A new method to estimate species and biodiversity intactness using empirically derived reference conditions

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ABSTRACT

Critical to the conservation of biodiversity is knowledge of status and trends of species. To that end, monitoring programmes have reported on the state of biodiversity using reference conditions as comparison. Little consensus exists on how reference conditions are defined and how such information is used to index intactness. Most use protected areas or an arbitrary year as reference. This is problematic since protected areas are often spatially biased, while arbitrarily defined reference years are often not sufficiently distant in time. We propose an alternative that relies on empirical estimates of reference conditions. Statistical ranges of reference are estimated and compared with observed occurrence and abundance to index status of individual species. When averaged among species, overall intactness is estimated. We demonstrate the approach using 202-winter mammal tracking sites from the boreal forest of Alberta, Canada. Intactness was estimated at 89 out of 100 with the southern boreal having lowest intactness and greatest human footprint. We suggest empirical predictions of reference conditions be used as baselines for comparing changes in the state of species and biodiversity. Reporting can occur at any spatial (e.g., ecosystem) or hierarchical (e.g., species, guilds, taxonomic group, or overall biodiversity) scale and is easily interpreted (scaled from 0-degraded to 100-intact). When used in a long-term monitoring framework, statistical trends in biodiversity intactness can be estimated, individual status of species assessed, and relevant policy evaluated.

1. Introduction

Biodiversity is threatened by modern human activities (Hooper et al., 2005). The current extinction crisis is one of the most significant in earth's history, with habitat loss, spread of non-native species, and global climate change the greatest threats (Wilcove et al., 1998; Chapin et al., 2000). Maintenance of biodiversity is important as its erosion will result in less stable ecosystems with reduced function (Naeem et al., 1994, 1995; Tilman et al., 1996; Stachowicz et al., 1999). Reduced function and stability eventually lead to greater uncertainty in ecosystem services, including a number critical for

human welfare (Costanza et al., 1997; Millennium Ecosystem Assessment, 2005). The value of such services is substantial, with global natural capital estimated at $33 trillion (US) per year in 1997; nearly double the global gross national product (Costanza et al., 1997). Given economic values and social-ethical concerns, governments, organizations, and scientists have attempted to quantify the 'state' of biodiversity by assessing status and trends, setting targets for mitigating biodiversity loss, and/or identifying hot spots for biodiversity protection (Dobson et al., 1997, 2001; Myers et al., 2000; Weber et al., 2004; Scholes and Biggs, 2005). Despite the need for consistency in monitoring programmes, no single method of measuring or reporting biodiversity has emerged (Purvis and Hector, 2000).

When biodiversity is measured and reported, it is not always evident what benchmark to use for comparison and indexing (Allen et al., 2003). Three general approaches have been used: (1) desired goal or target; (2) time-zero; and (3) protected areas. In desired goal or target, expert opinion or social values determine reference (benchmark) conditions (Young et al., 2004). Floristic quality assessments, for instance, have been used to assess ecological integrity of the Midwestern USA (Herman et al., 1997; Taft et al., 1997) using prior assignment of coefficients of conservation for each species (Wilhelm and Masters, 1995). Such assignments are impractical when dealing with hundreds to thousands of species necessary to inform biodiversity and for taxonomic groups about which little knowledge exists. Moreover, additional quantitative information, such as relative abundance (density, percent cover, etc.), is not fully considered. As an alternative to desired states, time zero referencing has been suggested. Here, a point in time is selected (normally the start of the monitoring programme) to compare and index against current conditions. The Living Planet Index uses 1970 as a benchmark to report on the state of the planet's ecosystems and species (Loh et al., 2005). Without a sufficiently distant past, time zero references fail to fully inform conservation-based boundaries for restoration and status assessments. Local areas within many ecosystems were already highly degraded in the year 1970. Furthermore, comparisons between monitoring programmes are compromised unless year of time zero and level of degradation are similar. Protected areas have also been used as comparison benchmarks. Sites of interest are compared against 'natural' or 'intact' reference sites, such as national parks (Mayer and Galatowitsch, 2001; Sinclair et al., 2002; Scholes and Biggs, 2005). Existing protected areas do not always contain a representative sample of biodiversity (Scott et al., 2001; Hansen and Rotella, 2002), since they often occur in remote high elevation areas lacking the potential for cultivation (Margules and Pressey, 2000; Scott et al., 2001). Without controlling for environmental gradients, differences among target and control areas can be solely due to natural patterns in species distributions, rather then anthropogenic influence. Furthermore, protected areas are being degraded over time by human activity resulting in sliding benchmarks.

We propose a fourth alternative for calculating benchmarks and biodiversity intactness. By estimating empirical relationships between species occurrence/abundance and human footprint we are able to estimate reference conditions under a pristine situation. These statistically-derived reference conditions are then compared to current species occurrence and abundance to index intactness. Deviation from reference (decreasing sensitive species or increasing non-native species) results in loss of intactness. With species as the basic unit of measure, numerous levels of organization can be reported (i.e., guilds, taxonomic group, or overall biodiversity). We demonstrate the utility of the approach using winter mammal monitoring data collected from the boreal forest of Alberta, Canada.

2. Estimating biodiversity intactness

2.1. What to measure?

Biodiversity encompasses numerous levels of natural organization. Species, however, are the focus of biodiversity, because they are the most easily defined (Noss, 1990; Huston, 1994). Although other levels of biodiversity organization, such as genetic diversity (Watson-Jones et al., 2006) and landscape configuration (Roy and Tomar, 2000; Lindenmayer et al., 2006), are important, we focus the development of our biodiversity index on species. Measures of species occurrence and abundance, rather than measures of diversity and evenness should be used to assess biodiversity status and trends. Changes in diversity based on richness do not indicate change in biodiversity when specialized species are replaced by generalist species, or when non-native species are introduced. Furthermore, managers are interested in both the status of individual species and groups of species (guilds). Thus, methods that estimate intactness at the species level that can be combined into other levels of biotic organization are desirable.

2.2. Estimating reference conditions and biodiversity intactness

We propose that generalized linear models or some statistical equivalent be used to determine reference conditions. Modelling species occurrence and abundance across environmental and anthropogenic gradients, allows occurrence and abundance (or expected range) for species in the absence of anthropogenic disturbance (i.e., intact conditions) to be estimated. For example, the occurrence and abundance of many mammals are correlated with road density (Carroll et al., 2001; Forman et al., 2003). By modelling changes in species with road density, estimates of occurrence and abundance at road densities of $0 \, km/km^2$ (i.e., intact) can be estimated. Deviation from intact reference conditions or range of reference conditions then allows us to estimate the degree of intactness for occurrence and abundance of each species over large spatial extents at points in time. Overall status of a species is estimated as the product of occurrence and abundance indices to emphasize simultaneous change in presence and abundance. To estimate intactness of guilds, taxonomic groups, or any other level of biodiversity the intactness of the species assemblage is based on the average of selected species scores. Reporting of intactness can occur hierarchically at any level, using the same species-specific values as the underlying data. Below, we describe how to derive reference conditions and calculate the intactness index.

2.3. Species-specific models of reference conditions

Before intactness can be calculated, reference conditions need to be estimated for species occurrence and abundance. Probability of occurrence for a species based on environmental covariates can be modeled using logistic regression taking the form,

$$\Pr(y = 1|x) = \frac{e^{LP}}{1 + e^{LP}}, \tag{1}$$

where the probability of outcome 1 (species being present) is estimated based on a set of x independent variables that describe the linear predictor (LP). In our demonstration using mammals, road density is used to predict occurrence. Additional covariates describing ecosystems or habitat types can be included to increase predictive capacity, allowing occurrence to vary as a function of ecosystem or habitat type. All variables chosen for setting reference should be readily available and easily updatable. After constructing a model for each species, reference conditions are estimated as the probability of occurrence under conditions with no human impact (e.g., the probability of occurrence at the intercept or 0 km/km^2 if using road density), holding other factors constant. Although estimates of reference conditions could be determined by only examining sites without human impact, modelling the relationship allows for predictions of future impacts to adjust management practices, increases the confidence around estimates of reference condition, allows for control of additional environmental covariates, and facilitates knowledge about direction and magnitude of population change (increase or decrease) with increasing human disturbance. Significance and confidence intervals around parameters and reference conditions can be estimated through randomization and re-sampling procedures like bootstrapping (Manly, 1991). Range of reference (i.e., the range at which occurrence or abundance is considered natural) can be defined from these confidence intervals. As a final step, predictive accuracy assessments, such as receiver operating characteristic (ROC) should be used to ensure that model predictions of reference condition are reasonable.

As well as estimating an occurrence model for reference conditions, reference levels for abundance are needed. To assure independence among presence–absence and abundance data all zeros (absences) are removed and a zero-truncated negative binomial regression model fit, taking the general form:

$$\Pr(y_i|x_i, \delta_i) = \frac{e^{-\tilde{\mu}_i}\tilde{\mu}_i^{y_i}}{y_i!}, \tag{2}$$

where the probability of a count of y_i is estimated by the mean $(\tilde{\mu})$ abundance of the species where present and related to the variables x_i. Negative binomial models are recommended over that of Poisson models, as the mean and variance of species abundances are rarely equal (e.g., overdispersion). Zero-truncated models have the added benefit of separating the presence–absence part of the relationship, which was previously modeled using Eq. (1), from that of abundance when present. Including absences in estimates of abundance after independently modelling occurrence would result in correlations between occurrence and abundance models (Wright, 1991; Nielsen et al., 2005) and therefore the indices of occurrence

and abundance. Based on the model's fit, reference conditions of abundance are estimated by zeroing out those human factor(s) that describe the abundance of the species. Significance and confidence intervals for abundance are derived through randomization and re-sampling procedures (Manly, 1991) and used to estimate the range of reference for abundance.

2.4. Occurrence index

Variations in observed species prevalence (rare to common) require standardization to ensure that each species receives equal weight. Between the lower and upper bounds of defined range of reference, an index value of 100 is assumed. If observed values are above the upper reference bound the occurrence index (OI) is estimated as,

$$OI_i = 100 - (|O_i - U_i| \times 100), \tag{3}$$

where OI_i is the occurrence index for species i ranging from 0 (i.e., degraded) to 100 (i.e., intact), O_i the observed proportion of sites occupied for species i, U_i the upper bounded probability of occurrence for species i under estimated intact (reference) conditions. If observed values are below the lower reference bound, the occurrence index is calculated as,

$$OI_i = 100 - \left[\left(\frac{|O_i - L_i|}{L_i}\right) \times 100\right], \tag{4}$$

where L_i is the lower bounded probability of occurrence for species i under intact (reference) conditions. Eq. (4) differs from Eq. (3) in that Eq. (4) is based on the relative difference between reference and observed values, while the former is based on the absolute difference between reference and observed values. Thus, a completely degraded state with an OI of 0 occurs for species above their upper bound only when a species' reference condition is predicted at 0 and the observed value is 1. In contrast, species occurring below their range of reference will decline to 0 when extirpated.

2.5. Abundance index

As well as determining the contribution of occurrence to the current state of biological intactness, the abundance of individual species is examined. We estimate the abundance index (AI) as:

$$AI_i = 100 - \left[\left(\frac{|(A_i + 0.5)^{0.5} - (E_i + 0.5)^{0.5}|}{(E_i + 0.5)^{0.5}}\right) \times 100\right], \tag{5}$$

where AI_i ranges from 0 (i.e., degraded) to 100 (i.e., intact) for species i, A_i represents the observed average abundance (where present) for species i, and E_i the expected abundance for species i using Eq. (2) and assuming pristine conditions. Since intact conditions are defined as a range of possible values, E_i is either the upper or lower reference value depending on observed abundance. When A_i is greater than E_i then the upper estimated reference is used, while the lower estimated reference is used when A_i is less than E_i. Values of A_i and E_i are square root transformed since samples were taken from a Poisson distribution (Bartlett, 1936). This transformation is further desirable since it stretches the range of values where A_i is not more than twice that of E_i. When transformed values of A_i are greater than or less than $2(E_i)$, AI_i is assumed to be 0.

Intact conditions (i.e., $AI_i = 100$) are assumed anytime observed abundance occurs within the defined upper and lower range of reference.

2.6. Species intactness

Using both the occurrence and abundance indices, intactness for each species is estimated as the product of the occurrence and abundance indices rescaled from 0 and 100, or more formally,

$$SI_i = \frac{(OI_i \times AI_i)}{100}, \tag{6}$$

where SI_i is the intactness index for species i, and OI_i (Eq. (3) or (4)) and AI_i (Eq. (5)) are the occurrence and abundance indices for that species respectively. By using the product of occurrence and abundance indices, simultaneous changes in both occurrence and abundance will be characterized by large decreases in intactness.

To estimate biodiversity intactness (BI), species intactness values are averaged:

$$BI = \frac{1}{R} \sum_i SI_i, \tag{7}$$

where BI is biodiversity intactness, SI_i species intactness for species i from Eq. (6), and R the number of species considered (e.g., species richness).

To estimate biodiversity intactness for more than one ecosystem, reference conditions specific to each ecosystem are estimated through individual models or as fixed factors (categorical variables) in Eqs. (1) and (2). Based on these estimates, occurrence and abundance indices are calculated for each ecosystem and used to derive individual biodiversity intactness scores. Reporting biodiversity intactness for more than one ecosystem, perhaps for a socio-political boundary or a large watershed, is accomplished using geographic weights to account for disparities in ecosystem size. More specifically, the geographically weighted biodiversity intactness index (BI_g) for a region of interest with more than one ecosystem would be,

$$BI_g = \sum_j (BI_j \times s_j), \tag{8}$$

where BI_j is the biodiversity intactness for ecosystem j estimated from Eq. (7) and s_j the relative size (proportion from 0 to 1) of ecosystem j relative to the total area of all ecosystems considered.

3. Intactness for mammals in the boreal forest of Alberta: a working example

To illustrate our method, we demonstrate the biodiversity intactness index using winter mammal monitoring data in the boreal forest of northeastern Alberta, Canada.

3.1. Winter mammal monitoring in the boreal forest of Alberta

We conducted snow-tracking surveys for mammals at 202 sites in the boreal forests of Alberta, Canada during the winters of 2001 through 2004 (Fig. 1). Survey locations were systematic long-term biodiversity monitoring sites for the Alberta Biodiversity Monitoring Program (see http://www.abmp.arc.ab.ca/). At each location, observers snowshoed a 9-km triangular transect following fresh snowfall. Surveys were conducted between 15 December and 15 March, following methods developed for the Finnish wildlife monitoring program (Linden et al., 1996). While traversing the triangle, observers used Global Positioning Systems to stay on pre-defined transects. All tracks crossing transects were counted and categorized by species. A more detailed description can be found in Bayne et al. (2005). Information on anthropogenic disturbance and ecosystem (natural sub-region) were noted for townships surrounding individual transects using databases maintained by Alberta Sustainable Resource Development. Sampled townships ranged from 0 km/km^2 of roads (52 of 202 sites) to a maximum of 1.4 km/km^2 of roads.

Using these data we demonstrate how empirical models of mammal occurrence and abundance can be used to estimate range of reference. Only species with an occurrence greater than 5% (>10 sites) were considered (14 mammals or groups of similar mammals). Road density (km/km^2 per 100-km^2 area) was used as a descriptor of human disturbance, while track numbers were used to index animal abundance. Based on these data and models, we estimate intactness for the 202 boreal sample sites in northeastern Alberta, Canada.

3.2. Occurrence models and the occurrence index for boreal mammals

Of 14 species or groups of species considered, 8 were significantly related (based on 90% bootstrapped bias-corrected confidence intervals) to road density (Table 1). Occurrence increased with increasing road density for domestic dog (*Canis domesticus*), coyote (*Canis latrans*), deer (*Odocoileus* sp.), and snowshoe hare (*Lepus americanus*), while decreasing for lynx (*Lynx canadensis*), marten (*Martes americana*), wolf (*Canis lupus*), and fisher (*Martes pennanti*). Using these relationships, we predicted range of reference using the 20th and 80th percentiles of 1000 bootstrapped models for each species and natural sub-region. Fig. 2 illustrates the probability of detecting lynx tracks, including the range of reference, as a function of road density. Both the central mixedwood and lower boreal highlands had narrow ranges of reference for lynx occurrence when compared to estimates of the dry mixedwood region, which were less precise (Fig. 2).

Using observed proportion of sites occupied and the range expected under intact conditions, an occurrence index was calculated for each species i and natural sub-region j (OI_{ij}) using Eqs. (3) and (4) (Table 2). For ubiquitous species present at all sites within a sub-region, reference conditions could not be estimated. To be conservative, we assumed OI_{ij} for such species to be 100. This occurred for deer (*Odocoileus* sp.), snowshoe hare (*Lepus americanus*), and red squirrel (*Tamiasciurus hudsonicus*) in the central mixedwood and mouse/voles in the lower boreal highlands. Intactness scores for these species were therefore dependent on the abundance index. Overall the occurrence index ranged from 100 for those occurring within defined ranges of reference to 71 for marten (*Martes*
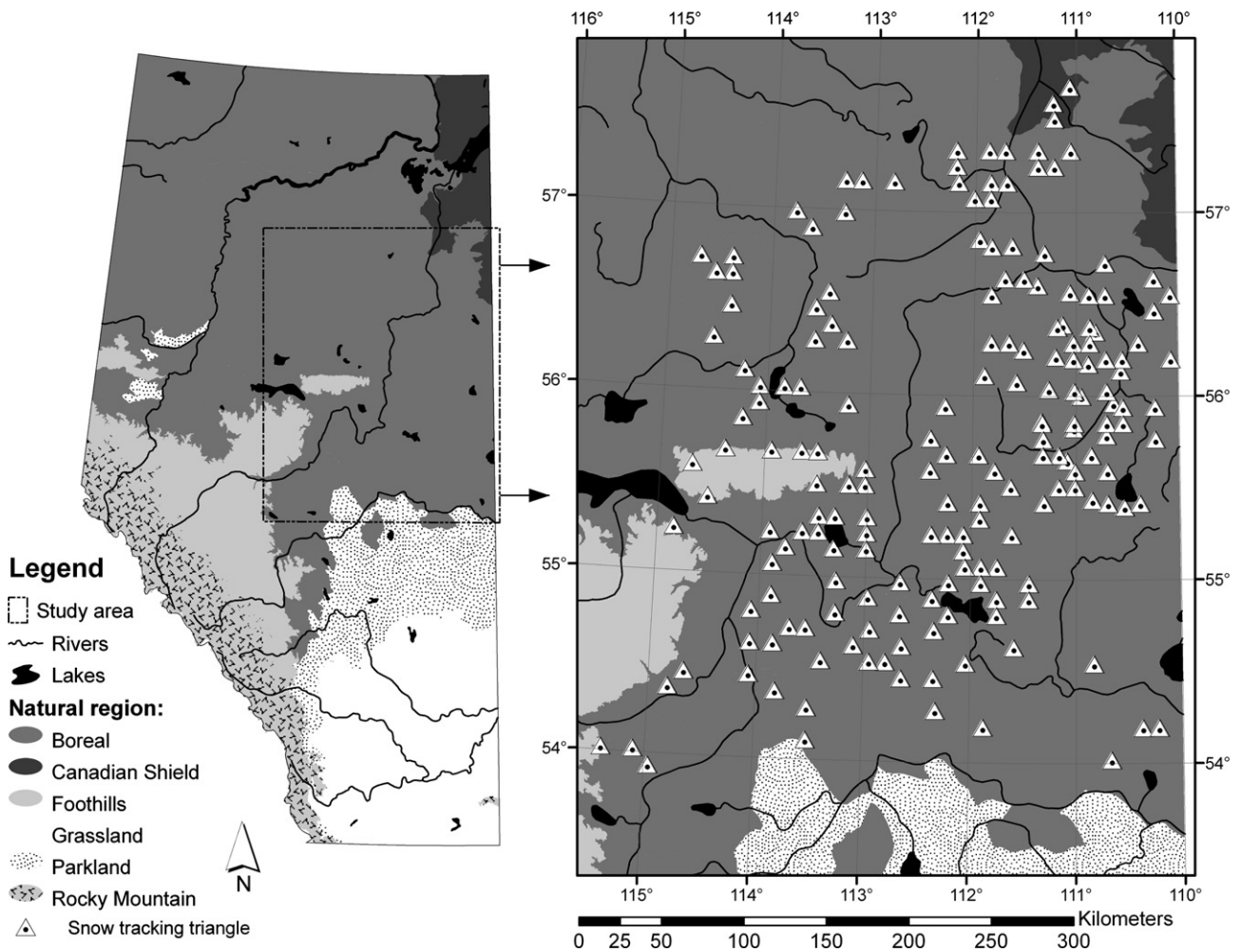
Fig. 1 – Location of the mammal tracking survey sites in northeastern Alberta, Canada. Natural sub-region as well as major rivers and lakes are defined. Locations of survey sites (white triangles with a dot) within the study region are illustrated in enlarged map on the right.

americana) in the dry mixedwood (Table 2). In the latter case, marten were detected at 33% of sites in the dry mixedwood, but was expected to occur at between 47% and 73% of sites under intact conditions.

3.3. Abundance models and the abundance index for boreal mammals

Of 14 species or groups of species, 6 had track abundances significantly related to road density (Table 3). Coyote (*Canis latrans*) and deer (*Odocoileus* sp.) tracks increased with increasing road density, while fisher (*Martes pennanti*), lynx (*Lynx canadensis*), marten (*Martes americana*), and weasel (*Mustela* sp.) abundance responded negatively to roads. Using estimated range of abundance at road densities of 0 km/km², observed abundance was compared with the range of reference and used to estimate an abundance index, AI_{ij}, using Eq. (5). For the northern river otter (*Lontra canadensis*) in the dry mixedwood sub-region, AI was not estimated due to absence of the species at all sites. Index values for individual species ranged from 100 for species within their range of reference to 46 for coyotes (*Canis latrans*) in the dry mixedwood,

which were much more abundant than expected under reference conditions (Table 4).

3.4. Species and biodiversity intactness for boreal mammals

Species intactness (SI_{ij}) was estimated for each species and sub-region by combining the occurrence and abundance indices using Eq. (6). Species intactness scores ranged from 100 for those species within their range of reference to a low of 39 for coyotes (*Canis latrans*) in the dry mixedwood sub-region (Table 5). Natural sub-region intactness (BI_j) ranged from 82 (dry mixedwood) to 94 (lower boreal highlands), while overall intactness adjusting for geographic extent of sub-regions was estimated at 89. Using model relationships, we predicted intactness for each township in the boreal forest of northeast Alberta, Canada using a geographic information system (Fig. 3). As only road density and natural sub-region were used as predictors of reference condition, maps reflect a basic depiction of intactness. Using these relationships, intactness for the region was estimated at 86, slightly lower then our sample sites, which were systematically distributed across a

Table 1 – Logistic regression coefficients describing occurrence of mammal tracks for each species along 9-km winter transects

Common name	Genus species	# obs.	Nat sub-region[a] DM	Nat sub-region[a] LBH	DSS	Road density	Constant
Coyote	*Canis latrans*	166	−0.173	−0.724	0.332[†]	3.799[†]	−0.582
Deer	*Odocoileus sp.*	171	$\perp_s$	−0.141	−0.001	9.002[†]	0.756
Domestic dog	*Canis domesticus*	17	0.959	−0.203	0.106	2.552[†]	−4.182
Fisher	*Martes pennanti*	68	0.408	0.319	0.114[†]	−1.659[†]	−1.081[†]
Red fox	*Vulpes velox*	29	−0.370	0.146	−0.219[†]	0.204	−0.728[†]
Snowshoe hare	*Lepus americanus*	187	$\perp_s$	−0.316	0.502[†]	4.085[†]	−0.252
Lynx	*Lynx canadensis*	125	−0.790	−0.255	0.215[†]	−1.706[†]	−0.107
Marten	*Martes americana*	103	0.008	0.027	−0.022	−1.572[†]	0.515[†]
Moose	*Alces alces*	170	−0.102	−1.012[†]	0.181[†]	−0.650	1.093[†]
Mouse/vole	Cricetidae family	181	−0.053	$\perp_s$	0.057	−1.097	2.023[†]
Northern river otter	*Lontra canadensis*	26	$\perp_f$	−0.988[†]	0.041	−1.413	−1.659[†]
Red squirrel	*Tamiasciurus hudsonicus*	197	$\perp_s$	−1.623[†]	0.111	−1.870	3.757[†]
Weasel	*Mustela sp.*	175	0.822	−0.156	0.116	−0.265	1.262[†]
Wolf	*Canis lupus*	64	−0.551	−0.931[†]	0.126[†]	−1.642[†]	−0.990[†]

$\perp_s$ and $\perp_f$ indicate perfect success and failure respectively of the prediction of species within natural sub-region categories. No coefficients estimated given the lack of variation (e.g., all absent or all present) in the response variable.

Number of observations (# obs) present for each species out of 202 total sample sites is provided. Days since snow (DSS) was included to accountfor accumulation of tracks over time. Road density was measured in km/km^2. Coefficients with a superscript † symbol represent those estimates that differ from a null value of 0 based on 90% bias-corrected confidence intervals from 1000 bootstrapped models.

a Indicator coding was used to estimate coefficients for the categorical 'natural sub-region' (DM, dry mixedwood; LBH, lower boreal highland) variable. Central mixedwood (CM) was used as the reference category. Significance for categorical variables represents differences from central mixedwood values.
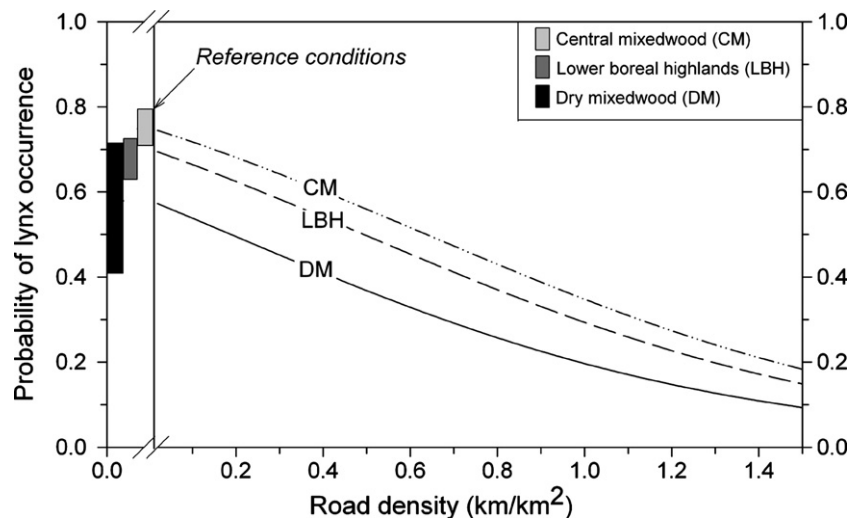
Fig. 2 – Example model estimating the probability of occurrence for lynx (*Lynx canadensis*) tracks by natural sub-region. Range of reference (rectangular boxes) under intact conditions (e.g., 0 km/km^2 of roads) estimated as the 20th and 80th percentiles of 1000 bootstrapped models.

human disturbance gradient. Along the southern boundary of our study area where human encroachment was most evident, intactness scores for some townships were half of their potential (Fig. 3).

4. Discussion

Indices of biodiversity integrity are desired by policy-makers as a mechanism to monitor change in ecological condition. Developing appropriate indices has proven to be difficult in practice (Purvis and Hector, 2000). There have been at least

three significant challenges to characterizing biodiversity condition: (1) establishment of appropriate reference conditions, (2) sensitivity to both rarity and overabundance, and (3) incorporating both native and non-native species in a single measure of biodiversity.

Explicit estimation of baseline or reference conditions is critical to biodiversity conservation (Allen et al., 2003). As such estimates provide the necessary context for interpreting change. Desired goals or targets, time-zero referencing, and protected areas all provide reference conditions but do not fully inform us about the state of biodiversity. As example,

Table 2 – Observed probability of occurrence for each species i by natural sub-region j (O_{ij}), predicted probability of occurrence by species and natural sub-region for the lower (L_{ij}) and upper (U_{ij}) reference conditions, and occurrence index (OI_{ij}) by species and natural sub-region

Common name	Observed occurrence – O_{ij}			Lower reference – L_{ij}			Upper reference – U_{ij}			OI_{ij}		
	CM	DM	LBH	CM	DM	LBH	CM	DM	LBH	CM	DM	LBH
Coyote	0.818	0.963	0.704	0.736	0.502	0.537	0.823	0.810	0.718	100	84.7	100
Deer	0.831	1	0.778	0.631	–	0.546	0.730	–	0.742	89.9	–	96.4
Domestic dog	0.047	0.333	0.037	0.015	0.020	0.017	0.034	0.142	0.041	98.7	80.9	100
Fisher	0.331	0.259	0.444	0.348	0.340	0.377	0.434	0.641	0.557	95.2	76.1	100
Red fox	0.149	0.111	0.148	0.094	0.037	0.081	0.147	0.173	0.192	99.8	100	100
Snowshoe hare	0.919	1	0.889	0.900	–	0.847	0.955	–	0.948	100	–	98.7
Lynx	0.662	0.333	0.667	0.714	0.410	0.631	0.791	0.718	0.772	92.7	81.2	100
Marten	0.534	0.333	0.556	0.555	0.467	0.510	0.640	0.733	0.688	96.2	71.4	100
Moose	0.865	0.815	0.741	0.863	0.772	0.683	0.920	0.943	0.821	100	100	100
Mouse/vole	0.892	0.815	1	0.890	0.811	–	0.939	0.958	–	100	100	–
Northern river otter	0.162	–	0.074	0.157	–	0.047	0.232	–	0.133	100	–	100
Red squirrel	0.98	1	0.926	0.979	–	0.902	0.995	–	0.967	100	–	100
Weasels	0.858	0.926	0.852	0.839	0.893	0.802	0.906	0.970	0.907	100	100	100
Wolf	0.365	0.148	0.222	0.386	0.185	0.142	0.473	0.439	0.301	94.5	79.9	100

Natural sub-region codes follow Table 1.

Table 3 – Zero-truncated negative binomial regression coefficients describing abundance of tracks along 9-km winter transects

Common name	Genus species	Nat sub-region[a]		DSS	Road density	Constant
		DM	LBH			
Coyote	*Canis latrans*	0.056	−0.110	0.144[†]	1.317[†]	1.651[†]
Deer	*Odocoileus* sp.	0.076	−0.510[†]	0.104[†]	0.913[†]	4.172[†]
Domestic dog	*Canis domesticus*	−1.570[†]	−0.670[†]	−0.140	0.281	2.670
Fisher	*Martes pennanti*	−0.215	0.028	0.102	−2.671[†]	1.255[†]
Red fox	*Vulpes velox*	−3.023[†]	−0.579	0.556	4.308	−12.445[†]
Snowshoe hare	*Lepus americanus*	−0.151	−0.011	0.155[†]	−0.475	4.841[†]
Lynx	*Lynx canadensis*	−0.196	0.003	0.237[†]	−1.617[†]	1.372[†]
Marten	*Martes americana*	−1.716	−0.368	−0.014	−1.859[†]	2.412[†]
Moose	*Alces alces*	−0.195	0.167	0.081[†]	0.242	2.786[†]
Mouse/vole	Cricetidae family	0.841[†]	0.036	0.098[†]	−0.168	2.389[†]
Northern river otter	*Lontra canadensis*	$\perp_f$	−3.080[†]	0.146	−0.488	−8.316[†]
Red squirrel	*Tamiasciurus hudsonicus*	−0.740	−0.099	0.069[†]	1.133	3.554[†]
Weasels	*Mustela* sp.	0.160	−0.118	0.025	−1.219[†]	3.316[†]
Wolf	*Canis lupus*	−0.970	−0.486	0.001	1.748	0.670

$\perp_f$ indicates that the sub-region lacks track numbers and thus no estimates provided.
Days since snow (DSS) was used to account for track accumulation over time. Natural sub-region abbreviations follow that of Table 1. Coefficients with a superscript † symbol represent those estimates that differ from a null value of 0 based on 90% bias-corrected confidence intervals from 1000 bootstrapped models.
a Indicator coding was used to estimate coefficients for the categorical 'natural sub-region' variable. Central mixedwood (CM) was used as the reference category. Significance for categorical variables represents differences from central mixedwood values.

the Living Planet Index (Loh et al., 1998) uses 1970 as a baseline. If little change has occurred since 1970, the index would be stable and at its benchmark (in this case 1.0), despite previous declines. Such ecosystems would be assumed to be doing well, while others in better ecological condition overall, but witnessing immediate changes, may not. Comparisons with other regional biodiversity assessments where time lines of human activity have been dissimilar would therefore be difficult. Reference conditions established using protected areas might also fail to adequately represent conditions outside of these areas, since the location and representation of protected areas are frequently biased (i.e., Margules and Pres-

sey, 2000; Scott et al., 2001; Hansen and Rotella, 2002). We suggest that reference conditions estimated from empirical relationships with human footprint provide a more scientifically defendable solution and thus avoiding some of the biases inherent in other methods of reference determination.

Our indices further enable decision-makers to concurrently assess the state of species that are increasing and species that are decreasing in frequency and abundance. Although biodiversity monitoring programmes focus on species that are becoming less common, species that become overabundant also are a management concern. For example, white-tailed deer (*Odocoileus virginianus*) and coyote (*Canis*

Table 4 – Average number of snow tracks where present (observed abundance, A_{ij}) and predicted (lower and upper) reference track numbers for winter mammal i by natural sub-region j

Common name	Observed abundance – A_{ij}			Lower reference – L_{ij}			Upper reference – U_{ij}			AI_{ij}		
	CM	DM	LBH	CM	DM	LBH	CM	DM	LBH	CM	DM	LBH
Coyote	19	41	15	10	8	7	13	17	14	79.8	46.0	96.6
Deer	151	253	88	99	95	49	139	165	89	95.8	76.2	100
Domestic dog	9	3	3	2	0	1	12	4	16	100	100	100
Fisher	8	3	7	4	2	4	8	18	9	100	100	100
Red fox	6	2	7	0	0	0	3	2	3	63.7	100	53.6
Snowshoe hare	309	244	392	274	201	235	327	324	349	100	100	94.0
Lynx	20	10	28	12	5	11	18	21	19	94.7	100	79.1
Marten	12	2	8	8	0	4	13	5	11	100	100	100
Moose	29	29	35	22	16	24	29	27	36	100	96.4	100
Mouse/vole	20	48	23	16	30	15	22	60	23	100	100	100
Northern river otter	4	–	1	0		0	3	–	1	86.6	–	100
Red squirrel	68	57	56	45	34	36	57	39	57	90.9	79.3	100
Weasels	27	23	28	28	28	21	36	50	36	98.2	90.8	100
Wolf	5	3	3	1	0	0	4	3	3	89.4	100	100

Table 5 – Estimated species intactness (SI) and biodiversity intactness (BI) for mammals in northeastern Alberta, Canada

Common name	OI_{ij}			AI_{ij}			SI_{ij}		
	CM	DM	LBH	CM	DM	LBH	CM	DM	LBH
Coyote	100	84.7	100	79.8	46.0	96.6	79.8	39.0	96.6
Deer	89.9	100[a]	96.4	95.8	76.2	100	86.1	76.2	96.4
Domestic dog	98.7	80.9	100	100	100	100	98.7	80.9	100
Fisher	95.2	76.1	100	100	100	100	95.2	76.1	100
Red fox	99.8	100	100	63.7	100	53.6	63.6	100	53.6
Snowshoe hare	100	100[a]	98.7	100	100	94.0	100	100	92.8
Lynx	92.7	81.2	100	94.7	100	79.1	87.8	81.2	79.1
Marten	96.2	71.4	100	100	100	100	96.2	71.4	100
Moose	100	100	100	100	96.4	100	100	96.4	100
Mouse/vole	100	100	100[a]	100	100	100	100	100	100
Northern river otter	100	–	100	86.6	–	100	86.6	–	100
Red squirrel	100	100[a]	100	90.9	79.3	100	90.9	79.3	100
Weasels	100	100	100	98.2	90.8	100	98.2	90.8	100
Wolf	94.5	79.9	100	89.4	100	100	84.5	79.9	100
Sub-region biodiversity intactness (BI)							90.5	82.4	94.2
Boreal biodiversity intactness (BI)							88.8		

Biodiversity value for the combined sub-regions was a weighted average (weight based on the aerial extent) of the three sub-regions.
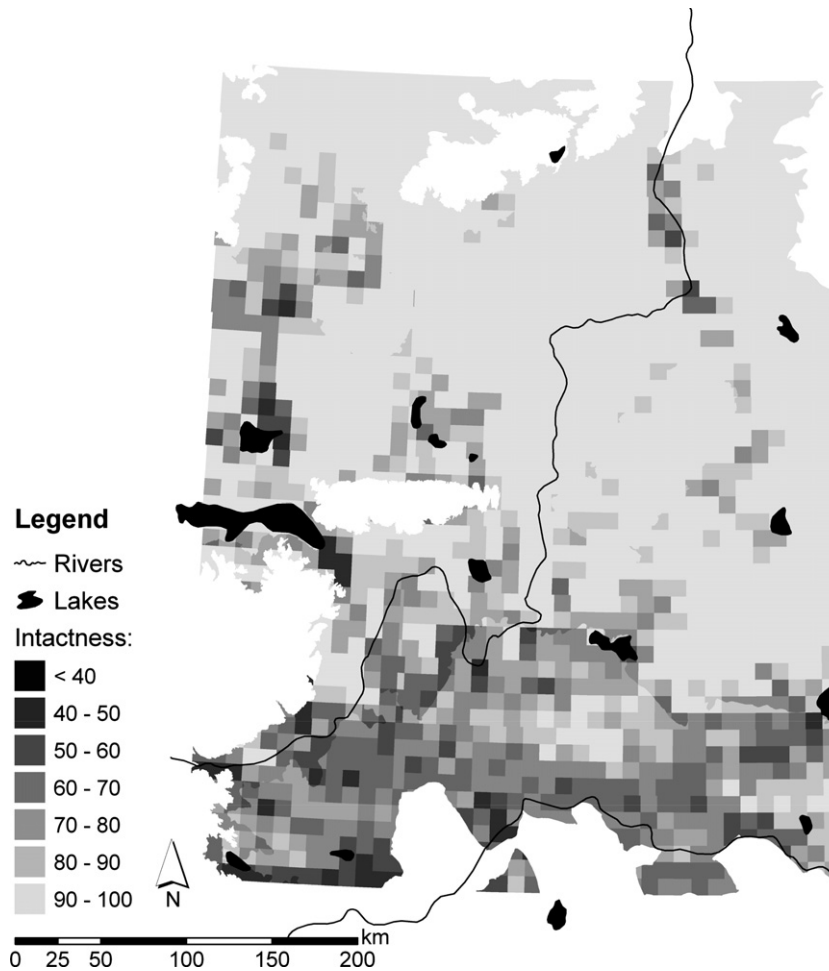
a Assumed to be at 100 in order to estimate *SI*.

latrans) are two species considered to be overabundant in many areas of North America, including boreal Alberta (Gompper, 2002; Cote et al., 2004). The resulting impact on biodiversity and ecosystem function can be substantial (Cote et al., 2004). For our index, both decreases and increases from reference are assumed to lead to degradation in biodiversity condition when they are beyond their natural range of reference.

Unlike other indices of biodiversity (e.g., Scholes and Biggs, 2005; Loh et al., 2005), we include both native and non-native species. Non-native species should be considered since they alter ecosystem function, compete with native species, and often are good indicators or precursors to the loss of biodiversity (Gundale, 2002; Arriaga et al., 2004; Hooper et al., 2005). In the United States there are now more than 50,000 non-native species accounting for approximately $120 billion dollars (US) per year in environmental damage

(Pimentel et al., 2005). Given such impacts, measures of biodiversity status need to include information on the status of non-native species. Increases in non-native species occurrence and/or abundance would be characterized in our index by decreasing intactness, consistent with the premise that non-native species reduce ecosystem integrity (Chapin et al., 2000). This avoids the problem of a higher biodiversity value from species richness-based indices as the number of non-native species increases, while also avoiding designation of native or non-native status of each species for each ecosystem, which may be difficult to determine for many taxonomic groups and ecosystems.

Using snow-tracking data for mammals in northeastern Alberta, Canada we demonstrated how species intactness could be estimated for 14 species or species groups based on road density and ecosystem type. We found intactness

Legend

~~ Rivers

🐟 Lakes

Intactness:

■ < 40

■ 40 - 50

■ 50 - 60

■ 60 - 70

■ 70 - 80

■ 80 - 90

■ 90 - 100

N

km
0 25 50   100   150   200

Fig. 3 – Example predictions of biodiversity intactness for the three natural sub-regions of the boreal forest in northeast Alberta, Canada. Predictions are based on the assumed relationship between road density, natural sub-region, and the occurrence and abundance of individual mammals, not monitoring data.

for these mammal species to be most eroded for the dry mixedwood sub-region, an area averaging 0.71 km/km^2 of roads, 4–6 times higher than either the central mixedwood or lower boreal highlands respectively. Based on the data analyzed and scaled for geographic extent of ecosystems, mammals in the boreal forest were at an intactness of 89. This analysis provides an example of how a biodiversity index can be calculated. Assessments of other human footprint variables, as well as taxonomic groups, such as plants, birds, arthropods, and aquatic biota, are required to fully estimate biodiversity intactness. Preliminary testing with birds, vascular plants, mosses, and lichens indicate that with rigorous monitoring protocols these taxa are equally amenable to this type of index structure.

4.1. Practical challenges

The biodiversity index described here can be used to: (1) establish 'intact' reference conditions for individual species, (2) estimate a species-level index of occurrence, (3) estimate a species-level index of abundance, (4) estimate the state of individual species by combining species-level occurrence and abundance indices, and (5) estimate the state of guilds,

taxonomic groups, or biodiversity by combining information on the state of individual species. The breadth of this information allows effective evaluation of changes in biodiversity as a whole, or components of biodiversity that are of special interest. Overton et al. (2002) suggested that biodiversity management and reporting be designed as an information pyramid, whereby data at the base level is integrated and generalized at higher levels of organization. Our approach provides a unified and transparent algorithm for doing this.

There are some challenges associated with the calculation of the index. The procedure works best in regions that have the complete range of natural habitats and human disturbances so that sites with little to no human footprint can be sampled, as well as sites with moderate to high levels of human development. This range of conditions may be most easily found in regions that are currently being developed, such as the boreal or tropical forests, but with careful planning a range of conditions are likely to be found in many regions of the world. Selection of appropriate spatial scale and suite of necessary human footprint, environmental, or biotic (including other species) variables for accurate estimation of reference conditions should be more fully considered. In highly altered landscapes where human footprint occurs

throughout, reference conditions must be extrapolated beyond existing data. Such extrapolations will increase uncertainty. Reference conditions may therefore have to be estimated at some pre-defined low level of human footprint. This problem is not unique to the method we have described.

Like other biodiversity indices, our index is sensitive to newly detected species, such as a new non-native species appearing at one or two monitoring sites. These new species will have a relatively high degree of intactness since they will be rare overall, limiting the ability to generate robust statistical relationships with human activity. Our intactness index averages the status of individual species, and as such new species, all with high intactness scores, cause the index to increase. This result is counter to what would be desired. One solution is to simply ignore all new species that are encountered and calculate intactness based only on species that were present at the beginning of the monitoring programme. This provides an overly liberal interpretation of intactness because new species invading an area are not considered. As an alternative, an update of the index can occur periodically to include all new species that have been detected and then back-calculate the index. Although this would invalidate comparisons with previously reported intactness estimates, biases due to changes in species richness would be countered. This is similar to what is done to account for inflation and other temporal trends in economic indices such as the consumer prince index.

An additional challenge is ubiquitous species. When species are present at all sites within a defined region, the occurrence index is 100 and thus the species intactness scores rely solely on estimates of the abundance index. As ecosystem size and ecosite variety increases, or as sample size increases, the likelihood of species being present at all sites should decrease.

A more difficult concern is the incorporation of rare species. Species with very low prevalence do not have enough variation in their response variables to effectively estimate reference conditions, and thus intactness cannot easily be determined for these species. This highlights the need to use monitoring protocols that are effective at sampling uncommon species so they can be included. If it is critical to incorporate rare species in the index, then expert opinion or other sources of information could be used to define range of reference.

Finally, we have chosen to use the product of the occurrence and abundance indices to emphasize simultaneous deviations from reference conditions. The multiplicative nature of the errors was not considered and therefore warrants further study.

5.   Conclusions

As many existing monitoring programmes already collect information on species occurrence and abundance, we suggest occurrence and abundance be used as a foundation for monitoring biodiversity intactness. By estimating a range of reference for each measure based on empirical models, current conditions can be compared with the estimated range of reference to determine whether current conditions are "normal". By scaling deviations between 0 (degraded) and 100 (intact), while leaving observations within their normal range of reference at 100, intactness can be easily interpreted and communicated. We argue reference condition should be informed by available monitoring data. However, the index as we derive it can utilize any reference condition deemed appropriate. As such, frequency of occurrence and abundance of species that no longer exist within an ecosystem could be included if expert opinion was deemed sufficiently robust to quantify what reference conditions should be. Since intactness is based on individual species, users can choose to aggregate information at any taxonomic level (i.e., specific guilds, taxonomic groups, total biodiversity) or spatial scale (i.e., ecosystems, watersheds, political boundaries).

For long-term monitoring, trends in intactness can be assessed using time series regression. Beyond simply measuring current conditions or trends in time, explicit targets (intactness value or rate of change) can be established and performance assessed. Trading markets (cap and trade), for instance, have been suggested and in some instances successfully implemented for other critical natural resources (Sandor et al., 2002; Woodward et al., 2002). The extension of such concepts for biodiversity has yet to be considered, but may be possible if systematic monitoring programmes are established and designed to detect trends in biodiversity using a common biodiversity currency. We suggest that one potential currency for biodiversity assessments are intactness based on the occurrence and abundance of individual species. Similar to the Kyoto protocol, a predetermined reference condition can be established and used as a baseline for maintaining future biodiversity. As well as tracking current trends, our index can be used proactively in evaluations of future land use practices through predictions of changes in species occurrence and abundance and subsequently intactness. We suggest that empirical reference conditions be used to standardize measures of intactness whenever possible.

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