The use of matrix models to detect natural and pollution-induced forest gradients

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Abstract: We sought to compare the efficacy of the stationary Markov model and conventional ordination techniques in describing compositional and structural changes in forest communities along natural and manmade spatial gradients at two scales, local and regional. Vegetation abundance and structure data are from six sites spanning a spatial gradient in the Great Lakes-St. Lawrence forests near Sudbury, Ontario, Canada. Ordination did not detect slope-related local gradients despite the general trend that, as distance from the pollution source increases, vegetation along the slopes begins to display Markovian spatial dynamics. We suggest that this is due to information loss resulting from static ordination analyses: information regarding transitions between observations along the natural ordering of quadrats is not maintained. Both ordination techniques and the Markov analyses detected strong regional pollution-induced gradients in abundance and structure.

Keywords: Correspondence analysis, Great Lakes-St. Lawrence forest, Hill-slopes, Perturbation gradient, Principal components analysis, Ordination, Stationary Markov model.

Abbreviations: CA - Correspondence Analysis, PCA - Principal Components Analysis.

Introduction

Forest models are extremely diverse in structure and implementation. In general, they serve as both descriptive and predictive tools for understanding forest dynamics. They can be constructed at various scales of interest, from landscapes to communities to populations to individuals (Lischke 2001). For obvious reasons, there is interest in scaling up from lower to higher levels (Bugmann et al. 2000, Picard and Alain 2001), and this has received considerable attention in the recent modelling literature. Models can also be classified with respect to how much emphasis is placed on temporal dynamics, spatial dynamics or both spatial and temporal dynamics. We are concerned here with matrix models to detect gradients in forest dynamics, whether in space or time. While we deal with population and community levels, the models can be scaled up or down, with the lower limits depending on the resolution of the data and the upper limits on extent.

Matrix modelling of gradients has a long history of application in community ecology. The advent of computational power led to the proliferation of applications of multivariate statistical methods heavily rooted in matrix algebra to the study of ecological gradients (Gauch and Whittaker 1972, Orlóci 1978, Ter Braak and Prentice 1988). The basic algorithm involves dimension reduction via minimization of (typically) linear correlations between variables in space or time using eigenanalysis, such that indirect gradients may be visualized. The success of dimension reduction and final choice for number of dimensions can be assessed objectively through various statistical tests (Legendre and Legendre 2000). Assumptions about the underlying data structures must be met, and these vary depending on the exact technique being used (Podani 2000). These multivariate techniques, or ordinations, are still being fine-tuned to account for problems arising from incomplete or non-random ecological sampling, unrealistic assumptions of normality and/or linearity, and the presence of noise (Legendre and Legendre 2000, Borcard et al. 1992, Doledec et al. 2000, De'ath 1999, McArdle and Anderson 2001, McCune 1997, Pillar 1999a.). Despite this, standard techniques such as Principal Components Analysis and Correspondence Analysis remain useful in the detection (and more importantly, parsimonious description) of strong, simple ecological gradients in space (e.g., systematic community change along moisture gradients) or time (e.g., succession) (Deutschman et al. 1997, Legendre and Legendre 2000, Anand and Kadmon 2000). In classical applications, these ordination techniques incorporate spatial and/or temporal information about gradients by averaging species associations

over space or time (e.g., through the calculation of variance/covariances). As such, information on the association between species and time and/or space and any explicit ordering therein, may be lost.

A more dynamic approach to gradient detection may be found in the application of a transition matrix model such as the stationary Markov chain. The application of stationary Markov models to forest dynamics was introduced in the early 1970's where mixedwood forest dynamics were modelled through time (Waggoner and Stephens 1970, Peden et al. 1973, Horn 1975). In one case (Waggoner and Stephens 1970), forest dynamics was modelled using states composed of dominant tree species and transition probabilities determined by measurement of the replacement of one state by another over very long timescales. In another case (Horn 1975), the number of tree saplings was used as a basis for the estimation of individual tree replacement by the same or new species. Since their introduction there has been wide interest in the application of Markov models to forest dynamics (van Hulst 1979, Binkley 1980, Culver 1981, Usher 1981, Valverde and Silvertown 1997, Logofet and Lesnaya 2000, Korotkov et al. 2001, Yemshanov and Perera 2002). Other well-known applications include the temporal dynamics of grassland (Balzter 2000), heathland (Legg 1980, Lippe et al. 1985, Orlóci et al. 1993, Anand and Heil 2000), and desert (McAuliffe 1988) plant communities. Markov matrix models have also been used in other ecological applications. For example, Wootton (2001) in intertidal mussel community dynamics and Usher (1979) for insect succession. Few applications have been made to spatial pattern detection (but see Kenkel (1993) for application to plant population dynamics of a plant and Li (1995) for vegetation patterns in a Texas savannah).

The main criticism of these models — that they are too simple – (van Hulst 1979) can also be considered their strength. A simple, stationary Markov chain is determined by the initial conditions of the system and a stationary transition matrix (the transition probabilities do not change within the spatiotemporal scale of the study system). Whether or not forest dynamics in time (or space) can be usefully modelled using such simple rules is still open to debate. Some recent approaches attempt to relax the assumption of a stationary transition matrix in the application of the Markov chain by using a non-stationary, non-homogeneous or fuzzy Markov chain (Li 1995, Anand and Orlóci 1997, Korotkov et al. 2001, Yoon and Korvin 2001). These approaches can often provide more accurate description at fine scales and under changing environmental conditions, but lose the most desirable property of the model, namely, simplicity. This property is

particularly important if the models are to be used for large-scale management purposes (Batabyal 1996).

Two things are key to the implementation of the stationary Markov model: First, there must be estimation of transition probabilities and second, there must be testing of the fit of the Markov model to the observed dynamics. Fine-scale direct observation of transition probabilities in heathland dynamics revealed that the transition probabilities were non-stationary in time due to the myriad of ever-changing site-specific environmental effects (Lippe et al. 1985). However, others (Orlóci et al. 1993, Anand and Heil 2000) have shown that using a less reductionistic approach to estimate transition probabilities, a stationary Markov chain modelled the recovery process of the same heathland data quite well. Over long periods of time and at fine-scales of resolution, ecological systems are inevitably subject to external perturbations and individual effects, and stationary transition probabilities are not realistic. However, over short periods of time and at meso and macro scales, a fixed transition matrix can provide reliable predictive power (Orlóci et al. 1993, Wootton 2001). Regarding testing of the fit of model to observations, there have been several approaches. Some (Binkley 1980, Lippe et al. 1985) used chi-square to evaluate the stationary nature of the model put forth by Waggoner and Stephens (1970). Others (Baltzer 2000) applied mean square error, Spearman's rank correlation coefficient and Wilcoxon's signed-rank test. The approach in Orlóci et al. (1993), however, is most appealing to us for two reasons: First, transitions may be estimated indirectly from phytosociological-type survey data, and second, statistical evaluation of the fitted Markov model is done using randomization testing, and thus unrealistic classical assumptions of random sampling and normality of underlying distributions need not be satisfied.

We sought to compare the efficacy of the stationary Markov model (using the general approach of Orlóci et al. (1993)) and conventional ordination techniques in describing compositional and structural changes in forest communities along natural and manmade spatial gradients representing local and regional scales near Sudbury, Ontario, Canada. The smelter damaged landscape of this area has been subject to vegetation studies in order to gauge the extent of pollution caused by historic nickel-copper sulphide ore smelting practices and to characterize the perturbation gradient that radiates outward from the point sources of atmospheric pollutants (Freedman and Hutchinson 1980a, Freedman and Hutchinson 1980b, Amiro and Courtin 1981, Anand et al. 2002). Naturally occurring gradients, however, are also important for plant community structure (Bridge and Johnson 2000), and the

Sudbury area is suitable for the study of potential topographically-induced gradients (due to abiotic conditions such as moisture availability and wind exposure). We were thus interested also in comparing the regional pollution gradient to 'naturally' occurring gradients that we believed to be important in spatial dynamics at the local scale.

Study site, sampling design and quantitative methods

Vegetation abundance and structure data are from six monitoring sites situated so as to traverse the anthropogenic perturbation gradient, starting near Sudbury area smelters decommissioned in 1972 and proceeding in a southerly direction for approximately 36 km (Fig. 1). The sites belong to the Canadian Ecological Monitoring and Assessment Network (EMAN; www.eman-rese.ca). At each site, south-facing slopes on hillsides were surveyed in 2001 using two parallel, 100 m transects which were believed to cross natural gradients relating to topography (soil moisture, soil nutrients). Moisture and nutrient gradients on hill slopes have been found to result in vegetation compositional changes (Bridge and Johnson 2000) and it was expected, from field observations, that these compositional changes should also be detectable on Sudbury area slopes using analytical techniques. Cover abundance of understory vegetation was estimated using the Braun-Blanquet method in 1m x 1m contiguous quadrats along each transect. These were transformed to percentage cover values. Overstory species were sampled for tree density and height in 5 m x 5 m contiguous quadrats. A total of 45 vascular plant species were detected in the surveys (Table 1). Local analysis involved examination of transect data from 100 m transects located at each monitoring site. Regional analysis examined data sets of mean values for species coverage or height classes at each of the six sites. Although understory and overstory analyses revealed similar behaviour of ordination techniques at local and regional scales, the overstory analyses are included because they illustrate a new application of the procedure outlined in Orlóci et al. (1993) and provide information about vertical forest structure.

Correspondence Analysis (CA) was used for gradient detection at both the local (transect) level and the regional (across sites) level, because it is well suited to the unimodal data structures we found at both scales. The ecological analysis software package SYN-TAX (Podani 2001) was used for the multivariate analysis. Correspondence analysis, also known as reciprocal averaging, is a technique that gives an ordination of both the species and the sampling units (Hill 1973). Symmetric weighting (α=0.5) of the

Table 1. Vascular plant species found in the surveys and corresponding codes used for ordination plots.

Species	Code
Abies balsamea (L.) Miller.	AB
Acer rubrum L.	AR
Agrostis scabra (Willd.)	AS
Alnus viridis (Villars) Lam.	AV
Amelanchier spp.	A
Aralia hispida Vent.	AH
Aralia nudicaulis L.	AN
Aster spp.	ASP
Aster macrophyllus L.	AM
Betula papyrifera Marshall.	BP
Carex scoparia Schk.	CS
Carex spp.	C
Clintonia borealis (Aiton) Raf.	CB
Comptonia peregrina (L.) J. M. Coulter.	CP
Cornus canadensis L.	CCA
Corylus cornuta Marshall.	CCO
Danthonia spicata (L.) F. Beauv.	DS
Deschampsia cespitosa (L.) P. Beauv.	DC
Deschampsia flexuosa (L.) Trin.	DF
Diervilla lonicera Miller.	DL
Dryopteris marginalis (L.) A. Gray.	DM
Gaultheria procumbens L.	GP
Hieracium aurantiacum L.	HA
Kalmia angustifolia L.	KA
Ledum groenlandicum Oeder.	LG
Lonicera canadensis Marshall.	LC
Lycopodium digitatum Dillen.	LDI
Maianthemum canadense Desf.	MC
Smilacina racemosa (L.) Desf.	MR
Monotropa uniflora L.	MU
Oryzopsis asperifolia Michx.	OA
Osmorhiza spp. Raf.	O
Picea glauca (Moench) Voss.	PG
Pinus banksiana Lambert.	PB
Pinus resinosa Aiton.	PR
Pinus strobus L.	PS
Populus grandidentata Michx.	PGR
Populus tremuloides Michx.	PT
Pteridium aquilinum (L.) Kuhn.	PA
Quercus rubra L.	QR
Salix spp.	S
Trientalis borealis Raf.	TB
Vaccinium angustifolium Aiton.	VA
Vaccinium myrtilloides Michx.	VM
Waldsteinia fragarioides (Michx.) Tratt.	WF

analysis results in a joint plot where the relative positions of variables (species) and objects (sampling units) in ordination space convey meaningful information regarding their association with one another (Podani 2000). That is, a gradient would be expected to appear as a systematic ordering of sampling units along the first and/or second ordination axis.

A stationary Markov chain is such that the state distribution at time t+1 is known from the state distribution at time t and a transition matrix:

$$X_{t+1} = X_t \times P \qquad (1)$$

where X_t is the previous state vector, P is the transition matrix, and X_{t+1} is the current state vector. In ecological applications, X_t is a multivariate vector of population abundance estimates and the elements of the transition matrix P represent the rates at which populations gain or lose ground to other populations. So, for the given transition matrix P, the element p_{ij} is a measure of the rate at which population i loses ground to population j after one time/space step.

If the model is temporal in nature the transitions are most often considered from one year to the next, but shorter or longer intervals may be used. In a temporal model, t refers to the temporally separated states (observations each year) between which transitions are examined. In a spatial model, transitions are examined along spatial intervals and t refers to the spatially separated states (quadrats or monitoring sites) between which transitions are examined. In either case, transitions are examined at the scale of the states that are of interest. Local analysis considers transitions between equidistant quadrats and is a fine scale examination of species dynamics along hill-slopes. Regional analysis considers transitions between monitoring sites and is an examination of species dynamics along the perturbation gradient. Note that the steps of the model at the regional level are not equidistant (Fig. 1). The intensity of perturbation does not necessarily have a linear relationship with distance, and our focus was on evaluating the transitions between obvious, perturbation-induced community states, not equally separated locations. The state vector, X, is the vector of variable measurements for the given sampling units. In understory

analysis the state vector is cover abundance values of species, while in overstory analysis the state vector is the species height classes that have been weighted by their respective frequencies. As illustrated in Fig. 2, the model can consider transitions between adjacent quadrats, in which case it is considered a first-order model, but Markov dynamics can also be investigated at increasingly higher orders (e.g., a second order model is where transitions are examined between every second quadrat). Next, we briefly review the Markov fitting procedure, but more details can be found in Orlóci et al. (1993).

The calculation of the transition matrix assumes that a population in transition loses most to or gains most from the largest coexisting population. Equation 2 illustrates the method of calculating the gain or loss from population i to population h:

$$D(i) = |X_{ik} - X_{ij}| \frac{X_{hk}}{X_{.k}} \qquad (2)$$

where $D(i)$ is the gain or loss of population i, X_{ik} and X_{hk} are quantities of populations i and h in relevé k, $X_{.k}$ is the sum of values in relevé k, and X_{ij} is the quantity of population i in relevé j. A transition matrix is calculated for each step (time/space) and the mean matrix is calculated to provide the transition matrix P. The Markov relevés, or model predictions of the system under investigation, are generated by successive iterations of Equation 1 using the first sampling unit vector of X and the transition matrix P.

The engineer's stress coefficient (σ^2) is employed to measure the degree of discordance between Euclidean distance matrices of the actual observations and the Markov relevés generated from the transition matrix, and randomization is used to generate an empirical distribution of stresses for hypothesis testing (Orlóci et al. 1993). The null hypothesis is that the coenosere is undirected;
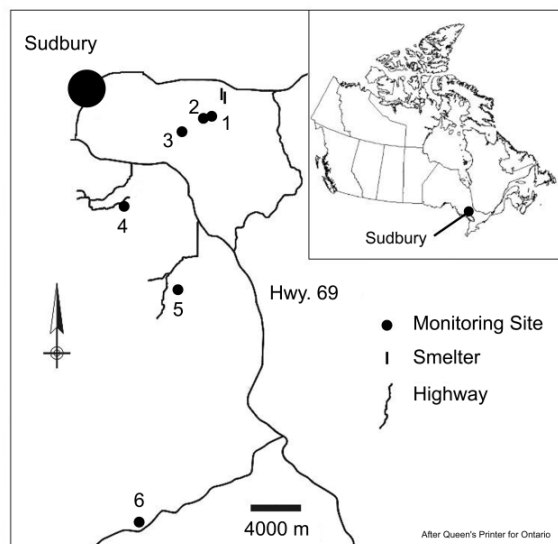

Figure 1. The locations of six ecological monitoring stations. Distances from decommissioned smelters are approximately: 1.7 km (1), 2.1 km (2), 4.2 km (3), 12 km (4), 16 km (5), 36 km (6). Note that sites are not equidistant.
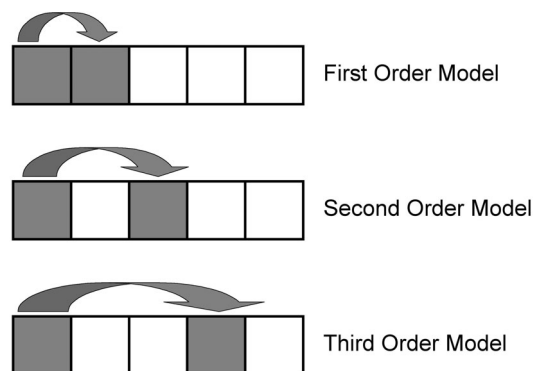

Figure 2. An illustration of Markov model orders applied to transects of contiguous quadrats.

that is, each state moves to the next via a separate and random transition matrix. It is possible to reproduce this behaviour by random permutations of the observed relevés where each permutation gives rise to a new stress value. After many permutations a sampling distribution of stress values is generated from which the probability of obtaining the actual observed stress value can be determined. Randomization testing provided by FitMarko was carried out for 1000 iterations for all analyses. H_o (that the process is random) is rejected if the proportion of simulated stress values equal to or smaller than the observed stress value is less than a desired limit (0.01, 0.05 or 0.1). When this proportion is low, the hypothesis that transitions are random is rejected, and it can be concluded that the coenosere is Markovian with a stationary transition matrix at the given order. The measure of stress (σ^2) between the two matrices is given by the square root of:

$$\sigma^2(D_X D_M) = \frac{\sum_{j<k}^{c}(d_{Xjk} - d_{Mjk})^2}{\sum_{j<k}^{c}(d_{Xjk} + d_{Mjk})^2} \qquad (3)$$

where X is the set of relevés, M is the set of Markov relevés, D_X and D_M are the distance matrices, d represents Euclidean distance. A Euclidean distance matrix is a matrix ($m \times m$) of the distances in variable space between all possible pairs of m points (Podani 2001). The computations are performed by the program FitMarko (Pillar 1999b).

Understory vegetation at the local level was analyzed at orders 1 to 5. Understory vegetation at the regional level was analyzed at the first order level only. The method assumes that the bare ground (BG) of a quadrat is the limiting resource. The values within each sampling unit were then standardized by total abundance/density. Overstory vegetation required development of a novel approach because the data collected in the overstory quadrats was not cover abundance, but rather density (# of individuals) and height (height class). Both parameters of overstory vegetation, height and density, were important in characterizing the regional perturbation gradient detected by Correspondence Analysis. The method proposed by Orlóci et al. (1993), however, is based on cover abundance of quadrat area and requires some measure of bare ground (available resource for which all populations compete). This can be interpreted as the maximum possible cover of the sampling unit after standardization and as the maximum potential for growth of the community (i.e., the understory can cover a maximum of 100% of the quadrat). Species frequencies were weighted by the mean of their respective height class resulting in values measured in "tree unit metres", where the value of a given variable (species height class) in a particular quadrat would be a function of height and density. This approach assumes that, aside from natural or anthropogenic stress factors, conditions along a given transect produce equal species numbers and height distributions. The maximum sampling unit sum along a given transect was used as the maximum allowable value for that particular transect and all other sampling units along the transect had, as a variable, a measure of unexploited resource. Understory unexploited resource is quantified as percent cover of bare ground while the overstory unexploited resource is quantified as the remainder of the difference, in unit metre height, between a given sampling unit sum and the maximum sum found along the transect. An artifact of this approach is that there will occur at least one sampling unit along each transect where the measure of unexploited resource is zero. This method provides a relative scale along each transect that takes into account both height and density of trees and avoids the situation where density or height are considered individually, leading to uneven consideration of variables. Overstory data at the local and regional levels were analyzed at the first order level.

Results

Correspondence Analysis did not detect slope related local gradients in either understory or overstory vegetation data (see Fig. 3 for an example). A slope related gradient would be expected to manifest itself as an ordering of quadrats in ordination space. A separation of the quadrats nearer to the top of the hill (lower numbered quadrats in Fig. 3) from the rest of the quadrats in the transect was also expected because the top portions of hill slopes showed the most dramatic changes in vegetation composition as one moved from the top of the hill to the midslope. The ordination scores of objects, however, did not indicate a particular ordering of sites along the CA axes. The failure of the ordination to detect these gradients may be the result of information loss resulting from static analysis, such as ordination, where information regarding transitions between observations along the natural ordering of quadrats is not maintained.

Markov analyses did detect local gradients in understory vegetation at some sites far from the smelter. These local gradients were significant at model orders 1 through 5 (Table 2). The general trend found in local Markov analysis was that, as pollution level decreases (distance from the smelter increases), slopes begin to show a Markov nature where local spatial dynamics are predictable.

Ordination, however, did detect the regional manmade gradient using understory as well as overstory data.

The horseshoe effect (Podani 2000) is present in all regional ordination plots, however, detrending of the CA was not required to capture the trends. Aside from unimodal species responses along the regional transect there was also an increase in species richness, which may account completely for the effect. Podani and Miklós (2002) have found that species richness gradients can in fact produce strong horseshoes in ordinations. This appears to be the case here. There is a strong correlation between the ordination axis 1 scores of sites in the CA plots and the species richness at those sites. This suggests that species richness changes may be largely responsible for the horseshoes in the ordination plots. A distinct ordering of sites occurred along Axis 1 in the CA joint plots of understory mean cover (Fig. 4a). The exception to this is the placement of sites 1 and 2, which are very similar in terms of both floristic components and distance from the smelter (±300 m). The joint plots show how the understory communities at these sites are indicators of the spatial proximity to the point source pollution. *Agrostis scabra* (AS), which is associated with sites 1 and 2, is the primary understory species at these heavily impacted, barren locations and has been found to be metal tolerant (Archambault and Winterhalder 1995). *A. scabra* was found primarily at sites 1 and 2 and the fact that it occurs at very few sites near the
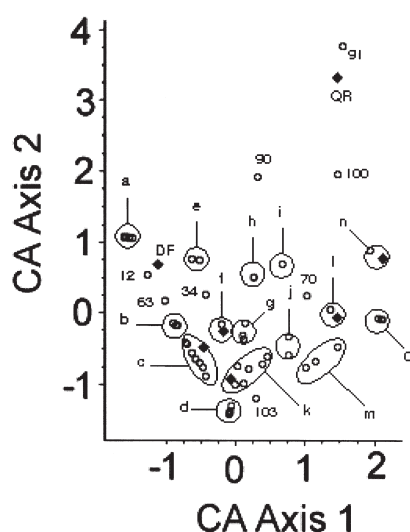
Table 2. Probabilities generated from randomization testing on the null hypothesis that transitions are random along 100 m transects at 6 sites. Each transect was tested at Markov orders 1 through 5. Transects at sites 4, 5, and 6 are deemed significant and indicate stationary Markov dynamics. Analysis performed with FitMarko and 1000 iterations for testing.

	Local Transects				
Site	1st Order	2nd Order	3rd Order	4th Order	5th Order
1	0.52	0.54	0.50	0.26	0.24
2	0.48	0.58	0.61	0.62	0.60
3	0.69	0.77	0.76	0.77	0.73
4	0.01	0.00	0.00	0.00	0.00
5	0.10	0.10	0.10	0.09	0.08
6	0.06	0.07	0.05	0.06	0.05

smelter, where abiotic conditions make it one of only a few species present, makes it distinct from virtually all other species studied. This difference manifests itself as the large distance between *A. scabra* and the rest of the species on the joint plot. This species tends to become less important in sites with greater numbers of understory species.

Betula papyrifera, *Deschampsia flexuosa* and *Vaccinium angustifolium* are placed near sites 3 and 4 and are major contributors to understory cover at these two locations. *B. papyrifera* and *D. flexuosa* are natural colonizers of the Barrens, with *D. flexuosa* usually appearing after the establishment of *B. papyrifera* (Winterhalder 2000). *V. angustifolium* also persists at these heavily impacted sites and has been noted as an early colonizer of heavily impacted soils in the Sudbury area, often associated with open canopy *B. papyrifera* (Gunn 1995). These species are present at sites closest to the smelter (1 and 2) as well, but in higher abundances in 3 and 4. Sites at increased distance along the pollution gradient are characterized by increased species richness and the presence of more sensitive, shade tolerant woodland species, such as *Aralia nudicaulis*, *Maianthemum canadense* and *Trientalis borealis*. The increased number of species at the sites distal from the smelters indicates a changing of understory dominance. Indeed, at site 5 *P. aquilinum*, *M. canadense* and *V. angustifolium* are the major contributors to understory vegetation cover. By site 6 the major contributors are *A. nudicaulis*, *A. rubrum*, *Aster macrophyllus*, *Corylus cornuta*, *M. canadense* and *P. aquilinum*. Not only are the dominant species changing, but they are also accounting for an increased amount of quadrat area, and bare ground is becoming less important.

Ordination of overstory regional data sets also helped to detect the pollution gradient. The monitoring sites displayed an ordering along axis 1 of the CA (Fig. 4b) where,
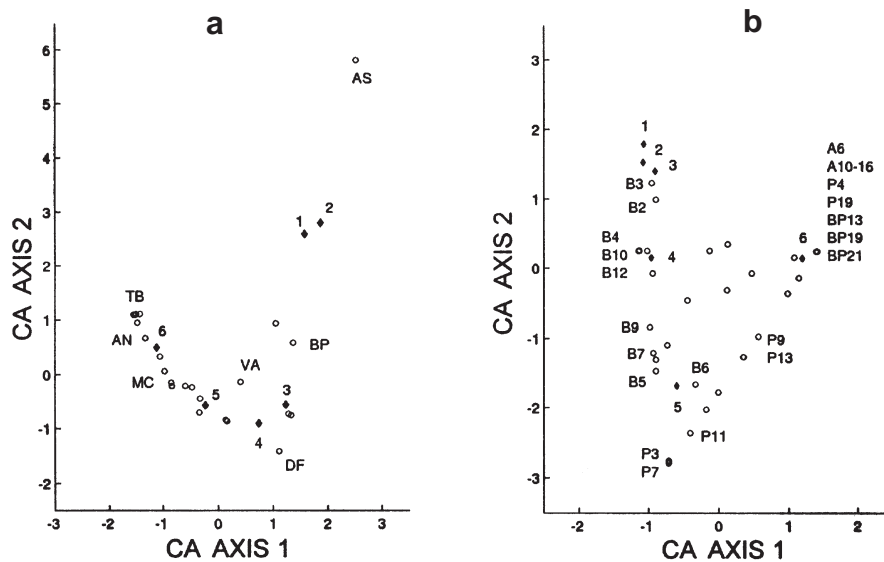

Figure 3. The result of a CA using SYN-TAX on a local understory transect at site 3. Solid dots are species and unfilled dots are sampling units (quadrats). No clear spatial trend could be detected in species or sampling units. Groups: **a** = 9,10,14-16,21,30-33, 36,39,40,42, 48, 54,64, 67, 68, 72, 75-77,80,81,83,84,86-89, 108,109; **b** = 18,20,24,35,38,85; **c** = KA,17,22, 29,37, 41,78, 79,82,110; **d** = 1,5,13, 19,49,65,74, 104-106; **e** = 23,71; **f** = VM,25; **g** = 47,50,55; **h** = 43,102; **i** = 2-4, 6-8,11,44,45,52,53, 66,93,107; **j** = 98,99; **k** = BP,26-28,46,59,97; **l** = VA, 101; **m** = 60,69,92; **n** = ARU, 56; **o** = 51,57,58,61,62,94-96. See Table 1, for species codes.

Figure 4. CA on understory cover means (**a**) and on height class overstory frequency means (**b**) at 6 sites (regional data, sites are solid diamonds and are labelled as numbers). Understory labels: *Agrostis scabra* (AS), *Betula papyrifera* (BP), *Deschampsia flexuosa* (DF), *Vaccinium angustifolium* (VA), *Maianthemum canadense (*MC), *Trientalis borealis* (TB), *Aralia nudicaulis* (AN) are labelled. Overstory labels: *Betula papyrifera* (B) *Pinus strobus* (P) and *Acer rubrum* (A) are labelled; number following alpha code is height class midpoint (m).

from left to right, the sites are arranged in order of their proximity to the smelter. Overstory species density and height are important in characterizing the spatial gradient. Tree height classes progressively increase from site 1 to site 6 in the ordination, with the tallest height classes (e.g., *P. strobus* 20 m, *P. resinosa* 30 m) being found at site 6. The species composition of the community also changes with the appearance of later stage successional species at greater distances. At sites close to the decommissioned smelters, *B. papyrifera* exists at low height classes and is the dominant species. As noted above, *B. papyrifera* is a natural colonizer of the highly degraded soils of the Sudbury area. The height of *B. papyrifera* increases with distance but near site 5, *P. strobus* also begins to characterize the monitoring sites. *P. strobus* has been shown to be particularly sensitive to atmospheric exposure to sulphur dioxide (SO_2) (Linzon 1958). The primarily unimodal response shown by both *B. papyrifera* and *Q. rubra,* with maxima occurring at sites closer to the smelters, may indicate successional changes in the forest structure, similar to what we may expect from temporal recovery. With increasing distance from the smelters more typical overstory species such as *Pinus strobus* are able to persist, effectively out-competing the early successional stage species.

Markov randomization testing for regional data sets of vegetation revealed highly significant results for a first-order Markov model: the Markov chain and calculated transition matrix closely fit the observed species dynam-

ics in understory data (p = 0.01) and in overstory data (p = 0.09). Understory species dynamics of the most abundant species is shown in Fig. 5. Bare ground decreases rapidly within the first 20 km away from the smelter, but then decreases to almost zero by site 6. *A. rubrum* shows a slight increase in cover abundance. *B. papyrifera* increases rapidly in the first 5 km but then begins a slow, continual decrease before disappearing prior to the site 6 (35 km). *D. flexuosa* follows the same pattern as *B. papyrifera* but at reduced cover amounts. This behaviour is expected when considering the fact that *D. flexuosa* tends to be present under cover of the taller *B. papyrifera*. *M. canadense* first appears at site 4 and increases at a continuous rate. *P. aquilinum* first appears in site 3 and increases to a maximum at site 5 then decreases at site 6. *Q. rubra* reaches a maximum at site 4, decreases and remains in low abundance for the remainder of the study range. *V. angustifolium* reaches a maximum at site 5 but then decreases to low abundance by site 6. Although the Markov projections closely fit the observed dynamics, there are notable differences. For example, unimodal responses of *B. papyrifera* and *D. flexuosa* are only very slightly captured in the Markov predictions of these two variables. The strong unimodal response of *V. angustifolium* is not captured in the Markov representation at all. Species that are absent from the site locations close to the smelter, such as *A. rubrum, M. canadense,* and *P. aquilinum,* are modelled as present at these sites by the Markov chain. Interestingly, model projections reveal that neither understory nor overstory have

reached stability at site 6 (Fig. 6). This indicates that the effects of perturbation may still be present at this distance.

The finding that the Correspondence Analysis was not capable of detecting the Markovian nature of several transects was explored in further detail. CA on a transect from site 6 is shown in Fig. 7a but does not reveal an ordering of quadrats along the ordination axes. A CA performed on a purely Markov coenosere generated from transition probabilities from the same transect is shown in Fig. 7b. The Markov process fit the data from this transect (p = 0.06) (Table 2). Sampling units 1-7 are systematically arranged along ordination axis 1, but there is no difference between quadrats 8-100. This is a reflection of the Markov analysis detecting the rapid change in vegetation community characteristics from the rocky hilltops to the

more heavily vegetated hillslopes, which is quite evident in the field.

In an attempt to explain the discrepancies between the Markov analysis and CA at the local level, Principal Components Analysis (PCA) was used to investigate the local Markov transects. An examination of the theoretical data structures of the Markov model, CA and PCA, will aid in the explanation (Fig. 8). CA is best suited for unimodal variable responses, while PCA assumes that the data are structured linearly. The Markov model is based on the data being structured monotonically. The PCA was able to detect the gradient at the regional level and, like CA, shows a systematic arrangement of sampling units when performed on a purely Markov system (Fig. 9). Although the vegetation data had a unimodal structure, and thus
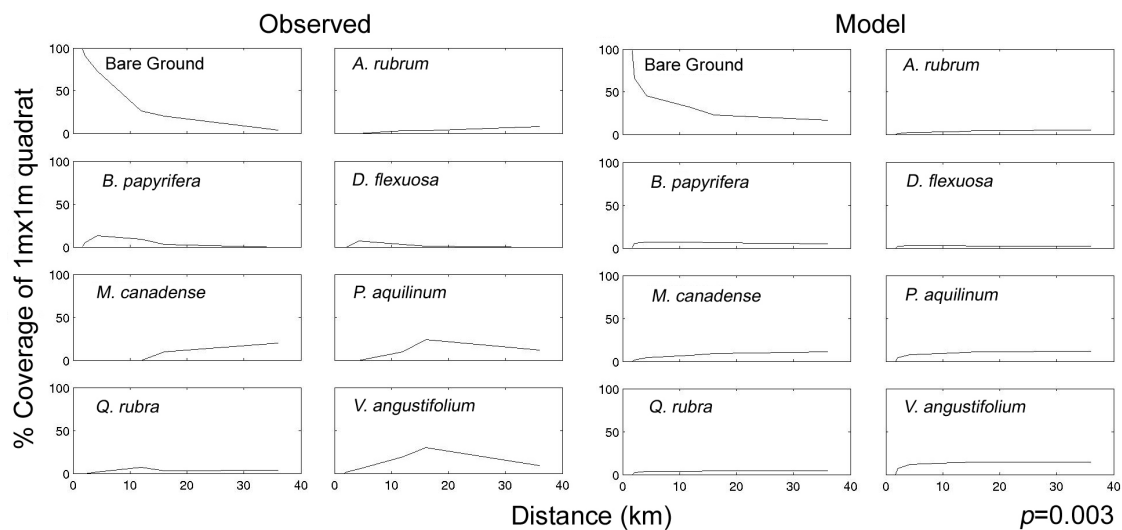

Figure 5. A comparison between observed and Markov dynamics in local understory transect data. Left: Actual percent cover in 1 m x 1 m quadrats of some understory species plotted against distance from the Sudbury area smelters. Right: Markov projections for the same species. Confidence level of fit (p=0.003) is from randomisation testing with 1000 iterations.
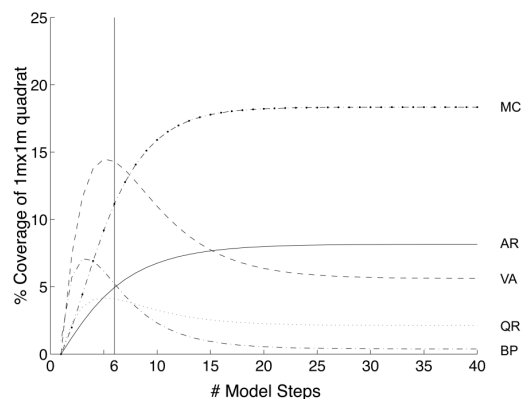

Figure 6. Markov projections for selected species beyond site 6 (35 km from pollution source). Site 6 is indicated by vertical line. Stability is not reached until model step 40. See Table 1 for species codes.
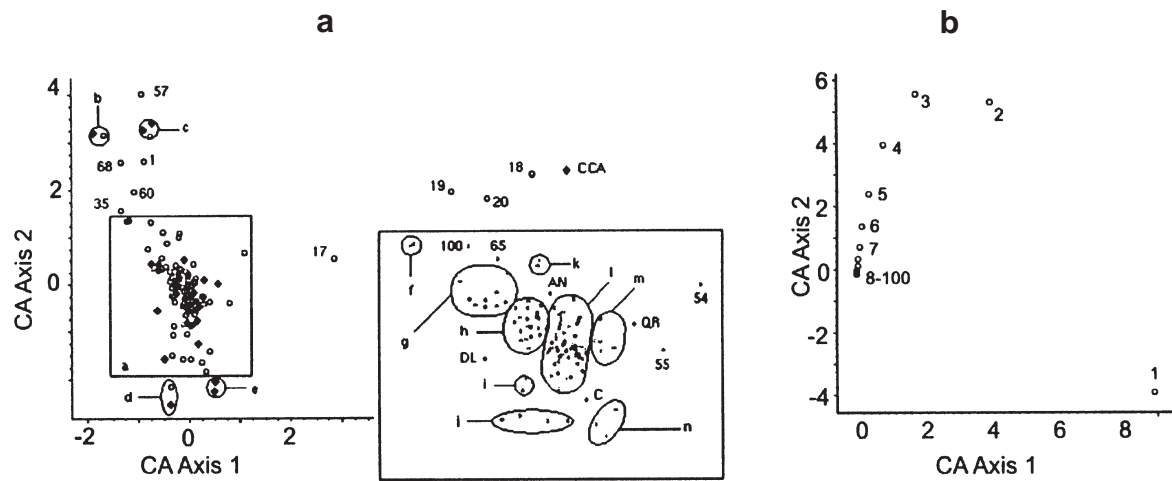
Figure 7. The results of a CA on understory percent cover from 1 m x1 m quadrats along a 100 m transect at site 6. (**a**) Solid dots are species and unfilled dots are quadrats. Groups: b = PG,98; c = ABA,OSP,97; d = PGR, 82; e = VM,AS; f = 40,42; g = CCO,MR,MU,17,21,30,34,41,52,83; h = GP, LC, PTR, 21-24, 31,33, 36, 37,39,43,50,66,75-78,93-96,99; i = 79,80; j = CB,81,88,92; k = 58,59; l = A, ARU, ASM,DM, LD, OA,PA,SAS,TB,2,5-13,15,25-29, 32, 38, 44-47,49,51,53,61-64, 67, 69, 70-74,84,85,87; m = 3,4,16,56; n = 89-91. Please see Table 1 for species codes. (**b**) The results of a CA on Markov relevés generated from data in (a). Open circles are sampling units. The Markov relevés fit the data local gradient very well in this case ($p = 0.06$).
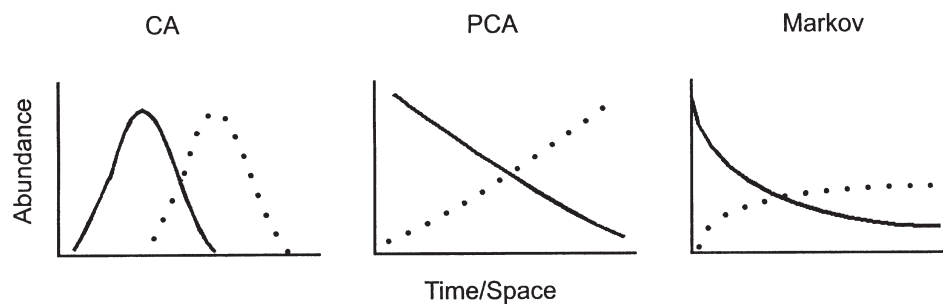

Figure 8. Data structures assumed by three gradient analysis techniques.
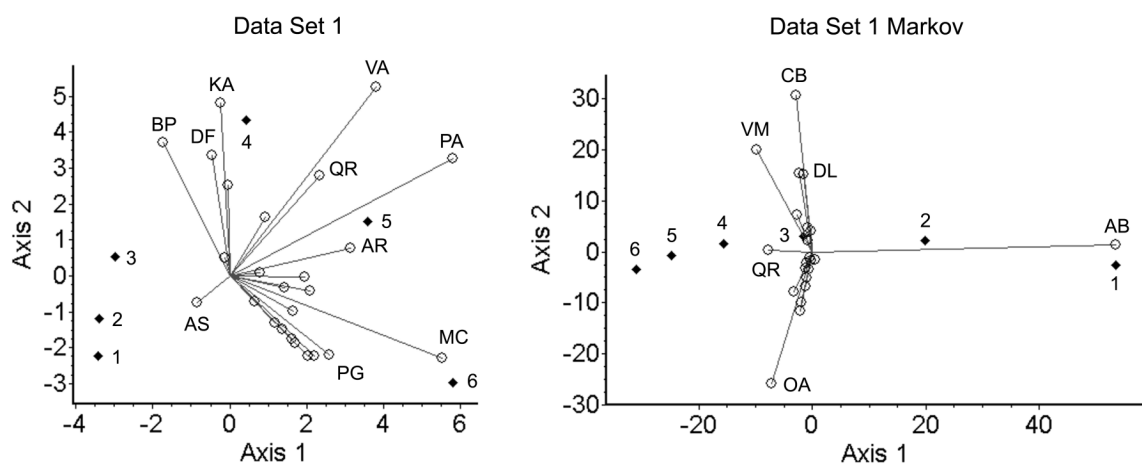

Figure 9. PCA Euclidean biplot of regional understory data (left, Axis 1 = 57.0% and Axis 2 = 26.6%) and Markov projections produced from model fit to understory data (right, Axis 1 = 99.3% and Axis 2 = 0.7%).

warranted the use of CA, a PCA was performed because of the similarity of the PCA and Markov data structures. The PCA, like the CA however, was unable to detect a difference between Markov and non-Markov transects at the local level.

Discussion

An analogy could be drawn between the spatial forest pattern observed across the pollution gradient and the temporal succession that occurs after a major perturbation (recovery). Nearest the perturbation source, in time or space the early succession species persist and, as distance from the source increases, these species give way to later stage successional species. The spatial dynamics of species around this impacted area tend to mimic temporal successional processes, with *A. scabra, B. papyrifera* and *D. flexuosa* occurring as colonizers in both space and time, but then giving way to later stage species. The primarily unimodal response shown by both *B. papyrifera* and *Q. rubra,* with maxima occurring at sites closer to the smelters, may indicate successional changes in the forest structure. At increasing distance from the smelters more typical overstory species such as *P. strobus* are able to persist, effectively out-competing the early successional stage species, such as *B. papyrifera*.

The perturbation gradient from past air pollution and subsequent degradation is detectable using ordination analysis of overstory and understory vegetation data. As such, there is a strong relationship between site location (distance from the point source of pollution) and vegetation community characteristics. The placement of understory species in relation to monitoring site locations, with few species associated with sites near the point source of pollution and increasingly more species with distance, is consistent with past work (Freedman and Hutchinson 1980a) and it suggests that the understory communities at these sites are good indicators of the spatial proximity to the site of point source pollution and, thus, the degree of perturbation. Increasing understory diversity in forests with increasing distance from a nickel-copper smelter has been found elsewhere as well (Salemaa et al. 2001). This may be a result of (1) less atmospheric fumigation in past smelting operations at these distal sites than site proximal to the source and (2) decreased metal and sulphur load in the soil at sites further from locations of smelters. Past work (Freedman and Hutchinson 1980b) confirms that metal concentrations in soil and foliage of trees decreased with increasing distance from Sudbury smelters along a southern track similar to the one used in our study.

The ordination of only relatively short overstory *B. papyrifera, A. rubrum* and *Q. rubra* at sites nearer the smelter is also consistent with other work. Several studies (Amiro and Courtin 1981, Freedman and Hutchinson 1980a, Gunn 1995) examine mechanisms to show how the overstory vegetation is critical in mediating temperature extremes at the soil surface. The increase in understory flora species may thus also be a function of the less extreme microclimate conditions that exist under the much more developed forest canopy at sites 5 and 6. The amount of shade provided by the overstory at these sites may also be a factor in allowing for diverse understory development. Species richness changes at the regional level, with increasing numbers of species being found at sites farther from the smelter, might account for the characteristic horseshoes in Fig. 4a and 4b. Ordination, however, was not found to be a useful model for detecting local slope-related gradients. This was surprising to us, as vegetation gradients seemed visually apparent during the field work, with tree height and species compositional changes occurring as we moved from the top of the rocky outcrops down towards the valleys.

The Markov model was found to be a good model of the regional understory and overstory dynamics associated with spatial proximity to the smelter. The method employed to estimate transition probabilities was developed specifically for coverage data from quadrats (the methodology used to measure the understory vegetation here), and the overstory vegetation required combining of measures (height class and density) prior to analysis for Markovity. Overstory (forest) modelling using Markov chains has been done primarily with the tree-by-tree replacement approach; this involves estimation of transition probabilities by determining the number and species of saplings in the understory of a particular overstory type (Horn 1975). The approach used here, however, allows for the consideration of not only species, but forest structure (vertical stratification) as well.

The Markov model deviates from the observed dynamics in that it does not accurately represent the unimodal responses of understory or overstory species. Although the Markov chain is capable of responding multimodally in the earliest state transitions, the variables reach dynamic equilibrium after a short time. The model does predict unimodal responses, such as the *B. papyrifera* and *D. flexuosa* understory signatures, but the amplitude of the response is greatly reduced. Unimodal responses at greater distances from the smelter (e.g., *V. angustifolium*) are not well captured by the model. This illustrates the model's inability to change trajectories once the system is nearing stability. Once stability has been reached the variable signatures will not fluctuate unless the transition matrix is altered, as in a non-homoge-

neous/non-stationary Markov model. The model also deviates from the observed where species are not present in all sampling units. *M. canadense* and *P. aquilinum* are not present in sites closest to the smelters. The model, however, inaccurately predicts the presence of these species. This displays another weakness in the Markov model: the trajectories of variables toward the stable states begin immediately at the first state transition. Situations where one variable remains zero for several transitions and then begins to increase, such as *M. canadense* being absent from the first four sites, is not possible in the model simulation.

It was interesting to find that local spatial dynamics (vegetation dynamics along slopes) did begin to show Markovian dynamics as we moved away from the pollution source. Dynamics thus appeared to be more predictable in less perturbed sites. Why might this be the case? One possible explanation is the fact that vegetation establishment on highly-perturbed sites may be highly dependent on random processes such as dispersal. However, it may also be due to the fact that colonizing assemblages may not be ones that reflect the original vegetation, and that species' associations in space have not had sufficient time to develop. For example, the grass *D. flexuosa* is replaced by the metal-tolerant *D. caespitosa* on barren sites. The failure of ordination techniques to detect these Markov transects seems to be related to the fundamental difference between static vs. dynamic analysis. The fact that the ordination techniques did not detect the local, slope related dynamics is illustrative of information loss that occurs during static analysis such as ordination. Ordination techniques use associations between observations during analysis and, as such, information regarding transitions between observations along the natural ordering of quadrats is not maintained. Dynamic analysis, such as the Markov approach used here, or spatial autocorrelation, maintains the natural ordering of sampling units. Ordination techniques, however, do not, but instead treat points in space and/or time as independent events (Anand and Kadmon 2000). It seems that new methods are needed to deal with the analysis of community dynamics subject to the effects of multiple stressors. Although the Markov chain was found to be useful at the regional level, future approaches will focus on methods that will reflect community dynamics with greater accuracy at both regional and local levels and perhaps even integrate the two.

One important difference between classic ordinations and dynamic models such as the stationary Markov model is in predictive power. The former provides very little and the latter, if well-fit to data, provides perfect predictive power. Realizing that the spatial pattern of vegetation dynamics is Markovian in nature and therefore should be approaching a state of stability, one might ask the question: What climax state, if any, is the impacted Sudbury vegetation headed toward? Parallelisms between temporal and spatial succession may give us a keyhole through which to catch glimpses of the answer. Indeed, our model projections indicate that stability has not yet been reached 35 km away from the pollution source, over 30 years since decommissioning of the smelter, suggesting that the effect may still be acting and that the community is still in a state of directional flux. Of course, long-term monitoring will provide a more complete picture of the recovery of the Sudbury landscape and on the persistence of natural and pollution-induced gradients throughout the recovery process (Anand et al. 2002).

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