

Potential indicators of the impacts of forest management on wildlife habitat in northeastern Ontario: A multivariate application of wildlife habitat suitability matrices

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Protocols to select ecological indicators of sustainable forest management will benefit from a proactive approach that identifies species likely to be most seriously impacted by management. Here, we use an objective approach that couples forest resource inventory information from logged and unlogged landscapes in northeastern Ontario with information from the provincial vertebrate habitat suitability matrix to assess habitat suitability (the amount of used and preferred habitats) in the landscapes and to identify potential indicators of the impacts of forest management activities. Because they may be most representative of potential future logged landscapes in the region, we contrasted the oldest post-clearcut landscapes in the region (1950s and 1960s era, $n = 27$) with unlogged landscapes ($n = 16$). Each landscape was a 2-km radius circle (12.6 km²). In light of reported invasions of hardwood species into logged conifer sites, we considered two regeneration scenarios for very young post-harvest stands: full and partial regeneration control. Logged landscapes differed markedly from unlogged landscapes with respect to forest age and forest type. These differences resulted in strong distinctions between logged and unlogged forests for bird and mammal communities, but relatively weak separation for herpetofauna. Redundancy analysis indicated that the percent variation in habitat suitability attributable to logging was 27% for birds, 17–18% for mammals, and 8–12% for herpetofauna. More than 40% of bird and mammal species showed highly significant differences in habitat suitability between the two landscape types ($P < 0.01$), with more species having higher suitability in unlogged than logged forests. This higher habitat suitability in unlogged forests was associated with a greater amount of older forests and a higher richness of forest types in unlogged compared to logged forests. The effect of the two regeneration scenarios was discernible for all communities, but had a relatively weak effect, with the possible exception of higher snowshoe hare (*Lepus americana*) densities under partial compared to full regeneration control. Various lines of evidence are presented suggesting that these differences between logged and unlogged landscapes may be maintained into the future unless actions are taken to ameliorate these effects of clearcut logging. The technique presented here may prove useful in forest monitoring and adaptive management planning because it is objective, can simultaneously consider a large number of forest taxa, focuses on real rather than projected landscapes, and outlines, in a succinct way, the main habitat-related gradients in habitat suitability matrices.

Key words: wildlife habitat supply, clearcut logging, boreal forest, indicator species, forest age, forest regeneration, multivariate analysis

Les protocoles pour sélectionner des indicateurs écologiques d'aménagement forestier durable tireront profit d'une approche proactive qui identifie les espèces qui seront vraisemblablement les plus sérieusement perturbés par l'aménagement. Dans le cas présent, nous utilisons une approche objective qui regroupe l'information de l'inventaire des ressources forestières tirée de sites récoltés et non récoltés du nord-est de l'Ontario avec l'information de la matrice provinciale de la pertinence de l'habitat des vertébrés afin d'évaluer la pertinence de l'habitat (l'importance et la préférence des habitats utilisés) dans les sites et pour identifier les indicateurs potentiels des conséquences des activités d'aménagement forestier. Parce qu'ils pourraient être les plus représentatifs du potentiel des sites à être récoltés dans le futur pour une région, nous avons mis en évidence les sites post-récolte les plus anciens de la région (époque des années 1950 et 1960, $n = 27$) par rapport aux sites non récoltés ($n = 16$). Chaque site était un cercle de 2 km de rayon (12,6 km²). À la lumière des invasions relevées d'espèces de feuillus dans les sites récoltés de conifères, nous avons considéré deux scénarios de régénération pour les très jeunes peuplements après récolte : suivi partiel et complet de la régénération. Les sites récoltés présentaient une différence marquée par rapport aux sites non récoltés relativement à l'âge de la forêt et des peuplements. Ces différences entraînaient d'importantes distinctions entre les forêts récoltées et non récoltées pour les communautés d'oiseaux et de mammifères, mais une différence peu marquée au niveau de la faune reptilienne. L'analyse de redondance a indiqué que le pourcentage de variation de l'habitat pertinent attribuable à la récolte était de 27 % pour les oiseaux, 17-18 % pour les mammifères et de 8-12 % pour la faune reptilienne. Plus de 40 % des espèces d'oiseaux et de mammifères ont démontré des différences très significatives pour l'habitat pertinent entre les deux types de site ($P < 0.01$), plus d'espèces ayant une pertinence plus élevée dans les sites non récoltés que récoltés. Cette pertinence pour l'habitat plus élevée dans les sites non récoltés a été associée au plus grand nombre de forêts âgées et à une richesse plus grande des peuplements forestiers dans les sites non récoltés comparativement aux sites récoltés. L'effet des deux scénarios de régénération était discernable pour toutes les communautés, mais avait eu un effet faible, à l'exception possible de densités plus élevées de lièvre d'Amérique (*Lepus americana*) selon le suivi partiel comparativement au suivi complet de la régénération. Plusieurs énoncés sont présentés laissant entendre que ces différences entre les sites récoltés et non récoltés peuvent être maintenues dans le futur à moins que des actions soient entreprises pour améliorer ces effets de la coupe à blanc. La technique présentée pourrait être utile dans le suivi des forêts et la planification de l'aménagement adapté parce qu'elle est objective, elle peut considérer simultanément un grand nombre d'espèces forestières, elle peut se concentrer sur les sites réels plutôt que ceux envisagés et elle peut souligner, d'une manière succincte, les gradients reliés à l'habitat principal dans les matrices de pertinence de l'habitat.

Mots-clés: quantité d'habitat faunique, coupe à blanc, forêt boréale, espèces indicatrices, âge des forêts, régénération forestière, analyse multivariée

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Introduction

The identification of appropriate indicators of sustainability is a key aspect of forest management and is an important part of forest monitoring and adaptive management planning (Noss and Cooperrider 1994). The indicator approach is now entrenched in forest management planning at both international and national levels (e.g., Santiago Declaration, Canadian Council of Forest Ministers 1995).

Typically, indicators of sustainable forest management from a biodiversity perspective reflect the current status of biodiversity; for example, as reflected in the numbers of threatened and endangered taxa. A valuable addition is a more proactive approach in which potential future problems in the conservation of biodiversity are identified. For example, Noss (1999) argued that whereas prescribing a desired future condition is often problematic; defining a future direction for management is easier. Monitoring of potentially problematic populations could provide early warning of future impacts, and test both the effectiveness of improved techniques in ameliorating future impacts and the science upon which the projections of future problems is based. Thus, identification of such indicators would prove useful in an adaptive management approach, either through successive monitoring and improvement of management techniques, or by providing a quantitative framework for evaluating and testing current understanding of wildlife responses under forest management.

At present, the biodiversity indicator approach for sustainable forest management in Ontario focuses on: 1) prescriptive guidelines for featured species and 2) indicator species whose habitat supply is tracked at a strategic level in assessing the impact of proposed management alternatives. Featured species include those at the provincial level such as moose (*Alces alces*) and marten (*Martes americana*) in the boreal region, and those at the regional level such as woodland caribou (*Rangifer tarandus*) in the northern part of the boreal region (McLaren *et al.* 1998). The strategic indicator set for the boreal east region of Ontario at present includes 18 species. Both the featured and indicator species were chosen with a variety of criteria in mind in addition to potential logging impacts, including representation of species from a broad range of forest types and ages and socioeconomic considerations (OMNR unpublished). Similarly, although habitat suitability matrices have been created for most of the forest vertebrate fauna of the province (e.g., D'Eon and Watt 1994), use of these matrices in the indicator approach so far has been limited to the identification of indicators to test the general hypothesis that forest management caus-

es changes in species richness, abundances, or distributions (McLaren *et al.* 1998) rather than the identification of indicators that are most likely to be impacted by logging.

In this paper, we use the provincial Forest Resource Inventory (OMNR 2001) in combination with the habitat suitability matrix (D'Eon and Watt 1994) to contrast vertebrate habitat suitability in a series of logged and unlogged landscapes in northeastern Ontario. Although both of these management tools are relatively crude at present, in concert they allow investigations at large spatial scales and with considerable taxonomic breadth. We take a community approach by simultaneously considering the vertebrate fauna within major taxonomic groups (herpetofauna, birds, and mammals). Such an approach sidesteps some of the criticisms levelled at the indicator approach (see McLaren *et al.* 1998, Lindenmayer *et al.* 2000); for example, the problem that habitat associations of one species may not be representative of those of other species is avoided when one focuses on the main habitat-related gradients in a community. We use a combination of univariate and multivariate techniques: the former to derive indicator sets, the latter to explore in a succinct way the main habitat-related gradients in species responses. Our specific objectives in this paper are to: 1) present an objective and proactive method for indicator selection, 2) compare the vertebrate faunas of logged and unlogged landscapes in northeastern Ontario, 3) use multivariate techniques to investigate the roles of forest type and age in contributing to differences between the two landscape types, and 4) identify sets of taxa that may indicate logging-related impacts through time and that may be useful in refining the list of indicator species used in Ontario.

Materials and Methods

Study area

Study sites were located in an area of approximately 7 million ha in northeastern Ontario (Fig. 1), including parts of Rowe's (1972) Northern Clay, Missinaibi-Cabonga, and Central Plateau boreal forest sections. We used a large study area to cover a wide range of boreal conditions and to obtain inferences applicable over a large area. The area included the relatively flat terrain of glacial Lake Ojibway in the northeastern section, the rolling terrain of the central Ontario height of land in the south, and flat well-drained plateaus in the western section (Rowe 1972). The area was characterized by a continental climate, with a mean annual temperature of -1 to 2°C , a mean July temperature of 15 to 18°C , and total annual precipitation of 660 to 760 mm (Hills 1959). Forests in the study area were a mosaic resulting

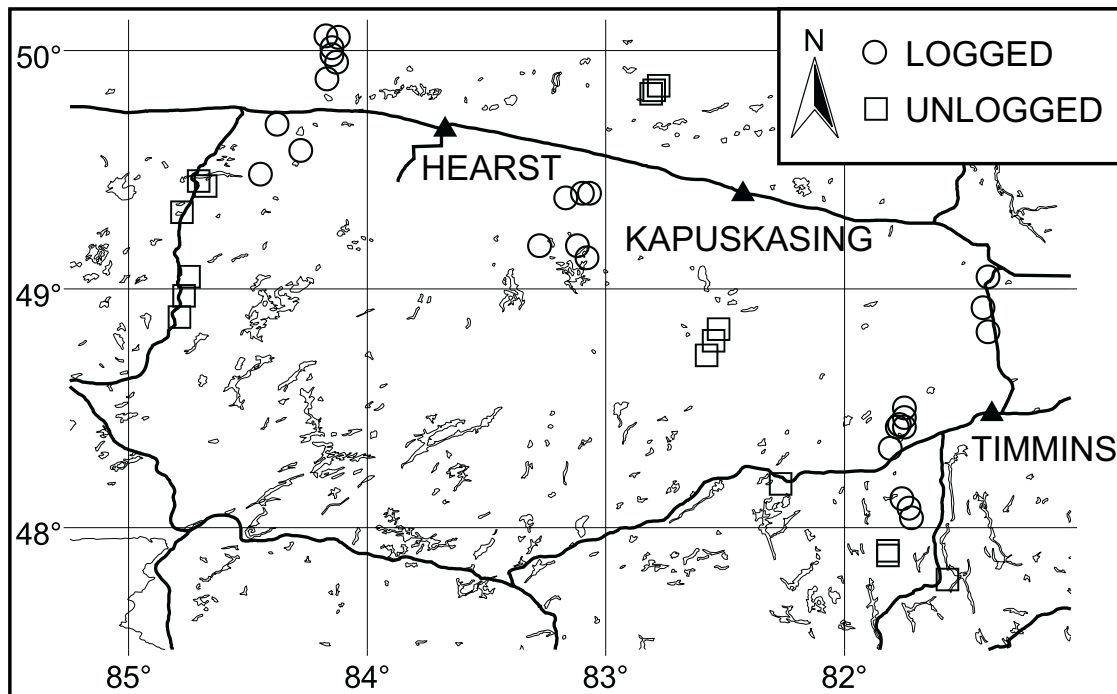


Fig. 1. Map of logged and unlogged study sites in northeastern Ontario, showing in addition major towns, roads, and lakes.

from fires, defoliation by spruce budworm (*Choristoneura fumiferana*), and, increasingly, forest harvesting by clearcut logging and associated forest management activities (Brumelis and Carleton 1988, Bonan and Shugart 1989, Hearnden *et al.* 1992, Gluck and Rempel 1996, Bergeron *et al.* 2001). Composition was predominantly black spruce (*Picea mariana*) and trembling aspen (*Populus tremuloides*), with other abundant species including balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), white birch (*Betula papyrifera*), and jack pine (*Pinus banksiana*). Other details on the climate, soil, geology, and vegetation of the region can be found in Hills (1959), Carleton and Maycock (1978), and Jones *et al.* (1983).

Study design

We reasoned that under clearcut silviculture, future managed landscapes of the northeast will come to resemble normal (or regulated) landscapes. In these landscapes, stand ages up to the rotation age are approximately equally represented whereas ages past the rotation age are rare (see Bergeron *et al.* 1998). In contrast, assuming that the probability of burning is independent of stand age, the age class distribution of an area subjected to stand-replacing fires in theory will follow a negative exponential distribution, with 37% of stands older than the mean fire return interval (Van Wagner 1978, Bergeron *et al.* 1998). Currently, forest management in the region is early in the transition to a regulated forest because large-scale clearcut silviculture only started in the 1950s and 1960s. We reasoned that these oldest logged landscapes are of particular interest for charting the potential future course of the region's forests because they are the closest to this presumptive future condition. At present, they are approximately one-half the rotation age (i.e., 40–50 years old) and hence, at least with respect to forest age, may represent an average future landscape condition. Also, because

rapid successional changes in forest composition tend to occur relatively early as stands age to the rotation age, it is reasonable to assume that the forest composition of these logged landscapes will change little at least until the next rotation.

This study was part of a larger research effort in which plant, vertebrate and insect communities were sampled in the study areas; therefore, our site selection protocol in part was designed to satisfy the demands of this sampling program. To identify logged and unlogged areas, we used two data sets: 1) maps of decadal clearcut logging activities between 1951 and 1990 (Pera and Baldwin 2000) and 1-km resolution Normalized Difference Vegetation Index values from the 1992/93 NOAA/NASA Pathfinder data set (Agbu and James 1994). We located six unlogged and six logged areas of about 150–400 km² each, and within each, selected a series of 2-km radius (12.6 km²) circular study sites (landscapes) for detailed study. Three sites were selected in five of the unlogged areas and one site in the remaining unlogged area for a total of 16 unlogged sites. Three or six sites were selected in each logged area for a total of 27 logged sites (Fig. 1). To satisfy the field-based sampling program: 1) the centre of each site was 100–300 m from a road, 2) the center of each site was an upland mixedwood stand that was at least 10% deciduous (*Populus tremuloides*, *P. balsamifera*, and/or *Betula papyrifera*) and 20% coniferous (*Picea glauca* and/or *P. mariana*), and 3) stands at the centre of logged sites had been clearcut via either horse logging (three sites in each of three of the logged areas) or mechanized logging (three sites in each of the six logged areas). It was not always possible to find unlogged sites that were completely devoid of logging, but any such logging covered at most a small area of the site. The requirement that the centre of each study landscape be a mixedwood stand helped to ensure that the logged and unlogged landscapes did not differ systematically from each other with respect to fea-

tures other than their disturbance history. In general, the unlogged sites had not been logged because they were relatively inaccessible, rather than because of some other characteristics of the site.

In addition to the logging itself, the logged landscapes also were the site of associated forest management activities, including in some cases site preparation followed by seeding or planting and subsequent tending (Hearnden *et al.* 1992). In addition, the variability of the forest causes portions of an area allocated for harvesting to be untouched; for example, pockets of unmerchantable tree species and sizes and inoperable terrain. In some cases, modified clearcuts were used in which blocks of unharvested forest and/or undesirable tree species were left on the site (Hearnden *et al.* 1992). In using “logging” in a generic sense in this paper, we are referring to the harvesting itself, as well as these associated forest management activities.

Habitat suitability

We used information from the Forest Resource Inventory (OMNR 2001) to quantify area in each of the habitat types in the Northeast Habitat Suitability Matrix (D'Eon and Watt 1994). Specifically, a provincial algorithm for the northeast region (Naylor 1994) was used to convert FRI information to FEC site types, and in concert with stand ages, was used to assign each FRI-based polygon to one of the matrix's 80 habitat types (five forest development stages for each of 16 FEC site types). Unfortunately, we could not determine habitat suitability directly from the FRI information because the habitat suitability matrix for the region instead makes use of FEC site types. The algorithm was a similar to that in Watkins and Davis (1999), but was modified to operate directly on the FRI data. The date of the most recent update of the FRI data varied from 1987 to 1992. For the purposes of this paper, all of the FRI ages were updated to 1999. We assumed that the stand composition at the time of the most recent update had not changed by 1999, with the exception of harvested stands in which “free to grow” surveys had not yet been undertaken (see Regeneration Scenarios section below). For most of the region's vertebrates, the habitat suitability matrix specified which habitat types were not used, used, or preferred. To derive an index of suitability, we recoded these classes as 0, 1, or 2, respectively. This recoded matrix was multiplied by the matrix of habitat areas (in km²) to give a matrix of species-specific habitat suitabilities for the sites. For example, if a species used habitat type *a* and preferred habitat *b*, but did not use any of the other 80 habitat types, then the index of habitat suitability for that species at a site was: (area of habitat *a* at the site) · 1 + (area of habitat *b* at the site) · 2. Our FRI information did not include “forest type” or “working group”; hence we modified the algorithm in two ways. First, assignment to FEC site type 1 (very shallow soil) was based only on the rule sets for stocking, age, and site class. Secondly, in addition to site class, we used information on dominant species to assign polygons to FEC site type 14 (Black Spruce/Leatherleaf). Specifically, we assumed that: 1) working group 11 in the original algorithm corresponded to dominance by black spruce and absence of white spruce and 2) working group 18 in the original algorithm corresponded to dominance by larch (*Larix laricina*).

Regeneration scenarios

FRI information is updated via new aerial photos only infrequently (at approximately 20 year intervals). Prior to “free to grow” surveys of regenerating sites, which typically take place 7–11 years after sites are regenerated, harvested stands are listed in the FRI data according to their presumed future composition (e.g., Sb10, Pj10, etc.) rather than their actual composition. For this paper, this procedure is potentially problematic because, as documented by Hearnden *et al.* (1992), many regenerating stands often become invaded by hardwoods (see also Carleton 2000, Thompson *et al.* 2003). For example, of approximately 316 000 ha of black spruce regenerated between 1970 and 1985 in boreal Ontario, only 11% was classified as black spruce in 1991 (see Table 1-ii in Hearnden *et al.* 1992). Therefore, we investigated two regeneration scenarios for these young stands: 1) full regeneration control: the stand composition remained as specified in the FRI and 2) partial regeneration control: stand composition changed in accordance with Hearnden *et al.* (1992). We investigated these two scenarios in part because of uncertainties regarding the actual composition of these regenerating stands. In addition, the full regeneration control scenario was of interest, in comparison to the partial regeneration control scenario, because it entailed a more coniferous species composition in the logged landscapes and thus showed affinities with more intensive forestry practices that have been proposed for the region (see Thompson *et al.* 2003). In calculating the second scenario, we used transition matrices in Hearnden *et al.* (1992) for 1970–74 that gave the probability of succession from an original forest type *x* to an eventual forest type *y*. Hearnden *et al.* (1992) used a coarser classification scheme than FEC; hence, an additional task was to convert their forest types to FEC types. To do this, we assumed that proportions of FEC types in each future Hearnden type *y* was the same as the historic proportions. The historic proportions were determined from stands that were not age zero (i.e., had been updated since harvesting). Because the “Hardwood” class of Hearnden *et al.* (1992) could be assigned unambiguously to FEC classes only by taking into account FRI site class, we developed the transition matrices for two different sets of site classes (Table 1). Note that although the regeneration scenarios defined the species composition (FEC site type) of the regenerating stands, they also affected forest development stage because development stages varied according to the site type (D'Eon and Watt 1994). For example, depending on the site type, the initiation phase varied from 0–5 years to 0–20 years.

Data analyses

Results from the habitat suitability calculations were analyzed separately for each regeneration scenario and major vertebrate group (herpetofauna, birds, and mammals). Principal components analysis (PCA) was used to investigate major patterns of variation in habitat suitability among landscapes. We used this linear approach because detrended correspondence analysis (DCA) indicated short ecological gradients in the matrices (gradient lengths along the first DCA axes were 1.2, 1.4, and 1.1 standard deviation units for herpetofauna, birds, and mammals, respectively). To examine the roles of forest composition and age in contributing to this variation, we calculated the amount of forest at each site in each FEC site type (all development stages combined) and in each development stage (all FEC site types combined) and used these variables passively

Table 1. Transition matrix for the “partial regeneration control” scenario showing probabilities of FEC site type membership for young stands originally classified as Pj (jack pine), Sp (spruce), or H (hardwood) under the Hearnden *et al.* (1994) classification scheme (two addition stand types, Mixed Softwood and Mixed Wood, did not occur in the study sites). See text for details

Forest type	FRI Site class	FEC site types											
		2	3	4	5	6	7	8	9	10	11	12	13
Pj	1+”X”	0.34	0.09	0.01	0.01	0.36	0.09	0.00	0.08	0.00	0.00	0.02	0.01
	2+3	0.34	0.10	0.01	0.01	0.40	0.00	0.00	0.08	0.05	0.00	0.02	0.01
Sp	1+”X”	0.07	0.06	0.01	0.02	0.36	0.21	0.03	0.14	0.00	0.06	0.03	0.02
	2+3	0.07	0.07	0.01	0.02	0.46	0.00	0.03	0.14	0.11	0.06	0.03	0.02
H	1+”X”	0.03	0.06	0.00	0.01	0.43	0.41	0.00	0.04	0.00	0.00	0.01	0.01
	2+3	0.03	0.07	0.00	0.01	0.62	0.00	0.00	0.04	0.21	0.00	0.01	0.01

in the PCA (i.e., as correlates rather than predictive variables). In addition, we used constrained ordination (redundancy analysis) to calculate the percent variation of habitat suitability that was explained by logging. This percentage was partitioned using the method of Borcard *et al.* (1992) to calculate the proportion of the variance attributable to the combined and independent effects of FEC site type and development stage.

Analysis of variance (ANOVA) was used to identify sets of potential indicator species by comparing species-specific habitat suitabilities between the logged and unlogged landscapes. Good indicators, i.e., those that had high variance in suitability between landscape types relative to within landscape types, had high significance levels in the ANOVAs. We used a relatively conservative criterion for inclusion in our sets of potential indicators ($P < 0.01$). CANOCO (v. 4.0) was used for the ordinations; other analyses were conducted using SAS (v. 8.01).

Results

Forest age and composition

The amount of forest in each of the five development stages differed significantly between the logged and unlogged landscapes under both regeneration scenarios (P 's < 0.01) (Fig. 2). Because many landscapes had zeros in one or another of the development or FEC classes, data were compared using median tests. Logged landscapes had more forest in the first three development stages than unlogged landscapes, whereas the converse was true for the last two development stages. In the logged landscapes, most stands were in the young development stage. The remaining forest area was approximately equally spread among the other development stages. In contrast, most forests in the unlogged landscapes were in the mature development stage, although old-growth forests were relatively common. In the unlogged landscapes, initiation and regeneration forests were rare or absent.

Of the 14 FEC site types present in the study landscapes, only six showed significant differences ($P < 0.05$) between the two landscape types in at least one regeneration scenario (Fig. 3). The amount of Mixedwood (FEC type 3), Black Spruce (FEC type 5), and Hardwood/Moist Soil (FEC type 10) was significantly greater in unlogged than logged landscapes, whereas the converse was true for Aspen/Spruce Mixedwood (FEC type 6) and Conifer/Moist Soil (FEC type 9). The Aspen/Spruce Mixedwood difference was significant only at $P = 0.08$ in the full regeneration control scenario. The amount of Black Spruce/Labrador Tea (FEC type 11) showed contrasting patterns in the two regeneration scenarios, being relatively more abundant in logged forests in the full control scenario, but relatively less abundant in logged

forests in the partial control scenario, although the difference was significant only for the former.

Herpetofauna

In both regeneration scenarios, most herpetofauna species showed a positive correlation with the first PCA axis (the partial control scenario is shown in Fig. 4; study sites scores are shown as circles). This axis was positively associated with young forests in Conifer/Moist Soil (FEC type 9) and Black Spruce/Leatherleaf (FEC type 14) forests and negatively associated with older forests in a variety of FEC types. In both scenarios, the second axis was driven primarily by a few logged stands that showed a large amount of boreal chorus frog habitat in initiation and regeneration stages (see Appendix 1 for scientific names of vertebrate species). In the partial control scenario, these very young forests were associated with Hardwood forests (FEC type 7), whereas in the full control scenario, they were associated with Black Spruce/Labrador Tea forests (FEC type 11). Compared to post-logged landscapes, unlogged landscapes tended to have small values on both axes, although separation between the two landscape types was weak. Percent variation of the species habitat suitability matrix that was explained by the logging was 8% and 12% for the partial and full regeneration control scenarios, respectively. Most of this variation (86% and 95%, respectively) was explained by the combined effects of FEC site type and development stage. FEC site type independently contributed 1% and 5%, respectively, of this variation and development stage 13% and 1%, respectively.

In both regeneration scenarios, all species except the eastern redbacked salamander had more habitat in the logged than unlogged landscapes. By contrast, in both scenarios this salamander had less habitat in the logged than unlogged landscapes. In the partial control scenario, the differences were not significant for four species (spring peeper, wood frog, blue-spotted salamander, mink frog); for the remaining four species, they were significant at $0.01 < P < 0.05$. In the full control scenario, only the difference in mink frog habitat was not significant; the rest of the habitat differences were significant at $0.01 < P < 0.05$.

Birds

Two FEC site types were absent from the study sites (Tolerant Hardwood Mixedwood and Sugar Maple/Yellow Birch), hence eight bird species restricted to those site types were absent as well and are not considered further here (house wren, indigo bunting, northern goshawk, northern oriole, red-shouldered hawk, scarlet tanager, warbling vireo, and white-breasted nuthatch).

The PCAs for birds showed strong separation of logged and unlogged landscapes with highly significant differences in

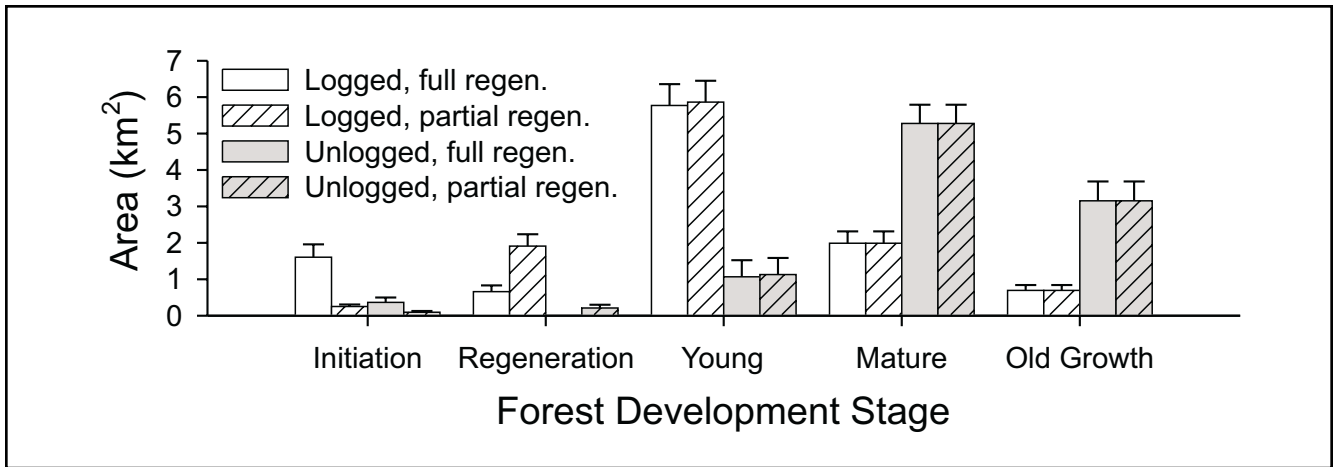


Fig. 2. The average amount of forest land (\pm SEM) in five development stages (all FEC site types combined) in 27 logged and 16 unlogged landscapes in northeastern Ontario. Averages are shown for each of two regeneration scenarios (full and partial regeneration control). See text for details.

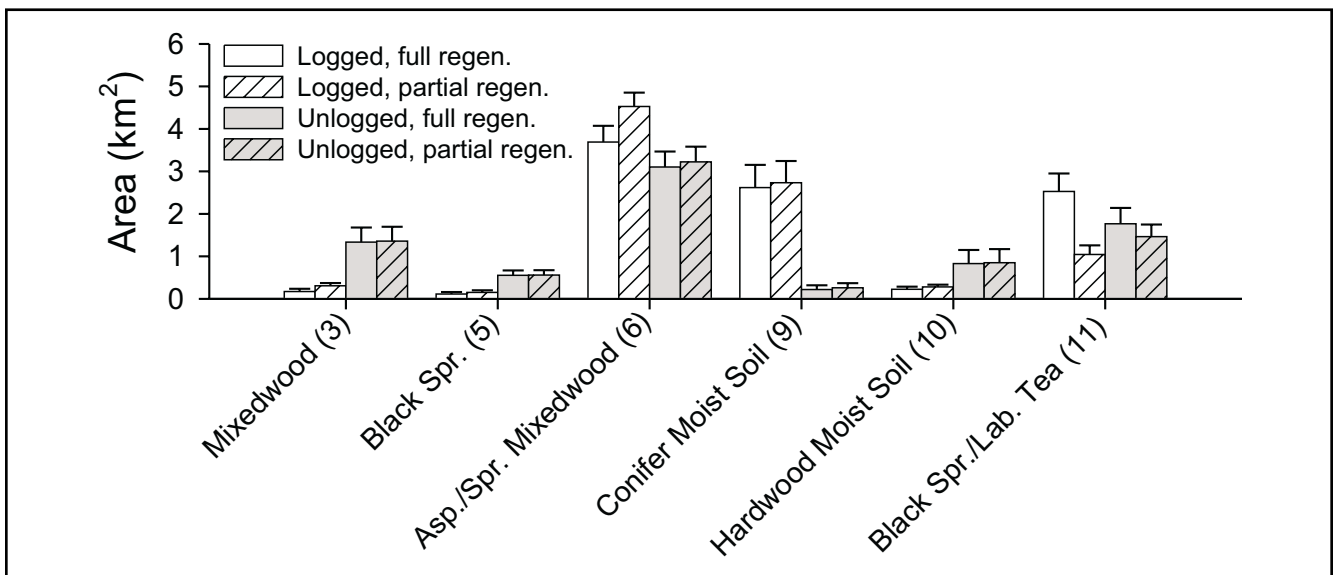


Fig. 3. As Fig. 2 except that the average amount of forest area in six FEC site types (all development stages combined) is shown (FEC numeric code is in parenthesis). Site types are shown that exhibited significant differences between logged and unlogged landscapes in at least one regeneration scenario.

habitat suitability in the two landscape types for many species. Both regeneration scenarios had similar patterns on axes one and two, with the study site scores showing a triangular distribution (the partial regeneration scenario is shown in Fig. 5). Logged landscapes defined one side of the triangle. One vertex was characterized by sites with young (age 3), Conifer/Moist Soil habitats. The other was characterized by sites with initiation and regeneration forests (age 1 and 2); however, associated forest types differed between the regeneration scenarios. In the partial control scenario, they tended to be Hardwoods (FEC type 7), whereas in the full control scenario, they tended to be Black Spruce/Labrador Tea forests (FEC type 11). Unlogged landscapes defined the final triangle vertex and were characterized by mature and old-growth habitats and contained a higher richness of FEC site types. Percent variation of the species habitat suitability matrix that was explained by the logging was

27% for both regeneration scenarios. Most of this variation (75% and 82% for the partial and full control scenarios, respectively) was explained by the combined effects of FEC site type and development stage. Of the remainder, more was due to the independent effect of development stage (17% and 11%, respectively) than FEC site type (8% and 7%, respectively).

Indicator species significant at $P < 0.01$ included 35 species that were more abundant in the unlogged compared to logged landscapes in both regeneration scenarios (Table 2) and 20 species that displayed the converse pattern and were significant ($P < 0.01$) in at least one regeneration scenario (Table 3). Differences between the two regeneration scenarios were relatively minor; for example, among the 20 species more abundant in logged than unlogged landscapes, means and levels of significance in the two habitat types were very similar in the two scenarios (Table 3).

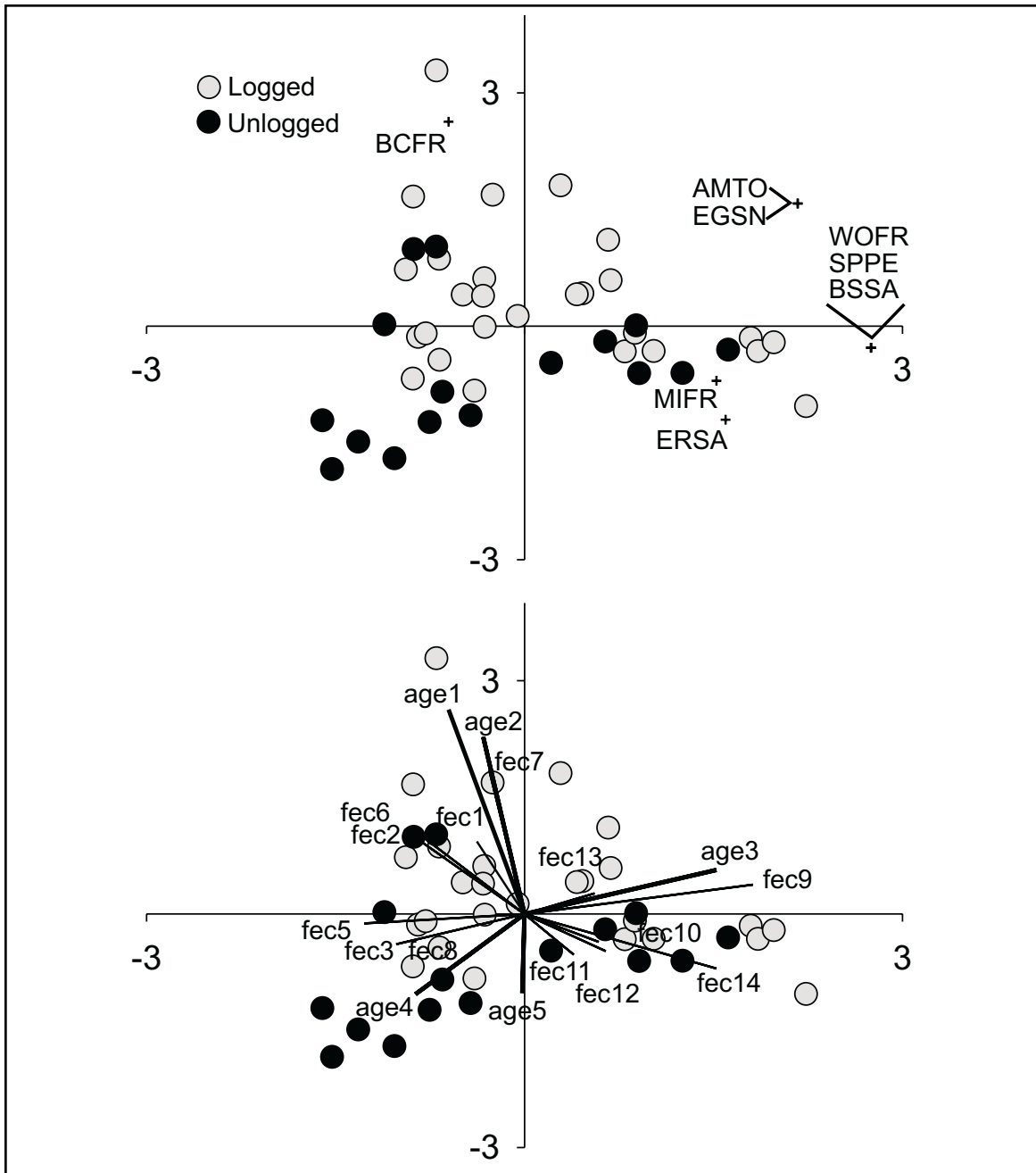


Fig. 4. Axes one and two from a principal components analysis on herpetofauna habitat suitability in logged and unlogged landscapes of north-eastern Ontario (partial regeneration control scenario). In part A, study site scores (black circles = unlogged sites, grey circles = logged sites) and species scores (pluses) are shown. Species scores are labelled using four letter acronyms (see Appendix 1). In part B, in addition to study site scores, vectors are shown that represent correlations between the principal component axes and the area of forest in five development stages and 14 FEC site types. See Figs. 2 and 3 for development stages and FEC classes (additional FEC types shown here that are not listed in Fig. 3 are Very Shallow Soil (FEC 1), Jack Pine/Coarse Soil (FEC 2), Jack Pine/Black Spruce (FEC 4), Hardwood (FEC 7), Black Spruce Feathermoss Sphagnum (FEC 8), Black Spruce/Alder (FEC 12), Conifer/Alder (FEC 13), and Black Spruce / Leatherleaf (FEC 14)).

Mammals

The triangular distribution of study site scores evident in the bird PCAs also was evident for mammals, although the distinction between the young and initiation/regeneration vertices was weak in the partial regeneration control scenario (Fig. 6). Variation of the species habitat suitability matrix that was explained by the logging was 17% for the partial regeneration control sce-

nario and 18% for the full regeneration control scenario. As with birds, most of this variation (75% and 84% for the partial and full control scenarios, respectively) was explained by the combined effects of FEC site type and development stage. Of the remainder, more was due to the independent effect of development stage (18% and 10%, respectively) than FEC site type (7% and 5%, respectively).

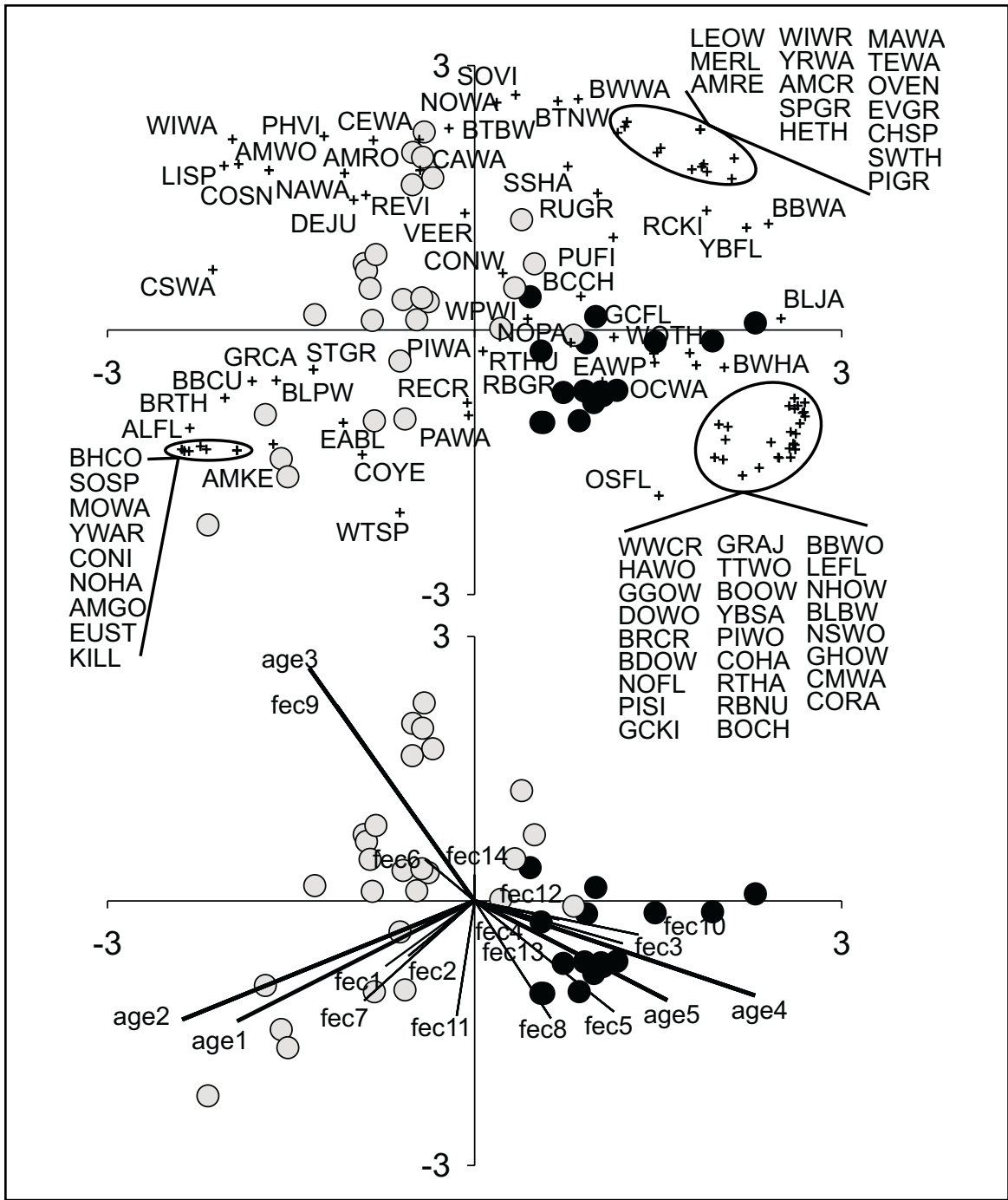


Fig. 5. As Fig. 4 except that the analysis is on the bird habitat suitability matrix.

Again, a large proportion of species showed highly significant differences in habitat suitability between the two landscape types. In both regeneration scenarios, the same 11 species had significantly more habitat in unlogged than logged landscapes ($P < 0.01$). Interestingly, although snowshoe hares and Canada lynx had more habitat in unlogged than logged forests in the full control scenario, and the differences were highly significant, in the partial control scenario they had more habitat in logged than unlogged forests (although not significantly so) (Table 2). Variation between the two regeneration scenarios was more pro-

nounced for species more abundant in logged than unlogged forests: of the nine species that showed highly significant differences in one or the other scenario, only two were common to both scenarios (Table 3).

Discussion

This study illustrates the potential value of habitat suitability matrices in identifying indicators of forest management activities, and also demonstrates that certain species and species groups may be more responsive than others. For the bird

Table 2. Mean habitat suitability (\pm SEM) for vertebrate species more abundant in unlogged than logged landscapes in northeastern Ontario. Species are listed only if analysis of variance indicated that differences were highly significant ($P < 0.01$) in one or both regeneration scenarios. If means differed between the two regeneration scenarios, both means are shown. See Appendix 1 for species acronyms

	Logged landscapes ^a (n = 27)	Unlogged landscapes ^a (n = 16)	Probability ^b
<i>Birds</i>			
HAWO	2.8 \pm 0.35	9.7 \pm 0.47	< 0.0001
NHOW	2.5 \pm 0.34	8.3 \pm 0.53	< 0.0001
BOCH	3.2 \pm 0.41	10.3 \pm 0.59	< 0.0001
PISI	4.2 \pm 0.56	13.1 \pm 0.66	< 0.0001
CMWA	2.5 \pm 0.36	9.2 \pm 0.63	< 0.0001
GRAJ	3.7 \pm 0.44	10.8 \pm 0.63	< 0.0001
GCKI	3.8 \pm 0.54	11.8 \pm 0.68	< 0.0001
RBNU	3.1 \pm 0.38	9.6 \pm 0.70	< 0.0001
WWCR	3.9 \pm 0.45	11.1 \pm 0.44	< 0.0001
NOFL	1.8 \pm 0.31	6.2 \pm 0.63	< 0.0001
GHOW	1.9 \pm 0.33	7.4 \pm 0.76	< 0.0001
RTHA	3.1 \pm 0.55	10.9 \pm 0.84	< 0.0001
BRCR	3.3 \pm 0.60	11.7 \pm 0.34	< 0.0001
CORA	1.8 \pm 0.31	5.8 \pm 0.61	< 0.0001
BDOW	1.3 \pm 0.30	6.3 \pm 0.58	< 0.0001
DOWO	1.3 \pm 0.27	5.9 \pm 0.38	< 0.0001
BLBW	1.8 \pm 0.28	5.6 \pm 0.89	< 0.0001
NSWO	1.5 \pm 0.29	7.6 \pm 0.39	< 0.0001
PIWO	1.5 \pm 0.30	5.2 \pm 0.82	< 0.0001
YBSA	1.3 \pm 0.28	6.8 \pm 0.71	< 0.0001
COHA	1.7 \pm 0.30	6.5 \pm 0.73	< 0.0001
LEFL	2 \pm 0.28	6.3 \pm 0.73	< 0.0001
TTWO	2.8 \pm 0.39	7.6 \pm 0.63	< 0.0001
OSFL	2 \pm 0.29	5.9 \pm 0.72	< 0.0001
GGOW	1.5 \pm 0.20	5 \pm 0.43	< 0.0001
BBWO	2.1 \pm 0.35	5 \pm 0.79	< 0.0001
BOOW	2.9 \pm 0.57	7.8 \pm 0.54	< 0.0001
BLJA	10.3 \pm 0.48	14.1 \pm 0.51	< 0.0001
OCWA	0.4 \pm 0.08	2.3 \pm 0.76	< 0.0001
BWHA	0.2 \pm 0.07	2.9 \pm 0.35	< 0.0001
EAWP	0.2 \pm 0.06	1.4 \pm 0.46	< 0.0001
YBFL	9.1 \pm 0.42	11.4 \pm 0.32	0.0011
GCFL	0.1 \pm 0.03	0.8 \pm 0.68	0.0032
BBWA	8.8 \pm 0.64	11.7 \pm 0.46	0.0059
RCKI	9.6 \pm 0.50	11.7 \pm 0.46	0.0093
<i>Mammals</i>			
NFSQ	2.7 \pm 1.73	8.4 \pm 1.66	< 0.0001
RACC	1.3 \pm 1.42	5.8 \pm 1.70	< 0.0001
WCAR	1.2 \pm 1.26	3.6 \pm 1.22	< 0.0001
WTDW	2.9 \pm 2.95	7.5 \pm 3.15	< 0.0001
STSH	11.9 \pm 1.38	14.6 \pm 2.46	< 0.0001
BBEC	11.6 \pm 1.46	13.7 \pm 1.78	0.0001
	(10.2 \pm 2.53)	(13.4 \pm 1.89)	< 0.0001
RSQU	9.6 \pm 1.99	12.2 \pm 2.13	0.0002
	(9.5 \pm 2.03)	(12.1 \pm 2.09)	0.0002
MART	9.7 \pm 2.84	13.0 \pm 2.45	0.0004
	(9.6 \pm 2.89)	(12.9 \pm 2.45)	0.0005
RBVO	12.0 \pm 1.65	14.2 \pm 2.00	0.0005
	(10.7 \pm 2.63)	(13.9 \pm 1.91)	0.0001
HVOL	0.7 \pm 0.84	1.8 \pm 1.46	0.0027
	(0.7 \pm 1.04)	(1.8 \pm 1.48)	0.0055
SNMO	0.5 \pm 0.32	1.2 \pm 1.25	0.0039
	(0.4 \pm 0.34)	(1.2 \pm 1.25)	0.0020
SNHA	12.0 \pm 1.48	11.7 \pm 1.68	0.4674
	(9.5 \pm 2.24)	(11.2 \pm 1.30)	0.0066
LYNX	12.0 \pm 1.48	11.7 \pm 1.68	0.4674
	(9.5 \pm 2.24)	(11.2 \pm 1.30)	0.0066

^aWhen means differed between the two regeneration scenarios, means for the partial control scenario are shown in the upper row and means for the full control scenario are shown in the second row (in parenthesis).

^bSignificance from one-way analysis of variance comparing means for logged and unlogged landscapes.

and the mammal communities, the differences between the two landscape types were pronounced, with landscape type explaining 27% and 17–18% of the total variability in habitat suitability, respectively. For both, more species showed higher habitat suitabilities in unlogged than logged landscapes than the converse, and the effect of the logging was highly significant ($P < 0.01$) for > 40% of the species in each group. The herpetofauna on the other hand was less responsive to the logging-induced landscape change, showing relatively weak separation of logged and unlogged landscapes (8–12% of the total species variability, depending on the particular regeneration scenario). This may reflect actual insensitivity of the group to the logging-induced landscape change, or it may reflect the fact that the FRI/FEC information is poor at capturing the resource needs of this group.

The utility of a multivariate approach in understanding the overall pattern of habitat change and species-habitat relationships also was illustrated by this study. For example, all vertebrate groups showed evidence of a triangular distribution of study sites (albeit weakly for mammals), with unlogged sites forming one vertex, young (development stage 3) forests another, and the youngest forests (development stages 1 and 2) the final one. The major axis of variation in habitat suitability distinguished between the unlogged vertex and the other two, and was highly correlated with forest age, in agreement with Thompson *et al.* (2003), who suggested that age-class truncation under silviculture was especially important in determining wildlife responses. Variation in all three faunal groups also reflected the regeneration scenarios, with the forest type affiliations of this last vertex reflecting conifer associations under the full regeneration control scenario, but a more deciduous composition under the partial regeneration control scenario that was based on Hearnden *et al.* (1992). The multivariate approach to indicator selection offers other advantages as well: it is objective, it potentially identifies a broad set of candidate species with a wide range of biological attributes, and, at least in a modelling context, it means that there is no particular reason to limit analyses to a subset of the fauna.

While the method used here may prove useful for the objective identification of potential indicator species, it is only a first step in implementing an indicator approach for monitoring forest condition. Any attempts to test the validity of the findings, or to design a monitoring system around the indicator set, would have to deal with practical realities of sampling. This will likely necessitate identification of a subset of the fauna that is selected primarily on the basis of practical considerations, particularly for mammals. Monitoring of all species clearly is not possible, although sampling methods such as point counts and territory mapping for birds simultaneously can provide information on many species. In deriving a relatively narrow set of indicator species, McLaren *et al.* (1998) considered a wide range of criteria, including habitat affiliations, conservation status, spatial scale, aspects of life history strategy, trophic level, and availability of monitoring methods. A similar approach would be useful in refining the lists in Tables 2 and 3, with the stipulation that candidate species be chosen from among those with the lowest probability values (i.e., those species most likely to be impacted by logging). From a conservation perspective, species that are predicted to be negatively affected by the logging are of special concern.

In light of our results, it is of some interest to examine the potential effectiveness as indicators of logging effects of the

Table 3. As Table 2 except that species more abundant in logged than unlogged landscapes are listed. See Appendix 1 for species acronyms

	Logged landscapes (n = 27)	Unlogged landscapes (n = 16)	Probability
<i>Birds</i>			
LISP	8.2 ± 0.55 (8.5 ± 0.56)	1.4 ± 0.37 (1.5 ± 0.40)	<0.0001 <0.0001
WIWA	10.6 ± 0.90 (10.4 ± 0.94)	1.3 ± 0.36 (1.3 ± 0.36)	<0.0001 <0.0001
CSWA	4.4 ± 0.35 (3.2 ± 0.34)	0.8 ± 0.31 (0.6 ± 0.31)	<0.0001 <0.0001
AMWO	4.2 ± 0.47 (5.1 ± 0.48)	0.4 ± 0.15 (0.5 ± 0.21)	<0.0001 <0.0001
PHVI	17.1 ± 0.66 (14.5 ± 1.01)	10.3 ± 1.00 (9.8 ± 1.08)	<0.0001 0.0048
COSN	4.6 ± 0.55 (5.6 ± 0.56)	0.7 ± 0.24 (0.9 ± 0.29)	<0.0001 <0.0001
REVI	14.5 ± 0.45 (12.1 ± 0.73)	9.9 ± 0.90 (9.5 ± 0.97)	<0.0001 0.0371
NAWA	10 ± 0.27 (8.7 ± 0.46)	7.2 ± 0.68 (6.9 ± 0.75)	<0.0001 0.0364
YWAR	2 ± 0.33 (2.1 ± 0.36)	0.3 ± 0.09 (0.4 ± 0.13)	0.0004 0.0010
CONI	2.2 ± 0.37 (2.3 ± 0.39)	0.3 ± 0.10 (0.4 ± 0.13)	0.0005 0.0007
SOSP	2.2 ± 0.37 (2.3 ± 0.39)	0.3 ± 0.10 (0.4 ± 0.13)	0.0005 0.0007
ALFL	0.9 ± 0.16 (2 ± 0.36)	0.1 ± 0.04 (0.3 ± 0.13)	0.0005 0.0011
MOWA	3.2 ± 0.57 (2.3 ± 0.40)	0.5 ± 0.15 (0.4 ± 0.13)	0.0007 0.0007
BRTH	0.4 ± 0.08 (0.2 ± 0.06)	0.1 ± 0.03 (<0.1 ± 0.01)	0.0010 0.0118
BHCO	1.7 ± 0.32 (0.4 ± 0.14)	0.3 ± 0.09 (<0.1 ± 0.02)	0.0012 0.0305
DEJU	11.1 ± 0.14 (12.5 ± 0.36)	9.9 ± 0.38 (10.2 ± 0.44)	0.0014 0.0003
CEDW	13.5 ± 0.65 (13.3 ± 0.67)	10.6 ± 0.55 (10.5 ± 0.54)	0.0036 0.0069
NOHA	0.2 ± 0.04 (1.6 ± 0.35)	<0.1 ± 0.01 (0.3 ± 0.13)	0.0058 0.0097
STGR	0.6 ± 0.13 (2 ± 0.36)	0.2 ± 0.08 (0.5 ± 0.16)	0.0353 0.0037
BLPW	0.6 ± 0.13 (2 ± 0.36)	0.2 ± 0.08 (0.5 ± 0.16)	0.0353 0.0037
<i>Mammals</i>			
MSHR	18.7 ± 2.99 (17.5 ± 3.57)	14.7 ± 2.81 (14.5 ± 2.67)	0.0001 0.0064
WTDS	2.7 ± 2.61 (0.4 ± 0.51)	0.4 ± 0.52 (0.1 ± 0.17)	0.0013 0.0403
MOOS	2.9 ± 2.82 (0.6 ± 0.89)	0.4 ± 0.56 (0.1 ± 0.17)	0.0014 0.0163
DMOU	10.3 ± 2.15 (7.8 ± 2.64)	8.1 ± 1.93 (7.6 ± 1.99)	0.0015 0.8575
BBEF	1.2 ± 1.19 (1.6 ± 1.81)	0.2 ± 0.24 (0.4 ± 0.53)	0.0020 0.0093
MVOL	0.4 ± 0.45 (1.8 ± 1.84)	0.2 ± 0.32 (0.5 ± 0.65)	0.1029 0.0089
MJMO	0.4 ± 0.46 (1.8 ± 1.84)	0.2 ± 0.32 (0.5 ± 0.65)	0.1423 0.0087

existing indicator sets for Ontario. In addition to the indicator set in McLaren *et al.* (1998), the Ontario Ministry of Natural Resources (OMNR) has recently defined 18 indicator species for the Northeast region (OMNR unpublished). Both of these sets were selected using a variety of criteria in addition to potential logging impacts; however, in both cases, a primary function of the indicator set was to evaluate the sustainability of for-

est management practices from a biodiversity perspective (McLaren *et al.* 1998, OMNR unpublished). In evaluating these indicator sets, we asked the question: based on our results, are the species in these lists any more likely to indicate logging effects than a random collection of vertebrate species? To answer this question, as a measure of the likelihood of logging effects for a species, we used the significance levels from our ANOVAs that compared habitat suitability between the logged and unlogged landscapes. Under the hypothesis that the indicator sets performed better in indicating logging impacts than a random collection of species, we expected the significance levels for the indicator species to average smaller than the overall mean across all species. For the McLaren *et al.* (1998) set, a one-tailed median test revealed little evidence of any such difference between the means, providing little evidence that the indicator set performed better than a random collection of species ($P > 0.30$ for both regeneration scenarios; for the purposes of this test, significance levels of < 0.0001 were set to 0.0001). The same was true of the subset of species that they used as indicators at the stand and forest levels ($P_s > 0.09$); however, indicators at the landscape level performed better ($0.01 < P < 0.05$). Similarly, the set of 18 species used by the OMNR for the NE region performed better than a random set ($P = 0.04$ and $P = 0.08$ for the full and partial regeneration control scenarios, respectively); however, five of the 18 species were absent from our indicator lists in Tables 2 and 3 (blue-spotted salamander, ruffed grouse, spruce grouse, white-throated sparrow, and moose winter habitat). To improve this list, one approach would be to drop these species and select other species that are both in McLaren *et al.* (1998) and have high significance levels in Table 2. For example, at the forest scale, ruffed grouse, spruce grouse, and white-throated sparrow could be replaced by boreal chickadee, golden-crowned kinglet, Cape May warbler, and hairy woodpecker. Candidates for inclusion in the list at the landscape scale are three-toed woodpecker, the two cross-bill species, and pine siskin. The approach that we use in this paper has numerous shortcomings and certainly falls short of a definitive examination of the potential effects of forest management (see below), but at the very least, these comparisons suggest that refinement of the current indicator sets for boreal Ontario is possible.

Perhaps the most common approach in habitat supply analysis is to compare projections of future conditions (Naylor 1994), including the potential effects of alternative management regimes (e.g., Hansen *et al.* 1993, Andison and Marshall 1999, Thompson *et al.* 2003). Our approach is different in that we focused on real landscapes (albeit characterized primarily by aerial photography) (see also Gluck and Rempel 1996, Elkie and Rempel 2001). This approach is advantageous in that landscape conditions are empirically based and so the approach is a potentially valuable complement to techniques that make use of future projections. However, in the present context, this empirical approach also entails several potential pitfalls. One is the extent to which our logged landscapes represent the presumptive regulated (or normalized) future condition expected under clearcut silviculture. At present, instead of the uniform distribution expected in a regulated forest, in which age classes up to the rotation age are approximately equally abundant (Bergerson *et al.* 1998), most forests in the logged landscapes tended to be in the young development stage (i.e., between 11 and 90 years old, depending on the FEC site type). Initiation and regen-

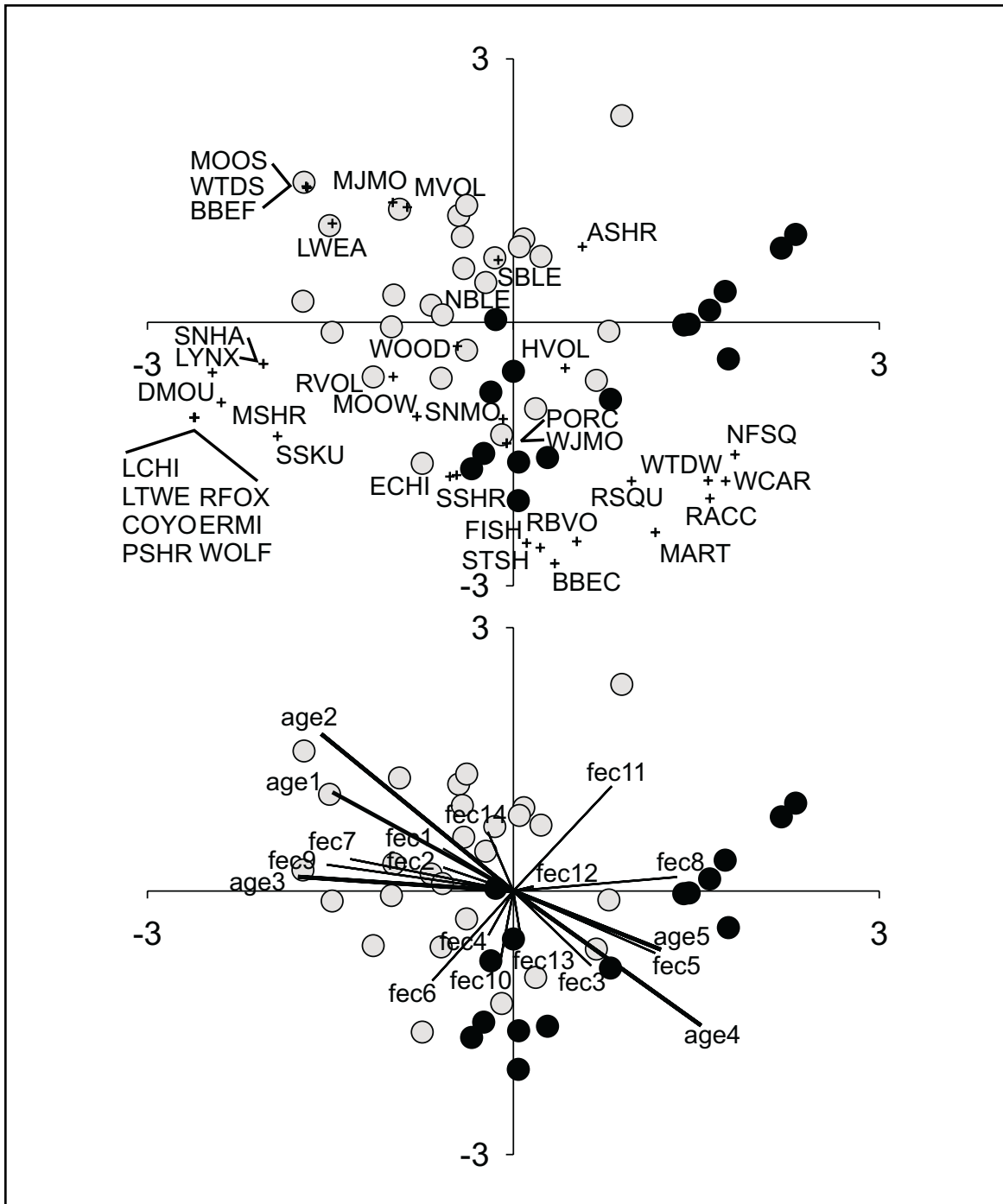


Fig. 6. As Fig. 4 except that the analysis is on the mammal habitat suitability matrix.

eration stages were rarer and old growth more common than expected. One reason for these differences from expectation is the small sizes of our landscapes (12.6 km²), which meant that they had been harvested over a relatively restricted time period (roughly 20–30 years) rather than over the full rotation cycle. However, for wildlife populations, perhaps the most significant aspect of these differences from expected future conditions is that our logged landscapes may mature considerably before they again reach merchantable age. At present, the logged and unlogged landscapes differ primarily from each other with

respect to the amounts of young (stages 1 to 3) and mature/old-growth forests (stages 4 and 5) and, as was evident in our ordinations of vertebrate habitat suitability in the two landscape types, the habitat suitability matrix for the northeast region proposes that this is a key distinction in determining faunal differences. However, examination of the matrix suggests that much of this age effect will be lost as the logged landscapes reach the mature stage: in the matrix, only nine bird and two mammal species show differences in habitat suitability between mature and old-growth forests. Thus, according to the matrix, much of the

age effect that we observed may be obliterated as forests age to > 40–90 years old (i.e., the cut-off used in the matrix between young and mature forests, which varies according to FEC site type). If this is the case, then the potential age-induced effects of forest management that we identified would largely disappear in these particular landscapes with time. In the larger context of regulated landscapes, the implication is that although large parts of the regulated landscape would be in the initiation, regeneration, and young development stages, and hence would show strong contrasts with the mature and old-growth forests of unlogged landscapes, the mature parts of the regulated landscape would adequately maintain old-growth taxa.

Several aspects of this problem are worth pointing out, however, and due to inaccuracies in the habitat suitability matrices, we doubt that the age effect will be obliterated as the logged forests reach the mature development stage. First, it should be born in mind that the matrix's lack of a distinction between mature and old-growth post-logged forests is purely hypothetical given that post-logged forests of these ages do not exist in the region. Given the importance of this feature of the matrix in determining future wildlife responses, and in keeping with an adaptive management approach (Holling 1978, Lindenmayer *et al.* 2000), this hypothesis is one that evidently bears close scrutiny and testing. Second, several considerations suggest that this lack of distinction between mature and old-growth post-logged forests in the matrix may be inaccurate. For example, in Fennoscandia, where regulated landscapes do exist, a strong faunal distinction is still maintained between managed and unmanaged landscapes (e.g., Virkkala *et al.* 1994). Our field studies in the stands at the centres of the landscapes showed that habitat features such as the amount of coarse woody material and canopy heterogeneity continued to increase well past 100 years and that some habitat features continued to show linear increases up to the oldest stand ages examined (Malcolm *et al.* in prep.). The implication here is that for organisms that use these features as habitat, habitat supply may continue to increase well past the mature development stage. Third, an additional concern is the possibility that logging may impact biodiversity independently of forest age; for example, through decreases in the amount of coarse woody debris due to the export of wood through harvesting (Hansen *et al.* 1991, Thompson *et al.* 2003). Finally, an important issue is the potential difficulty of assigning ages to natural boreal stands. For example, if a second or third cohort of trees assumes dominance in the canopy (Bergeron *et al.* 1998, Cumming *et al.* 2000), stands ages will be underestimated using aerial photography (Cumming *et al.* 2000). In support of this possibility, although the shape of the age class distributions that we observed in unlogged landscapes was similar to those reported for eastern Ontario and western Quebec by Bergeron *et al.* (2001), the FRI-based mean age of our unlogged forests was younger than the means that they obtained via reconstruction of fire histories (96 vs. 111–172 years, respectively). The FRI data also indicated proportionally less forest area > 100 years of age than they found (43% vs. 54–78%). The implication is that the mature and old-growth stands in the habitat suitability matrix may in some cases be older than their FRI ages, making it less likely that rotation-age, post-logged forests will attain comparable habitat characteristics. An alternative hypothesis is that these differences in forest age represent regional variation in disturbance regimes, which is poorly understood (Bergeron *et al.* 2001). In light of these considerations, it

seems reasonable to hypothesize that logging-induced age effects could remain well into the future in northeastern Ontario. Under this hypothesis, our comparisons of different-aged landscapes may prove useful in predicting these future effects of logging. They also may prove useful in evaluating forest management practices that could serve to ameliorate some of the potential negative effects of clearcut silviculture; in particular, the use of partial cutting regimes (e.g., Bergeron *et al.* 2001) and the establishment of targets for maintenance of old-growth forests.

Even under the assumption of no age effects with increasing stand maturity, the observed differences in forest composition between logged and unlogged landscapes are of concern because they present the possibility that even as the post-logged landscapes age, composition differences will remain. For example, relative to unlogged landscapes, a notable feature of the logged landscapes was the decrease in FEC site diversity, which was most marked under the full regeneration control scenario. Although these compositional differences had a relatively minor effect on habitat suitability in the present analysis, this may change as the post-logged forests age. The potential negative effects of full regeneration control on snowshoe hare habitat are of particular interest in that it is a keystone species in this system (being a major determinant of the abundance of most predators). In their model of the effects of silvicultural practices on selected vertebrate species at a site in northeastern Ontario, Thompson *et al.* (2003) also suggested that the regeneration scenario had an important effect on the relative densities of this species, with lowest densities under the scenario with the greatest amounts of coniferous regeneration (the scenario that included Intensive Forest Management). In this sense, our full regeneration control scenario shows affinities with their Intensive Forest Management scenario because it was assumed in both scenarios that forest composition will end up being more coniferous. Thompson *et al.* (2003) also provided a review of studies on the effects of boreal silvicultural on vertebrates, identifying the important effects of forest composition (in addition to stand structure and age) on vertebrate species. Hobson and Bayne (2000a) document the adverse effects on boreal birds of silvicultural practices that promote the creation of monospecific, single-aged stands, which historically has been a common goal of silviculture in northeastern Ontario.

A final issue related to projection of our findings into the future concerns fire management in the boreal forest. Compared to the theoretical negative exponential curve (Van Wagner 1978), it appears that a larger proportion of old forests and a paucity of young stands is a natural phenomenon in these forests, especially in light of historic increases in fire intervals (Bergeron *et al.* 2001). These features served to accentuate the difference between the logged and unlogged landscapes. Unfortunately, however, baseline unlogged forests from which to evaluate empirical conditions are becoming increasingly rare south of the managed forest boundary in the province. For example, nearly all of the old-growth landscapes studied here have since been extensively logged. South of the 51st parallel, natural forests are becoming increasingly restricted to parks. A broad set of regionally representative reserve areas is needed for empirical baseline studies. Because of the large areas affected by disturbances events, such reserve areas must be large in order to provide replicates of seral stages (Pickett and Thompson 1978).

Several other important caveats of the present analysis should be mentioned. One is the possibility of systematic dif-

ferences between the logged and unlogged landscapes with respect to features other than their disturbance history. We do not believe this to be an important factor, in part because of the stipulation that the centre of each landscape be a mixedwood stand, and in part because the unlogged landscapes remained unlogged because of were inaccessible rather than because of physical characteristics of the site. Nonetheless, because logging is not a random process, the possibility of such a bias remains. Another caveat concerns the fact that we entirely ignored the spatial context of the habitats. Other analyses have focussed nearly entirely on spatial configuration, including measures of fragmentation, edge effects, etc. (e.g., Gluck and Rempel 1996, Andison and Marshall 1999, Perera and Baldwin 2000). In our view, because the forested matrix in boreal Ontario provides broad connectivity between patches, in developing a first-order view of likely future changes it is most important to focus on the sheer amount of habitat rather than its spatial pattern. Empirical studies indicating the importance of habitat amount rather than spatial configuration include McGarigal and McComb (1995), Drolet *et al.* (1999), and Drapeau *et al.* (2000). This is not to say that changes in the spatial configuration of habitats will not importantly modify logging effects (see Chapin *et al.* 1998, Thompson *et al.* 2003).

A final set of caveats concerns the specific protocol that we used, namely, combining aerial photography of habitat features with a habitat suitability matrix. Many species may respond to microhabitat features quite independently of overstory composition (Naylor 1994), measurements of single habitat features may be relevant only to particular groups of species (Jonsson and Jonsell 1999), and as a general tool, the FRI data has limited resolution, scope, and accuracy (Naylor 1994, Watt 1994). This is especially true if it is used to classify forests into FEC types, which in reality are defined based upon additional characteristics of the plant community (including understory plants) and soil characteristics. Although the habitat suitability matrices are based on empirical information in some instances, professional judgement figures prominently. Other potential problems include the breakdown of habitat relationships into simple scores, which may introduce artefacts into the analysis, and the absence of information on wetland uses (Naylor 1994). Perhaps most seriously, habitat suitability may provide only limited, or even misleading, information on population productivity (Van Horne 1983).

At the same time, although is beyond the scope of the present paper, our results find support from other studies, holding out hope for the validity of our conclusions and indicator sets despite these numerous caveats. For example, considering just birds, of the nine species that Hobson and Bayne (2000b) found to be most indicative of old-growth conditions in Saskatchewan, seven are listed as potential indicators in Table 2. Similarly, in a comparison of natural and managed landscapes in the Northern Claybelt of Quebec and Ontario (Drapeau *et al.* 2000), of the nine species most affiliated with natural landscapes, four are in Table 2. Thompson *et al.* (2003) cited five studies that all indicated that black-backed woodpeckers (*Picoides arcticus*), three-toed woodpeckers (*P. tridactylus*), and brown creepers (*Certhia americana*) would be negatively affected by a logging-induced reduction in forest age: all three species are in Table 2. Finally, all six Canadian boreal forest bird species with the highest number of threat factors in Imbeau *et al.* (2001) are in Table 2. These authors noted that

past logging has had a disproportionately negative effect on Fennoscandian woodpeckers, which is of particular concern given that this keystone guild creates habitat for many other species (McLaren *et al.* 1998). In agreement with their conclusions from Fennoscandia, all seven woodpeckers in the northeast Ontario habitat suitability matrix are in Table 2. Continuing efforts to improve the forests management tools that we used no doubt will improve their accuracy and utility; for example, ongoing efforts to base the habitat suitability matrix on empirical information (Naylor, personal communication), the incorporation of field-based and satellite information on habitats and forest ages into the forest inventory, and efforts to incorporate density, productivity, scale, and life history characteristics into the habitat suitability matrices.

In conclusion, our comparison of logged and unlogged landscapes in northeastern Ontario indicated strong differences in habitat suitability between the two landscapes that were attributable to both forest age and composition effects, with more species showing negative than positive responses to logging. The result was a list of species that are predicted to be strongly impacted by logging; these species bear close monitoring over time. The use of coupled forest resource information, habitat suitability matrices, real landscapes, and multivariate techniques holds out the promise for the identification of wildlife indicators of ongoing impacts of logging and for identifying habitat changes that simultaneously may affect many species.

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Appendix 1. Acronyms and scientific names of species. Acronyms for birds are from the American Ornithologists Union

Herpetofauna

AMTO	American toad	<i>Bufo americanus</i>
BCFR	Boreal chorus frog	<i>Pseudacris triseriata</i>
BSSA	Blue-spotted salamander	<i>Ambystoma laterale</i>
EGSN	Eastern garter snake	<i>Thamnophis sirtalis</i>
ERSA	Eastern redback salamander	<i>Plethodon cinereus</i>
MIFR	Mink frog	<i>Rana septentrionalis</i>
SPPE	Spring peeper	<i>Pseudacris crucifer</i>
WOFR	Wood frog	<i>Rana sylvatica</i>

Appendix 1. Continued

<i>Birds</i>		
ALFL	Alder flycatcher	<i>Empidonax alnorum</i>
AMCR	American crow	<i>Corvus brachyrhynchos</i>
AMGO	American goldfinch	<i>Carduelis tristis</i>
AMKE	American kestrel	<i>Falco sparverius</i>
AMRE	American redstart	<i>Setophaga ruticilla</i>
AMRO	American robin	<i>Turdus migratorius</i>
AMWO	American woodcock	<i>Scolopax minor</i>
BAWW	Black-and-white warbler	<i>Mniotilta varia</i>
BBCU	Black-billed cuckoo	<i>Coccyzus erythrophthalmus</i>
BBWA	Bay-breasted warbler	<i>Dendroica castanea</i>
BBWO	Black-backed woodpecker	<i>Picoides arcticus</i>
BCCH	Black-capped chickadee	<i>Poecile atricapillus</i>
BDOW	Barred owl	<i>Strix varia</i>
BHCO	Brown-headed cowbird	<i>Molothrus ater</i>
BLBW	Blackburnian warbler	<i>Dendroica fusca</i>
BLJA	Blue jay	<i>Cyanocitta cristata</i>
BLPW	Blackpoll warbler	<i>Dendroica striata</i>
BOCH	Boreal chickadee	<i>Poecile hudsonica</i>
BOOW	Boreal owl	<i>Aegolius funereus</i>
BRCR	Brown creeper	<i>Certhia americana</i>
BRTH	Brown thrasher	<i>Toxostoma rufum</i>
BTBW	Black-throated blue warbler	<i>Dendroica caerulescens</i>
BTNW	Black-throated green warbler	<i>Dendroica virens</i>
SOVI	Blue-headed vireo	<i>Vireo solitarius</i>
BWHA	Broad-winged hawk	<i>Buteo platypterus</i>
CAWA	Canada warbler	<i>Wilsonia canadensis</i>
CEDW	Cedar waxwing	<i>Bombycilla cedrorum</i>
CHSP	Chipping sparrow	<i>Spizella passerina</i>
CMWA	Cape may warbler	<i>Dendroica tigrina</i>
COHA	Cooper's hawk	<i>Accipiter cooperii</i>
CONI	Common nighthawk	<i>Chordeiles minor</i>
CONW	Connecticut warbler	<i>Oporornis agilis</i>
CORA	Common raven	<i>Corvus corax</i>
COSN	Common snipe	<i>Gallinago gallinago</i>
COYE	Common yellowthroat	<i>Geothlypis trichas</i>
CSWA	Chestnut-sided warbler	<i>Dendroica pensylvanica</i>
DEJU	Dark-eyed junco	<i>Junco hyemalis</i>
DOWO	Downy woodpecker	<i>Picoides pubescens</i>
EABL	Eastern bluebird	<i>Sialia sialis</i>
EAWP	Eastern wood pewee	<i>Contopus virens</i>
EUST	European starling	<i>Sturnus vulgaris</i>
EVGR	Evening grosbeak	<i>Coccothraustes vespertinus</i>
GCFL	Great crested flycatcher	<i>Myiarchus crinitus</i>
GCKI	Golden-crowned kinglet	<i>Regulus satrapa</i>
GGOW	Great gray owl	<i>Strix nebulosa</i>
GHOW	Great horned owl	<i>Bubo virginianus</i>
GRAJ	Gray jay	<i>Perisoreus canadensis</i>
GRCA	Gray catbird	<i>Dumetella carolinensis</i>
HAWO	Hairy woodpecker	<i>Picoides villosus</i>
HETH	Hermit thrush	<i>Catharus guttatus</i>
KILL	Killdeer	<i>Charadrius vociferus</i>
LEFL	Least flycatcher	<i>Empidonax minimus</i>
LEOW	Long-eared owl	<i>Asio otus</i>
LISP	Lincoln's sparrow	<i>Melospiza lincolnii</i>
MAWA	Magnolia warbler	<i>Dendroica magnolia</i>
MERL	Merlin	<i>Falco columbarius</i>
MOWA	Mourning warbler	<i>Oporornis philadelphia</i>
NAWA	Nashville warbler	<i>Vermivora ruficapilla</i>
NHOW	Northern hawk owl	<i>Surnia ulula</i>
NOFL	Northern flicker	<i>Colaptes auratus</i>
NOHA	Northern harrier	<i>Circus cyaneus</i>
NOPA	Northern parula	<i>Parula americana</i>
NOWA	Northern waterthrush	<i>Seiurus noveboracensis</i>
NSWO	Northern saw-whet owl	<i>Aegolius acadicus</i>
OCWA	Orange-crowned warbler	<i>Vermivora celata</i>
OSFL	Olive-sided flycatcher	<i>Contopus cooperi</i>
OVEN	Ovenbird	<i>Seiurus aurocapilla</i>
PAWA	Palm warbler	<i>Dendroica palmarum</i>
PHVI	Philadelphia vireo	<i>Vireo philadelphicus</i>
PIGR	Pine grosbeak	<i>Pimicola enucleator</i>
PISI	Pine siskin	<i>Carduelis pinus</i>
PIWA	Pine warbler	<i>Dendroica pinus</i>

Appendix 1. Continued

PIWO	Pileated woodpecker	<i>Dryocopus pileatus</i>
PUFI	Purple finch	<i>Carpodacus purpureus</i>
RBGR	Rose-breasted grosbeak	<i>Pheucticus ludovicianus</i>
RBNU	Red-breasted nuthatch	<i>Sitta canadensis</i>
RCKI	Ruby-crowned kinglet	<i>Regulus calendula</i>
RECR	Red crossbill	<i>Loxia curvirostra</i>
REVI	Red-eyed vireo	<i>Vireo olivaceus</i>
RTHA	Red-tailed hawk	<i>Buteo jamaicensis</i>
RTHU	Ruby-throated hummingbird	<i>Archilochus colubris</i>
RUGR	Ruffed grouse	<i>Bonasa umbellus</i>
SOSP	Song sparrow	<i>Melospiza melodia</i>
SPGR	Spruce grouse	<i>Falcapennis canadensis</i>
SSHA	Sharp-shinned hawk	<i>Accipiter striatus</i>
STGR	Sharp-tailed grouse	<i>Tympanuchus phasianellus</i>
SWTH	Swainson's thrush	<i>Catharus ustulatus</i>
TEWA	Tennessee warbler	<i>Vermivora peregrina</i>
TTWO	Three-toed woodpecker	<i>Picoides dorsalis</i>
VEER	Veery	<i>Catharus fuscescens</i>
WAVI	Warbling vireo	<i>Vireo gilvus</i>
WIWA	Wilson's warbler	<i>Wilsonia pusilla</i>
WIWR	Winter wren	<i>Troglodytes troglodytes</i>
WOTH	Wood thrush	<i>Hylocichla mustelina</i>
WPWI	Whip-poor-will	<i>Caprimulgus vociferus</i>
WTSP	White-throated sparrow	<i>Zonotrichia albicollis</i>
WWCR	White-winged crossbill	<i>Loxia leucoptera</i>
YBFL	Yellow-bellied flycatcher	<i>Empidonax flaviventris</i>
YBSA	Yellow-bellied sapsucker	<i>Sphyrapicus varius</i>
YRWA	Yellow-rumped warbler	<i>Dendroica coronata</i>
YWAR	Yellow warbler	<i>Dendroica petechia</i>
<i>Mammals</i>		
ASHR	Arctic shrew	<i>Sorex arcticus</i>
BBEC	Black bear (cover)	<i>Ursus americanus</i>
BBEF	Black bear (fall foraging)	<i>Ursus americanus</i>
COYO	Coyote	<i>Canis latrans</i>
DMOU	Deer mouse	<i>Peromyscus maniculatus</i>
ECHI	Eastern chipmunk	<i>Tamias striatus</i>
ERMI	Ermine	<i>Mustela erminea</i>
FISH	Fisher	<i>Martes pennanti</i>
HVOL	Heather vole	<i>Phenacomys ungava</i>
LCHI	Least chipmunk	<i>Eutamias minimus</i>
LTWE	Long-tailed weasel	<i>Mustela frenata</i>
LWEA	Least weasel	<i>Mustela nivalis</i>
LYNX	Lynx	<i>Lynx canadensis</i>
MART	Marten	<i>Martes americana</i>
MJMO	Meadow jumping mouse	<i>Zapus hudsonius</i>
MOOS	Moose (summer)	<i>Alces alces</i>
MOOW	Moose (winter)	<i>Alces alces</i>
MSHR	Masked shrew	<i>Sorex cinereus</i>
MVOL	Meadow vole	<i>Microtus pennsylvanicus</i>
NBLE	Northern bog lemming	<i>Synaptomys borealis</i>
NFSQ	Northern flying squirrel	<i>Glaucomys sabrinus</i>
PORC	Porcupine	<i>Erethizon dorsatum</i>
PSHR	Pygmy shrew	<i>Sorex hoyi</i>
RACC	Raccoon	<i>Procyon lotor</i>
RBVO	Red-backed vole	<i>Clethrionomys gapperi</i>
RFOX	Red fox	<i>Vulpes vulpes</i>
RSQU	Red squirrel	<i>Tamiasciurus hudsonicus</i>
RVOL	Rock vole	<i>Microtus chrotorrhinus</i>
SBLE	Southern bog lemming	<i>Synaptomys cooperi</i>
SNHA	Snowshoe hare	<i>Lepus americanus</i>
SNMO	Star-nosed mole	<i>Condylura cristata</i>
SSHR	Smoky shrew	<i>Sorex fumeus</i>
SSKU	Striped skunk	<i>Mephitis mephitis</i>
STSH	Short-tailed shrew	<i>Blarina brevicauda</i>
WCAR	Woodland caribou	<i>Rangifer tarandus</i>
WJMO	Woodland jumping mouse	<i>Napaeozapus insignis</i>
WOLF	Gray wolf	<i>Canis lupus</i>
WOOD	Woodchuck	<i>Marmota monax</i>
WTDS	White-tailed deer (summer)	<i>Odocoileus virginianus</i>
WTDW	White-tailed deer (winter)	<i>Odocoileus virginianus</i>