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A network approach for evaluating and communicating forest change models

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Summary

1. Knowledge of forest change is often formalized in state-and-transition models (STMs). These models generate forecasts of forest condition that are widely used for forest management planning. Common techniques for evaluating such models are complex, requiring specialized skills not available to non-modellers. Consequently, model transparency can be limited, hampering collaborative resource modelling that otherwise may increase the chances of management success.

2. We demonstrate evaluation of STMs through network visualization that produces intuitively accessible results, comparable to results of more commonly applied, complex techniques. To evaluate this approach, we statistically test model similarities with empirical data. As examples, we use STMs of forest change, alternately parameterized with information from experts and literature, and compare them to our empirical reference information.

3. Graph theoretical analyses revealed differences in structure and dynamics between alternate STMs. For example, compared to empirical STMs, expert STMs were less complex while literature STMs were more complex. Overall, expert STMs were less similar to empirical STMs than were literature STMs, suggesting information in the expert STMs may deviate more strongly from empirical reference data.

4. We used several techniques that provided complementary information, which produced a comprehensive view of network similarity. We speculate that differences between expert and empirical STMs result from lower complexity of mental models compared to empirical data. While we illustrated our approach using a simple matrix model, it could be adapted for more complex STMs. Improvements of the proposed approach could involve representation of forest change rates with waiting times depicted by multigraphs.

5. *Synthesis and applications*. Common evaluations of forest change STMs involve complex techniques not easily accessible to non-modellers. Approaching such models as networks makes their evaluation and statistical testing intuitively accessible to many audiences. Benefits of this approach to modellers include improved communication about models with non-modellers, while benefits to stakeholders and decision makers include enhanced understanding of models. This may aid a collaborative resource modelling process and should improve the chances of successful resource management plan implementation. While we used an example from boreal forests, our approach could be applied to many other vegetation types globally.

Key-words: boreal forest, forest change, forest management planning, graph analysis, matrix model, model evaluation, network analysis, stakeholder, state-and-transition model

Introduction

Forest management planning is largely based on analyses of forest inventories and forecasts of future forest states (USDA 1996). Modelling is increasingly used for forecasting future forest states, because it enables information from various disciplines to be integrated, at various space and time scales, and performing simulated management experiments (Dale 2003). However, successful resource management is more likely if resource modelling is a collaborative process among ecological modellers, local stakeholders and decision makers (Theobald *et al.* 2005). This collaborative process is dependent upon a similar level of knowledge and understanding among all parties. Nevertheless, most resource models are complex

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and their communication requires specialized skills (Dale 2003). This makes information exchange between modellers and non-modellers difficult (Richardson & Berish 2003). It also limits transparency about model assumptions and concepts, which may reduce confidence in model applications (Harwell & Gentile 2003). Here, we propose a new approach to communicating and evaluating forest change models that is more easily accessible to non-modellers than many more common approaches. We believe that it could facilitate a collaborative resource modelling process and may increase the chances of successful resource management.

State-and-transition models (STMs), which represent forest types as *states* and forest change as *transitions*, are often employed to formalize knowledge of forest change (Yemshanov & Perera 2003). STMs can be used to model the dynamics of forest landscapes (Vavra, Hemstrom & Wisdom 2007) and other vegetation types (Balzter, Braun & Köhler 1998). A Markov model is a particular type of STM that, despite criticism of some (Usher 1981), often is used for modelling forest change (Hall *et al*. 1991). It uses a stochastic matrix (transition probability matrix, cf. Otto & Day 2007) that formalizes knowledge about forest types and the probabilities of transitions among them. For illustrative reasons, we focus this paper on first-order Markov models because of their easy analytical tractability. This allows comparison of our approach to a mathematically more sophisticated and commonly applied approach: eigenanalysis (Caswell 1989). However, our approach could also be applied to other matrix models (e.g. semi-Markov: Acevedo, Urban & Ablan 1995) or even non-matrix STMs (Perry & Enright 2007) and does not depend on analytical tractability of the model (see Discussion).

We propose to approach STMs as networks and to represent them as graphs. Matrix models of forest change have previously been depicted as graphs (Johnson & Fryer 1987), but the full value of this approach has not been widely explored. When approaching STMs as graphs, they can be analysed with graph theoretical methods (Harary 1969). Such methods have been used for network analyses in other disciplines ranging from social sciences (Wolfe 1978) to biochemistry (Noack *et al*. 2007), and landscape ecology (Urban *et al*. 2009). Graph theory provides many tools for analysing ecological networks (Chartrand 1984). For example, local graph structure statistics can be calculated (Jordan, Liu & Davis 2006) and randomization approaches can be used to statistically compare graphs (Hubert & Golledge 1981), aiding their objective evaluation. Through their pictorial nature, graphs enable easy visualization of model structure and dynamics while graph theoretical methods for evaluating STMs are easily illustrated. Such visualizations can improve model understanding by non-modellers (Zimmerman *et al*. 2006) and are useful for communicating model structure and evaluations among modellers, stakeholders and decision makers (Harwell & Gentile 2003).

Here, we propose a novel approach for communicating and evaluating STMs of forest change using networks. It requires less mathematical sophistication, is more intuitively accessible to non-technical audiences, and lends itself more to visualization then many more common methods. Despite its simplicity, the approach is sufficiently sensitive to locate and quantify STM differences. By supporting collaborative resource modelling among modellers and non-modellers, we believe that this approach can contribute to successful forest resource management. Our objectives are to demonstrate the easy visualization of model structure and dynamics as networks, to illustrate graph theoretical evaluation and statistical comparison of STMs of forest change, and to evaluate our approach by comparison to results from eigenanalysis. We do so using example models of forest change in boreal Ontario that were alternately parameterized using information from experts or published research studies, and that were compared to a reference model parameterized with our own empirical data.

Materials and methods

STUDY REGION

Driven by disturbances such as fire and insect pests (Holling 1992; Payette 1992), the North American boreal forest is a shifting mosaic of forest types that are often defined on the basis of tree species composition (Ride *et al*. 2004). Within the boreal forest, ecogeographical areas can be differentiated based on systems such as the National Ecological Framework for Canada (ESWG 1995). We used information for one such area that straddles Lake Nipigon (49°50′N and 88°30′W), north of Lake Superior in northwestern Ontario, Canada. The dominant tree species are white spruce *Picea glauca* (Moench) Voss, black spruce *P. mariana* (Mill.) B.S.P., balsam fir *Abies balsamea* (L.) Mill., jack pine *Pinus banksiana* Lamb., trembling aspen *Populus tremuloides* Michx., and paper birch *Betula papyrifera* Marsh. (ESWG 1995). For simplicity, we coded different forest types as broadleaved (BRD1 to BRD3: conifer content ≤30%), mixed (MIX1 and MIX2: conifer content 30–70%) and coniferous (CON1 to CON5: conifer content ≥70%). For details on forest type species compositions see Table S1 in Supporting Information.

PROBABILITIES OF FOREST CHANGE

Forest change probabilities were estimated using information from (i) expert opinion, (ii) research studies on natural forest change, or (iii) empirical observations of forest change. Expert opinion was taken from a report (Ride *et al*. 2004) of forest ecology and management experts that is considered to be a compendium of expertise for the study region. In this report, forest change was expressed as the proportion of forest stands that changed type or were self-replacing. The report does not describe elicitation method and group composition and data quality is thus unknown but it is the only available source of expert opinion for the study region. The research studies comprised 63 studies of boreal forest change in North America (hereafter: literature) published in a 40-year period prior to 2004. They were selected from popular literature data bases using natural forest change as the main criterion. All publications were screened for relevant forest types and information was extracted about the direction of forest change, which resulted in approximately 1000 data records. Our empirical observations are based on time series of historical aerial photographs (9100 ha of forest) supplemented with data from permanent sample plots (28 plots) from the study region. The data comprised individual time series for 352 forest stands from which we extracted information about direction of forest change. As for the literature, the empirical data were used to calculate the proportion of forest stands that changed type or were self-replacing. For each of the three sources, this information was treated as estimates of probabilities and was used to populate transition probability matrices of expert, literature, and empirical Markov models.

FOREST TRANSITION NETWORKS

Forest transition networks (FTNs) were derived from expert, literature and empirical transition probability matrices of forest change. The forest types in FTNs are connected by transition probabilities. Each transition probability, p_{ij}, describes a change of forest type i to j. When addressing all p_{ij} simultaneously, a network emerges that embodies the changes between all forest types. Such a network represents the overall structure of forest changes of the complete forest system.

For subsequent analyses, we represented FTNs in two different forms called *probabilistic* and *binary*. In probabilistic FTNs, transitions between forest types are quantified by the probability of change. In binary FTNs, transitions between forest types and self-replacement are formalized as binary indicators (forest change and self-replacement can occur: yes/no). We investigated both probabilistic and binary FTNs to investigate whether FTNs differed more in assessments of exact transition probabilities (e.g. 0·2 vs. 0·0) or general structure of transition pathways (e.g. yes vs. no). If FTNs differ more in exact probabilities, then similarity among probabilistic FTNs should be lower than among binary FTNs.

GRAPH THEORY

Graph theory (Harary 1969) is a mathematical discipline focused on relationships among objects. Here, we describe the application of graph theory to FTNs as relevant to this study; for a thorough introduction to graph theory, we refer to detailed textbooks (Diestel 2005).

In a FTN graph, *nodes* represent forest types and *edges* represent changes between forest types (Fig. 1, Table 1). As nodes represent specific forest types, they are *labelled*. Because change among forest types is directional, edges between nodes are *directed* and *weighted*, indicating direction and probability of change. Reciprocal change between forest types is indicated by two edges pointing in opposite directions. Self-replacement of forest types is represented by an edge originating and ending at the same node called a *loop*. The numbers of edges entering and exiting a node are respectively its *in-degree* and *out-degree*. The sum of in-degree and out-degree is the node's *total degree*. All degree values are calculated excluding loops. Forest types that are exited but not entered by forest stands are represented by nodes with in-degree zero and out-degree > zero called *sources*; the reverse is true for forest types that are *sinks*. When neither in-degree nor out-degree of nodes are zero, we interpret the ratio of in-degree to out-degree as indicating source- and sink-like properties of nodes. A *cascade* is a hierarchical graph with a highest level *root* node and several lower level nodes where edges are always directed at lower level nodes (Gopal, Ramesh & Zionts 2001).

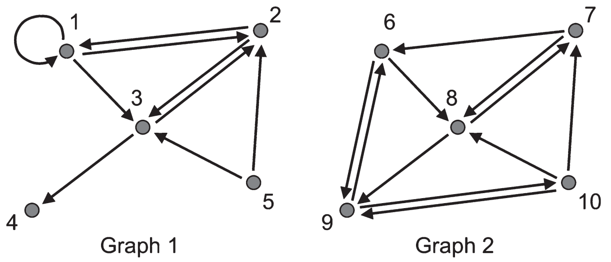

Fig. 1. Illustration of some graph theoretical terminology relevant to this study. Circles are *nodes* symbolizing forest types, identified here by node *labels* as numbers. Arrows are *directed edges* connecting the nodes, symbolizing forest type change and self-replacement. For details see *Graph theory* section and Table 1.

CHARACTERIZING NETWORK STRUCTURE

Network structure can be described using various statistics (Jordan *et al.* 2006). We used degree analysis as a convenient tool for simple characterization of local and global network structure excluding labelling information.

To investigate local network structure, we determined in-degree, out-degree, total degree, and ratio of in-degree to out-degree for different forest types. Investigating degree values of forest types is a simple way to support conclusions about location and extent of sink and source properties within FTNs (Table 1).

To investigate global network structure, we determined mean total degree over all forest types and standard deviations of in-degree, out-degree, and total degree for each FTN. Mean total degree measures network edge density and indicates complexity of overall forest changes in FTNs. Degree standard deviation measures variation of in-, out-, and total degrees among nodes, indicating variability of the structure of forest changes within FTNs (Table 1).

To compare expert/literature FTNs to empirical FTNs, we calculated differences of degree values (degree, mean degree or degree standard deviation) between respective networks ($\text{degree}_{\text{Emp}}$–$\text{degree}_{\text{Exp/Lit}}$). A positive difference indicates lower degree values for expert/literature FTNs compared to empirical FTNs.

Graphical exploration of FTN dynamics was compared to results from eigenanalysis. The long-term, dynamic equilibrium of forest types (stable distribution) was found by re-scaling the eigenvector of the dominant eigenvalue of FTNs. Rate of approach to the stable distribution was assessed with the convergence rate that is positively related to the damping ratio, $1/|\lambda_2|$ (Caswell 1989), where λ_2 is the sub-dominant eigenvalue.

QUANTIFYING NETWORK SIMILARITY

To include forest type labelling information, which is not considered in degree analysis, we performed additional analyses of network similarity between expert/literature and empirical FTNs. We calculated Pearson's product-moment correlation (r) for networks following Butts & Carley (2005) and used it as a network similarity index:

$$r = \frac{\mathrm{cov}(H, E)}{\sqrt{\mathrm{cov}(H, H)\mathrm{cov}(E, E)}}$$

$$\mathrm{cov}(H, E) = \frac{1}{N!/(2!(N-2)!)} \sum_{ij} \left(A_{ij}^{H} - \mu_H\right)\left(A_{ij}^{E} - \mu_E\right)$$

Here, H and E symbolize expert/literature and empirical FTNs, respectively, N is the set of forest types, A_{ij}^{H} and A_{ij}^{E} are adjacency matrices of FTNs H and E, and μ_H and μ_E are their means. The value of r varies from −1 to + 1; increasing r indicates higher similarity. We calculated r for probabilistic and binary FTNs and calculated confidence limits (95%) on r with Fisher's z' transformation where $z' = 1/2[\ln(1 + r) - \ln(1 - r)]$.

Table 1. Description of graph elements and characteristics used in this study. Examples refer to Fig. 1

Graph elements and characteristics	Description	Ecological interpretation for network models of forest transition	Example
Node	Object whose relationships are of interest	Forest type	
Edge	Relationship between nodes	Connection between two forest types, i.e. a forest stand in one forest type can change into another forest type or self-replace	
Loop	Edge starting and ending at same node	Self-replacement, i.e. forest stands are replaced by forest stands of the same forest type. Not counted in degree values	Node 1 has a loop indicating self-replacement
In-degree	Number of edges arriving at a node	Number of forest types that can change to a focal forest type	Node 1 has in-degree 1, node 8 has in-degree 3
Out-degree	Number of edges leaving a node	Number of forest types that a focal forest type can change to	Node 1 has out-degree 2, node 8 has out-degree 2
Total degree	Total number of edges arriving at and leaving a node	Total number of change relationships that a focal forest type has with other forest types. High total degree may indicate a forest type that is central for the overall change dynamics of a forest landscape	Node 1 has total degree 3, node 8 has total degree 5
Mean total degree	Mean of total degree of all nodes in a graph	Mean number of change relationships that a forest type has with other forest types. High mean total degree may indicate higher complexity of change dynamics of a forest landscape	Graph 1 has mean total degree 3·6, graph 2 has mean total degree 4·4
Standard deviation of in-degree	Standard deviation of in-degree of all nodes in a graph	Variation of number of forest types that can change to focal forest types. High in-degree standard deviation may indicate strong variation among forest types in degree to which they are aims of change dynamics	Graph 1 has in-degree standard deviation 1·3, graph 2 has in-degree standard deviation 0·8
Standard deviation of out-degree	Standard deviation of out-degree of all nodes in a graph	Variation of number of forest types that focal forest types can change to. High out-degree standard deviation may indicate strong variation among forest types in degree to which they are origins of change dynamics	Graph 1 has out-degree standard deviation 0·9, graph 2 has out-degree standard deviation 0·4
Standard deviation of total degree	Standard deviation of total degree of all nodes in a graph	Variation of total number of change relationships of forest types. High total degree standard deviation may indicate strong variation among forest types in degree of centrality for overall change dynamics	Graph 1 has total degree standard deviation 1·8, graph 2 has total degree standard deviation 0·5
Source	Node with in-degree of zero and out-degree larger than zero	Forest type that can only change to other forest types	Node 5 is a source
Sink	Node with in-degree larger than zero and out-degree of zero	Forest type to where other forest type can only change to	Node 4 is a sink
In/out-degree ratio	Ratio of in-degree and out-degree of a node	Ratio of number of forest types that can change to a forest type and number of forest types that this forest type can change to. High ratio may indicate sink-like property of a forest type, while low ratio may indicate source-like property	Node 2 has in/out-degree ratio 1·5, node 10 has in/out-degree ratio 0·3
Cascade	Group of nodes organized by hierarchical levels with one highest level, root node and several lower level nodes. Edges never connect same level nodes and are always directed at lower level	Hierarchy of forest types * change steps. Represents all forest types that a focal forest type can change to or self-replace. Each level represents all forest types that a forest type can succeed to in one change step	The cascade starting from node 2 in graph 1 leads in the first change step to nodes 1 and 3, and in the second change step to nodes 1, 2, 3 and 4. See Fig. 3 for cascade graphs

STATISTICAL TEST OF NETWORK SIMILARITIES

Classical hypothesis testing is not recommended for networks, because the relationships among nodes are not independent. Further, reasonable null hypotheses are necessary for hypothesis testing (Gotelli & Graves 1996) but to generate reasonable null networks, underlying network data structure created by node relationships should be preserved. For these reasons, the quadratic assignment procedure (QAP) was proposed for statistical network testing (Hubert & Schultz 1976). QAP is a generic algorithm used for nonparametric significance testing of network statistics. It is based on comparisons between observed data and a random sample generated by Monte Carlo simulation. Essentially a null model method (Gotelli & Graves 1996), QAP consists of random permutation of rows and columns of a network-representing data matrix, thus creating null networks. By simultaneously permuting row k and column k of a $m \times m$ matrix (where $k \leq m$), row and column marginals are preserved, diagonal cells remain on the diagonal, and the general structure of the original network is maintained. Comparison of an observed statistic to the simulated distribution of the statistic for null networks allows an empirical assessment of the likelihood of the observed statistic. We modified QAP (mQAP) by relaxing the degree of network structure preservation, leading to a more conservative test then ordinary QAP: the cells in one row of the data matrix represent changes from one forest type to other types as well as self-replacement. This was the only network structure relevant to us, and to maintain it, we needed only to preserve the groupings of cells in rows. Accordingly, mQAP consisted of random permutation of whole rows combined with random permutation of individual cells within rows, thus preserving row marginals but not column marginals or diagonal identity. Otherwise, mQAP and QAP proceed identically: using the empirical FTN as a reference, we compared the similarity between expert/literature FTNs and the empirical FTN to the distribution of similarities between null FTNs and the empirical FTN.

We programmed mQAP using R, version 2.2.1 (RDCT 2005), with the sna package, version 1.5 (Butts 2007). We constructed null FTN distributions using 10 000 random permutations for each separate test of probabilistic and binary expert/literature FTNs.

Results

FOREST CHANGE DYNAMICS

We explored expert, empirical and literature FTNs graphically (Fig. 2, see Table S2 in Supporting Information for transition probability matrices). As an example we show cascade graphs of four forest type transitions, using forest type BRD2 as root node (Fig. 3).

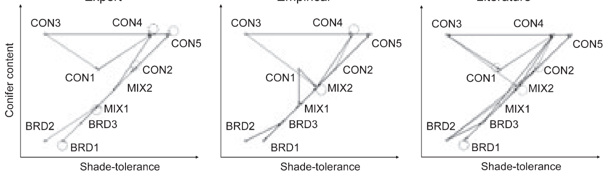

Fig. 2. Literature, empirical and expert forest transition networks (FTNs). Forest types are arranged by conifer content and shade-tolerance for illustrative purposes only.

Expert forest transition networks

The four transition steps show forest type changes from BRD2 to mixed and coniferous forest types (Fig. 3). Initially forest transitions involved few forest types and it took three transition steps before forest types diversified. Only after a fourth step did forest type transitions converge toward a small number of coniferous forest types (CON2, CON4 and CON5).

These findings were congruent with results from eigenanalysis. The stable distribution indicated that forest stands starting from BRD2 have the highest probability of changing to forest type CON5, followed by CON4 and CON2. The damping ratio, indicating the rate of movement toward the stable distribution, was 1·21.

Literature forest transition networks

The initial transition step indicated that forest types change from BRD2 to the BRD3, MIX2, and CON2 forest types, constituting one-third of forest types (Fig. 3). The second transition step led to two-thirds of forest types. With the third step the diversity of forest types increased further, although most transitions converged toward mixed and coniferous forest types (MIX2, CON4 and CON5). The fourth transition step mainly repeated the pattern of the third step.

The graphical findings corresponded with results from eigenanalysis. The stable distribution, approached with a damping ratio of 1·51, indicated that a BRD2 forest stand had the highest probability of changing to forest type MIX2, followed by CON5 and CON4 and several less important forest types.

Empirical forest transition networks

Complexity of forest changes of the empirical FTN was intermediate between expert and literature FTNs (Fig. 3). The first transition step from BRD2 was as simple as that of the expert FTN. However, the second transition step reached multiple forest types. With the third step, the diversity of forest types increased, but transitions simultaneously converged toward a group of mainly mixed forest types (MIX1, MIX2 and CON5). The fourth transition step repeated the pattern of the third step.

The findings were similar to the results of eigenanalysis. The stable distribution of forest types indicated that BRD2 forest stands had the highest probability of changing into forest types MIX1 and MIX2, followed by CON5, BRD3 and CON3. The stable distribution was approached with a damping ratio of 1·78.

COMPARISON OF LOCAL NETWORK STRUCTURES

Expert forest transition networks

The differences of all degree types (in-, out- and total) between expert and empirical FTNs ranged from −2 to 7, with most differences being larger than zero, indicating that the expert FTN was generally less complex (i.e. lower edge density) than the

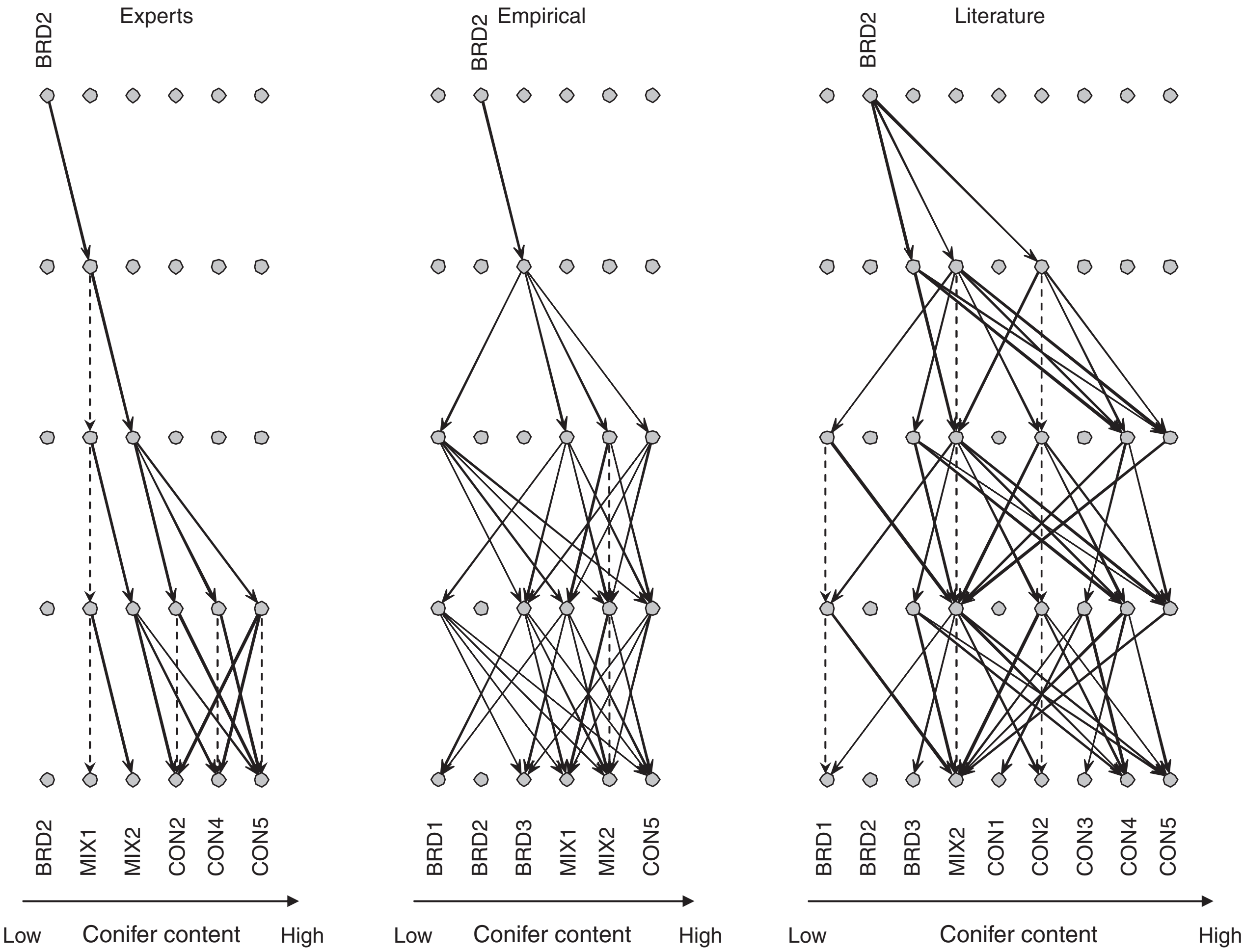

Fig. 3. Cascade of four forest transition steps starting from forest type BRD2 as derived from the literature, empirical and expert forest transition networks (FTNs) depicted in Fig. 2. Each row represents one transition step and is not necessarily proportional to the passing of time. Solid lines indicate transitions between forest types, broken lines indicate self-replacement. Sets of forest types differ from Fig. 2 because not all types can be reached from BRD2. Forest types are arranged by approximate conifer content for illustrative purposes only.

Table 2. Results of the comparison between expert and literature FTNs to empirical FTNs based on degree analysis. Shown are differences in degree values between empirical vs. expert/literature FTNs for all forest types

	Forest type									
FTN source and graph characteristics	BRD1	BRD2	BRD3	MIX1	MIX2	CON1	CON2	CON3	CON4	CON5
Experts										
In-degree difference	2	0	4	2	7	−1	−2	0	−2	2
Out-degree difference	3	0	3	3	−1	1	1	0	1	1
Total degree difference	5	0	7	5	6	0	−1	0	−1	3
In/out-degree ratio difference	0·5	0·0	1·0	−1·8	3·7	−1·0	−2·0	0·0	−3·0	0·2
Literature										
In-degree difference	1	0	2	5	0	−1	−2	−2	−3	1
Out-degree difference	3	−2	1	3	−3	0	−1	−1	−1	2
Total degree difference	4	−2	3	8	−3	−1	−3	−3	−4	3
In/out-degree ratio difference	−0·5	0·0	0·3	1·3	2·4	−0·5	−0·7	−0·7	−0·7	−2·3

empirical FTN (Table 2). Degree differences were mainly positive for broadleaved and mixed forest types indicating lower complexity for these types in the expert FTN. Degree differences were often negative for coniferous forest types indicating higher complexity in the expert FTN. In-/out-degree ratio differences for some coniferous forest types were negative, signifying that these types had stronger sink character in the expert FTN.

Literature forest transition networks

The degree differences (in-, out- and total degree) between literature and empirical FTNs varied from −4 to 5 and were balanced between negative and positive values, indicating that the literature and empirical FTNs overall were equally complex (Table 2). Most positive degree differences were found for the broadleaved forest types, MIX1, and CON5, indicating lower complexity for these types in the literature FTN than the empirical FTN. Degree differences for most coniferous forest types were negative indicating higher complexity in the literature FTN. In-/out-degree ratios for all coniferous forest types were negative, indicating that they had stronger sink character in the literature FTN.

Comparison of degree differences between expert and literature FTNs indicated that for all but one forest type (MIX1), the literature FTN was locally more complex than the expert FTN (Table 2).

COMPARISON OF GLOBAL NETWORK STRUCTURES

Expert forest transition networks

The difference of mean total degree was positive indicating that overall complexity in the expert FTN was lower than in the empirical FTN (Table 3). The difference of in-degree standard deviation was positive indicating lower variation in sink character for the expert FTN than the empirical FTN; the difference in out-degree standard deviation was near zero indicating similar variation in source character for the two. A positive difference in total degree standard deviation indicates that forest types in the expert FTN showed lower variation in connectedness than in the empirical FTN, i.e. the expert FTN was a more regular network than the empirical FTN.

Literature forest transition networks

All differences (mean total degree and degree standard deviations) were close to zero (Table 3), indicating that, as long as forest type identities (labelling) are ignored, the overall structures of literature and empirical FTNs are very similar.

Table 3. Results of comparison of expert and literature FTNs to empirical FTNs based on aggregated degree analysis results. Shown are differences in mean total degree ($\bar{x}$) and in standard deviations (s) of in-degree, out-degree and total degree

	FTN source	
Graph characteristics	Experts	Literature
Total degree $\bar{x}$ difference	2·4	0·2
In-degree s difference	1·3	0·3
Out-degree s difference	0·4	−0·2
Total degree s difference	1·8	0·0

Table 4. Results of expert and literature FTN testing with the modified quadratic assignment procedure. Similarity between expert/literature and empirical FTNs was quantified with Pearson's product-moment correlation for networks (r) for binary and for probabilistic FTNs. 95% confidence intervals are shown in parentheses

	r	
FTN source	Binary	Probabilistic
Experts	$0{\cdot}10^{ns}$ (−0·10–0·29)	0·23* (0·04–0·41)
Literature	0·29** (0·10–0·46)	0·47*** (0·30–0·61)

$^{ns}P > 0{\cdot}05$, $*P < 0{\cdot}05$, $**P < 0{\cdot}01$, $***P < 0{\cdot}001$.

STATISTICAL TESTS OF FOREST TRANSITION NETWORKS

An analysis of FTN similarities showed that neither expert nor literature FTNs were very similar to the empirical FTNs (Table 4, max. $r = 0{\cdot}47$). However, similarity and its significance varied by FTN source and form (Table 4): the similarity of expert FTNs to empirical FTNs was low, and was not significant for binary networks. The literature FTNs were always significantly similar to empirical FTNs, and the similarity of literature FTNs to empirical FTNs was always higher than for expert FTNs. The similarity for probabilistic FTNs was higher than for binary ones.

Discussion

Collaboration between modellers and non-modellers will increase the chances of successful resource management (Theobald *et al.* 2005). It has been shown that output visualization of mathematical resource models can improve model understanding by non-modellers more so than non-visualized output (Zimmerman *et al.* 2006). Hence, we propose a versatile network approach that, depending on the purpose, can enable both model communication and evaluation. This approach requires less mathematical sophistication, is more intuitively accessible, and is more amenable to visualization than many other approaches. Benefits of this are improved communication about models by modellers and understanding of models by stakeholders and decision makers. We believe this facilitates transparency, communication and collaborative resource modelling, thus strengthening support from all parties (Argent, Grayson & Ewung 1999) and increasing chances of successful resource management.

Our graphical exploration of FTNs revealed network properties and differences. The results of this simple technique were confirmed by results from eigenanalysis (Caswell 1989; Otto & Day 2007). The empirical FTN initially had simple dynamics becoming more complex after two transition steps and soon converging on some broadleaved, mixed and coniferous forest types. Both the literature and expert FTNs differed from this pattern. Compared to the empirical FTN, the expert FTN transition pattern was simple: the group of forest types expanded more slowly, transitions tended to occur within the groups of mixed and coniferous forest types, and self-replacement was relatively more frequent. These dynamics led to a slower approach to the stable distribution than in the empirical FTN, also indicated by the lower damping ratio. Further, the group of forest types toward which transitions converged, overlapped only partially with the empirical FTN. The literature FTN, however, showed a more complex pattern of forest transitions than the empirical FTN and many transitions occurred among the groups of broadleaved, mixed, or coniferous forest types. The group of forest types expanded rapidly but was dominated by a smaller number of forest types. This suggests that the dynamics are more diverse than in the empirical FTN and, despite this fast spread, lead to a slower approach to the stable distribution, as also indicated by the lower damping ratio. Again, the group of forest types toward which transitions converged overlapped only partially with the empirical FTN. Eigenanalysis largely confirmed the partial overlap of converging forest type groups between FTNs as indicated by the cascade graphs.

Comparing the results of degree analyses indicated that the expert FTN was locally less complex than the empirical FTN. The expert FTN was also more regular (cf. Diestel 2005), showing less variation in sink character and connectedness among forest types, although source character variation was similar to the empirical FTN. The literature FTN varied more in local complexity then the empirical FTN, in particular the broadleaved forest types were less connected while the coniferous types were more connected. This pattern was also found at the global network level. The overall complexity, convergence and variation in connectedness of the expert FTN were lower than for the empirical FTN. The overall structure of the literature FTN was similar to the empirical FTN.

Taking into account labelling information, i.e. identity of forest types, neither the expert nor the literature FTNs were very similar to empirical reference FTNs. However, all binary and the probabilistic literature FTNs were significantly similar to the empirical FTNs, suggesting that this similarity is not spurious and the information in the literature overlaps with empirical forest change data. Expert FTNs were less similar to empirical FTNs than were literature FTNs, and were not significantly similar in binary form. This may suggest that the information provided by experts might correspond less well with empirical forest change data than the information in the literature. Probabilistic expert/literature FTNs were almost twice as similar to empirical FTNs than were binary ones. The reason for this is that differences about individual forest change directions between binary expert/literature FTNs and binary empirical FTNs always contribute 1 (value later normalized) to dissimilarity. For probabilistic FTNs, however, these differences can range from just over 0 to 1. Consequently, because forest changes occur often with a probability much smaller than 1, but only seldom with a probability close to 1, most disagreements about forest changes decrease similarity more strongly in binary FTNs than in probabilistic FTNs. Surprisingly, our data suggest that modelling of infrequent forest changes enjoyed stronger support from empirical data than more frequent forest changes.

The different techniques used for evaluating FTNs provide complementary information. A comparison of cascade graphs indicates the dynamics and end result of several transition steps, whereas degree analysis and correlation analysis present a static picture. An important difference between degree and correlation analysis is that the former focuses on general complexity and connectivity while the latter centres on a comparison of individual transitions between specific forest types. Not unexpected, detailed examinations show that, depending on technique and forest type, either expert or literature FTNs can be more similar to empirical FTNs. For example, variation in source character among forest types in the expert and literature FTNs is about equally similar to the empirical FTN. Variation in sink character among forest types in the expert FTN, however, is much lower and dissimilar to the empirical FTN than is the case for the literature FTN. Clearly, assessing different aspects of network similarity with a suite of indicators will always provide a more comprehensive picture.

We used eigenanalysis results to evaluate the validity of results obtained with cascade graphs. However, while cascade graphs indicate forest type distribution after a fixed (small) number of steps, eigenanalysis indicates forest type distribution after an infinite number of steps. Consequently, there might be differences in the results although these should decrease with increasing step number in cascade graphs. The specific research interest may determine the more relevant type of information: for relatively stable ecosystems asymptotic model dynamics may be more important, while in frequently disturbed systems transient dynamics may be more important.

Evaluation of models by comparison to empirical observations is a commonly accepted approach, although we do not state here that our empirical data are *true*. Multiple error sources may affect our data, such as incorrect derivation of species distributions from aerial photography. However, our main intent was not to evaluate whether models were *accurate*. Instead, we used empirical data as a reference to evaluate whether the models were *similar* to them and, if not, to determine how the models differed. This approach was chosen because our objective was to demonstrate visualization of model structure and dynamics and to illustrate the use of graph theoretical tools for evaluation and statistical comparison of models. However, this does not mean that our approach could not be used to evaluate model accuracy. This is not so much a question of our method but rather of the trust put in the empirical data used for evaluation.

We evaluated network models based on information from experts and published studies (literature) by comparing them to empirical observations, although the literature, naturally, is based on its own empirical data. Because we ensured that our empirical data and the data from other studies did not coincide, there should be no overlap between the parameterization and evaluation data that could explain higher similarity between the literature and empirical FTNs. However, we speculate that empirical data naturally may be more complex than mental models of experts. For example, the practical experiences of experts are confined by natural limits to the scale of personal observations, while this is not necessarily so for empirical studies (Fazey *et al.* 2006). Thus, expert knowledge of forest changes may be more limited, possibly explaining their lower complexity compared to empirical data. Additionally, there may be cognitive bias (cf. Meyer & Booker 2001) in expert observations: if experts focus on higher valued forest types or familiar changes (i.e. anchoring, Morgan & Henrion 1992), they may underestimate or ignore infrequent forest changes leading to lower complexity of expert FTNs. Nevertheless, we treated both the experts and the literature as equally valid information sources because they are often used similarly for model parameterization in practical applications.

While degree analysis and cascade graphs can be used to compare networks of different sizes, we recommend caution. A matrix example illustrates the point: to compare matrices describing different forest types, it is not possible to simply 'merge' several forest types into one 'overarching' forest type. The dynamics of the matrices before and after 'merging' will differ even if transition probabilities outside the group of 'merged' forest types remain identical. Further, we calculated Pearson's product-moment correlation for networks including double-zeros that indicate non-edges in both networks and thus contribute to network similarity. Consequently, two sparse matrices are more likely to be spuriously similar than two non-sparse matrices. Exclusion of double-zeros from the calculation of network correlations could compensate for this, although arguably double-zeros are part of the network structure and should therefore be retained. This links to the problem of meaningful null-models for hypothesis testing: we modified QAP (Hubert & Schultz 1976) by relaxing the requirement of preserving matrix diagonal identity, meaning that loops in graphs are not preserved. Therefore, we implicitly state that the only important underlying network structure is the number of edges per forest type and their associated weights. Arguments for preserving other aspects of network structure could be made leading to different null-models, interpretations and test conservatism.

We illustrated our approach using first-order Markov chains that produce comparatively simple dynamics, but the approach is not limited to this model type. Also semi-Markov (Acevedo *et al.* 1995), second-order Markov (Aaviksoo 1995), or even non-matrix STMs that produce more complex dynamics can be approached as networks and evaluated and described with graphs. For any of these models, it is possible to follow the fate of individual model units (e.g. individuals, patches or forest stands) and tally their transitions. The proportions of such transitions can be expressed in transition matrices (Perry & Enright 2007) and analysed with graph theoretical means as proposed by us. Admittedly this would simplify temporal dynamics. However, temporal effects could be investigated by generating separate transition matrices for various periods (Usher 1981) and comparing their corresponding networks with our approach.

Just as Markov chains, FTNs in our study experience passing of time in discrete steps. Rate of change in a forest type can thus be calculated as amount of forest changing divided by time [= amount forest/(number steps × time per step)]. This rate is positively related to the probability of transition and the amount of forest that can change. Unfortunately, the expert information available to us did not include time-scales of change and consequently we did not attach explicit time-scales to any network. Clearly, our approach implies that all transitions in networks take the same time. This is a strong simplification because transition length may vary by forest type (Acevedo *et al.* 1995) and future extensions of our work that would allow for variable step length would be interesting. Methods could be borrowed from network flow analysis (Ford & Fulkerson 1958) or water supply networks (Klemes 1970) involving expressions of waiting times between states. Graphical expression of such networks could use multigraphs (Diestel 2005) representing transition probabilities and waiting times by separate edges within the same graph.

Conclusions

Forest state forecasts are widely used in forest management decision making and often based on STMs of forest change. Many common techniques for investigating such models are not easily accessible to non-modellers. Consequently, model communication and evaluation remain ambiguous to them. This may impede a collaborative resource modelling process and limit successful forest management planning. Visualization of model results can enhance model understanding by non-modellers and therefore we propose visualizing STMs as graphs to improve model communication and evaluation. Following this approach, we used simple cascade graphs to illustrate model behaviour and found support by evaluation with mathematically more sophisticated methods. We further quantified network characteristics with graph theoretical techniques and were able to evaluate models by comparing them to empirical reference data. The pictorial basis of our results makes them intuitively accessible to non-modellers offering salient information about general model structure as well as about detailed relationships. While we illustrated our approach using boreal forest change as an example, we believe it can be applied to many other vegetation types globally. The information gained with our approach would benefit modellers because it facilitates communication about models with non-modellers, while it would enhance model understanding by stakeholders and decision makers. Ultimately, this should aid a collaborative resource modelling process and improve the chances of successful resource management plan implementation.

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References

Aaviksoo, K. (1995) Simulating vegetation dynamics and land use in a mire landscape using a Markov model. *Landscape and Urban Planning*, **31**, 129–142.

Acevedo, M.F., Urban, D.L. & Ablan, M. (1995) Transition and gap models of forest dynamics. *Ecological Applications*, **5**, 1040–1055.

Argent, R.M., Grayson, R.B. & Ewung, S.A. (1999) Integrated models for environmental management: issues of process and design. *Environment International*, **25**, 693–699.
Balzter, H., Braun, P.W. & Köhler, W. (1998) Cellular automata models for vegetation dynamics. *Ecological Modelling*, **107**, 113–125.
Butts, C.T. (2007) sna: tools for social network analysis (Version 1.4) [Computer software]. Retrieved 15 August 2007; available at: http://cran.r-project.org/web/packages/sna/index.html.
Butts, C.T. & Carley, K.M. (2005) Some simple algorithms for structural comparison. *Computational & Mathematical Organization Theory*, **11**, 291–305.
Caswell, H. (1989) *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer Associates Inc., Sunderland, MA, USA.
Chartrand, G. (1984) *Introductory Graph Theory*. Dover Publications, New York, NY, USA, 320 pp.
Dale, V.H. (2003) Opportunities for using ecological modeling for resource management. *Ecological Modeling for Resource Management* (ed. V.H. Dale), pp. 3–21. Springer Verlag, New York, NY, USA.
Diestel, R. (2005) *Graph Theory*. Springer Verlag, New York.
ESWG [Ecological Stratification Working Group] (1995) *A National Ecological Framework for Canada*. Agriculture and Agri-Food Canada, Research Branch, Centre for Land and Biological Resources Research and Environment Canada, State of the Environment Directorate, Ecozone Analysis Branch, Ottawa/Hull, Ontario/Quebec, Canada. Retrieved 4 December 2008; available at: http://www.ec.gc.ca/soer-ree/English/Framework/default.cfm.
Fazey, I., Fazey, J.A., Salisbury, J.G., Lindenmayer, D.B. & Dovers, S. (2006) The nature and role of experiential knowledge for environmental conservation. *Environmental Conservation*, **33**, 1–10.
Ford, L.R. Jr & Fulkerson, D.R. (1958) Constructing maximal dynamic flows from static flows. *Operations Research*, **6**, 419–433.
Gopal, R.D., Ramesh, R. & Zionts, S. (2001) Cascade graphs: design, analysis and algorithms for relational joints. *INFORMS Journal on Computing*, **13**, 2–28.
Gotelli, N.J. & Graves, G.R. (1996) *Null Models in Ecology*. Smithsonian Institute Press, Washington, DC, USA.
Hall, F.G., Botkin, D.B., Strebel, D.E., Woods, K.D. & Goetz, S.J. (1991) Large-scale pattern of forest succession as determined by remote sensing. *Ecology*, **72**, 628–640.
Harary, F. (1969) *Graph Theory*. Addison-Wesley, Reading, MA, USA.
Harwell, M.A. & Gentile, J.H. (2003) Overcoming barriers to the use of models in environmental decision making. *Ecological Modeling for Resource Management* (ed. V.H. Dale), pp. 89–108. Springer Verlag, New York, NY, USA.
Holling, C.S. (1992) The role of forest insects in structuring the boreal landscape. *A Systems Analysis of the Global Boreal Forest* (eds H.H. Shugart, R. Leeman & G.B. Bonan), pp. 170–195. Cambridge University Press, Cambridge.
Hubert, L.J. & Golledge, R.G. (1981) A heuristic method for the comparison of related structures. *Journal of Mathematical Psychology*, **23**, 214–226.
Hubert, L.J. & Schultz, J. (1976) Quadratic assignment as a general data analysis strategy. *British Journal of Mathematical & Statistical Psychology*, **29**, 190–241.
Johnson, E.A. & Fryer, G.I. (1987) Historical vegetation change in the Kananaskis Valley, Canadian Rockies. *Canadian Journal of Botany*, **65**, 853–858.
Jordan, F., Liu, W. & Davis, A. (2006) Topological keystone species: measures of positional importance in food webs. *Oikos*, **112**, 535–546.
Klemes, V. (1970) A two-step probabilistic model of storage reservoir with correlated inputs. *Water Resource Research*, **6**, 756–767.
Meyer, M.A. & Booker, J.M. (2001) *Eliciting and Analyzing Expert Judgment: A Practical Guide*. Society for Industrial and Applied Mathematics, Philadelphia, PA, USA.
Morgan, M.G. & Henrion, M. (1992) *Uncertainty: A Guide to Dealing with Uncertainty in Quantitative Risk and Policy Analysis*. Cambridge University Press, New York, NY, USA.
Noack, S., Wahl, A., Qeli, E. & Wiechert, W. (2007) Visualizing regulatory interactions in metabolic networks. *BMC Biology*, **5**, 46 (doi: 10.1186/1741-7007-5-46).
Otto, S.P. & Day, T. (2007) *A Biologist's Guide to Mathematical Modeling in Ecology and Evolution*. Princeton University Press, Princeton, NJ, USA.
Payette, S. (1992) Fire as controlling process in the North American boreal forest. *A Systems Analysis of the Global Boreal Forest* (eds H.H. Shugart, R. Leeman & G.B. Bonan), pp. 170–195. Cambridge University Press, Cambridge.
Perry, G.L.W. & Enright, N.J. (2007) Contrasting outcomes of spatially implicit and spatially explicit models of vegetation dynamics in a forest-shrubland mosaic. *Ecological Modelling*, **207**, 327–338.
RDCT [R Development Core Team] (2005) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Retrieved 11 June 2007; available at: http://www.R-project.org.
Richardson, J.R. & Berish, C.W. (2003) Data and information issues in modeling fore resource management decision making: communication is key. *Ecological Modeling for Resource Management* (ed. V.H. Dale), pp. 167–179. Springer Verlag, New York.
Ride, K.R., Longpre, T.W.F., Racey, G.D. & Elkie, P.C. (2004) Estimates of ecoregional forest composition derived using modeled bounds of natural variation in Northwestern Ontario. NWSI Tech. Rep. TR-136. Ontario Ministry of Natural Resources, Northwest Science and Information, Thunder Bay, ON, Canada.
Theobald, D.M., Spies, T., Kline, J., Maxwel, B., Hobbs, N.T. & Dale, V.H. (2005) Ecological support for rural land-use planning. *Ecological Applications*, **15**, 1906–1914.
Urban, D., Minor, E.S., Treml, E.A. & Schick, R.S. (2009) Graph models of habitat mosaics. *Ecology Letters*, **12**, 260–273.
USDA [USDA Forest Service] (1996) *Timber Resource Planning Handbook*. Forest Service Handbook 2409.13. USDA Forest Service, Washington, DC, USA. Retrieved 16 April 2008; available at: http://www.fs.fed.us/cgi-bin/Directives/get_dirs/fsh?2409.13.
Usher, M.B. (1981) Modeling ecological succession, with particular reference to Markovian models. *Vegetatio*, **46**, 11–18.
Vavra, M., Hemstrom, M.A. & Wisdom, M. (2007) Modeling the effects of herbivores on the abundance of forest overstory states using a state-and-transition approach in the upper Grande Ronde River Basin, Oregon, USA. *Landscape and Urban Planning*, **80**, 212–222.
Wolfe, A.W. (1978) The rise of network thinking in anthropology. *Social Networks*, **1**, 53–64.
Yemshanov, D.G. & Perera, A.H. (2003) Synthesizing published knowledge of boreal forest cover change for large-scale landscape dynamics modelling. *Forestry Chronicle*, **79**, 132–145.
Zimmerman, D.E., Akerelrea, C., Kapler Smith, J. & O'Keefe, G.J. (2006) Communicating forest management science and practices through visualized and animated media approaches to community presentation: an exploration and assessment. *Science Communication*, **27**, 514–539.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Forest type definitions.

Table S2. Transition probability matrices for experts, empirical and literature.

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