classification and soil investigation on lake Edward Forest Experiment Area. Can. Depart. Mines and Resources. Sylvicultural Research Note No. 66. 49 pp.

Hilden, O. 1965. Habitat selection in birds: a review. Ann. Zool. Fenn. 2:53–75.

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

Hurd, L.E.; Mellinger, M.V.; Wolf, L.L.; McNaughton, S.J. 1971. Stability and diversity at three trophic levels in terrestrial successional ecosystems. Science 173:1134–1136.

Hutchinson, G.E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? Am. Nat. 93:145–159.

James, F.C. 1971. Ordinations of hahitat relationships among hreeding birds. Wilson Bull. 83:215–236.

Johnston, D.W.; Odum, E.P. 1956. Breeding bird populations in relation to plant succession on the Piedmont of Georgia. Ecology 37:50–62.

Johnston, V.R. 1947. Breeding birds of the forest edge in Illinois. Condor 49:45–53.

Karr, J.R. 1971. Structure of avian communities in selected Panama and Illinois habitats. Ecol. Monogr. 41:207–229.

Karr, J.R.; Roth, R.R. 1971. Vegetation structure and avian diversity in several New World areas. Am. Nat. 105:423–435.

Kendeigh, S.C. 1944. Measurement of bird populations. Ecol. Monogr. 14:67–106.

Kendeigh, S.C. 1945. Community selection by birds on the Helderberg Plateau of New York. Auk 62:418–436.

Kendeigh, S.C. 1946. Breeding birds of Beech-Maple hemlock community. Ecology 27:226–244.

Kendeigh, S.C. 1948. Bird populations and biotic communities in Northern Lower Michigan. Ecology 29:101–114.

Kikkawa, J. 1968. Ecological association of bird species and habitats in Eastern Australia: similarity analysis. J. Anim. Ecol. 37:143–165.

Krebs, C.J. 1972. Ecology, the experimental analysis of distribution and abundance. Harper & Row, New York. 694 pp.

Kricher, J.C. 1972. Bird species diversity: the effect of species richness and equitability on the diversity index. Ecology 53:278–282.

Kruskal, J.B.; Carmone, F. 1969. How to use M-D-Scal (version 5M) and other useful information. Bell Telephone Laboratories (New Jersey). Mimeographed. 54 pp.

Lack, D. 1933. Habitat selection in birds, with special reference to the effects of afforestation on the Breckland avifauna. J. Anim. Ecol. 2:239–262.

Lack, D. 1937. A review of bird census work and bird population problems. Ibis (Ser. 14) 1:369–395.

Lloyd, M.; Ghelardi, R.J. 1964. A table for calculating the equitability component of species diversity. J. Anim. Ecol. 33:217–225.

MacArthur, R.H. 1955. Fluctuations of animal populations and a measure of community stability. Ecology 36:533–536.

MacArthur, R.H. 1957. On the relative abundance of bird species. Proc. Natl. Acad. Sci. U.S.A. 43:293–295.

MacArthur, R.H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599–619.

MacArthur, R.H. 1960. On the relative abundance of species. Am. Nat. 94:25–36.

MacArthur, R.H. 1964. Environmental factors affecting species diversity. Am. Nat. 98:387–397.

MacArthur, R.H. 1972. Geographical ecology: patterns in the distribution of species. Harper & Row. 269 pp.

MacArthur, R.H.; MacArthur, J.W. 1961. On bird species diversity. Ecology 42:594–598.

MacArthur, R.H.; MacArthur, J.W.; Preer, J. 1962. On bird species diversity II. Prediction of bird census from habitat measurements. Am. Nat. 96:167–174.

Margalef, D.R. 1968. Perspectives in ecological theory. Univ. of Chicago Press. 111 pp.

Martin, N.D. 1960. An analysis of bird populations in relation to forest succession in Algonquin provincial Park, Ontario. Ecology 41:127–140.

Mayr, E. 1946. History of the North American bird fauna. Wilson Bull. 58:3–41.

McIntosh, R.P. 1967. An index of diversity and the relation of certain concepts to diversity. Ecology 48:392–404.

Morse, D.H. 1967. Competitive relationships between Parula Warblers and other species during the breeding season. Auk 84:490–502.

Morse, D.H. 1968. A quantitative study of foraging of male and female spruce-woods warblers. Ecology 49:779–784.

Morse, D.H. 1976. Variables affecting the density and territory size of breeding spruce-woods warblers. Ecology 57:290–301.

Murdoch, W.W.; Evans, F.C.; Peterson, C.H. 1972. Diversity and pattern in plants and insects. Ecology 53:819–829.

Odum, E.P. 1950. Bird populations of the Highlands (North Carolina) Plateau in relation to plant succession and avian invasion. Ecology 31:587–605.

Odum, E.P. 1971. Fundamentals of ecology 3th ed. W.B. Saunders Co. 574 pp.

Orians, G.H.; Willson, M.F. 1964. Interspecific territories of birds. Ecology 45:736–745.

Pearson, D.L. 1971. Vertical stratification of birds in a tropical dry forest. Condor 73:46–55.

Pianka, E.R. 1971. Species diversity. *In* Topics in the study of life: the bio source book. pp. 401–406. Harper & Row.

Pielou, E.C. 1966. Species-diversity and pattern-diversity in the study of ecological succession. J. Theor. Biol. 10:370–383.

Pitelka, F.A. 1941. Distribution of birds in relation to major biotic communities. Am. Midl. Nat. 25:113–137.

Pough, R.H. 1950. Comment faire un recensement d'oiseaux nicheurs? Terre Vie 4:203–217.

Power, D.M. 1971. Warbler ecology: diversity, similarity, and seasonal differences in habitat segregation. Ecology 52:434–443.

Recher, H.F. 1969. Bird species diversity and habitat diversity in Australia and North America. Am. Nat. 103:75–79.

Roth, R.R., 1976. Spatial heterogeneity and bird species diversity. Ecology 57:773–782.

Schoener, T.W. 1969. Optimal size and specialisation in constant and fluctuating environments: an energy-time approach. Brookhaven Symp. Biol. 22:103–114.

Schoener, T.W. 1971. Theory of feeding strategies. Annu. Rev. Ecol. Syst. 2:369–404.

Shannon, C.E.; Weaver, W. 1949. The mathematical theory of communication. Univ. of Illinois Press. 117 pp.

Shimwell, D.W. 1972. The description and classification of vegetation. Univ. of Washington Press. 322 pp.

Simpson, E.H. 1949. Measurement of diversity. Nature (Lond.) 163:688.

Slobodkin, L.B.; Sanders, H.L. 1969. On the contribution of environmental predictability to species diversity. Brookhaven Symp. Biol. 22:82–95.

Smith, A. 1973. Stratification of temperate and tropical forests. Am. Nat. 107:671–683.

Snyder, D.P. 1950. Bird communities in the coniferous forest biome. Condor 52:17–27.

Sokal, R.R.; Rohlf, F.J. 1969. Biometry. W.H. Freeman, 776 pp.

Svärdson, G. 1949. Competition and habitat selection in birds. Oikos 1:157–174.

Terborgh, J. 1971. Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. Ecology 52:23–40.

Terborgh, J. 1977. Bird species diversity on an Andean elevational gradient. Ecology 58:1007–1019.

Terborgh, J.; Diamond, J.M. 1970. Niche overlap in feeding assemblages of New Guinea birds. Wilson Bull. 82:29–52.

Tramer, E. 1969. Bird species diversity: components of Shannon's formula. Ecology 50:927–929.

Vernon, C.J. 1970. The application of botanical ordination techniques to the analysis of avian communities. Ostrich, Suppl. 8:299–313.

Vuilleumier, F. 1972. Bird species diversity in Patagonia (Temperate South America). Am. Nat. 106:266–271.

Wallwork, J.A. 1970. Ecology of soil animals. McGraw-Hill. 283 pp.

Whittaker, R.H. 1965. Dominance and diversity in land communities. Science 147:250–260.

Whittaker, R.H. 1969. Evolution of diversity in plant communities. Brookhaven Symp. Biol. 22:178–196.

Whittaker, R.H. 1970. The population structure of vegetation. *In* Tüxen, R. *(red.)*. Gesellschaftsmorphologie. pp. 39 – 62. La Haye.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. Taxon 21:213–251.

Whittaker, R.H.; Lewin, S.A.; Root, R.B. 1973. Niche, habitat and ecotope. Am. Nat. 107:321–338.

Woodwell, G.M.; Smith, H.M. *(eds.)*. **1969.** Diversity and stability in ecological systems. Brookhaven Nat. Lab. Publ. no 22. 264 pp.

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