THE WEST CHAMPLAIN HILLS

PART II: SUMMARY OF FINDINGS, 2004–2007

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THE WILDLIFE CONSERVATION SOCIETY and the ADIRONDACK NATURE CONSERVANCY

CONTENTS

1 Introduction

This part of the Champlain Hills report summarizes the scientific findings from fieldwork in 2002, 2004, 2006, and 2007. For completeness, and to allow this part of the report to stand alone, some material is repeated from Part I.

The field work described here was funded by the Nature Conservancy and the Wildlife Conservation Society; some of the analysis and many of the graphics in this part were prepared during a Bullard Fellowship at Harvard Forest. Jerry Jenkins was the principle investigator throughout the study and wrote and illustrated the reports. Bill Brown, John Davis, Brett Engstrom, and several others helped with the field work in 2004. John Davis, Leah Nelson, and Patti Smith helped in 2006. Celia Evans, Peter Jenkins and Barbara Lott were full-time field assistants in 2007. Barbara did the geological sampling and determined the rock specimens, and Peter processed the soil samples and determined the soil pHs. The Eddy Foundation provided housing for us at Black Kettle Farm in Essex, and we are indebted to them and to the residents of Black Kettle for making us at home during our stay.

This part of the report is a summary of the main findings of the study, presented as a series of graphics with brief annotations. For a fuller description of geography and flora see *The West Champlain Hills, Part I: Geography, Rare Species, Disturbance, the Two Kinds of Richness, and the Calcareous Oak-Hickory Community.* For details of the individual sites see: *The West Champlain Hills, Part I: Site Descriptions and Species Lists.*

PART I: OCCURRENCE & DISTINCTNESS

2 Geography

For about 50 miles, from the north end of Lake George to the mouth of the Ausable river, the west shore of Lake Champlain (New York, USA) is bordered by low rocky hills, which often have rounded summits and open cliffs on their south and east sides. The hills are quite dramatic, especially in winter, and have more exposed rock than many higher mountains, and more open summits than most alpine areas.

So far as I can tell, from 30 years of flying and photographing New England from the air, these may be the some of rockiest low hills in the Northeast.
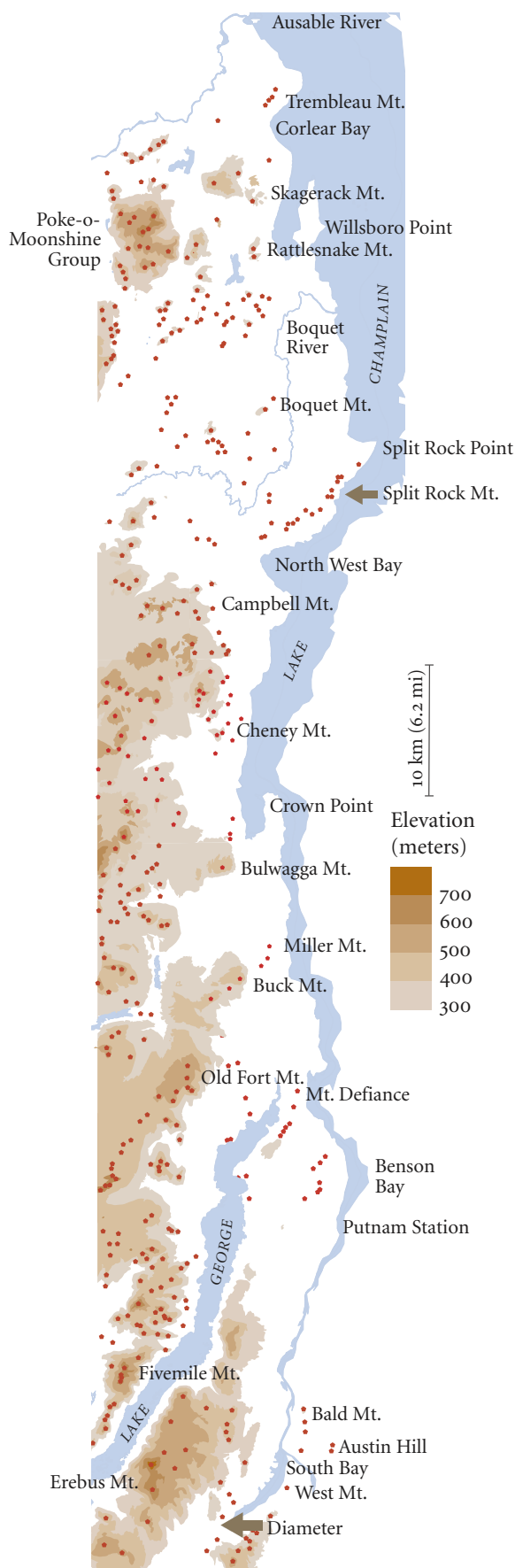
3 Geology

Like the rest of the Adirondacks, the bedrock in the West Champlain Hills is largely igneous. Granitic gneisses with much quartz are the commonest rocks. Anorthosite, a base-rich rock with much plagioclase and little quartz, is the dominant rock in the Westport area. Gabbro, amphibolite, and various meta sediments occur locally in small amounts.

Barbara Lott collected and identified about 100 bedrock samples from 20 study sites in 2007. She found that, with the exception of minor amounts of amphibole, and one or two sites where there was both gabbro and gneiss, the bedrock at each site tended to be homogenous, and to accord well with the regional geological map.

4 The Champlain Hills Dry-Rich Community

The typical forests of the western Champlain Valley, as of the Adirondacks as a whole, are continuous-canopy northern hardwoods forests, typically of fairly low diversity and with an acid-loving flora. Forests of this sort dominate the post-agricultural lands of the valleys and north-facing slopes, but tend to give way to open, glady, oak-hickory-hornbeam forests on south slopes and rocky summits.

The oak forests and their associated balds and glades differ sharply from the surrounding northern hardwoods forests: they are lower, much more open, much richer in herbs and graminoids, and much more likely to contain calcium-loving species.

I call this mixture of oak-woods and grassy openings the Champlain Hills Dry-Rich Community, and regard it as a distinctive plant community that is very different from the northern hardwoods forests in which it is embedded.

It shows this distinctness in three ways: in structure, in situation, and in composition.

In structure it is a low, open community, never with tall trees, always with much sun on the floor, and always with many grasses, sedges, shrubs, and tall herbs. It usually mixes open forests with about 50% canopy and soils that are 0.2 m deep or more with open rocky barrens with no canopy and thin soils interrupted with much bare rock.

The forests and the barrens are distinct vegetation types, and if we want to slice our communities finely they might be regarded as different communities. But they intergrade and are interspersed on a scale of a few meters, and because for practical reasons I like my communities bigger and more mappable, I regard them as two vegetation types within a single community.

Granite & gneiss (G)

Anorthosite (A)

Ga
Gabbro & amphibolite (Ga)
Ga

Granite & gneiss (G)

10 km (6.2 mi)
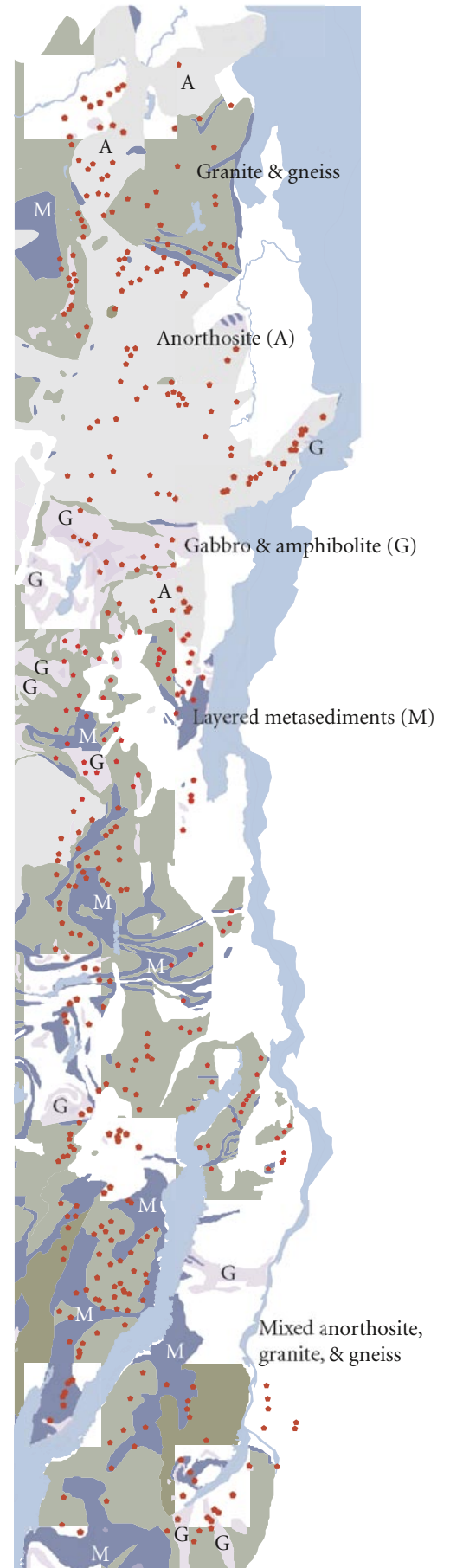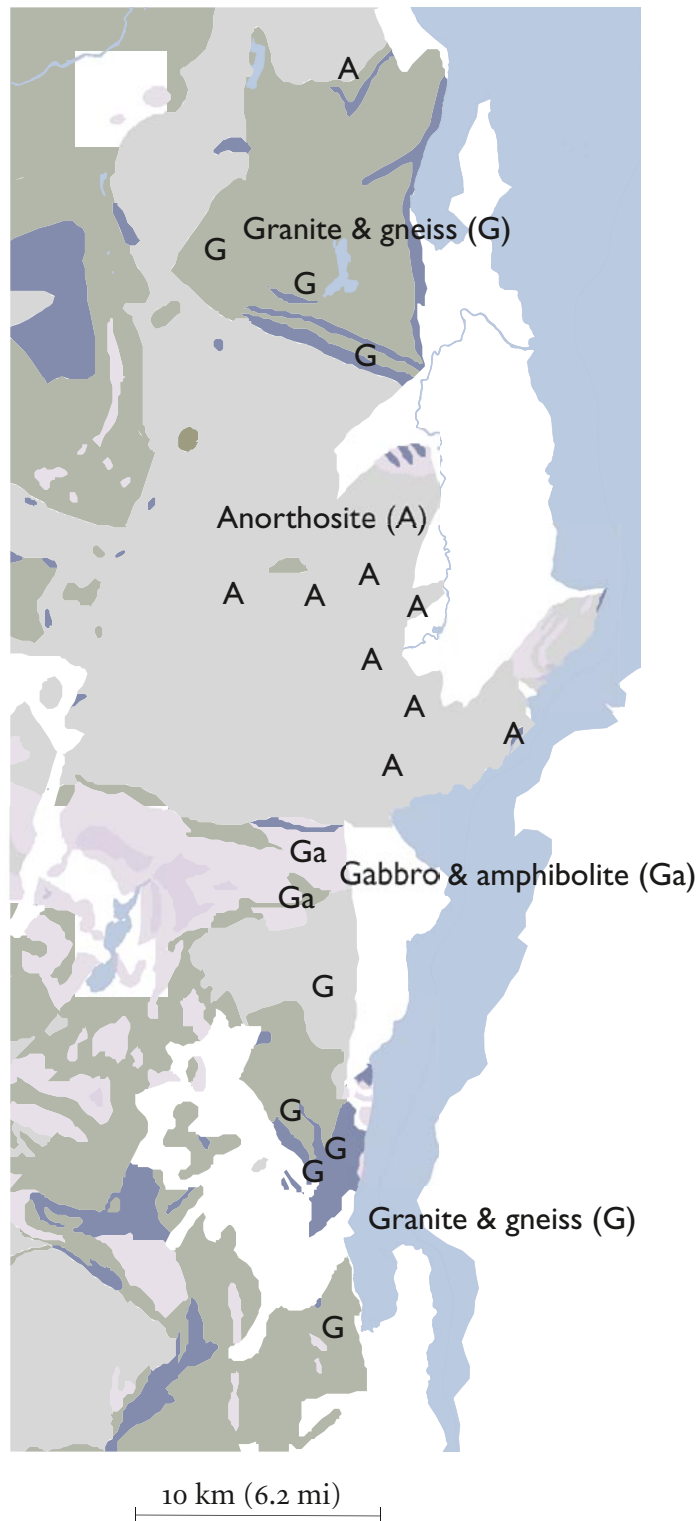
Left, bedrock lithologies of 2007 study sites determined by Barbara Lott (capital letters), compared with those given on the New York State geological map (p. 5). The agreement is quite good, except at two sites near the

Right, two characteristic vegetation types of the Champlain Hills community, open glades with a partial canopy and grassy understory and vegetated ledges with bryophytes and herbs. Both have many characteristic indicator species that are rare outside this community.

Glades on Coon Mt.

Vegetated ledges on Harper Mt.

In situation, the community is usually south or south-east facing (occasionally southwest), and restricted to dry benches, ledges, and slopes.

In composition the community is variously grass, oak, hickory, or hornbeam dominated, and about 170 ecologically specialized species, many with dominantly southern distributions and near the northern range limits here, that are restricted to dry or calcareous sites or both. At least 100 of these require dry warm sites and almost never occur in northern hardwood forests. The other seventy require calcareous sites but not necessarily dry ones. They are found widely in fertile hardwood forests but only rarely in acid ones.

5 Formal Community Definition

The Champlain Hills Dry-Rich Community occurs in the Champlain Valley and adjacent Taconic and Adirondack mountains. Physiographically is found on rocky, south-facing slopes, benches and summits, on both igneous and metasedimentary rocks, where the soils are thin and there is much exposed bedrock. Structurally it is a glade community, with low sparse forests, many openings, and a grassy understory. Floristically the community is dominated by plants of the Oak- Zone, with many shrubs and herbs, and in particular many grasses and sedges. Ecologically, the herb species most commonly clump-forming, winter-deciduous perennials. Annuals, creepers, evergreens, and rhizomatous species all occur but are rarer. Taxonomically the grasses and "advanced" zygomorphic families (Beans, Snapdragons, Composites ...) are much commoner and more diverse in this canopy than they are in ordinary woods. Many of the herbs are drought-tolerant, wilting and recovering during dry periods in the summer, and many bloom in the late summer or fall. About 135 of the species are commonly found in areas with calcareous bedrock and absent from areas of exclusively acid rocks. Another 35 of the species are characteristic of dry soils and rock exposures but are not uniformly calciphilic.

Right, two characteristic vegetation types of the Champlain Hills community: an open, somewhat barren summit with low trees and shrubs and sparse herbs and grasses; and a hillslope forest with rocky glades. The summit community usually is low diversity and has few calcareous indicators. The wooded slopes with outcrops are typically high diversity and have a mixture of dry-rich and moist-rich indicators.

Summit barrens community on Coot Mt.

Wooded slope with glades, Harper Mt.

For the purposes of analysis I divide the 170 ecologically specialized species into three groups. The 66 *moist-rich* species are encountered widely in mesic forests on calcareous soils. The 74 *dry rich species* are encountered most commonly on dry sites, and are often found on or seemingly restricted areas of calcareous bedrock. And the 35 *other-dry* species are other species of dry and usually barren sites which either occur regularly on non-calcareous bedrock (juniper, sweet fern), or whose calcium status is unknown (Douglass's knotweed, rock spikemoss).
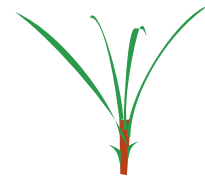
Carex pedunculata

Carex laxiflora
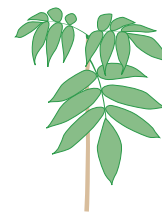
Red Elderberry
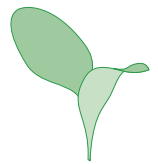
Wild Leek
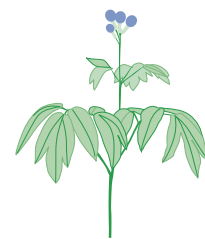
Blue Cohoosh

Sweet Cicely

Right, examples of the three groups of indicator species in the Champlain Hills community. Even though the community is characteristically dry (and in fact subject to extreme summer drought) moist-rich species occur regularly within it. This is in part because the community is a mosaic of moist and dry habitats, and in part because the groups are artificial constructs and the species have a range of preferences from mesic and drought intolerant to xeric and drought tolerant,

Prickly Gooseberry

Allegheny Vine

DRY-RICH SPECIES

Broad-leaved
Mountain Rice

Purple Melic

Woodland Sunflower

Purple Clematis
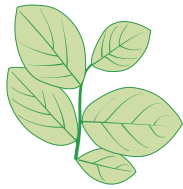
Leatherwood

Fragrant Sumac
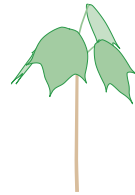
Limber Honeysuckle

Stiff Sandwort

OTHER DRY SPECIES

Common Pinweed

Sharp-leaved
Mountain Rice

Douglas's Knotweed

NON-RICH SPECIES

Marginal Woodfern

Striped Maple

Red Trillium

DRY-RICH SPECIES

33% of median

MOIST-RICH SPECIES

71% of median

NONINDICATOR SPECIES

36% of median
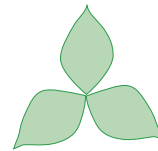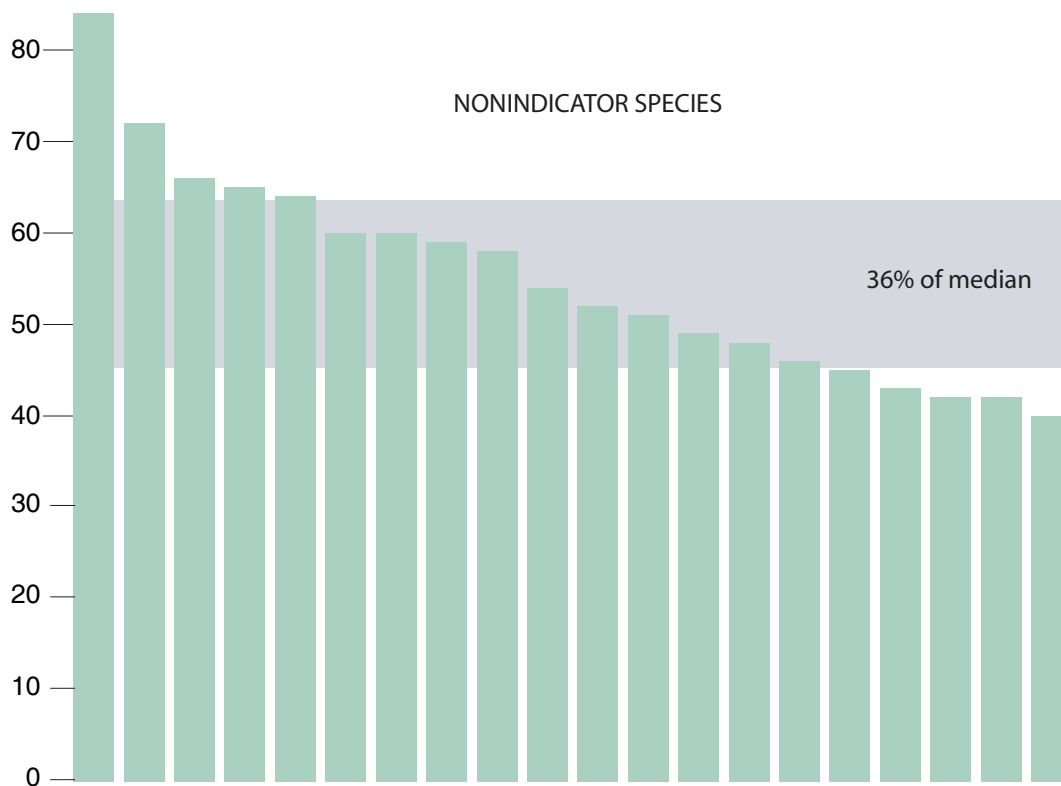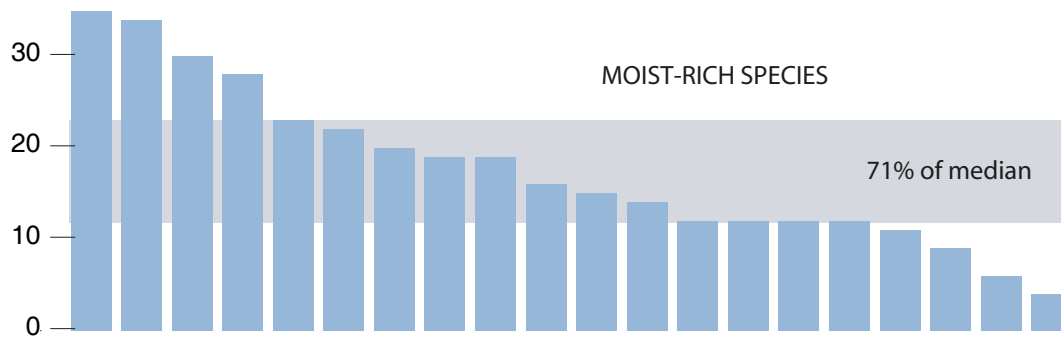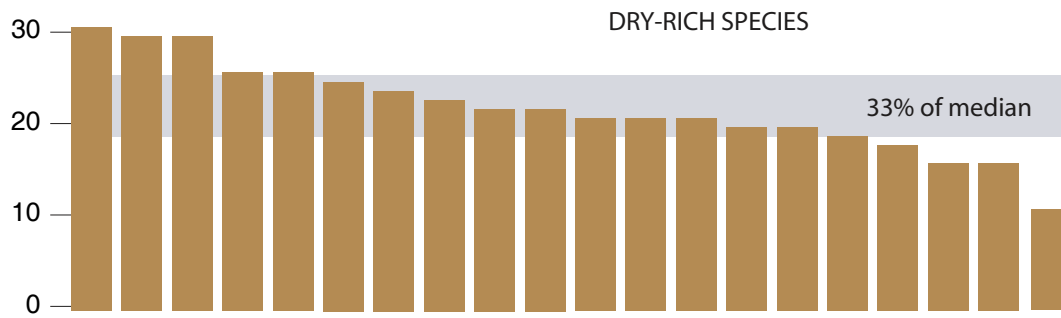
Gray boxes give the range of the middle 11 sites (55% of all sites). The percentages compare height of the gray box (range of middle 11 sites) to the median species richness.
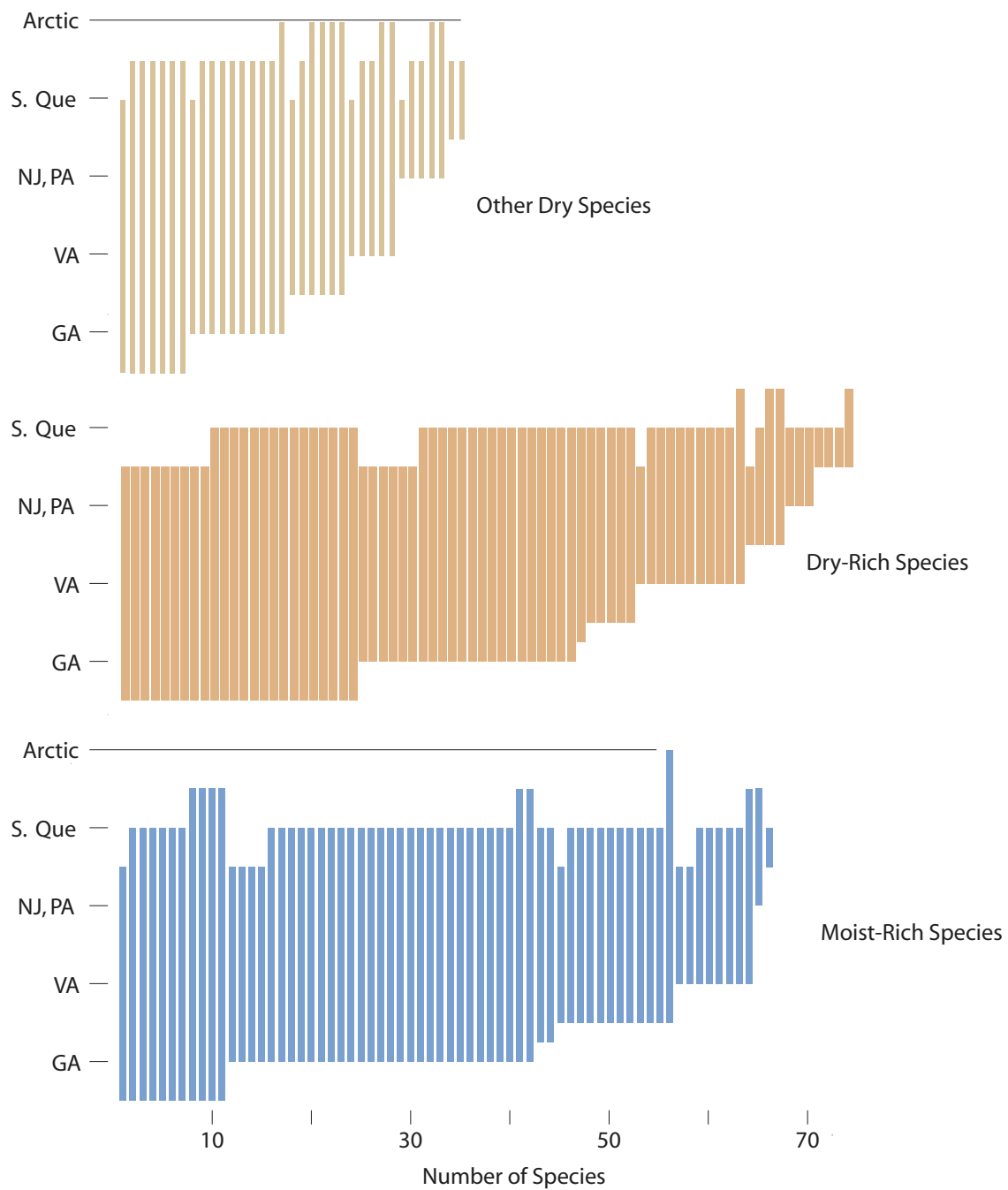
Left, the ranked diversities of indicators and nonindicators. The moist-rich species are more variable between sites than the dry-rich species and nonindicators, but are still present at all sites. Above, the latitudinal ranges of 170 indicator species. The dry-rich and moist-rich species are largely warm temperate species that are near or at their northern range limits here. The other-dry species are more wide ranging and have cold-temperate and subarctic species.

7 Physiographic Boundaries

The CHC is restricted to dry, convex, terrain with thin soils and much exposed rock. It requires some surface water flow and at least a thin soil, and so is not found on cliff faces or on the driest summits and ledge crests. It is thus a middle- and upper-slope community on hills with a southerly exposure.

As such, it is often sharply bounded. The community is absent from lower slopes where the soils are deeper and moister, from ravines, and from northern slopes, even from rocky northern slopes with thin soils that might otherwise appear suitable. Its boundaries are often abrupt: on the south faces it usually starts at the first major outcrop, and you can often go from ordinary northern hardwoods to a well developed CHC in 10 meters or less.

Its currently known elevation range is from lake level (30 meters) on Split Rock Mountain to somewhere around 400 meters, with many examples between 250 and 350 meters. It is present at 400 meters on Cheny Mountain, 410 meters on Drake Mountain, and 450 meters on Cook Mountain. It is absent at 450 meters on Pokamoonshine, 500 meters on Mud Pond Mountain, and 550 meters on Bald Pond Mountain.

8 Geological Boundaries

So far, the community doesn't seem to have any. Many of our examples were on anorthosite, but we also found it on gneiss and granite—which is to say on all the major igneous rocks of the western Champlain Valley. It also occurs on marble and calcareous schists on the Vermont side of the lake, and similar communities occur on basalt in Massachusetts

9 Geographic Boundaries

We have clear examples of the community from Drake Mountain, about 5 miles south of the Ausable River, south to the Diameter at the southern tip of Lake Champlain, and inland to Mount Discovery in Elizabethtown. On the Vermont site of the lake examples occur somewhat farther to the north, from around Colchester south to Benson, and inland to Snake Mountain in Addison, the Great Ledge in Fairhaven, Twin Mountain in West Rutland, and possible St. Catherine Mountain in Poultney.

The northern, eastern, and southern limits seem fairly certain: I have looked for, but not found, any really comparable communities north of the Ausable River, south of Whitehall, or in the eastern Taconics. The western limit is uncertain. The community seems to become less common as you move westward into the higher and
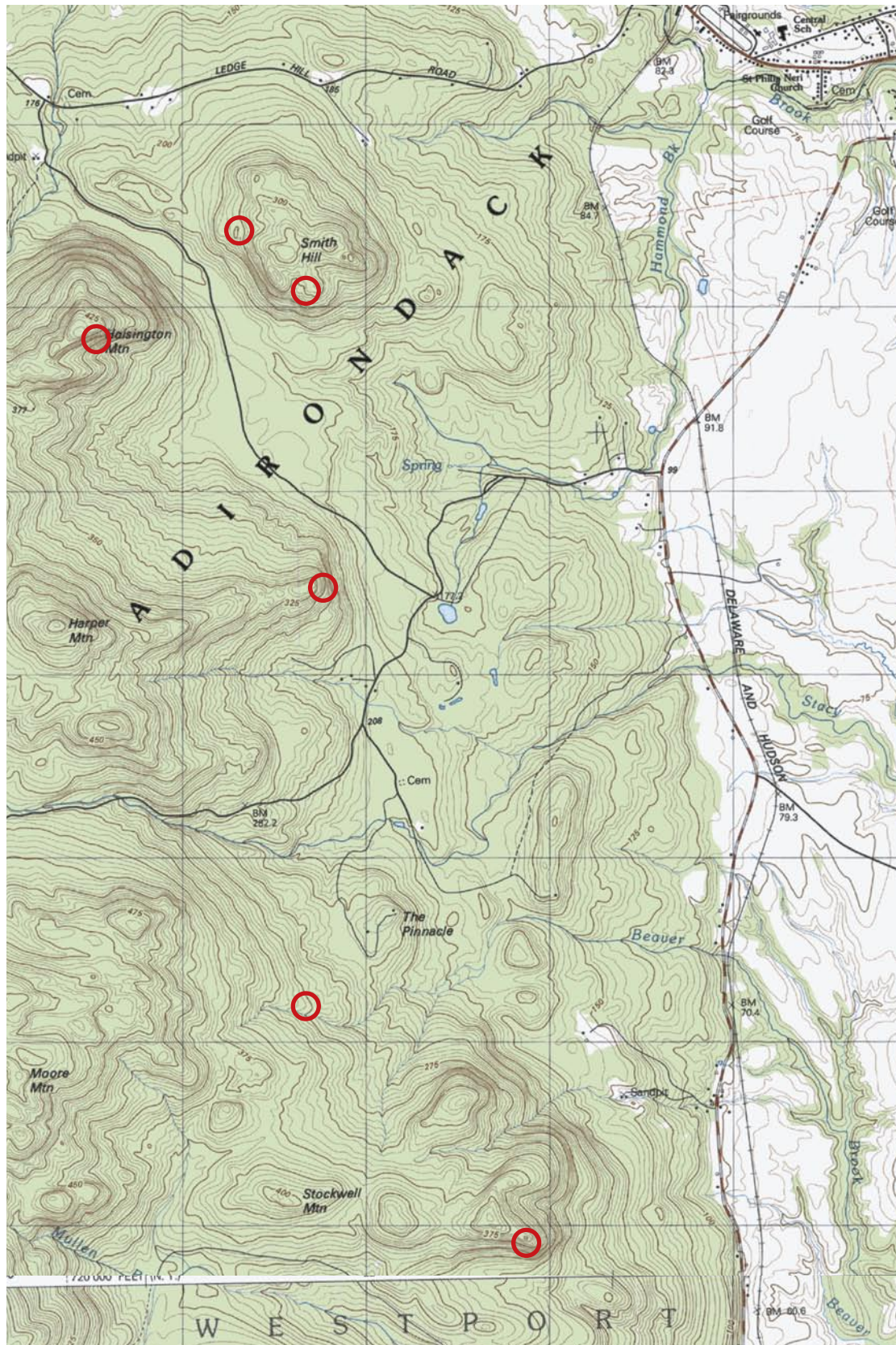
wetter Adirondacks, but we have not done enough fieldwork to be sure where the boundary lies.

10 *Incidence*

The CHC is of remarkably consistent incidence: over and area of at least 300 square miles, between Willsboro and Port Henry, almost every suitable rocky, south-facing slope under 500 meters in elevation that we examined had an example of this community.

North and south of this area the incidence is less well known, simply because we have done less fieldwork. In particular, there are many rocky hills between Moriah and Lake George Village that we have not checked.

The regular incidence strongly suggests that the CHC is a true *physiographic community*, controlled by bedrock and topography, and not just an interesting aggregation of plants produced in a few places by chance or history.

11 *Numbers of Known & Possible Champlain Hills Sites*

Currently we know of about 33 CHC sites between the Ausable River and the south end of Lake Champlain. In the area north of Port Henry where most of our work was concentrated there are at least twenty more sites that are near to ones we have already studied and which, based on exposure and topography and the high incidence in this area, are likely to additional examples. Outside this area there are many rocky hills around Lake George, between Ticonderoga and Port Henry, and in Wilmington and Chesterfield which have not been investigated. Any of these might be a possible CHC site.

12 *Number of Protected Sites*

Currently Split Rock is in the Forest preserve, Coon Mountain is owned by the Adirondack Nature Conservancy, Boquet Mountain and Kinglet Hill by the Eddy Foundation, and Mount Defiance by the Fort Ticonderoga Association. All the other sites are privately owned, and most by different owners. Shirely Forests, a private timber company, owns three sites, Blais Hill, Ferguson Mountain, and Cob Hill. The Westport Hills property, formerly owned by International Paper and currently by Lyme Timber, has about a dozen known sites and at least a half-dozen more likely ones. It is the richest single ownership, public or private, that we currently know. It is currently protected by a conservation easement. Adding public ownership or explicit protection for the CHCs and

Right, topographic situations of known Champlain Hills community sites between Westport and Port Henry, continued from p. 15. The red circles are sites that we checked that contained the community. The two black circles, are sites that we checked that did not contain the community.
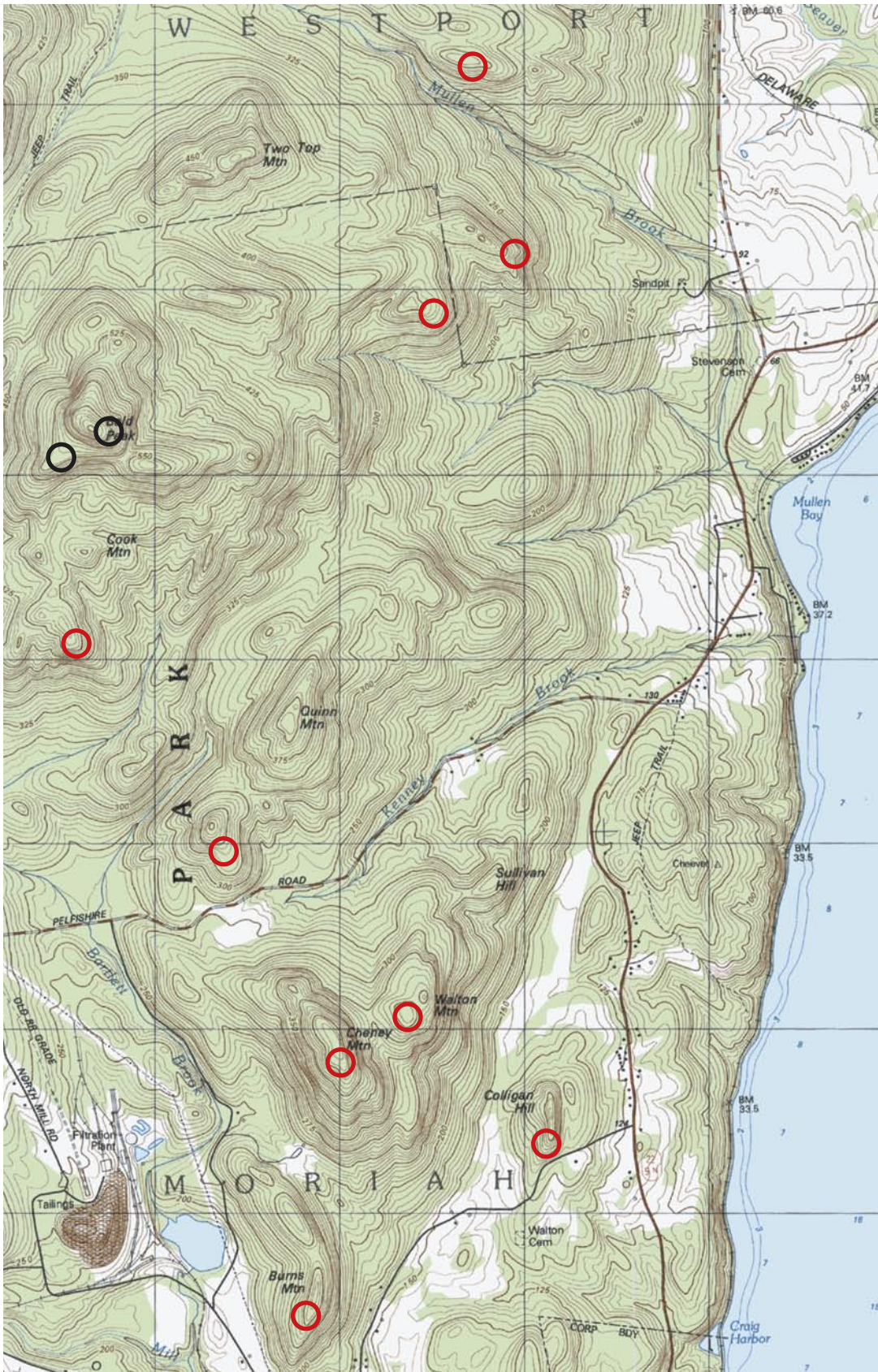
their associated woods would be a major conservation achievement.

13 *Regularly Associated Communities*

The Champlain Hills Community is usually surrounded by northern mixed forests, most commonly dominated by sugar maple, red maple, or hemlock. At many sites there are, in addition, small amounts of rich mesic woods with calciphilic but not drought-tolerant herbs. Commonly these woods occur in ravines and below ledges. Only rarely do they seem well developed and equivalent to the rich mesic woods that develop on carbonate rocks in moister situations. More often they consist of a few indicators scattered, often in small quantities, in more or less ordinary northern hardwoods forests.

Many hills with CHCs on their flanks have open rocky summits with drought-tolerant species but few or no dry-rich indicators. I regard this as a separate community—it is not forested and lacks calcium indicators—but as one that differs only in degree, and grades into and may be indistinguishable from some open slabs in the CHC.

14 *How strongly does the CHC contrast with these associated communities?.*

It contrasts very strongly, in both appearance and composition with ordinary northern hardwoods and with postagricultural successional mixed forests. It is lower, grassier, shrubbier, much more open, and has a suite of indicator species that do not occur in ordinary forests. The median indicator richness for our 2007 study sites was 16 moist-rich species, 22 dry-rich species and 10 other-dry species, only a very few of which are likely to be encountered in the adjacent woods.

It contrasts less strongly but still clearly with the moist rich community, which is usually darker, maple-dominated rather than oak-dominated, more ferny and less grassy, restricted to mesic sites, and less likely to have dry-rich species. The two communities often occur together and share species and can grade into one another. All our dry-rich communities, for example, had at least some moist-rich indicators on their lower slopes. But they are none the less distinct in appearance and composition, even though boundary is not sharp.

The regular presences of moist-rich species within dry rich communities suggests that the separation between the dry-rich and moist-rich groups is not fundamental, and that they may form a continuum. While the extreme members of the groups do not overlap at all—maiden hair fern doesn't grow with rusty woodsia

Wood lily and rusty woodsia, two characteristic Champlain Hills species. Neither is ordinarily thought to be a calciphile, but both are relatively common in this community and largely absent from acid-rock communities outside it.

or poke milkweed with four-leaved milkweed— many other spe-
cies can, give the right habitats, occur with members of the other
group, and most of our CHCs include members of both groups.

The CHC also grades into a more common open summit com-
munity of drought-tolerant and acid-rock-tolerant species that I
call the open-dry community. The open-dry community shares
many species with the dry-rich community, and is distinguished
primarily by its lower diversity, and the lack of calcium-requiring
species. Its limits are uncertain, both because is often found on
summits just above benches that have dry-rich communities, and
because we are not sure of the calcium requirements of some of the
species involved.

15 Summary: The CHC is Well Defined

Plant communities can be defined in different ways at different
scales. For me, a plant community is a group of plants, covering
an area significantly larger than that of a single individual and its
neighbors, that occurs in a particular physiographic situation or
in particular ecological conditions, and has a distinct structure
(physiognomy) and distinct composition that reflects its situation
and ecology.. As a working rule, I like vascular plant communities
to be at least a few hundred square meters in area, and to have less
than 70% of their species in common with related communities.

By these criteria, the CHC is quite well defined. It occurs in a
distinctive topographic situation, within a definite altitude band.
It has a distinct structure and a distinct composition: on average
about 50 species per site, or 48% of the flora, were indicator spe-
cies that did not occur in the ordinary northern hardwoods flora,
and 22 species per site, or 21% of the flora, were species that were,
at least in the Adirondacks, largely restricted to this community.
And finally it had a high incidence (high probability of occurring
on topographically suitable sites) indicating a strong relationship
between situation, physiognomy, and composition.

PART II: PATTERNS WITHIN AND AMONG SITES

This part of the report deals with vegetation structure at medium and large scales in the Champlain Hills. It focus on correlations between the groups of indicator species—the species which offer the sharpest definition of the community—and either other indicator groups or environment. The aim, in other words, is to explore the extent to which the vegetation changes as its setting changes, and the extent to which the changes in different components of the vegetation are coherent.

By medium and large scales I mean over distances from 5 meters, the size of our smallest plots up to an area of about 300 square kilometers, the area for which I currently have quantitative information.

My interest in these particular scales is that they define the range over which the notion of plant community seems best defined. As explained in Section 14 above, me a plant community is a chunk of vegetation in a distinct physiographic situation, whose spatial and ecological structure depends upon, and is in some extent peculiar to, that situation.

Thus, for example, bouldery taluses common have a patchy vegetation that favors certain life forms and taxonomic groups, and varies in a predictable way from the bottom to the top of the talus. These patterns—spatial, life history, life form, taxonomic—are, again in my view, what define the community. It is not just a list of plants, but rather a list of plants that have been selected and arranged in a definable way by the physical characteristics of a particular place.

Defined this way, a community will only be visible at scales large enough for the characteristic relations between place and plants to emerge, and small enough that these relations are relatively uniform.

Both the "large enough" and "small enough" are important.

At smaller scales, you have too little information—too few species and too little sense of their relation to physiography—to get a sense of the community. At large scales, climate and physiography become less comparable, species often change their edaphic behavior, and range-limits change the species pool, all of which muddy the boundaries between communities.

There is, of course, much botanical order at larger and small scales. At larger scales you have turnover, endemism, and the other processes that differentiate floras and create tension zones between them. On small scales you have a rich array of local processes, especially the choice of sites by individuals and the competition between neighbors, which create structure. These sorts of large- and small-scale order are obvious and easily documented features

NUMBERS OF MOIST AND DRY CALCIUM INDICATORS

Moist calciphiles
Xeric calciphiles

NUMBERS OF DRY-RICH AND OTHER-DRY INDICATORS

Other xeric species
Xeric calciphiles
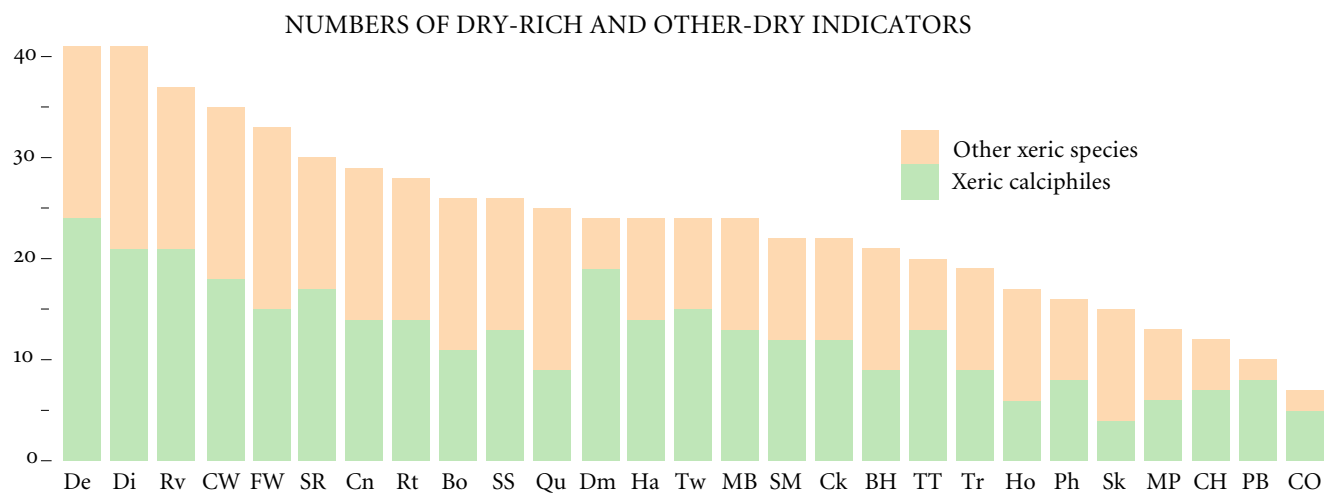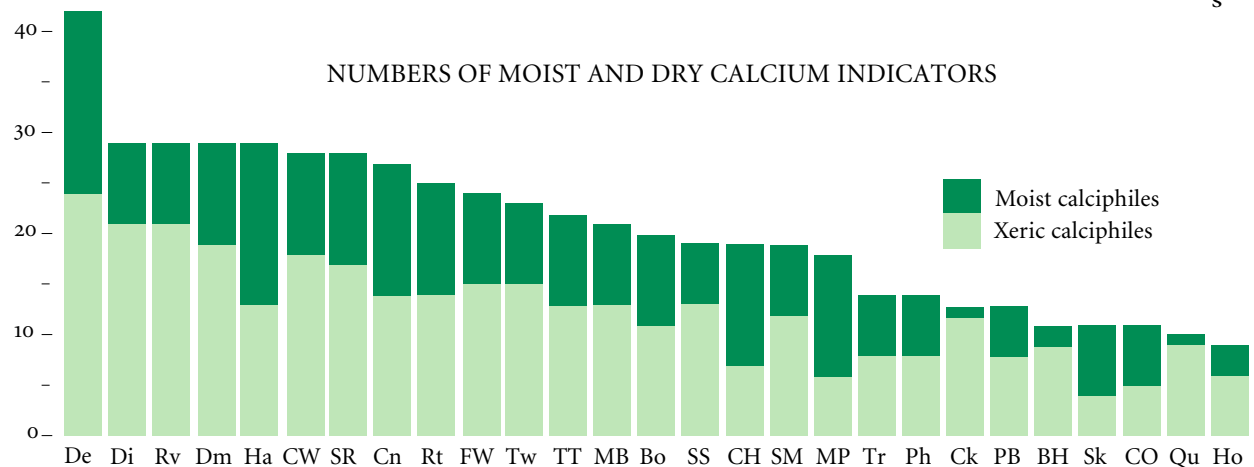
Numbers of indicators at sites visited prior to 2007, mostly from fall data.
The numbers of dry-rich and other-dry indicators show a weak correla-
tion; the numbers of moist-rich and dry-rich vary independently.

of vegetation and so familiar to every field botanist. But they do not, by themselves, help define communities.

Thus my question here is whether there are vegetation patterns at the intermediate scale appropriate for describing communities. It is clear (Section 13) that the community *contrasts* sharply with other communities and so deserves its name and is, to some extent, a conceptually useful biological entity. And it is also true (and in fact universal) that the plants within it have microhabitat and competitive relations, and are arranged in orderly ways with respect to gradients and each other. But it is not at all clear that the community as a whole has a pattern—that its composition relates in some predictable way to geography, for example, or that it contains groups of species that are arranged in predictable ways.

If it does, then we know something important, which is that it is either organizing itself, or being organized by larger ecological forces. And if it does not, we also know something, which is that, like a sandpile or the rings of Saturn, an entity that looks highly patterned from the outside can look quite patternless once you look inside it.

16 *What sorts of internal order do communities have?*

By *internal order* I mean patterns involving only examples of that community. These may be patterns within a single site: differences in composition and diversity associated with topographic gradients, associations between different indicator groups, patterns (which I call generically *sample-pool* patterns) in the relative abundance of species or the increase in diversity with area.

Or they may be patterns that arise when sites are compared: variations in diversity or composition with bedrock, physiography, or soils; sample-pool patterns computed between sites.

17 *What data were available to look for these patterns?*

We had two sorts of data:

> - Species presence data for 33 sites. The data were gathered in different seasons with surveys of different intensity and so cannot be used for quantitative comparisons.

> - Plot- and transect-based data, gathered at 20 sites in 2007. The data include rock samples, soil samples, species presence in 5-meter square plots and species presence in 5-meter segments of 100-meter transects.

We also have aspect, elevation, and topographic information for each site. Because many of the sites face the same way and are at

CHAMPLAIN HILLS SITES FOR WHICH
WE HAVE FLORISTIC DATA

- Trembleau
- Drake
- Skagerack
- Poke-o-Moonshine
- Rattlesnake
- Sugarloaf
- Bristol
- North Bouquet
- Ferguson, Whipple
- South Bouquet
- Blais
- Cobb
- Discovery
- Kinglet
- Rattlesnake
- Phinney
- Little Raven
- Coon
- Split Rock
- Raven Hill
- Barn Rock
- Kronk, Twin
- Hoisington, Smith
- Harper
- Stockwell
- Bald Peak
- Two Tops
- Cook
- Cheney, Walton
- Quinn
- Colligan
- Burns
- Coot
- Mt. Defiance
- The Diameter

- Examined 2002–2006
- Examined 2007
- Examined previously

5 x 5 m plot
on knoll or
bench

20 Sites, 2 -10 hectares

1 x 100 m transect,
with 20 1 x 5 m segments

Other arrangements of plot and transect

The sampling plan used in 2007. We record species presence for the entire site in each 5-meter segment of a 100-meter transect, and in a 5 x 5 meter plot located at the highest point of the transect.

similar elevations, only limited use could be made of this information.

We did not gather cover information, both because it would have been hard to gather accurately for the 5-meter sampling units we were using, and because I felt it would be more likely to reflect local; features (soil depth, shading…) than overall properties of the site.

18 Intersite Comparisons I: The Range of Site Diversities.

Here and in what follows I use DR for dry-rich, MR for moist-rich, and OD for other-dry.

Our sites typically have about a hundred species, of which about 20 are DR, 15 MR, and 10 OD. The data are spread out and the standard deviations are large, up to 50% of the mean. Interestingly, all the distributions are asymmetrical, with more sites on the high-diversity side of the peak than on the low. It seems that once you decide, as we did to survey a whole hill, there are threshold values for richness—80 species overall, 10 MR species, 15 DR ones— below which only a few sites will fall. The median values are near the threshold, while values above the median form an upper tail, which is often truncated. Even though there are 66 MR indicators and 74 DR ones, no site went above 35 MR ones or 31 DR ones, and no site had more than 73 of the 170 indicators that occur in the community.

The DR diversities are somewhat more concentrated than general, MR, or OD diversities, and have a higher low-diversity threshold and a higher peak. (This is also shown in the ranked bar graph.) This reflects that fact that we were deliberately sampling DR communities, and did not sample sites at which the community was poorly developed.

Thus there is no such thing as a characteristic diversity of a CHC. The diversities form a range, tending to be truncated above and below. Few sites sample less than a quarter and none much more a half of any of the three pools of indicator species.

Said in another way, the pool of species in the community is significantly larger than the pool in even the richest sample; the individual sites are samples, and often fairly small samples, from a rich pool, rather than replicates of a standard pattern; and that—conservationists attend—no single site or small collection of sites can represent the whole community very well.

19 The Range of Transect and Plot Diversities

The distributions of the transect and plot diversities are more compressed because less area was sampled. The plots, which were placed on knolls or summits, were usually quite dry, have only about a

DISTRIBUTION OF TOTAL AND INDICATOR DIVERSITY, 2007
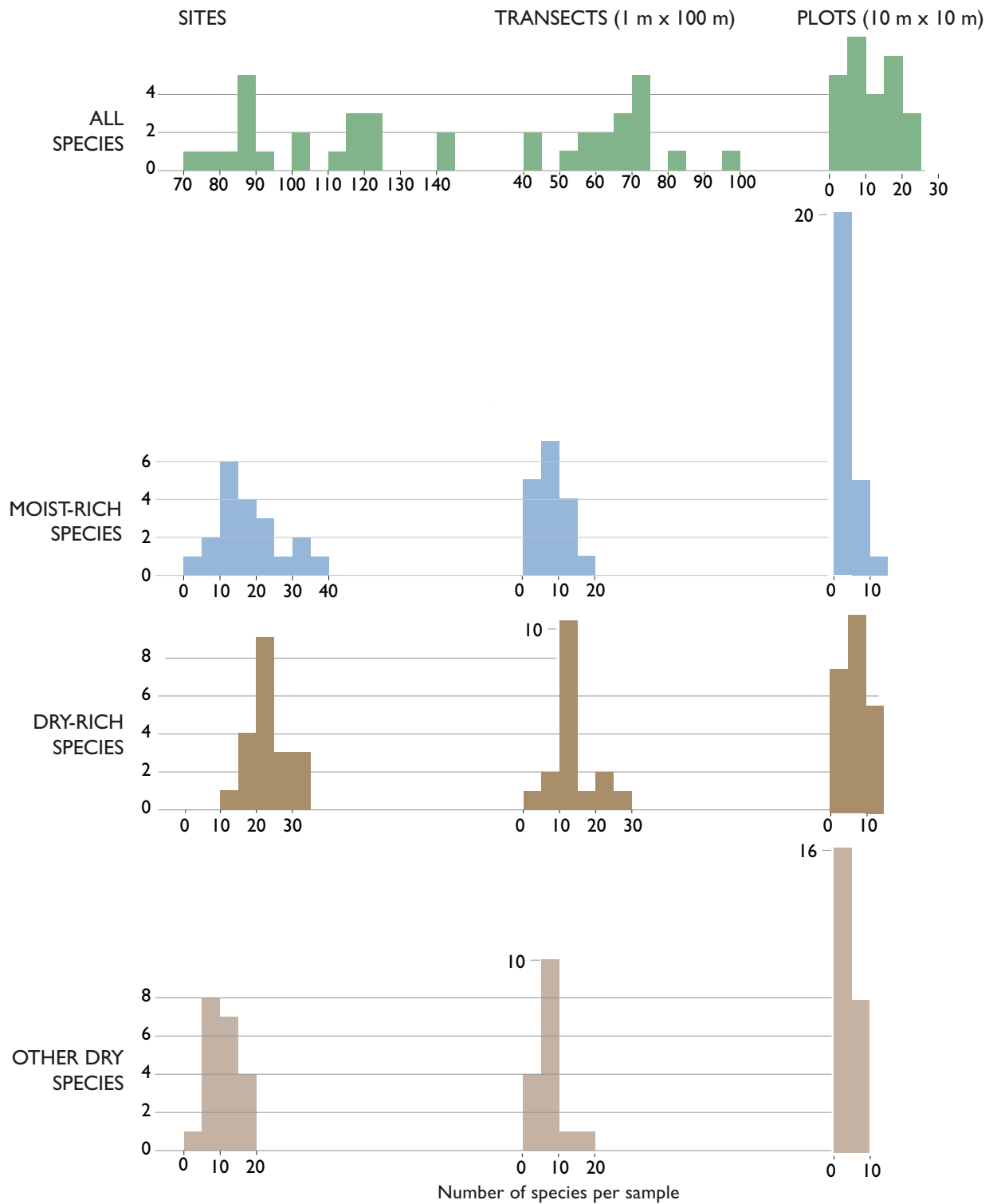
Y-axis gives the number of samples per 5-species range of species diversity. The y-axis are identical.
The x-axis have identical scales, but are shifted to the left in the pots for sites and transects
in the upper row.

third of the DR and OD species of the site and very few (14%) of the MR species at all. The transects, which typically extended down from the plot into more shaded habitats, do significantly better. They capture, on average, 69% of the DR species of the site, 64% of the OD species, and even a surprising 59% of the MR species. Thus they provide a reasonable sample of the total diversity of the site, and might be used as a standardized way of comparing sites.

20 Differences Between Summer and Fall Surveys

The mean diversities of MR and DR species recorded in the summer surveys of 2007 were about twice that recorded in the fall surveys of 2004 and 2006. This was in part the result of some species being more visible or determinable in the summer, and in part the result of more intense surveying. In 2004 and 2006 I often worked by myself or with an assistant who was not a botanist; in 2007 we had a four-botanist team and, because we did transects and plots, spent more time at each site, and often covered a larger area.

Other-dry species varied much less: the mean number of species recorded in the summer surveys of 2007 was almost the same as that recorded in fall ones of 2004 and 2006.

The effect of survey intensity is probably at least as important as that of survey season. This is shown nicely by diversities from sites that were visited twice. At Harper Mountain, where the 2006 and 2007 surveys followed the same route and covered almost the same area, the total number of indicators seen in 2006 was 40 and the number seen in 2007 was 57, a gain of 42% in the summer survey. At Cob, where the 2006 survey was brief and the 2007 both more intensive and over a large area, the numbers were 23 and 61, a gain of 165%. And at Coon, where two 2004 surveys covered a large area and the 2007 survey was restricted to the south summit, the reverse was true. The total numbers of indicators in 2004 and 2006 were 42 and 31, a decrease of 26%.

21 How common are uncommon species?

The answer, of courses, depends on what is meant by uncommon. The 33 sites we have studied probably comprise less than 200 hectares of land, and yet contain at least 73 species that (within the Adirondacks) are either restricted to the CHC or very rare outside of it. Some of these plants (shagbark hickory, woodland sunflower) are common within the community. Others (spring for-get-me-not, Missouri rockcress) are only known from a single site each. None the less, all of these 73 could with some justice be called uncommon in the Adirondacks.* Under that definition, the known examples of the CHC have about 560 occurrences of uncommon communities, or about 17 per site. These are surprising numbers,

*About 25 of these species are frequent or common within at CHC sites, and the remaining 48 uncommon or rate at CHC sites. Applying Heritage Program categories to the Adirondacks, the fiorst 25 species would be s3 species within the Adirondack region, and the other 48 s2 or s1 species within the Adirondack region.

NUMBERS OF INDICATOR SPECIES AT 2007 SITES
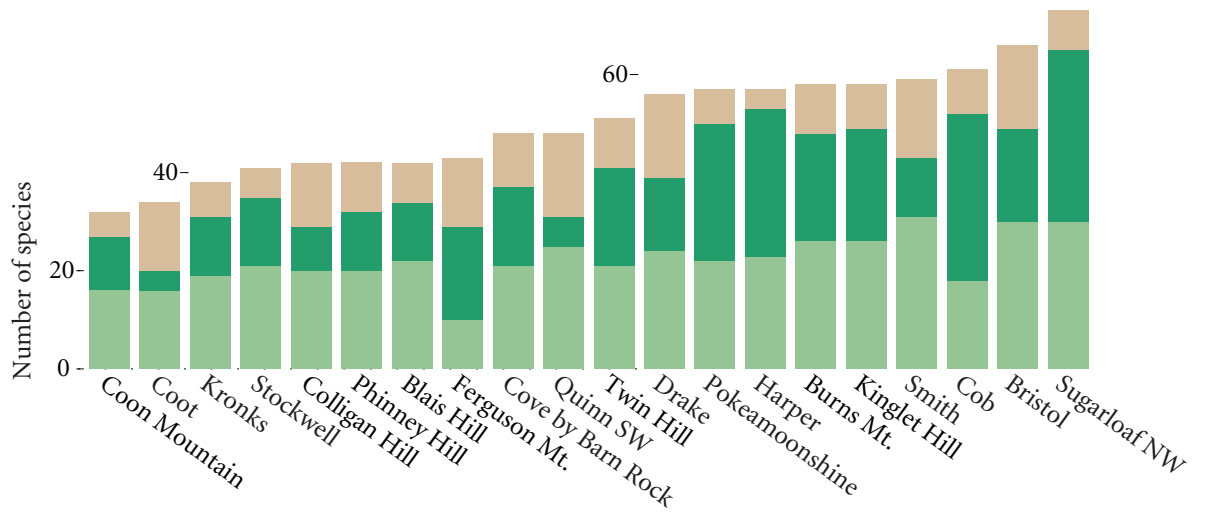
NUMBERS OF DRY-RICH SPECIES AT 2007 SITES
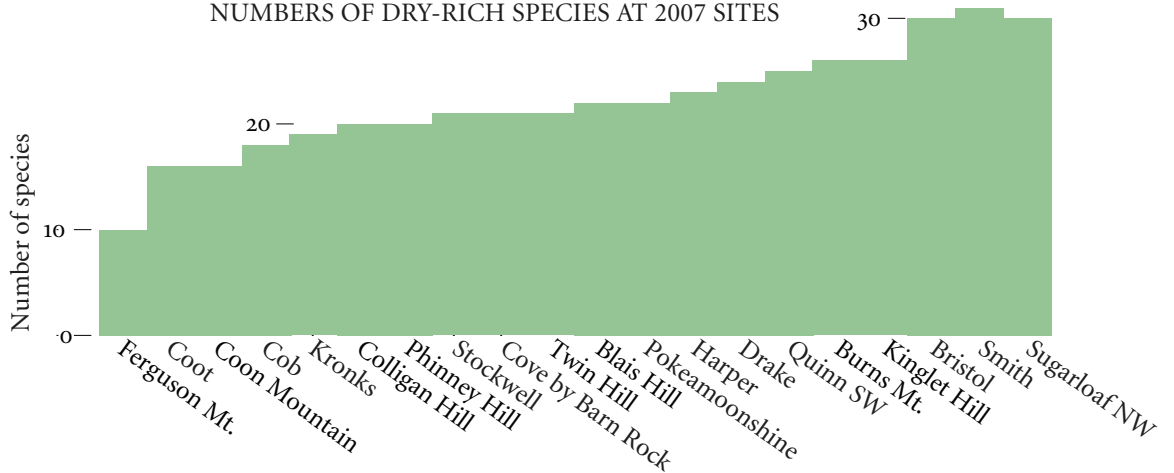
Indicator species at 2007 sites, from summer data.
Compare the fall data on p. 21.

which speak both to the distinctiveness of the community and the level of ecological specialization of its characteristic species.

The map of the number of uncommon species per site shows a fairly uniform distribution, with most sites having at 10 or more, and no apparent geographic pattern in which sites have few and which many.

22 Intersite comparisons II: Geographic Variation in Indicator Diversity

The maps on pages 30 and 31 show the variation of indicator diversities between sites. There is no obvious geographic pattern in either the summer or the fall data, and also no obvious correlation between the different indicator groups, which seem to vary independently of each other. The scatterplots of the 2007 data show

NUMBERS OF SITES FOR SOME UNCOMMON SPECIES

Arabis lyrata	1	Carex cephalophora	3	Dirca palustris	11
Arabis missouriensis	1	Celtis occidentalis	3	Rhus aromatica	11
Carex hitchcockiana	1	Cerastium arvense	3	Asplenium platyneuron	12
Carex merritt-fernaldii	1	Clematis occidentalis	3	Asplenium trichomanes	12
Carex peckii	1	Dicanthelium xanthophysum	3	Carex laxiculmis	12
Conopholis americana	1	Geranium bicknellii	3	Desmodium paniculatum	13
Cypripedium calceolus	1	Lonicera hirsuta	3	Lonicera dioica	13
Dicanthelium columbianum	1	Parietaria pensylvanica	3	Schizachne purpurascens	13
Draba sp.	1	Penstemon hirsutus	3	Asclepias quadrifolia	14
Myosotis verna	1	Poa saltuensis	3	Carex backii	14
Panax quinquefolius	1	Cardamine parviflora	4	Arenaria stricta	16
Shepherdia canadensis	1	Carex sprengelii	4	Ribes hirtellum	16
Solidago squarrosa	1	Corallorhiza maculata	4	Waldsteinia fragarioides	18
Staphylea trifolia	1	Symphoricarpos albus	4	Amelanchier cf. sanguinea	22
Ulmus rubra	1	Woodsia obtusa	4	Viburnum rafinesquianum	23
Uvularia perfoliata	1	Juncus secundus	5	Dicanthelium latifolium	24
Xanthoxylon americanum	1	Lespedeza intermedia	5	Aster undulatus	26
Adlumia fungiosa	2	Phryma leptostachya	5	Galium lanceolatum	26
Arabis drummondii	2	Lilium philadelphicum	6	Quercus alba	26
Carex siccata	2	Oryzopsis pungens	6	Hepatica americana	27
Hieracium scabrum	2	Polygonum douglasii	7	Helianthus divaricatus	28
Phegopteris hexagonoptera	2	Ceanothus americanus	8	Woodsia ilvensis	29
Prunus pumila	2	Silene antirrhina	8	Carya ovata	31
Vitis aestivalis	2	Potentilla arguta	9		
Bromus kalmii	3	Specularia perfoliata	9		

NUMBER OF RARE OR UNCOMMON SPECIES PER SITE

Trembleau

Drake
Skagerack

Rattlesnake

Pokamoonshine
Sugarloaf NW

Bristol

Bouquet

Ferguson, Whipple
Blais
Discovery
Cob
Kinglet

Phinney
Coon
Split Rock
Barn Rock

Raven Hill
Hoisington
Kronk, Twin

Smith
Harper

Stockwell

Cook
Two Tops

Cheney, Walton
Colligan
Burns

Coot

5 species
15 species
30 species

Mt. Defiance

Blais Hill	19
Boquet Mountain	14
Bristol Mt.	26
Burns Mt.	18
Cheney and Walton Mts.	16
Cob Hill	16
Colligan Hill	18
Coon Mt.	20
Coot Hill	13
Cove N of barn rock Bay, Split	16
Drake Mt.	23
Ferguson and Whipple Mts	19
Harper Mt.	22
Hill NW of Sugarloaf	20
Hoisington Mt.	5
Kinglet Hill	20
Kronks Hill	16
Mountain SE of Mud Pond	4
Mt. Defiance	24
Mt. Discovery	19
Paintball Hill	4
Phinney Hill	20
Quinn Mt.	4
Rattlesbake Mountain, Willsboro	14
Raven Mt.	16
Ridge South of Two Top Mt.	12
S slopes of Pokamoonshine	12
SW slopes of Quinn Mt.	27
Skagerack Mt.	4
Smith Hill	27
South Slopes of Cook Mt.	10
Split Rock Mt.	18
Stockwell Mt. Middle	11
Stockwell Mt. S	21
Trembleau Mt.	9
Twin Hill	17
Twin Mountains, Rutland	15
All sites	589
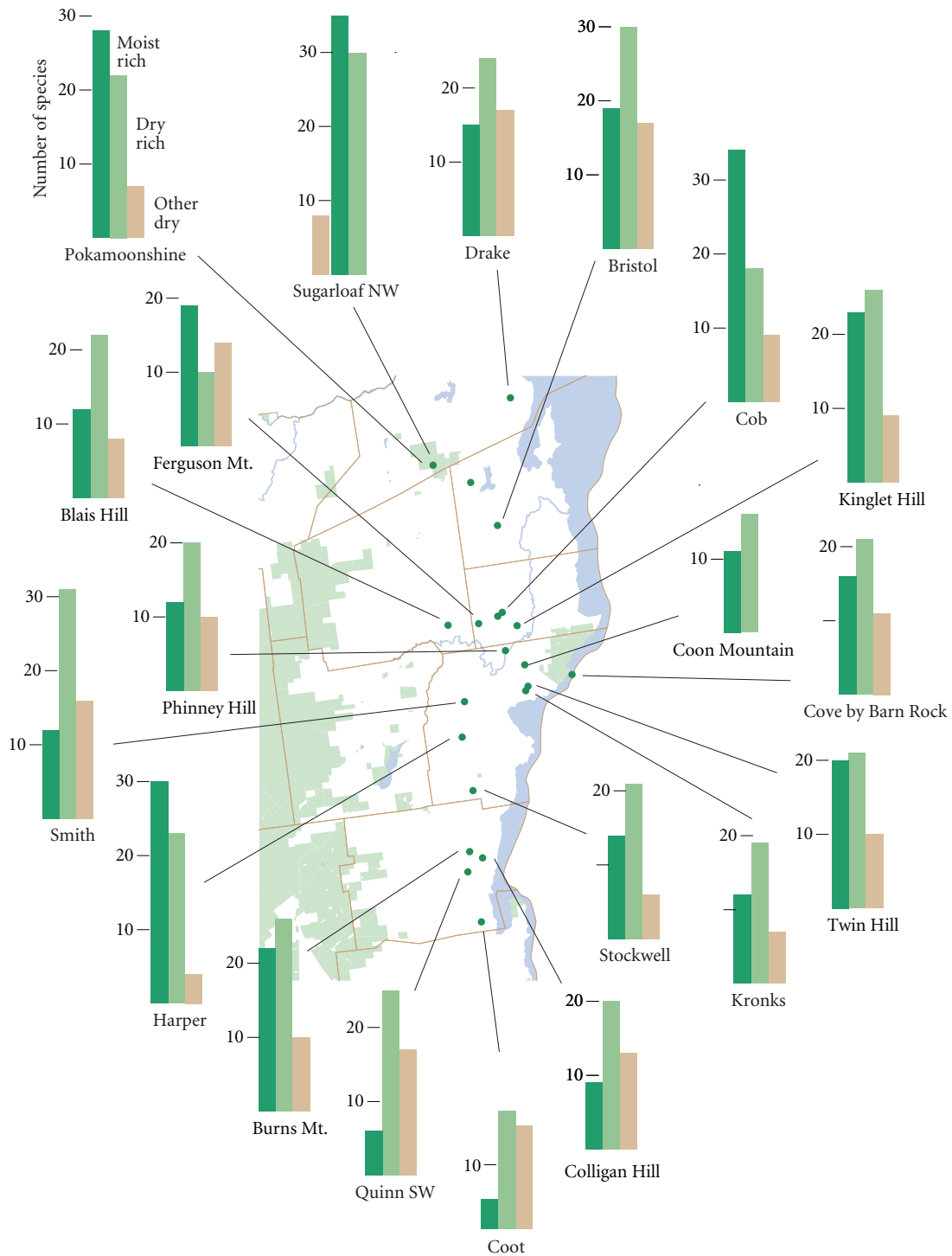
Above and left, the diversities of the three indicator groups (dark green = MR, light green = DR, tan = OD) at Champlain Hills sites. The vertical scale of the bar graph is the same in both figures. The 2007 data, above, were taken in the summer. The data from previous years, with the exception of Mt. Defiance and the Diameter, were taken in the late fall.

Blais Hill

Cob Hill

Skagerack Mt.

Trembleau Mt.

Rattlesnake Mt.

N&S Bouquet

Ferguson & Whipple

Discovery & Rattlesnake

Phinney Hill

Raven & Little Raven

Mud Pond Mt.

Split Rock Mt.

Coon Mt.

Two-Tops, SE

Hoisington Mt.

Harper Mt.

Cook Mt. S

Stockwell Mt. S

Stockwell Mt. E

Quinn Mt. SW

West of Mullen Bay

Twin Mt., Vermont

Cheney & Walton

Mt. Defiance

The Diameter

Paintball Hill, Johnsburg

Examined 2002–2006

Examined previously

Mesic calcium-indicators (moist-rich species)

Xeric calcium-indicators (dry-rich species)

Other xeric glade and summit species

31

this is in fact the case and that the diversities of the groups are largely independent.

23 *Diversity and Bedrock*

Anorthosite and gabbro have more calcium than gneiss. If, as botanists commonly assume, plants derive much of their calcium from the local bedrock, than the number of calcium-dependent species should vary with the bedrock type. In addition, since total diversity in many plant communities seems to be related to calcium status, we should expect higher total diversity on calcium-rich bedrock.

Our 2007 data for the 20 sites from which we have bedrock samples, showed no such pattern. There were no significant differences between the median total diversity or diversity of calcium indicators between anorthosite and gneiss, the two common rock types. The diversities on gabbro were slightly higher, but we have only two sites (and did intensive studies with multiple visits and both of them), and so can not say if this is a general pattern.
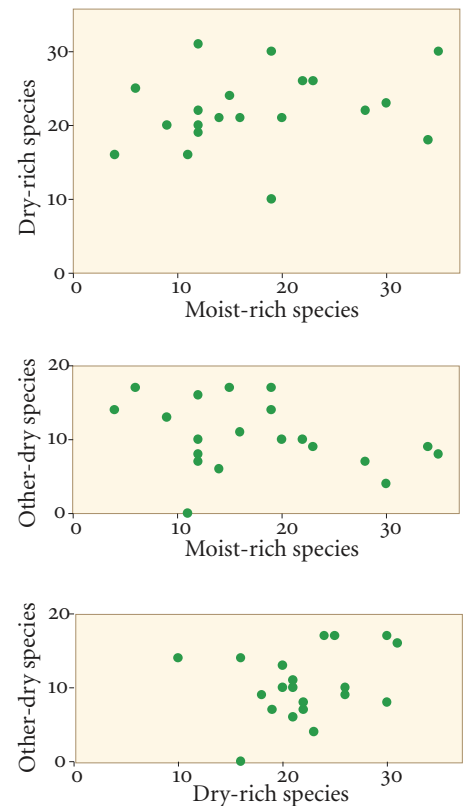
Above, the correlations between the three indicator groups at the 2007 sites. The diversities are almost uncorrelated: there is a weak (and nonsignificant) negative correlation between moist-rich diversity and other-dry diversity. Moist-rich and dry-rich diversity are uncorrelated, as are dry-rich rich and other dry.

RICH DIVERSITY OF SITES VS ROCK TYPE

TOTAL DIVERSITY OF SITES VS. ROCK TYPE
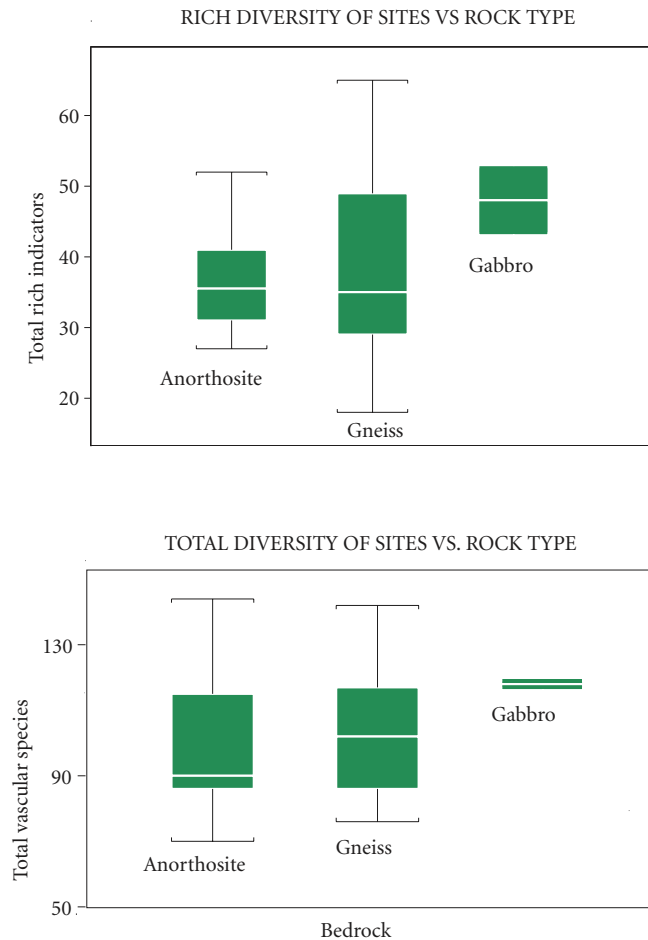
TOTAL DIVERSITY OF STUDY SITES
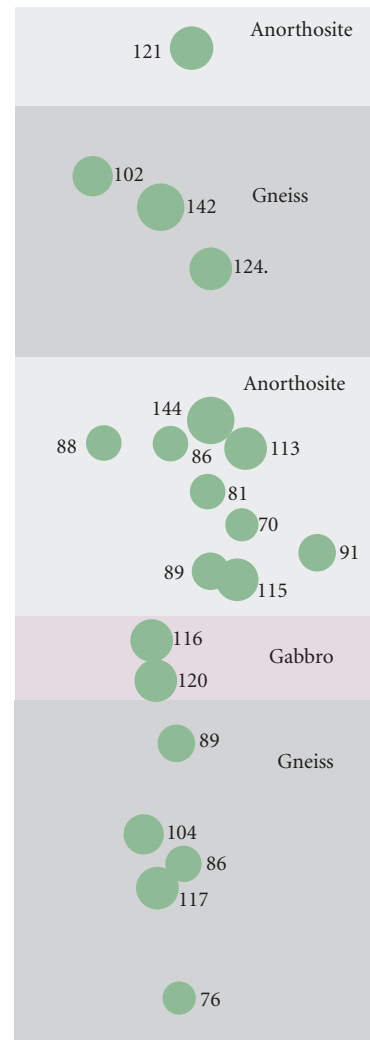
Above left, boxplots of the total and calcium-indicator diversity of the 2007 sites against rock type. There are only two gabbro sites, and the values may not be representative. Right, a schematic map showing the geographic distribution of rock types and total site diversity. The map on p. 30 may be used to identify the sites.

We took pooled soil samples from 17 of our 5 x 5 meter plots. Peter Jenkins measured the pHs in 2007; we have not yet done general nutrient analysis.

The pHs of woodland soils typically run between about 4 and 6; in acid woods where there are no carbonates in the till they are often less than 5. They are buffered by organic acids at the low end and bicarbonate at the high end, and so don't change that much as the calcium status of the soil changes. For this reason calcium concentrations and base saturation are clearer indicators of calcium availability than pH.

Our pHs ran from 4.51 to 5.68. Because the pHs were often taken on exposed summits, they probably represent the acid end of the pH range for each site. At Cob Hill, where we have two plots and 2 pHs, the summit pH was 4.51, the lowest we recorded. The pH in an oak glade in a saddle, 100 meters away, was 5.68, the highest we recorded.
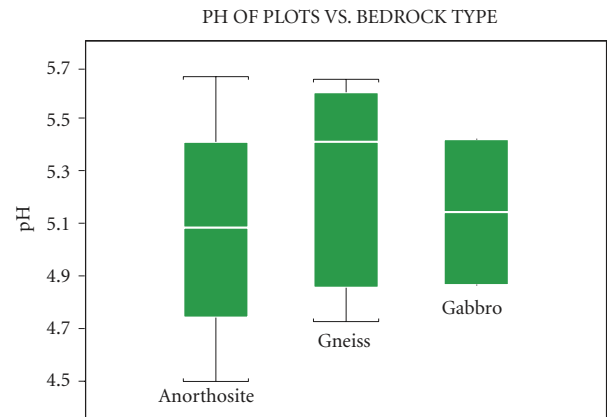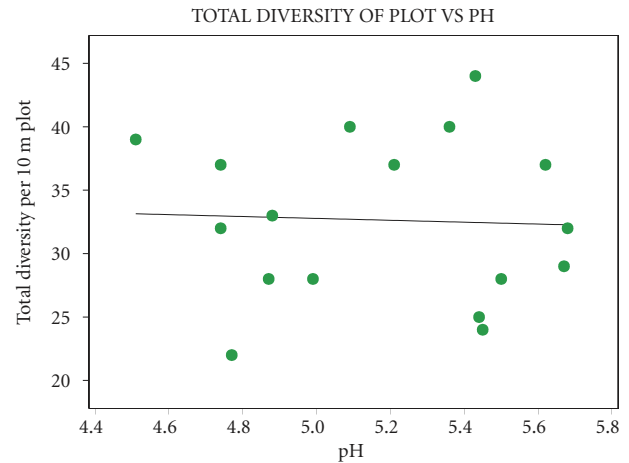
The distribution seemed to be bimodal, with a peak around 4.8 and another around 5.5. Ten of the 17 pHs were over 5.0 and thus high by normal woodland standards.

Surprisingly, the soil pH showed no relation to the bedrock type. The median value for gneiss, supposedly the most acid rock, was actually somewhat higher than those of anorthosite and gabbro, the basic rocks. The ranges overlapped and there were no significant differences.

The diversity of the indicator groups is clearly related to pH, though the relationships are not particularly strong. The median pHs at which dry-rich and moist-rich indicators are found are 5.2 and 5.4; those of other-dry and all other species are both 5.1. More significantly, the diversity of both dry-rich and moist-rich species increases with pH. About 75% of the occurrences are at pH 5.0 or higher.

pH DISTRIBUTION OF PLOTS

pHS OF INDICATOR GROUPS
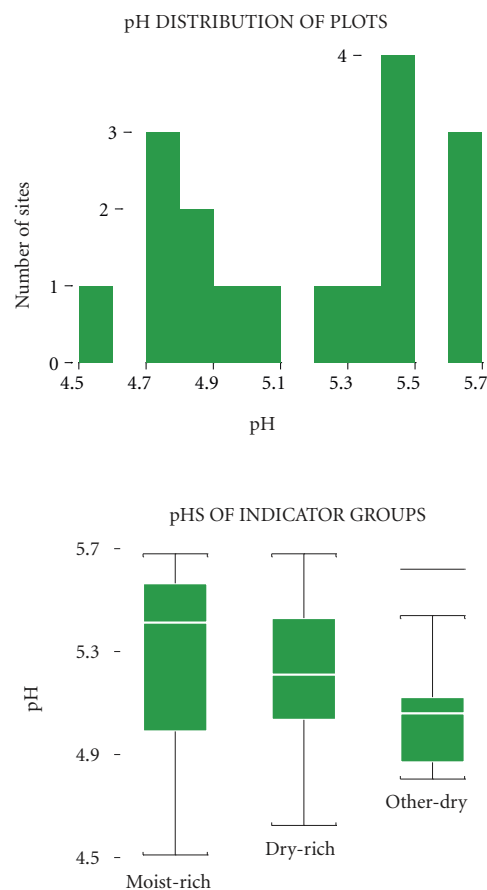
Above, the pH distribution of 17 5-meter by 5-meter plots sampled in 2007. Below, the distribution of the pHs of the indicator species found in those plots. The plots were always placed at the highest point of the transect, and tended to be relatively dry, and often more barren than other parts of the site.

NUMBER OF DRY-RICH SPECIES VS. PH

NUMBER OF MOIST-RICH SPECIES VS. PH

NUMBER OF NON-RICH SPECIES VS. PH

TOTAL DIVERSITY OF PLOT VS PH

PH OF PLOTS VS. BEDROCK TYPE
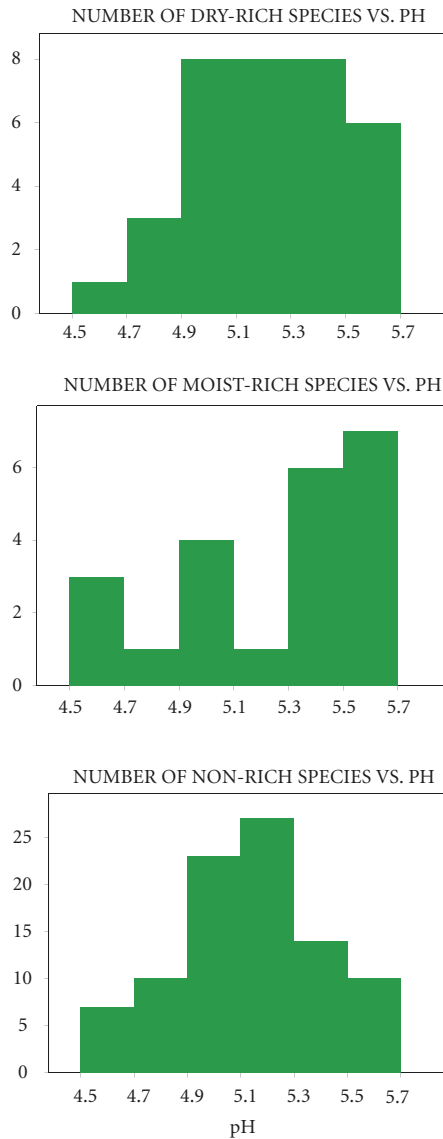
Distributions of the indicator group diversities by pH interval, for the 17 plots sampled in 2007. The dry-rich and moist-rich species prefer pHs over 4.9, with the dry-rich species uniformly distributed at pHs over 4.9 and the moist-rich species favoring pHs over 5.3. The other-dry species are symmetrically distributed; they may either favor pHs around 5.1, or (more likely) be widely distributed and tolerant.
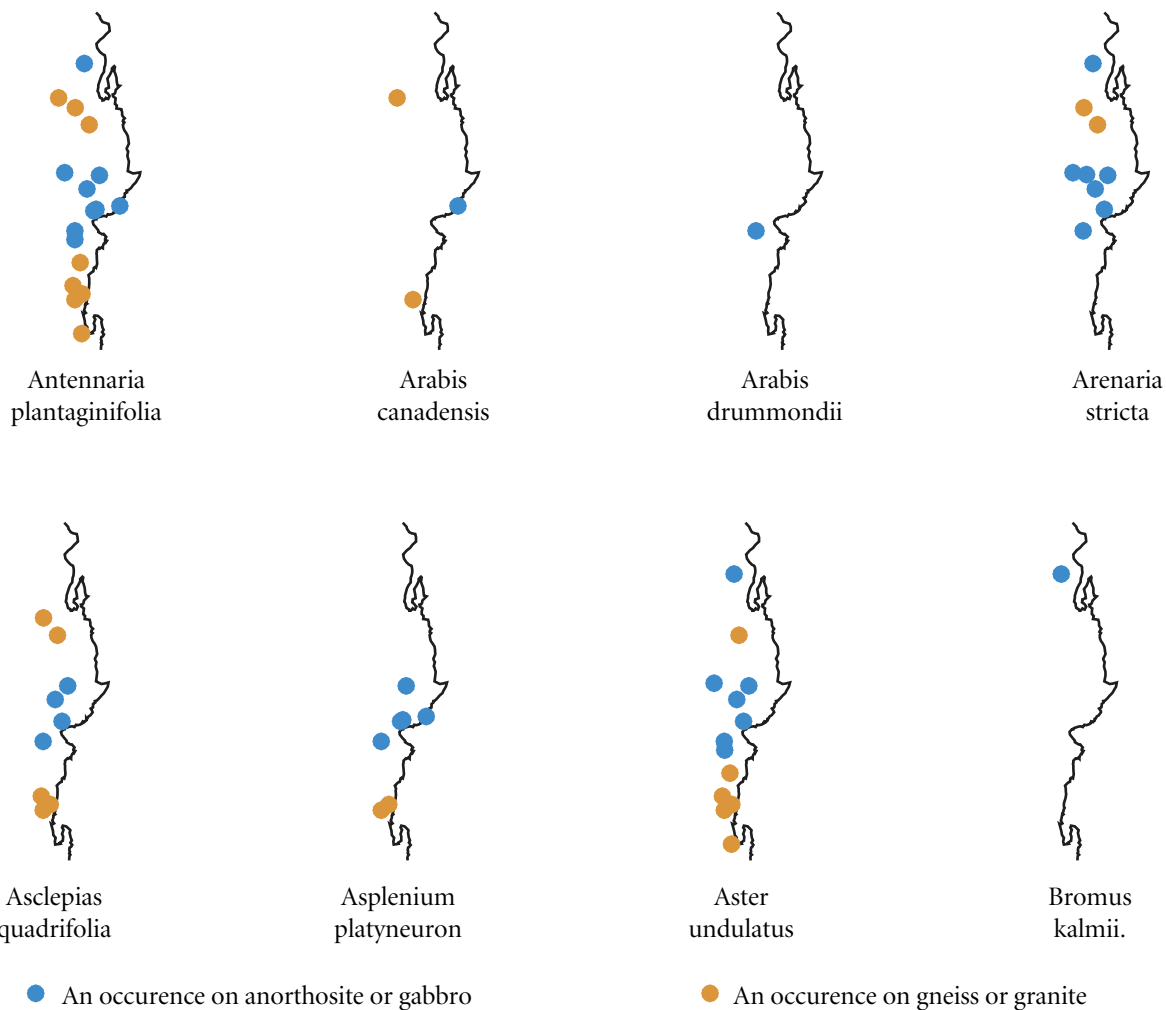
Above, total diversity of the 17 plots sampled in 2007; there is no relationship to pH. Below, the distribution of the pHs of the sample plots by rock type; rock type seems to have no effect on pH.

We mapped the occurrences of all indicator species on small range maps and examined these for geographical patterns. The full set of maps are on page 64 and following. Most species occurred on both of the main types of bedrock, and, except for rarities, were not restricted to particular parts of the study area.

A few species, shown on the map on the opposite page, were largely restricted to one rock type, or absent from the northern part of the study area. Only a few of the 170 indicators had distributions like this, and they could be accidental patterns and not controlled by bedrock or geography at all.

DISTRIBUTION OF SOME DRY-RICH INDICATORS

Antennaria
plantaginifolia

Arabis
canadensis

Arabis
drummondii

Arenaria
stricta

Asclepias
quadrifolia

Asplenium
platyneuron

Aster
undulatus

Bromus
kalmii.

● An occurence on anorthosite or gabbro   ● An occurence on gneiss or granite

INDICATOR SPECIES WITH RESTRICTED DISTRIBUTIONS

LARGELY ON GABBRO AND ANORTHOSITE

| Polygonym douglasii (OD) | Adiantum pedatum (MR) | Rhus aromatica (D) | Potentilla arguta (DR) | Saxifraga virginiensis (DR) |
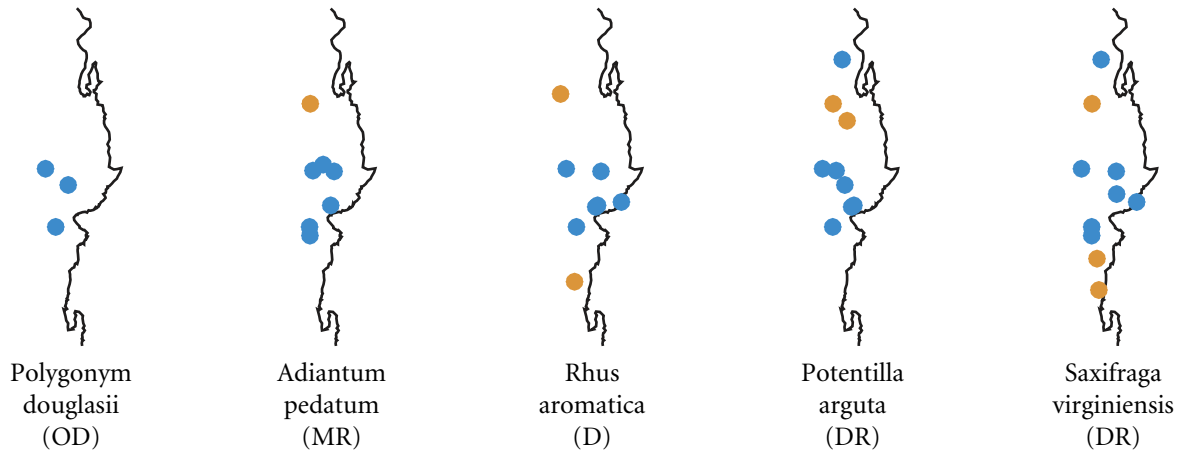
ONLY ON GRANITE AND GNEISS

ONLY SOUTH OF SPLIT ROCK

Lilium philadelphicum (DR)

Arctostaphylos uvi-ursi (OD)

Viburnum rafinesquianum (DR)
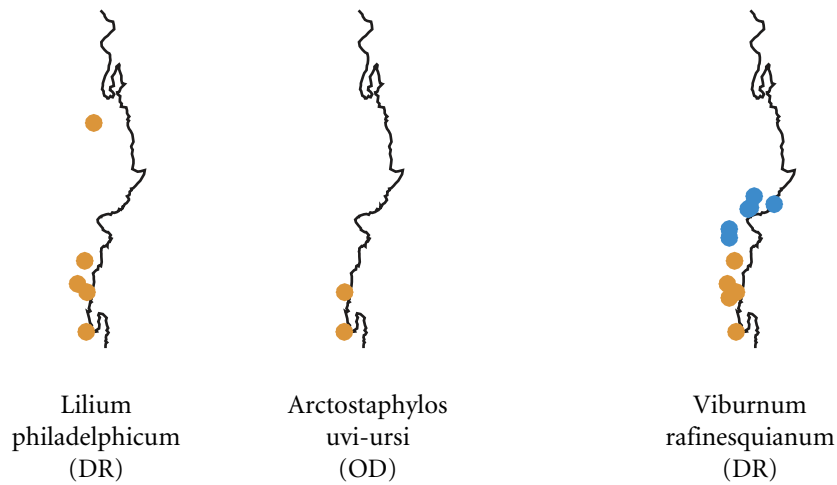
● An occurence on anorthosite or gabbro   ● An occurence on gneiss or granite

Left, occurrences of eight dry-rich indicators, showing that many species occur on both calcareous and noncalcareous bedrock. Above, seven species that seem to be more abundant on one type of rock than another, and one that was restricted to the southern part of the study area. The maps include all the records from this study. The map on p. 22 may be used to identify the individual sites.

Because our plots are small and located on knolls, they probably give us both a limited sense of the range of pHs encountered at the sites, and a limited sense of what a species prefers. In particular, for some of the strongly calciphilic species, they may be catching only the lower end of its pH range—telling us, in effect, more about what it tolerates than what it prefers.

The commonest species, occurring in 5 or more plots each, almost all had wide pH ranges, and may well have been common because they had wide ranges. None the less, the species at the right end of the graph, with median pH's of 5.1 or higher, are mostly species we think of as at least moderate calciphiles.

The less common species in the plots are actually more informative, even though their pHs are corresponding less certain. The table gives the species whose mean pH was 5.4 or high; the species with asterisks only occurred in plots whose pH was 4.0 or higher. The list contains 33 species. Seventeen of these are usually thought of as definite calciphiles, and nine more as at least weak calciphiles.

pH MEANS OF HIGH pH SPECIES

5.40	Fraxinus americana
5.43	Dicanthelium acuminatum
5.43	Desmodium paniculatum
5.43	*Carya cordiformis
5.44	*Sanicula marilandica
5.44	*Mitella diphylla
5.45	*Fragaria vesca
5.45	*Lactuca sp.
5.44	*Hepatica americana
5.44	Poa saltuensis
5.44	*Cornus alternifolia
5.45	Bromus pubescens
5.50	Tilia americana
5.50	*Asclepias quadrifolia
5.50	*Amphicarpaea bracteata
5.55	*Acer saccharum
5.56	*Galium lanceolatum
5.56	*Thalictrum dioicum
5.56	*Galium triflorum
5.60	*Acer pensylvanicum
5.62	*Quercus alba
5.62	*Specularia perfoliata
5.68	*Aster divaricatus
5.68	*Lonicera canadensis
5.68	*Prenanthes sp.
5.68	*Asclepias exaltata
5.68	*Hepatica acutiloba
5.68	*Oryzopsis racemosa
5.68	*Osmorhiza claytonii
5.68	*Viola pubescens
5.68	*Dirca palustris
5.68	*Festuca subverticillata
5.68	*Uvularia grandiflora

Above, the mean pH preferences of 33 species that occurred on plots whose mean pHs were 5.4 or higher. The species with asterisks did not occur on any plots with a pH of less than 5.4.

pH RANGES & MEDIANS OF COMMON SPECIES, 2007 PLOTS
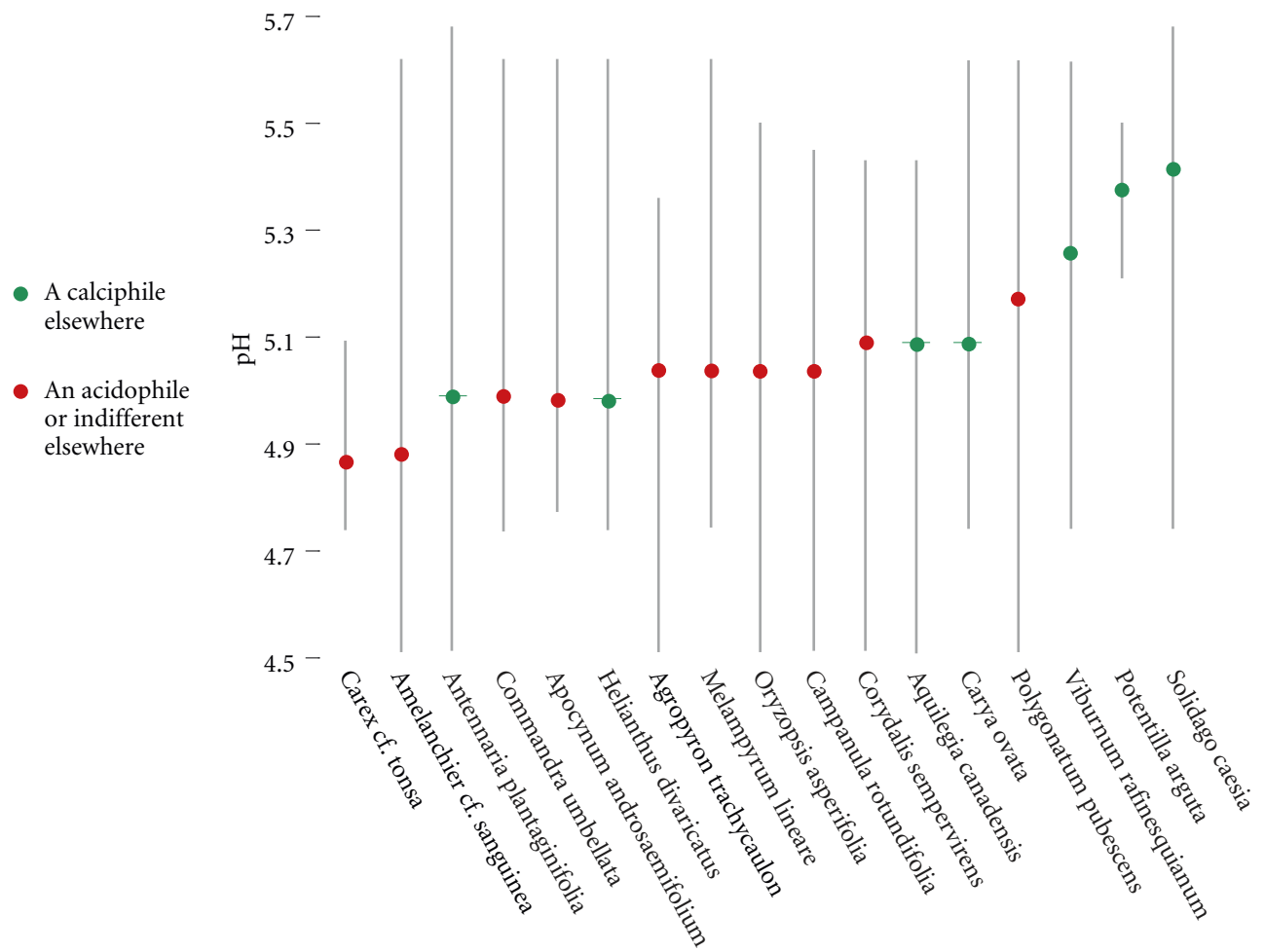
Above, the pH ranges and median pHs of
14 species that occurred on 5 or more plots
each.

27 Intrasite Comparisons I: Topographic Control of Indicator Diversity

Our field work gave us a strong sense that the number of dry-rich indicators was highest on partially shaded ledges, lower on benches and in glades with deeper soil and less rock, and lowest in dense woods and on open summits. We wondered if there were similar patterns for the other indicator groups, and if these translated into regular relations between indicator diversity and typography, and hence between the diversities of different groups.

We investigated this by picking the highest point in the community, usually a summit or a knoll and, depending on the topography, either running the transect down from down the steepest slope or running the transect through the knoll and down the slopes on either side.

The figures on the next two pages show the results. The basic data is the number of moist-rich, dry-rich and nonindicator species in each 5-meter segment. The data has been smoothed, which makes the curves easier to compare but a lot less jagged than they actually are.
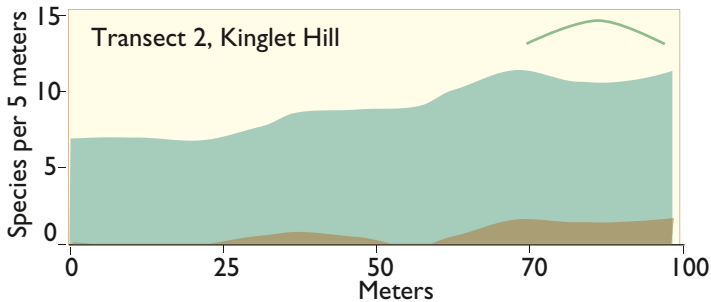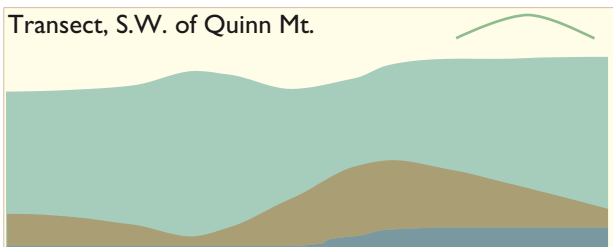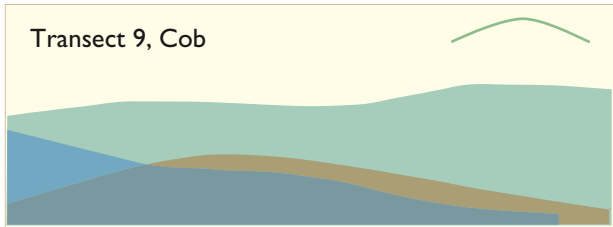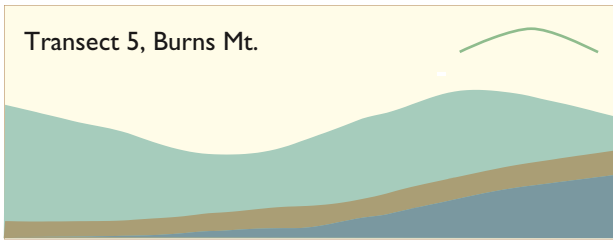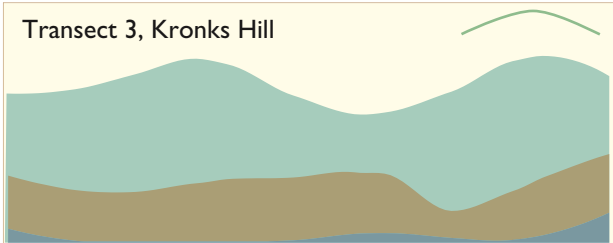
The results show that indicator diversity certainly varies with topography, but that way in which this happens is different on different hills. Sometimes diversity peaks at the high points, sometimes at the low points, sometimes in the middle. Sometimes a topographic gradient introduces strong variations in diversity; other times a similar gradient causes little change. Sometimes the different diversities are in phase, sometimes out of phase, sometimes seemingly independent of each other.

Based on our field observations, we have no doubt that many of the individual peaks and dips in the curves have direct explanations. Dry slabs and oak thickets with abundant shrubs are always low diversity; moist ledge faces and ridgetop glades are often high. This is the sort of small-scale variation that occurs in most communities. But what the figures seem to show is that, while all the sides had this sort of local variation, there is no evidence that it is organized into some larger-scale pattern that repeats from site to site.

Right, the smoothed variation of dry-rich, moist-rich, and nonindicator diversity along transects. The diversity is measured as the number of species per 5-meter segment. The green lines, which do not have a vertical scale, show whether the transect was across a knoll (and thus sloping in both directions) or down a slope with a high point at the end.

East-West Transects Over Knolls

Transect 6, Colligan Mt.

Nonindicators

Dry-rich

Moist-rich

Transect 3, Kronks Hill

Transect 5, Burns Mt.

Transect 9, Cob

Transect, S.W. of Quinn Mt.

Transect 2, Kinglet Hill

Species per 5 meters

Meters
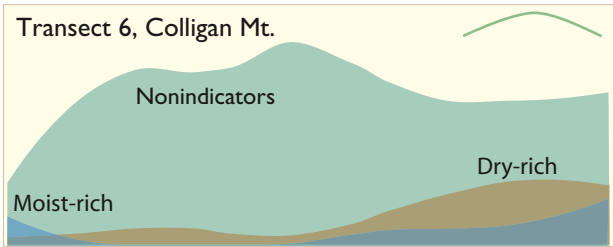
East West Transects Down Slopes
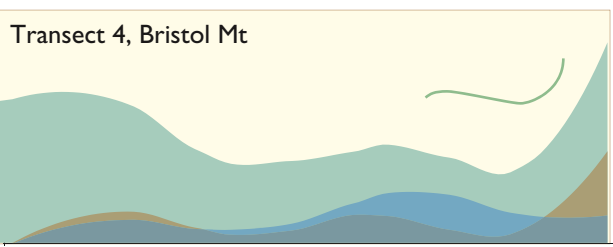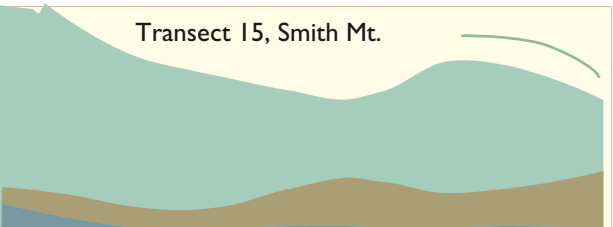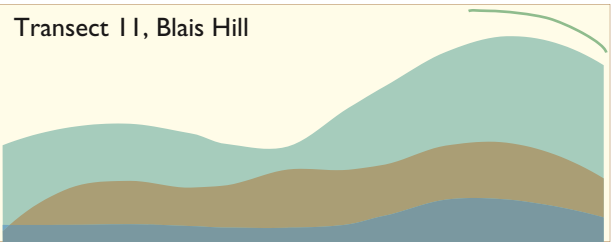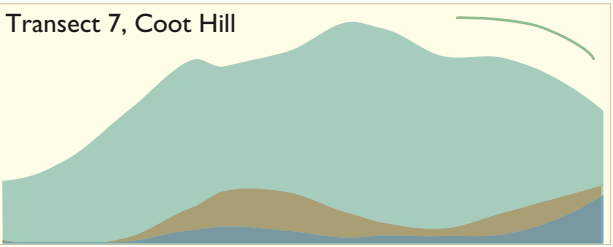
Transect 7, Coot Hill

Transect 11, Blais Hill

Transect 14, Stockwell Mt.

Transect 15, Smith Mt.

Transect 4, Bristol Mt

Profile of transect

North-South Transect Down Slopes

Transect 12, Coon Mt.

Nonindicators

Dry-rich

Moist-rich

Transect 16, Ferguson Mt.

Transect 10, Phinney Hill

Transect 8, Drake Mt.

Species per 5 meters
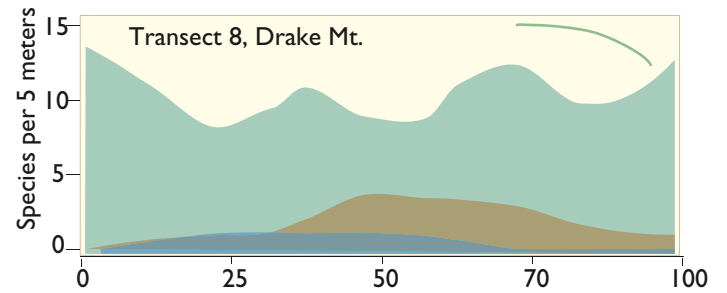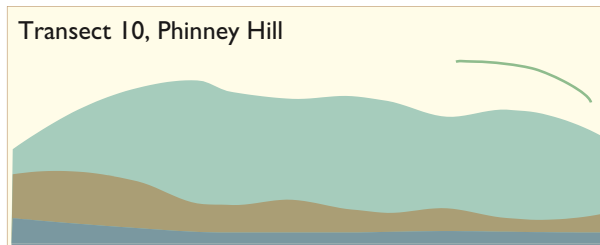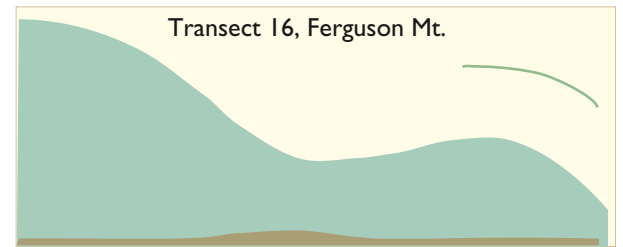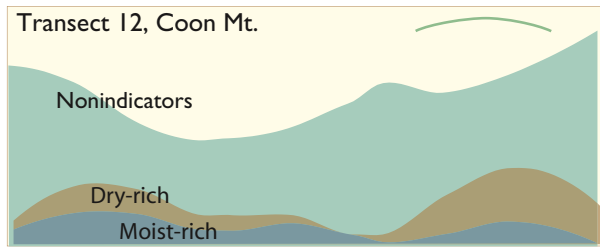
Long Southwest-Northeast Transects

Transect 17, Harper Mt.

Species per 5 meters

Meters

Transect 13AB, Smith Hill

Species per 5 meters
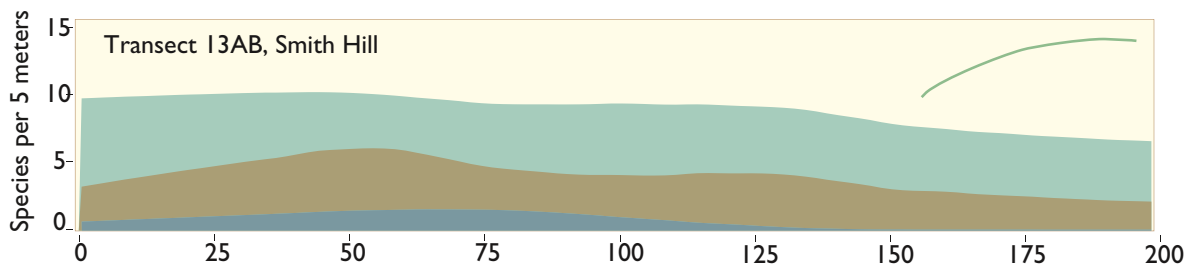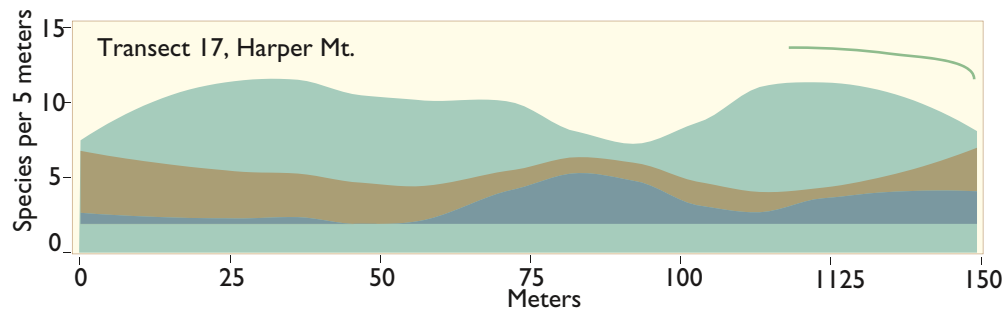
Additional graphs for north-south transects and two extended transects.
Scales and colors as on p. 41.

Bristol Mountain

Kronks Hill

Two areas of relatively high diversity on transects: above, a steep, open, vegetated slab on Bristol Mountain; below, glades on a bench in Kronks Hill. Areas of locally high diversity usually a well developed groundlayer, some outcrops and some deeper soils, and often a mixture of sun and shade. They are usually not summits, but otherwise may occur in a variety of topographic positions.

By a correlation I mean a co-occurrence: two groups are correlated when their diversity is high in the same places and low in the same places.

There are several reasons why the indicator groups might be correlated.

> The MR and DR groups both require calcium.

> The DR and OD groups both occur in open, xeric sites.

> The MR group requires moist, usually shady sites, and so might be anticorrelated with the DR and OD groups.

> Substrate diversity often controls plant diversity, and this might generate correlations between the nonindicators (NI) and any of the indicator groups.

We have measurements at three spatial scales—site, transect, and plot—and can look for correlations both with and between each scale. Thus we can ask if, for example, the MR diversity of a site correlates with the DR diversity; or we can ask if how well the MR diversity of a transect predicts the MR diversity of the associated plot or transect.

I have previously, noted, based on figures, the apparent lack of coordination between the diversities of the indicator groups at the site scale (Section 22) and at the transect scale (Section 27). To look at this more formally, I calculated the correlations between the four species groups (MR, DR. OD, NI) at three different scales, and then represented the correlation matrix graphically.

The simplest thing you can say about the results are that some things correlate and many don't. The strongest correlations are

> Between moist-rich and nonindicator species at the site and transect level, and between the plots and sites and transects and sites. The latter means that moist rich diversity on a transect or a plot is a good predictor of high nonindicator diversity at a site.

> Between all the indicator groups (MR, DR. OD) on a plot and the same group on the associated transect. Also, though generally more weakly, between the indicator groups on plots or transects and those on sites.

The only strong anticorrelations are between moist-rich and other-dry species at the plot and plot-site levels.

Right, the correlation matrix for the 2007 site, transect, and plot data. The correlations are calculated between the diversities of different indicator groups, either at the same (DR diversity of sites x MR diversity of sites) or at different scales (DR diversity of sites x MR diversity of plots). A circle indicates a correlation between two different indicator groups, either at the same or at different scales. A square is a correlation between the same group at two different scales. The saturated colors are correlations that are significant at the 5% level.

CORRELATIONS BETWEEN DIVERSITIES OF SPECIES GROUPS, 2007 DATA
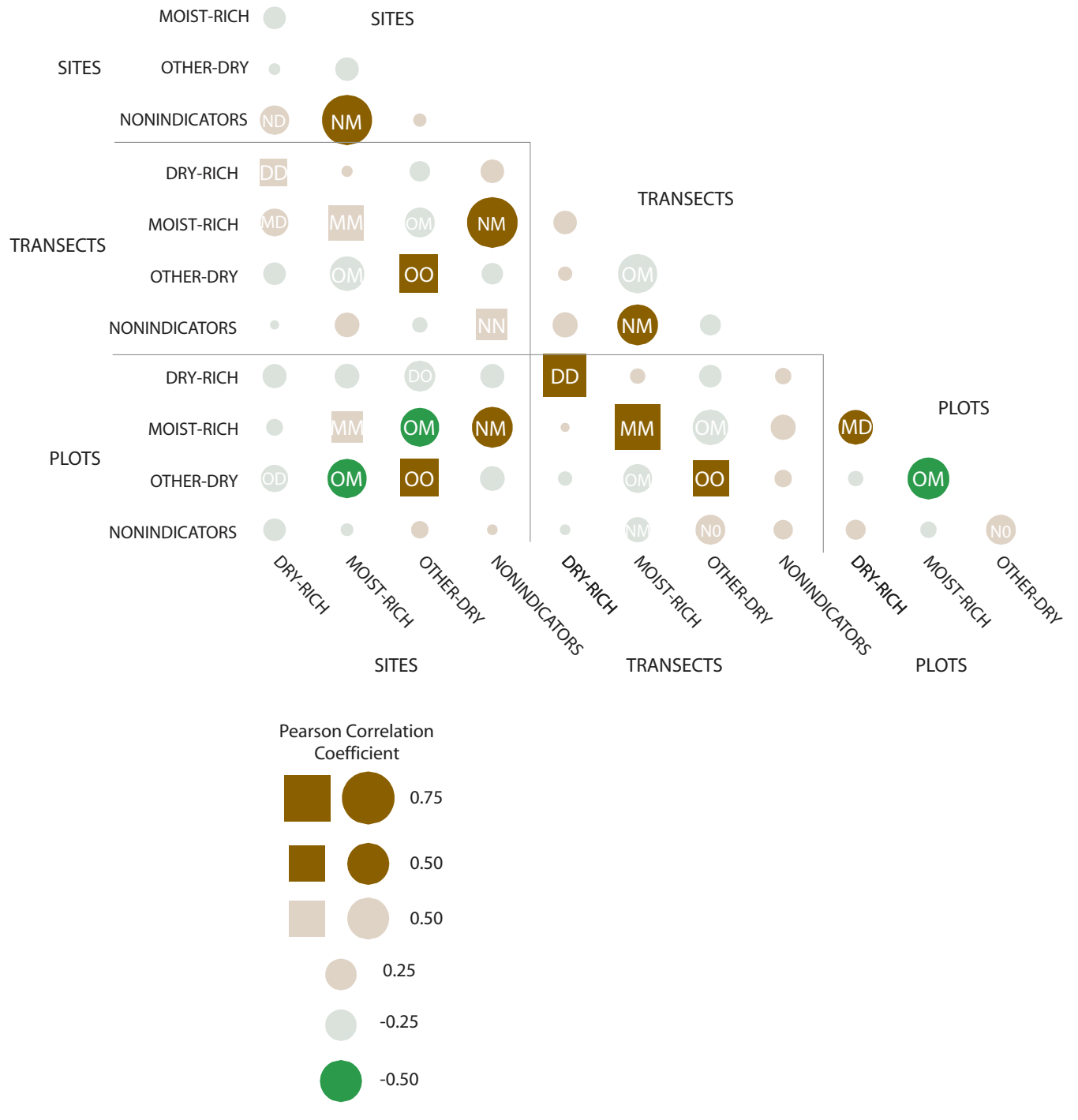
All these correlations have some biological logic. Moist rich sites elsewhere tend to be rich in both indicators and nonindicators, and so it stands to reason the MR diversity in a dry site could increase the NI flora as well. Plots and transects are spatially associated and so we would expect correlations between, say, the diversities of DR species at plot and transect scale. And moist-rich and other-dry species are at opposite ends of both the fertility and moisture gradients, and so their anticorrelation is not surprising.

What is surprising, given our intuitive sense of their ecology, is the lack of significant correlations, at any scale between MR and DR species and DR and OD species. This suggests either a surprising independence of behavior of the part of the species involved, or a surprising lack of understanding of their behavior on the part of those of us who are studying them.

29 *Intrasite comparisons III: Correlations Between Indicator Species*

The three groups of indicators that I use in this analysis have been chosen by comparing the species behavior outside the Champlain hills. Thus *Carex plantaginea* is considered a moist-rich species because it grows in fertile mesic forests elsewhere, and *Carex siccata* an other-dry species because it often grows in acid sand plains. It would be nice to verify these groups by showing that the species in each group do tend to occur together.

This could, and perhaps should, be done through ordination or clustering. I do it in a simpler way here because I want to limit my attention to the strongest relationships.

My analysis uses presence data for 18 transects, and is given in the following three graphs. This analysis was confined to MR and DR indicators but it could be extended to other groups.

First I eliminate species that occurred less than three times; they have little information content and can generate false associations by chance. This leaves 40 species. I calculate the correlations and then, after some testing of significance levels, eliminate the ones for which r <= 0.5. The remaining ones (33 of 760) are all significant at the 5% level.

The remain correlations (lower diagram, opposite) involve about 20 species. As expected, these are species of medium frequency. The common species that occur on almost every transect are, in a sense, associated with everything, and so their correlations with other species are generally not significant.

In the diagrams on the opposite page each dot represents a significant correlation between two species. By connecting the correlations that have a common species, the dots become a network (p. 48). By redrawing the network (each line becomes a dot representing a species, each dot becomes a line representing a connec-

Left, the correlation matrix for 40 dry-rich and moist-rich indicators that occurred three times or more on our 2007 transects. The rows and columns are species; each circle is the correlation between two species. Thus the dark brown circle near the top of the diagram is the correlation between *Aster undulatus* and *Asclepias quadrifolia.* Brown correlations are positive, green negative; saturated colors are the correlations for which r is equal or greater than 0.5 or equal or less than -0.5, and thus (for this data set), significant at roughly the 5% level. The upper diagram shows all the correlations, the lower only the significant ones. The correlations are calculated for the whole transect and not the segments; thus two species are considered to co-occur if they are found anywhere in the same segment.
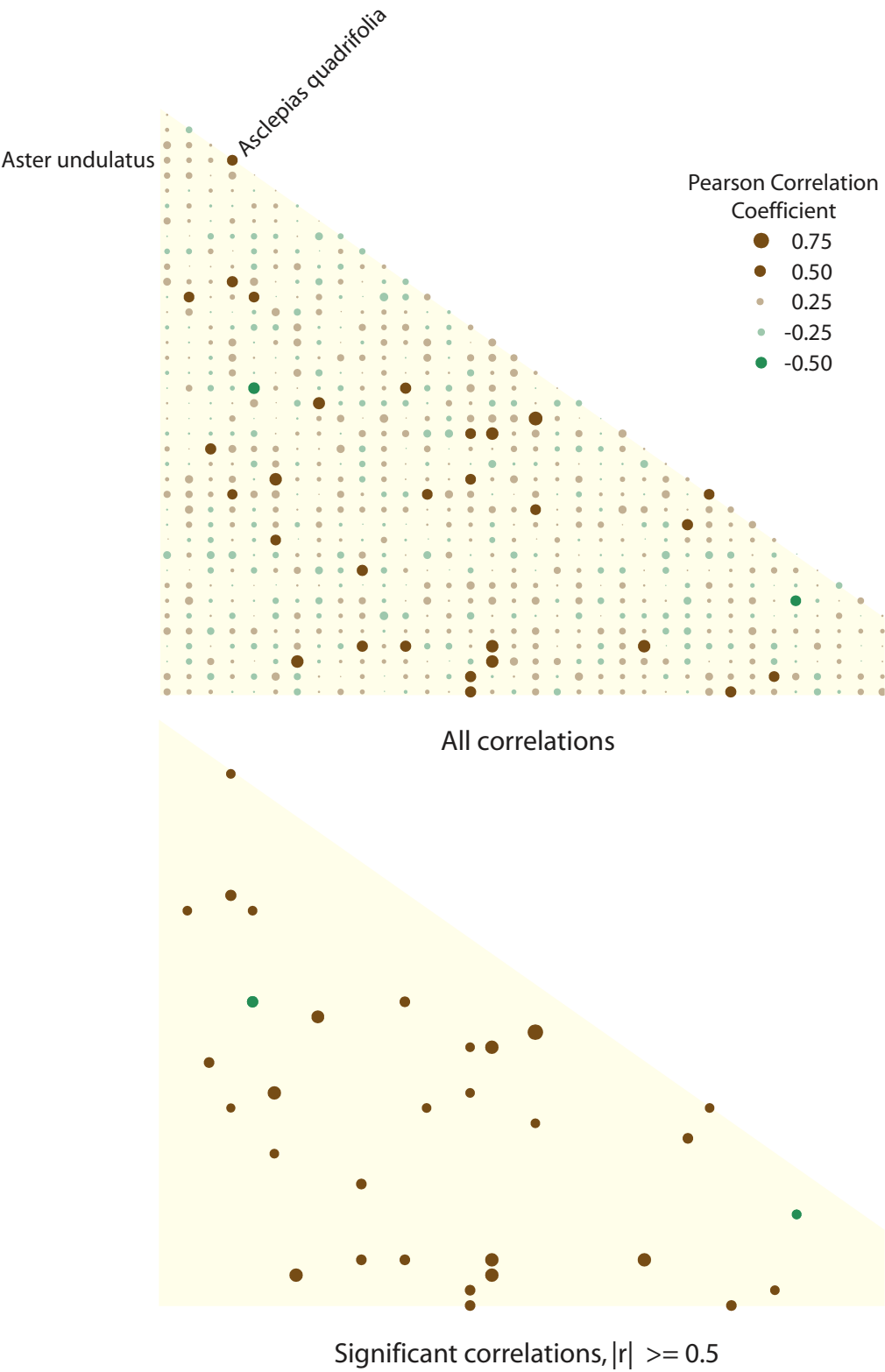
All correlations

Significant correlations, |r| >= 0.5
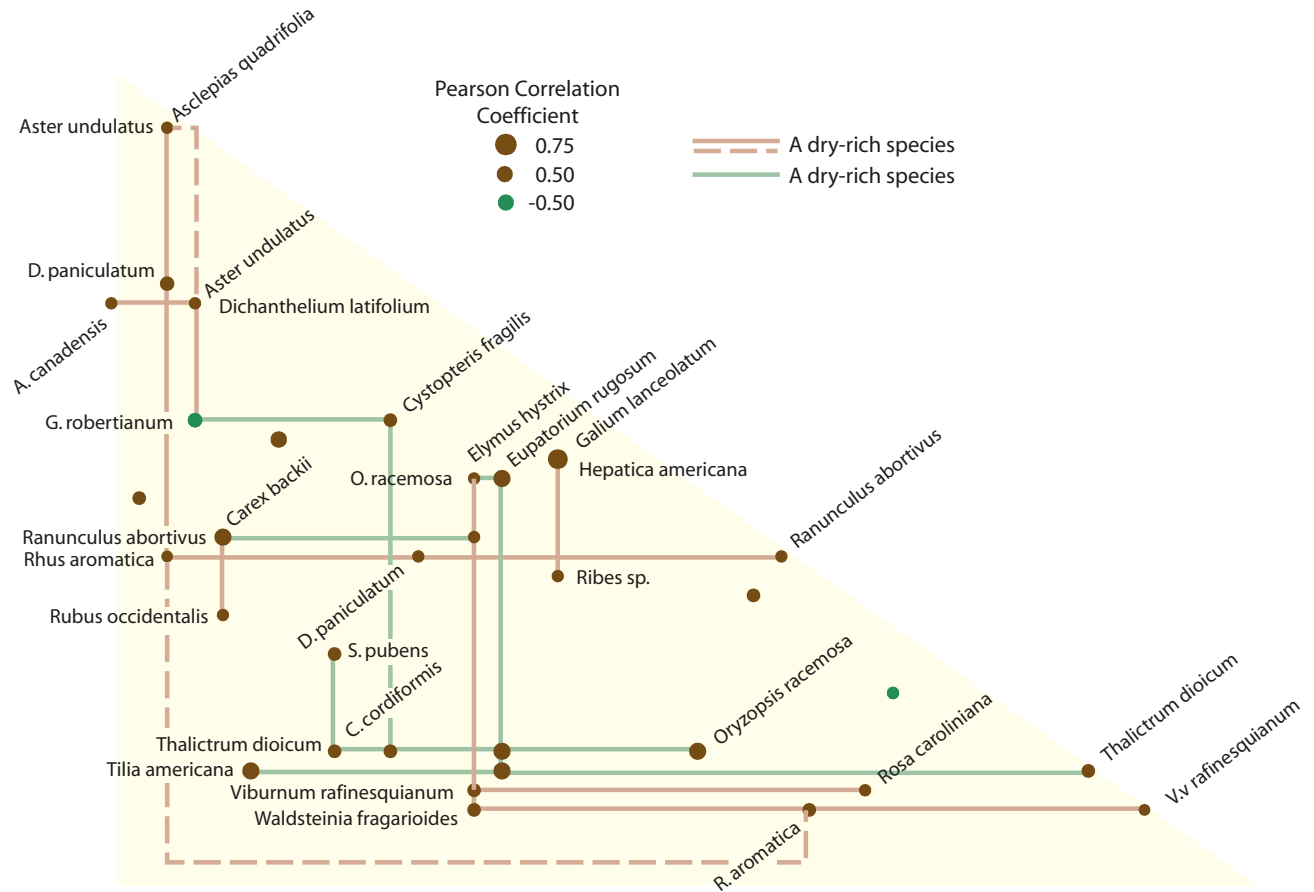
A correlogram in which the significant correlations (circles) that have a species in common are connected by lines. In the correlation matrix the rows and columns are species, and so any correlations in the same row or same column have a species in common. Thus, at the top of the diagram, *Asclepias quadrifolia* (name at an angle, indicating a column) is correlated with *Aster undulatus, Desmodium paniculatum, and Rhus aromatica*, and shown by a tan line, indicating that it is a dry-rich species. Further, because each species occurs once as a row and once as a column, there are two additional links shown by the dotted lines; these connect parts of the network that have *Aster undulatus* or *Rhus aromatica* in common.

The result is a single correlation network that includes 26 of the significant correlations, a much shorter network with two correlations, and 5 isolated correlations without any species in common with any other correlations.

Dichanthelium latifolium
Aquilegia canadensis
Asclepias quadrifolia
Waldsteinia fragarioides
Viburnum rafinesquianum
Rosa caroliniana
Aster undulatus
D. paniculatum
Rhus aromatica
Elymus hystrix
Oryzopsis racemosa
Rubus occidentalis
Carex backii
Ranunculus abortivus
Eupatorium rugosum
Carex laxiflora s.l.
Tilia americana
Thalictrum dioicum
Sambucus pubens
Carya cordiformis
Cystopteris fragilis
Geranium robertianum

Dry-rich species   Moist-rich species   — — Anticorrelation between moist-rich and dry-rich species

Untangling the main network and redrawing it in a more conventional way so that species are circles and correlations are lines, we get the above picture. No attempt has been made to represent the strengths of the correlations, and so only the topology matters. The network divides into two intercorrelated parts, one containing dry-rich and one moist-rich species. In between these are a group of bridging species of mixed affinities.

tion) and rearranging, the topology starts to make sense, and the result is a network with two interconnected ends separated by a narrow bridge (p. 49). Very satisfyingly, one end consists of all dry-rich species and the other end all moist-rich species. Interestingly, the bridging group between the two ends is a mixture of dry-rich and moist-rich species.

PART III: PATTERNS IN THE FREQUENCY OF SPECIES

In many floras there are strong quantitative patterns in the relative abundance or frequency of species. These in turn generate characteristic patterns of how diversity varies with sample size, or with the area sampled. species-frequency curves, like the one on the opposite page, are examples of the first sort of pattern. Species-pool curves, shown on the next two pages, are examples of the sampling curves that they generate.

These curves are favorites of quantitative naturalists, including myself, because they are some of the strongest and most regular relations that we see. Unfortunately, they are also some of the least interpretable. There is a large, technical, and mirky literature surrounding them. The upshot of this literature that many different models will generate similar patterns. Thus far it is not possible to say which, if any, models best represent the biological processes that generate these patterns, and hence it is not possible to look at a pattern and say what it means.

Even if we can't interpret the frequency patterns we still may be able to use them. It is possible that they differ for different communities. If so, then they say something, though what we do not know, about what makes one community different from another.

That level of analysis will require the comparison of comparable frequency data from different communities, and is beyond the scope of this report. What I will do here is simple exhibit the patterns and note that these patterns might or might not be a sort of quantitative fingerprint that distinguishes one community from another.

30 Species-Frequency Distributions at Different Scales

The figures at the right are species-frequency distributions, showing the number of species that occur in different frequency ranges. The left bar in the uppermost left figure says that 26 dry-rich species occur at a in the frequency range of 1 site out of 21 to 5 sites out of 21. Note that the heights of the figures have been scaled so that the left bar in each figure is the same height.

In all the figures low-frequency (relatively uncommon) species are more numerous than high frequency ones, and, for all species

Right, species frequency distributions by species group and sampling scale. The figures give the number of species that are found in a certain frequency range. The lower left figure, for example, says that about 160 species occur at frequencies of 1 site each to five sites each, and 60 species at frequencies of 6 sites to 10 sites each. The x-axis are equal; the y-axis have been scaled so that the left hand bars are all equal, to facilitate comparison of the shapes of the distributions.

SPECIES FREQUENCY DISTRIBUTIONS BY GROUP AND SCALE
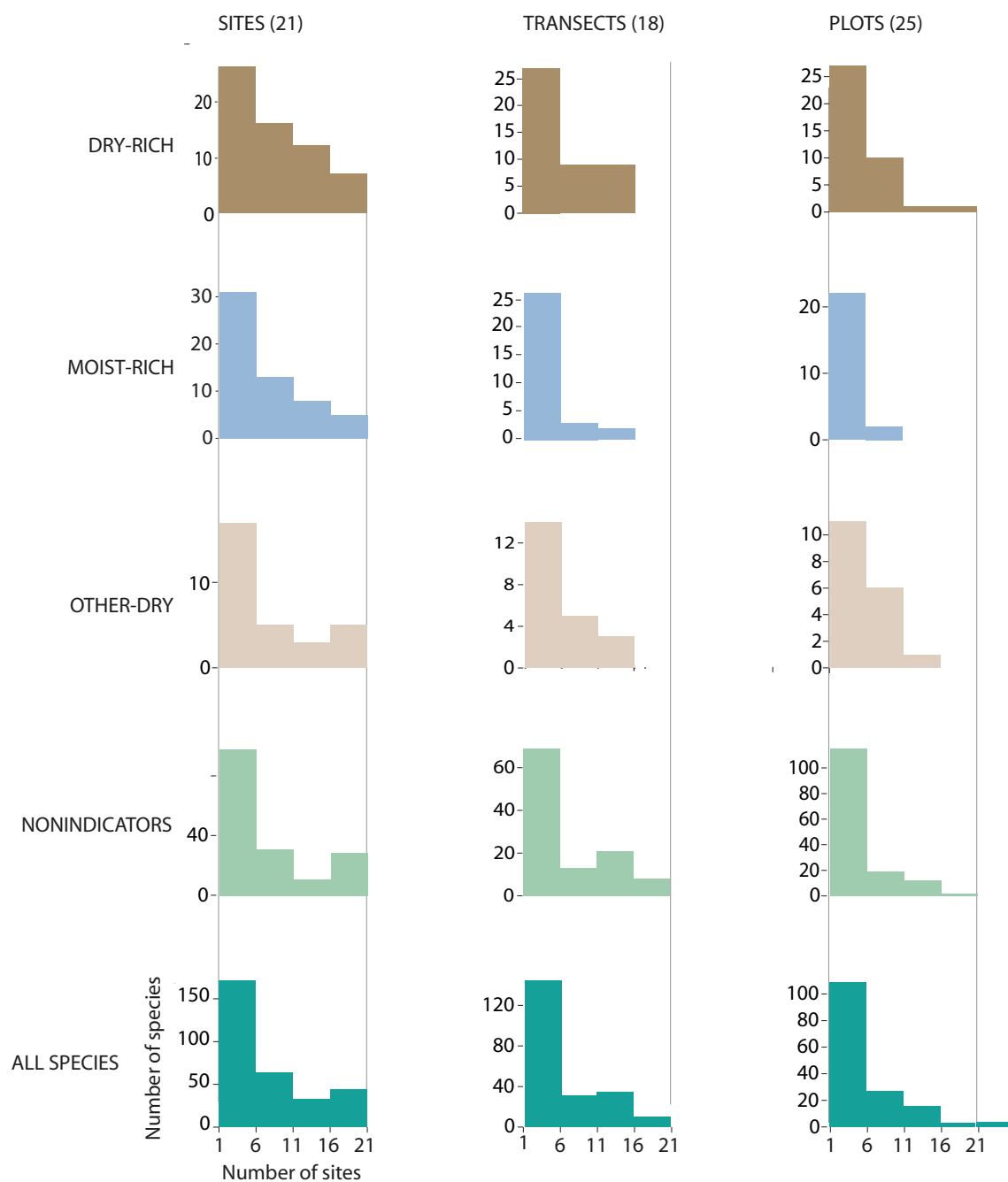
groups, are more predominant on plots than in transects and in transects than on sites.

Where the distributions differ is in the abundance of mid-frequency species. The dry-rich site distribution has 43% of its species in the left bar, 45% in the middle two bars, and 12% in the right bar. As I have scaled it, it looks like a steep ramp. The moist-rich site distribution is more L-like: the corresponding figures are 54%, 37%, and 9%. The nonindicator site distribution is more L-shaped yet: the figures for it are 56%, 26%, and 18%. Thus the DR species, which are the species most clearly specialized for this community have fewer rare and common species than the less specialized nonindicators, but more species at intermediate frequency. The nonindicators have some very common species, but also a lot of infrequent ones. Interestingly, as shown at the table at right, these changes affect the shapes of the frequency distribution more than the mean frequencies. The average frequencies of all the species groups at the site level are quite similar.

31 Sample-Pool Relationships for Transects

A sample-pool graph compares the mean number of species in a single sample with the total number of species in all the pooled samples. It is thus a measure of the rate at which you add new species as you continue sampling.* This in turn depends on the species frequency distributions. If the average frequency is near 1, so that most samples contain most species, you will not add many new species by repeated sampling. If it is very low, so that most species are seen only once, the total diversity will climb rapidly as you continue to sample.

Thus the sample-pool distribution contains, somewhere inside it, information about how many species are rare and how many are common. And this, we would like to believe, says something about the diversity of microhabitats and how species compete and how specialized they are and things like that. But just where that information is and how it is encoded, we still do not know.

I give two examples of sample-pool relationships based on our 2007 data. The graph on p. 53 shows a small-scale relationship, the number of species in a 100-meter transect as a function of the average number of species in a 5-meter segment of the same transect. Thus the sample is a 5-meter segment and the pool a set of 20 such continuous segments. Each point is for one species group on one transect. The regressions for three of the four species groups are significant, and the regression for all the groups together is highly significant.

Note two things about this relation. The first is that it represent a genuine increase in information, and not just a reshuffling of data. To see this imagine that you sample a transect but never

MEAN SPECIES FREQUENCIES
At sites

All species	6.63
Dry-rich species	7.34
Moist-rich species	6.18
Other-dry species	7.10
Nonindicator species	6.56

On transects

All species	5.34
Dry-rich species	5.22
Moist-rich species	3.74
Other-dry species	5.27
Nonindicator species	5.95

On plots

All species	4.91
Dry-rich species	4.33
Moist-rich species	2.67
Other-dry species	4.56
Nonindicator species	3.90

Above, the mean frequencies (number of samples in which a species is present) for different groups and different sample types.

*Species-pool graphs are similar in concept to species area curves but are more statistically robust because they start with the mean of a number of small samples rather than a single sample, and they ignore the samples of intermediate size, which turn out not to contribute any information beyond what is contained in the mean small sample and the total pooled sample.
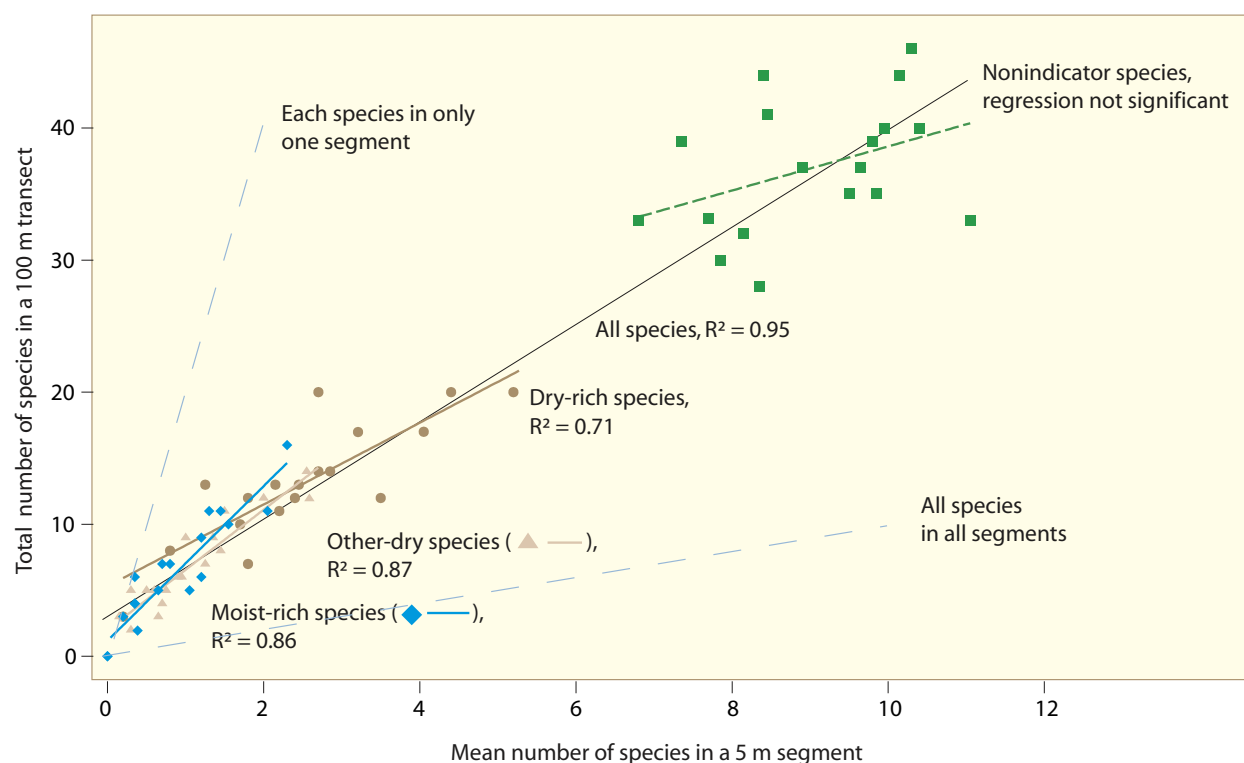
A sample-pool graph for transects. Each point represents the data for one species group on one transect, and gives the total number of species of that group on the transect versus the mean number of species from that group in a 5-meter segment of the transect. The regressions for the three indicator groups and for all species are highly significant. It seems, for example that there are likely to be, on average, four times as many total species and six times as many moist-rich species in the whole transect as there are in a single segment.

The slopes of the regression lines for each group are determined by the species-frequency distribution of that group, and are bounded by two extreme distributions. When (lower dotted line) all species are so common that every segment contains all the species, the segment mean = the total species pool. When (upper dotted line) the species are so rare that no species is seen more than once, the species pool = the number of segments × the number of segments per transect, in this case 20.

write down the names of the species. Instead, all you do is count how many species are in each segment. You do not have any idea whether, say, the 8 species in this segment are the same as or different from the 12 in the last segment. None the less, if you when you get to the end you find that there on average 10 species per segment, you can predict, fairly confidently, that the total number of species you have seen will be 3.4 + 3.7 · 10 = 40.4.

The second is that this particular relationship is only one of many possible ones. If more species were rare the lines would be steeper; the upper dotted line represents the limit where each species occurs only once and each segment adds all new species. If they were commoner the lines would be flatter; the lower dotted line is the limit where the same species occur in all segments.

32 Sample-pool Relationships for Sites

The second example, shown on he opposite page, shows a similar relationship at a much larger scale. In this case each point compares the mean diversity of a single sample (plot, transect, or whole sites) of one species group at one site to the total diversity of the pooled samples of that species group from all sites. Thus the four red triangles, for example, estimate the ratio (total diversity of all plots)/(mean diversity of one plot) for DR, MR, OD, and NI species. The regressions for plots, transects, and sites are parallel. In each case the relation between sample and pool is about the same, give or take an additive constant.

33 What do the sample-pool relationships say?

Besides being pretty, they say several unexpected things.

First, if you do one sample at each of 20 sites, the total number of species in all your samples will be about 2.7 times the average numbers of species per sample. There is a thus a regular relation between individual samples and an ensemble of such samples spread out over a large area, in our case some 300 square kilometers.

Second, this relation is the same for four ecologically different groups of plants. It does not vary with indicator status.

Third this relationship is also invariant with sample size: it works with 25-square-meter plots, 100-square-meter transects, and, amazingly, sites of variable sizes that are typically 10,000 square meters or more.

And fourth a similar relation holds at a much smaller scale: the mean number of species in a 5-square-meter segment predicts the total number of species in a 100-square-meter transect. Once again the relationship is strong and does not vary with indicator status. And interestingly, the slope is even similar: 3.7 for the expansion

SAMPLE-POOL RELATIONSHIPS FOR DIFFERENT SAMPLE TYPES

Each point represents a different subgroup (moist-rich, dry-rich, nonindicator, other-dry) of the flora.
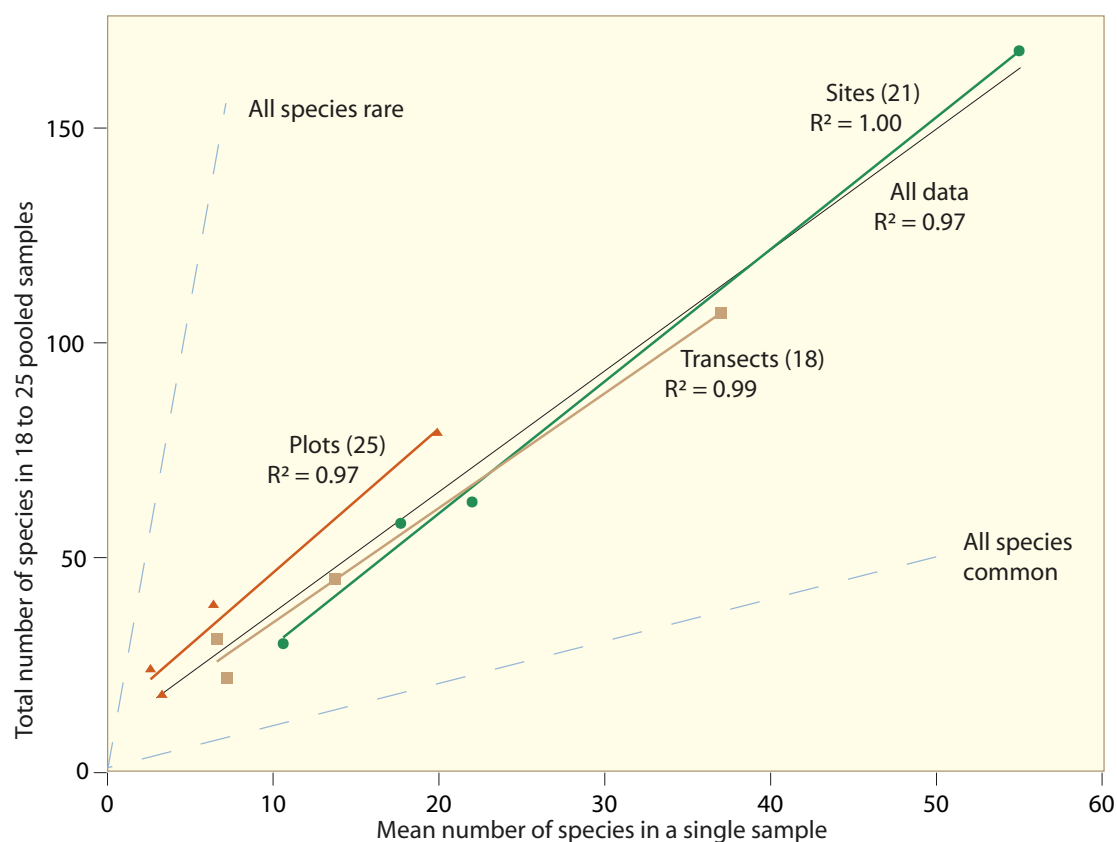
from 1 segment to 20 segments, 2.7 for the expansion from 1 site to 21 sites.

All of this is satisfying, but leaves the most important question unanswered: are these slopes, and the species-frequency distributions that generate them, a community property, or a more general property? Would they be different for, say, alpine tundra, CHCs, and beaver marshes? If so they would be worth investigating further, because on the one hand a quantitative signature of each communities, and on the other a thread that might be followed to learn something substantive about how communities work.

SUMMARY

34 What do we know about the geography, composition, and incidence of the Champlain Hills community?

That there are now over thirty known examples in the main area that we have explored between Crown Point and the Ausable River,

A sample-pool graph for three different sample units. In this case the sample is a mean diversity of, say, the individual plots, and the pool the diversity of all the plots put together. A sample-pool point for each the four species groups (DR, MR, OD, NI) is computed for each sample type. Interestingly, both the overall regressions for all data points, and the individual regressions on the species groups in each sample type are highly significant and nearly parallel to each other. As with the sample-pool relation for transects, the regression lines lie near the middle of the angle formed by the dashed lines showing the limits in which all species are very common and all are very rare.

plus at least twenty more possible sites in this area, and at least that many in the relatively unexplored area between Crown Point and the south end of the lake.

That the community has a very distinctive appearance and composition, and is characterized by about 170 indicator species that don't occur in ordinary woods.

And that, again in our main area of study, its incidence is topographically regular and independent of rock type. It occurred on almost every dry, south-facing rocky slope and bench under 500 meters in elevation that we examined, and was equally well developed on gneiss, gabbro, and anorthosite.

35 What are its chief conservation values?

Its chief values are that it is an unusual community, uncommon in New York and rare in New England; that it is exceptionally attractive and scenic; that it has received little use and is largely intact and good condition; that it is in part a grassland community and natural grasslands are rare in the Northeast; that it contains the richest woodland floras in northern New York; and that it contains some 560 occurrences of 73 species which are largely restricted to this community and so rare or uncommon in northern New York.

36 What is the current level of protection and what are the chances for increased protection?

Currently one site is in the New York State Forest Preserve and four others are owned by private nonprofits. The Westport Hills tract, formerly owned by International paper and now by Lyme Timber, is protected by a conservation easement that prevents development. It has the largest number of known and potential sites of any single ownership; it will come on the market in about ten years, and would an extraordinarily important conservation acquisition.

37 How sharply does the Champlain Hills community contrast with the matrix forests in which it is embedded?

Very sharply and cleanly. It generally begins abruptly and is marked by clear changes in vegetation structure and composition.

38 Is there a pattern to the way individual sites differ from one another?

The analyses I have done so far have not found one. The sites differ in composition and diversity, but there is no obvious geographic

or physiographic pattern to the differences. There is no association between the bedrock type and either the diversities of the different indicator groups or the distribution of individual species, and very little association between the diversities of different indicator groups.

39 Are there mid-scale internal patterns within individual sites?

By mid-scale I mean a pattern that involves a group of species at a scale larger than that of individual microhabitats or neighborhoods. On this scale there are at most weak patterns. High pH plots tend to have more moist-rich and dry-rich species. There are strong variations in indicator diversity with topography at individual sites, but no tendency for these patterns to recur at other sites with similar topographies. As a result, the indicator diversities of different groups were at most erratically and weakly correlated.

40 Are there patterns in the distribution or association of individual species?

Yes, but again many are not particularly strong. The strongest one is that many dry-rich species are very faithful to this community, occurring regularly within it and almost never outside of it. Beyond this, there are patterns of association between indicator species at middle-frequencies that allow us to detect a correlated group of 11 dry-rich species and another of about 11 moist-rich species. And there is a weak patterns suggesting that some individual species have pH preferences. But beyond this there is much ecological noise. We have many species without clear associations or pH preferences, and only a very few that seem to have any preference for specific types of bedrock.

41 Are there multiscale patterns in diversity?

Yes there are, and, as with other communities I have studied, they are very sharp. There are predictable sample-pool relationships, independent of the species group, between the segments of a transect and the whole transect. And there are similar relationships, also independent of both the species group and the size of the sample, between measurements at a single site and the pooled measurements at all sites.

42 What does this suggest about the nature of plant communities?

I have the following thoughts:

The CHC is a natural vegetation unit, contrasting sharply with the matrix forests in which it is embedded. As such it has a natural scale. If we attempted to merge it into a larger community we would have something that was clearly composite. If we attempted to divide it into several subcommunities they would lack distinctness.

Though the matrix forests in which it is embedded vary greatly, they don't divide into sharp subcommunities. This suggests a general observation, which is that the best-defined plant communities are local. They tend to be small-scale formations and gain their sharpness by contrast to larger, and inherently vaguer, regional communities in which they are embedded.

The CHCs refusal to vary consistently with rock type is likely telling us something, but what we don't know. Perhaps it is saying that we have not made the right measurements, or enough measurements. Or that we need to understand the relation between rock type and calcium on the one hand and rock type and pH on the other. Or that glaciers and weathering are homogenizing forces, and that the soils on different rocks are more alike than we know. Or the reverse: that glaciation makes for heterogeneity, and there are pockets of acid soils on limy rocks and limy soils on acid rocks.

The CHCs relative lack of internal pattern is something encountered in many self-organized systems, where pattern exists at a certain scale and not at larger are small scales. In these systems, the components—sand grains in a dune, molecules in a snowflake—cooperate to produce a pattern, but in such a way that the pattern is surprisingly independent of just who they are and what they are doing.

In the same way, because the CHC is an excellent habitat for many of the indicators in it, there may be little regularity in just where they live and who they live next to. Outside the community a dry-rich plant like blue-stemmed goldenrod is in basically poor habitat and is likely to occur only in particular places and there to be associated with other dry-rich species. But within the community it is in optimal habitat, and can occur almost anywhere. And since it can its ecological relations—its topographic preferences, its pH range, and it associates—will be much less sharply defined than they would be if we are observing it outside the community.

If this model is correct, then communities of this sort—ones that depend on a particular physical setting but don't have strong environmental gradients within the community—are going to be strongly distinct as an ensemble but rather pat-

ternless as individuals. They will certainly vary, but the variations may not tell you much about what they contain. The size and shape of a dune tells you almost nothing about the kinds of sand grains it contains. And the physiography, bedrock, and total diversity of a CHC seems to tell you equally little about how diverse the different indicator groups will be or which species will be present.

The lack of within-site pattern was often manifest in the field. As we approached a site we often had a clear sense of just where the community was going to start. But once we were within a site we usually did not know where the peak diversity would be (except that it would never be on dry summits) or where particular species were most likely to be found. And though we recognized many individual habitats, we had very little sense that the community included anything like a distinct subcommunity.

The sample-pool relations are scaling relations: they say that if you have some information about diversity on one scale you are able to predict it on another scale. They are surprisingly strong, extend from 5-meter plots to an ensemble of sites spread out over several square kilometers or more, and are independent of which species group you use to calculate them. They are cousins of the much-studied species-area relations, which may be the most reliable predictive relations in ecology. Like species-area relations, they are constant over different scales, and so may be called fractal. And like the species-area relations, they are rooted in an un-understood fact: nature, which has many possible choices for the distribution of species frequencies, seems choose only a few.

All of which points at something potentially interesting. We know that the CHC displays sharp sample-pool relationships. But we don't know if these relationships are different from, or the same as, those in other communities. If the first (which might be expected from the uniquely high diversity of this community) they may be an interesting, though hardly intuitive, metric for comparing communities. If the later (which might be expected from their kinship to species-area relations) then they are less informative but, given their surprising exactness, even more mysterious.

Barbara Lott of the southeast slopes of Quinn Mountain

Peter Jenkins on Kronks Hill

Celia Evans on Bristol Mountain

Large anorthosite crystals on Kronks Hill

Spotted coralroot and sharp-lobed hepatica

Young plants of Douglass's knotweed in a mat of polytrichum moss

Stiff sandwort and maidenhair spleenwort, with apple moss and *Peltigera* lichens.

Field chickweed

Actaea pachypoda

Actaea rubra

Adiantum pedatum

Adlumia fungiosa

Agropyron trachycaulon

Allium tricoccum

Amelanchier cf. sanguinea

Anaphalis margaritacea

Andropogon scoparius

Anemone virginiana

Antennaria plantaginifolia

Aquilegia canadensis

Arabis canadensis

Arabis drummondii

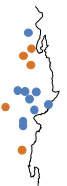Arabis lyrata

Arabis missouriensis

Aralia hispida

Aralia racemosa

Arctostaphylos uvi-ursi

Arenaria stricta

Arisaema triphyllum

Asarum canadense

Asclepias exaltata

Asclepias quadrifolia

Asplenium platyneuron

Asplenium trichomanes

Aster undulatus

Athyrium thelypteroides

Botrychium virginianum

Bromus kalmii

Bromus pubescens

Bulbostylis capillaris

Campanula rotundifolia

Cardamine parviflora
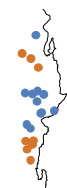
Carex albursina

Carex arctata

Carex backii

Carex blanda

Carex cephalophora

Carex cf. laxiflora

Carex peckii

Carex pedunculata

Carex plantaginea

Carex platyphylla

Carex rosea

Carex siccata

Carex sparganioides

Carex sprengelii

Carex swanii

Carex virescens

Carya cordiformis

Carya ovata

Caulophyllum thalictroides

Ceanothus americanus

Celtis occidentalis

Cerastium arvense

Chenopodium gigantospermum

Clematis occidentalis

Comptonia peregrina

Conopholis americana

Conyza canadensis

Corallorhiza maculata

Cornus rugosa

Corydalis sempervirens

Cypripedium calceolus

Cystopteris bulbifera

Cystopteris fragilis

Dentaria diphylla

Desmodium glutinosum

Desmodium nudiflorum

Desmodium paniculatum

Desmodium sp.

Dicanthelium cf. depauperatum

Dicanthelium columbianum

Dicanthelium latifolium

Dicanthelium xanthophysum

Dicentra cucullaria

Dirca palustris

Draba sp.

Dryopteris goldiana

Elymus hysterix

Epigaea repens

Eupatorium rugosum

Festuca subverticillata

Galium circaezans

Galium lanceolatum

Galium triflorum

Gaylussacia baccata

Geranium bicknellii
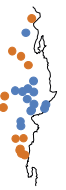
Geranium robertianum

Hackelia virginiana

Helianthus divaricatus

Hepatica acutiloba

Hepatica americana

Hieracium scabrum

Juglans cinerea

Juncus secundus

Juniperus communis

Juniperus virginiana

Laportea canadensis

Lechea intermedia

Lespedeza intermedia

Lilium philadelphicum

Lonicera dioica

Lonicera hirsuta

Milium effusum

Muhlenbergia glomerata

Muhlenbergia mexicana

Myosotis verna

Oryzopsis pungens

Oryzopsis racemosa

Osmorhiza claytonii

Panax quinquefolius

Parietaria pensylvanica

Penstemon hirsutus

Phegopteris hexagonoptera

Phryma leptostachya

Poa saltuensis

Polygonum douglasii

Potentilla arguta

Potentilla tridentata

Prunus pumila

Quercus alba
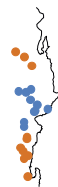
Ranunculus abortivus

Rhus aromatica

Ribes cynosbati

Ribes hirtellum

Ribes sp.

Rosa carolina

Rubus occidentalis

Rubus odoratus

Sambucus pubens

Sanguinaria canadensis

Sanicula marilandica

Sanicula sp.

Saxifraga virginiensis

Schizachne purpurascens

Shepherdia canadensis

Silene antirrhina

Solidago arguta

Vitis aestivalis

Waldsteinia fragarioides

Woodsia ilvensis

Woodsia obtusa

Xanthoxylon americanum

LISTS OF INDICATOR SPECIES

Moist-rich Species

Actaea pachypoda
Actaea rubra
Adiantum pedatum
Adlumia fungiosa
Allium tricoccum
Aquilegia canadensis
Aralia racemosa
Arisaema triphyllum
Asarum canadense
Asclepias exaltata
Asplenium trichomanes
Botrychium virginianum
Bromus pubescens
Carex albursina
Carex arctata
Carex blanda
Carex cf. laxiflora
Carex communis
Carex deweyana
Carex digitalis
Carex gracillima
Carex laxiculmis
Carex pedunculata
Carex plantaginea
Carex platyphylla
Carex rosea
Carex sparganioides
Carex swanii
Carex virescens
Carya cordiformis
Caulophyllum thalictroides
Cystopteris bulbifera
Cystopteris fragilis
Dentaria diphylla
Depraria acrostichoides
Dicentra cucullaria
Dryopteris goldiana
Eupatorium rugosum
Galium triflorum

Geranium robertianum
Hepatica acutiloba
Juglans cinerea
Laportea canadensis
Milium effusum
Oryzopsis racemosa
Osmorhiza claytonii
Panax quinquefolius
Phegopteris hexagonoptera
Ranunculus abortivus
Ribes cynosbati
Rubus occidentalis
Rubus odoratus
Sambucus pubens
Sanguinaria canadensis
Sanicula marilandica
Saxifraga virginiensis
Solidago flexicaulis
Sphenopholis obtusata
Staphylea trifolia
Thalictrum dioicum
Tilia americana
Viola canadensis
Viola conspersa
Viola pubescens
Viola rostrata

Dry-rich Species

Anemone virginiana
Antennaria plantaginifolia
Aquilegia canadensis
Arabis canadensis
Arabis drummondii
Arabis lyrata
Arabis missouriensis
Arenaria stricta
Asclepias quadrifolia
Asplenium platyneuron
Aster undulatus
Bromus kalmii
Cardamine parviflora
Carex backii
Carex hitchcockiana
Carex peckii
Carex sprengelii
Carya ovata
Celtis occidentalis
Cerastium arvense
Chenopodium simplex
Clematis occidentalis
Conopholis americana
Corallorhiza maculata
Cornus rugosa
Cypripedium calceolus
Desmodium glutinosum
Desmodium nudiflorum
Desmodium paniculatum
Dicanthelium latifolium
Dirca palustris
Elymus hysterix
Festuca subverticillata
Galium circaezans
Galium lanceolatum
Geranium bicknellii
Geranium robertianum
Hackelia virginiana
Helianthus divaricatus
Hepatica americana
Juniperus virginiana
Lespedeza intermedia
Lilium philadelphicum
Lonicera dioica
Lonicera hirsuta

Muhlenbergia glomerata
Myosotis verna
Parietaria pensylvtanica
Penstemon hirsutus
Phryma leptostachya
Poa saltuensis
Polygonum douglasii
Potentilla arguta
Quercus alba
Rhus aromatica
Ribes cynosbati
Ribes hirtellum
Rosa carolina
Quercus alba
Saxifraga virginiensis
Schizachne purpurascens
Shepherdia canadensis
Solidago arguta
Solidago caesia
Solidago squarrosa
Symphoricarpos albus
Triosteum aurantiacum
Ulmus rubra
Uvularia grandiflora
Uvularia perfoliata
Viburnum rafinesquianum
Viola conspersa
Vitis aestivalis
Waldsteinia fragarioides
Woodsia obtusa
Xanthoxylon americanum

Other-dry Species

Agropyron trachycaulon
Amelanchier cf. sanguinea
Anaphalis margaritacea
Andropogon scoparius
Aralia hispida
Arctostaphylos uvi-ursi
Bulbostylis capillaris
Campanula rotundifolia
Carex cephalophora
Carex cf. tonsa
Carex merritt-fernaldii
Carex siccata
Ceanothus americanus
Comptonia peregrina
Corydalis sempervirens
Dicanthelium cf. depauperatum
Dicanthelium columbianum
Dicanthelium xanthophysum
Gaylussacia baccata
Hieracium scabrum
Juncus secundus
Juniperus communis
Lechea intermedia
Oryzopsis pungens
Polygala polygama
Polygonum douglasii
Potentilla tridentata
Prunus pumila
Selaginella rupestris
Silene antirrhina
Solidago bicolor
Solidago nemoralis
Solidago puberula
Specularia perfoliata
Woodsia ilvensis