Alberta Biodiversity
Monitoring Institute

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Manual for Species Modeling and Intactness

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Summary

The Alberta Biodiversity Monitoring Institute (ABMI) monitors hundreds of species of vertebrates, invertebrates, plants, lichens and habitat structures at 1656 sites systematically located across the province of Alberta, and at additional targeted sites. Two of the main goals of the institute are to support natural resources management by providing: i) empirical models of the relationship of species and habitat elements to natural vegetation types, human footprint and climate and geographical gradients, and ii) credible and understandable indices of the status of biodiversity. This document details the statistical methods used to produce models for species, and to derive reference conditions and the indices ABMI has developed to assess the intactness (or deviation from reference condition) for species, groups of species and habitat features. The methods presented here are continuously in revision, and updated versions of this document will be released periodically.

1. Background on ABMI

The Alberta Biodiversity Monitoring Institute (ABMI) was initiated in 1997 through a broad partnership of industry, government, and academia. ABMI is tasked with providing an effective way to track status and change to biodiversity at local, regional and provincial scales, and provide relevant and objective information to policy-makers, scientists, and the general public.

The institute collects information on thousands of terrestrial and aquatic species (mammals, birds, mites, vascular plants, bryophytes, lichens, and aquatic macro-invertebrates) and habitat structures at 1656 sites spaced systematically on a 20-kilometre grid across the entire province. At full implementation, each of the 1656 sites will be sampled once every 5 years using a set of scientifically reviewed protocols. The same protocols are used in additional "off-grid" sites targeted to complement the main sites to address species questions, such as the effects of gradients of human disturbance. This standardized data collection is designed to reduce duplication and increase cost efficiency for provincial and regional monitoring commitments, and provide a more complete understanding of cumulative impacts on the environment from multiple industries and human activities.

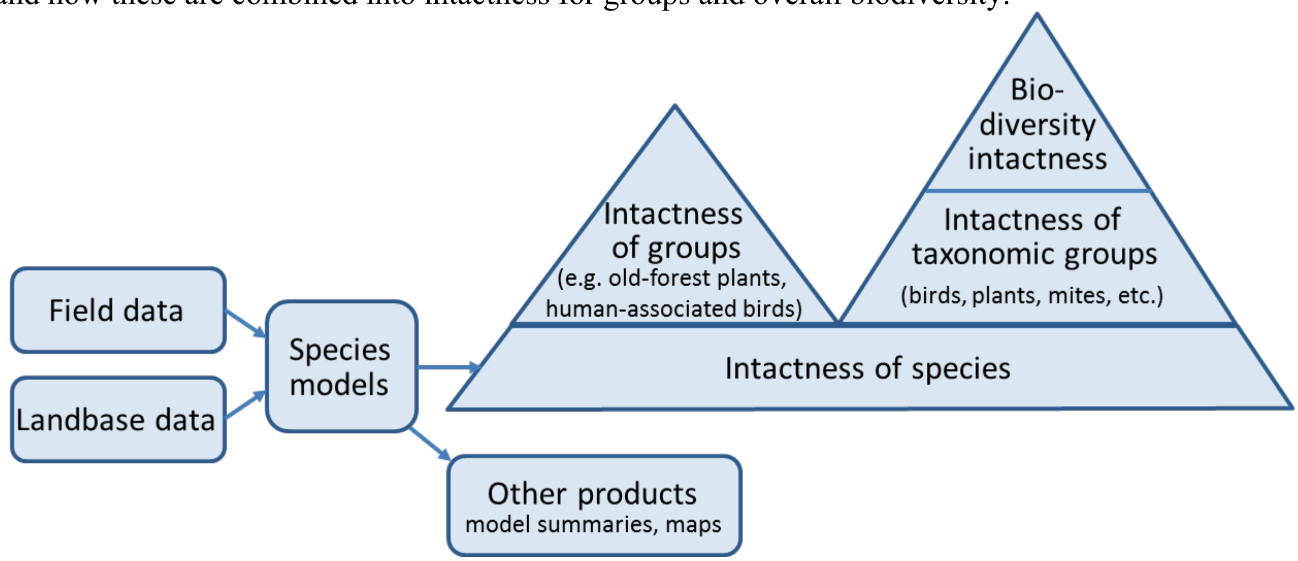
A main goal of the institute is to provide scientifically valid models of the relationships between species or habitat elements and vegetation types, human footprint and climate and geographical gradients (collectively referred to as "habitat models"). These habitat models have several purposes. One of these is to generate indices of the intactness of biodiversity for regions within the province and for the entire province of Alberta. These indices identify how the state of biodiversity has changed in comparison to an estimated reference condition.

This document describes the analysis methods used to generate the habitat models for species and habitat elements, and how these models are used to estimate intactness indices at the regional scale. Species level indices, along with important habitat structures, are ABMI's focus because they are the most clearly defined level of biodiversity. However, information is also rolled up to provide indices for groups of species, and for biodiversity overall.

1.1 Overview

Figure 1 outlines the general procedure for producing species models and using them to calculate intactness for species, groups of species and overall biodiversity. Field surveys provide data on the relative abundances of species and habitat elements at ABMI sites. We use province-wide maps of vegetation and human footprint created by ABMI to describe the landbase at each site. Statistical analyses generate models of how each species' abundance relates to the vegetation and human footprint at the sites. These models are summarized and applied in different ways to generate several products, including estimates of relative abundance in each vegetation or human footprint types, and maps of the predicted current distribution of the species across the province. The models are also applied to "reference" vegetation maps, in which human footprint has been replaced or "back-filled" with the original vegetation. Intactness of a species compares the predicted current abundance of a species with the abundance predicted under the reference condition with no human footprint. Intactness of a group of species, such as old-forest plants or human-associated birds, or of a larger taxonomic group, such as all mites, is calculated by averaging the intactness of all species in the group. Overall biodiversity intactness is an average of the intactness values for the larger taxonomic groups.

Field protocols are described in Standards and Protocols, Field Protocols (http://www.abmi.ca/abmi/reports/reports.jsp?categoryId=0) The landbase data are described in Standards and Protocols, Landscape Mapping Protocols (http://www.abmi.ca/abmi/reports/reports.jsp?categoryId=0&subcategoryId=232). Section 2 of this document details the statistical analysis that combines these into habitat models for each species. Section 3 outlines how the models are used to generate intactness values for species, and how these are combined into intactness for groups and overall biodiversity.



2. Habitat Models for Species

Modeling the relationship of species to habitat is at the heart of many of our analyses, including direct descriptions of those habitat relationships, mapping and species intactness. "Habitat" is used in a broad sense, including: 1) Human footprint, 2) Descriptions of the natural ecosystems – vegetation (stand types by age classes) in forested areas, or soils and natural subregions in prairie areas, 3) Climate and spatial variables (latitude, longitude), 4) Footprint surrounding a site. We use a flexible analysis for the habitat modeling, which can be adopted to address specific questions, such as the effects of particular industrial sectors.

2.1. Relative abundance by human footprint and ecosystem type

2.1.1. Modeling species

The first, most basic step of the analysis is to estimate the relative abundance of a species in different human footprint types and ecosystem types. Because most ABMI sites fall in several types, we use a multiple regression approach to separate the effect of each type. The main footprint and ecosystem variables used in the models (section 2.1.2) and modeling procedure (section 2.1.3) are the same between taxa, but details of the modeling differ slightly due to different sampling methods for the taxa and habitat elements.

Birds: Birds are modeled as the number of occurrences in the 9 point counts at a site, using a logit-link binomial distribution with 9 trials. The raw data for the bird surveys records the number of individuals of a species at a point count station, but we reduced this to presence/absence at a station, because most values are 0 or 1, and repeatability of the data for multiple individuals at a station is low. Vegetation and human footprint variables are summarized for the total area occupied by 150m-radius circles around each of the 9 count stations at a site.

Vascular plants and mites: The data for both taxa are treated as occurrences in 4 quadrats (plants) or soil samples (mites) in the 1-ha central area of each site, using a logit-link binomial distribution with 4 trials. Vegetation and human footprint variables are summarized for the 1ha central area.

Bryophytes and lichens: The data since 2009 are similar to the vascular plant data, and are also analyzed as 0-4 quadrat occurrences per site. Prior to 2009, these taxa were surveyed with a more complex design that stratified by microhabitat across the central 1-ha plot. Those data are reduced to simple presence/absence at the site. The pre- and post-2009 data are analysed together, using a logit-link binomial distribution with 1 (pre-2009) or 4 (post-2009) trials, and an additional factor for old versus new protocol. The protocol factor adjusts for the different area of each occurrence (1ha versus 50mx50m) and different search protocol.

Mammals: Mammals were originally surveyed with a triangle of 3km per side. The protocol was changed to a 10km linear transect in 2005. In both methods, occurrences of mammal species were recorded separately for 1km segments. Mammals are analysed as presence/absence on each 1km segment, with vegetation and human footprint summarized in a 250m buffer around each segment. Adjustments are made to estimated standard errors to compensate for the dependence of segments along the same transect, and transects are resampled together in bootstrapping (section 3.3). A factor is included in the analysis to account for the change in protocol from triangles to transects. Additionally, tracking data is directly affected by days-since-snow when the survey was conducted. A quadratic relationship with days-since-snow is included in the models to account for this.

Habitat elements – trees, snags and logs: Counts of these structures, divided into classes by diameter and species groups, are analysed with log-link negative binomial count models, which can capture the highly aggregated nature of some structures (a few high counts, many zeroes). For predicting, predicted counts can be converted into densities (/ha) and then into basal areas of trees or snags (m^2/ha) or volumes of downed wood (m^3/ha), using quadratic mean diameters of the size classes and the known sampling areas or transect lengths.

Habitat elements – cover layers: Canopy, shrub, etc. cover layers are analysed as a logit-linked binomial variable, as this produced more stable models than alternatives such as beta distributions or other transformations.

Habitat elements – miscellaneous: pH is modeled as a log-normal distribution. Organic depth and soil carbon have a normal error distribution.

2.1.2. Human footprint and ecosystem variables

The human footprint types and way of describing ecosystems differ between the North (boreal, foothills, Canadian shield and Rocky Mountains) and the South (grasslands, parklands, dry mixedwood and some of the central mixedwood subregion of the boreal).

North: Human footprint types in the North are grouped as cultivation, hard linear (non-vegetated: roads, railways, etc.), soft linear (vegetated: pipelines, powerlines, road margins, seismic lines, etc.), urban/industrial (combining industrial sites like well-pads, compressor stations, factories, with urban and rural residential areas, which cannot currently be distinguished reliably in our footprint maps), human-made water bodies and forestry. Forestry sites are classified according to their original stand as deciduous or mixedwood, upland spruce+fir or pine, and their age (0-10yr, 10-20yr, 20-40yr, 40-60yr, 60-80yr). Ecosystems are described using vegetation types, which are combinations of broad forest types (deciduous, mixedwood, upland spruce+fir, pine, black spruce, larch fens) and age classes (0-10yr, 10-20yr, 20-40yr, 40-60yr…140+ yr), along with open vegetation types – grass, shrub, open wetlands, open water, rock and other barren areas. All area in the North is classified as one of these human footprint or natural vegetation types.

South: Human footprint types in the South are grouped as cultivation, hard linear, soft linear, urban-industrial and human-made water body. There is no forestry in the South region. Ecosystems are currently described by two variables: Soil groups and pAspen. Soil groups are productive (loamy, silty types), clay, saline and rapid-draining (sandy and badlands). pAspen is the probability that aspen would be found under natural (no footprint) conditions in a plot at the site, based on a model of the species that uses climatic, topographic and lithology variables.

2.1.3. Estimating species' relative abundances in human footprint and ecosystem types

North: In the North analysis region, a two-stage procedure is used to estimate species relative abundances in the human footprint and vegetation types. The first step estimates relative abundances for the human footprint types and the broad vegetation types (combining stand ages within the forested types). The second stage estimates the species' relationship with age of forest within the broad stand types.

The first stage uses a set of 5 models. The first includes each human footprint and vegetation type (broad stand types, no age classes). The other models combine similar human footprint or vegetation types that are difficult to estimate into coarser groups. The estimates from the 5 types are combined with AIC-based model-averaging, which weights each model based on a metric of how well the data for the species supports each model. These models provide estimates of a species' relative abundance in each human footprint type (including the age classes and stand types of forestry cutblocks, although classes or stand types are combined in some models and hence have the same estimate), in the non-forest vegetation types, and in the broad stand types.

The second stage estimates how the species' relative abundance within each of the broad stand types changes as a function of stand age. The age analysis is done separately for each stand type. Only sites with >10% of their area in the target stand type are included. Sites included in the analysis are weighted by the proportion of their area in that stand type (for example, a site with 20% pine would have a weight of 0.2, compared to a weight of 1 for a site that was 100% pine). Some recently burned upland forests are classified as grass or shrubs in our vegetation data. Grass and shrub sites are therefore included as age 0-10 or age 10-20 stands, respectively. They are weighted as 0.5 X the proportion of the target upland stand type in the surrounding quarter section. The 0.5 weighting is to reflect the fact that some of these grass and shrub sites are edaphic (permanent) openings, not early-seral stages of the stand types. With this dataset for each stand type, a curve is fit between the relative abundance of the species and age. A predicted abundance of the species at each site is first generated from the relative abundance coefficients in step 1, and this value is used as an offset in the age analysis. The analysis is therefore looking at the residual (incremental) effect of age on the species' abundance in the stand type. These age curves are used to predict the relative abundance of the species in each age class of each stand type.

After estimates of relative abundance have been generated for each human footprint and vegetation type using the above models, two adjustments are made: 1) Estimates for hard and soft linear features are often highly uncertain, because these features never occupy a high proportion of our sites, making it difficult to separate their effect from the effects of other vegetation types. We therefore modify the estimate for hard linear features by combining it with the estimate for the similar urban/industrial footprint type, using an inverse-variance weighted estimated (the weight given to the original hard linear or urban/industrial estimate is proportional to 1/variance of the estimate). For soft linear features, we use an inverse-variance weighted average with recent forestry cutblocks (for upland sites) and the youngest age class of black spruce (for lowland sites). With inverse-variance weighting, the poorer the estimate for hard or soft linear footprint, the more strongly the final estimate is pulled towards urban/industrial or forestry/young lowland estimates. 2) Estimates for cutblocks >20yr are poor, because there are few sites with old forestry. We adjust the estimates for cutblocks >20yr so that they converge on natural stands by age 80yr. Based on expert opinion of the timing of convergence of harvested and natural stands, the estimate for spruce and pine cutblocks 20-40yr is adjusted 50% of the way towards the estimate for natural 20-40yr stands, 40-60yr cutblocks are adjusted 85% of the way and 60-80yr cutblocks 96% of the way. Convergence rates are somewhat higher for deciduous stands: 70%, 91% and 97% at 20-40yr, 40-60yr and 60-80yr.

<u>South:</u> There are no stand ages in the South analysis, so relative abundances in each human footprint and soil type can be estimated in a single step. Eight models are used in an AIC-based model-averaging framework. The first four models combine difficult-to-estimate soil types or human footprint types in different ways. The other four models add a term for pAspen to the first four models. These models are used to estimate species' relative abundances in each human footprint and soil type. (For presenting results, separate estimates are generated for sites with pAspen=0 and pAspen=1 – i.e., sites predicted to be completely treeless or completely forested prior to human disturbance). As in the North, estimates for hard linear footprint are modified using an inverse-variance weighted average with urban/industrial footprint. There are no estimates for forestry in the South, so estimates for soft linear features are not adjusted.

2.2. Additional variation due to climate, geographic location and surrounding human footprint

The analyses in section 2.1 provide estimates of species' relative abundances in human footprint and ecosystem types that are the same throughout the analysis zone. In addition to varying due to these factors, we also know that species vary geographically and/or along climate gradients. Species may also be affected by the amount of footprint in an area around a site, not just the footprint at the site. For example, a species that uses native vegetation may be less common at a site with native vegetation if it is surrounded by human footprint than if it is part of a larger area of native vegetation.

The estimates of abundance by human footprint and ecosystem type are first used to predict a species' abundance at each site. These are then used as offsets in models to estimate the residual effects of geographic location, climate and surrounding human footprint. We use 14 models with different individual or combined climate variables, such as mean annual temperature, potential evapotranspiration, etc. An additional 14 models add latitude and longitude, and a further 14 models add latitude, longitude and latitude*longitude. The best of these 42 models of residual effects of climate + geographic location is selected using BIC. The climate and/or spatial variables from this best model are then used as covariates in a set of 7 models estimating the residual effects of human footprint in the quarter section area surrounding each site. The 7 models use different ways of grouping the human footprint types. These 7 models of surrounding-footprint effects, including the best climate and spatial covariates, are combined using BIC-weighted model-averaging.

2.3 Products from the habitat models – Model summaries and maps

We use the human footprint + ecosystem models (section 2.1) and the models of residual effects of climate, geographic location and surrounding human footprint (section 2.2) to produce several products:

1. Relative abundances by footprint and ecosystem type. For each species, we make predictions for sites that are 100% of each human footprint or natural ecosystem type (vegetation, including age class for forest stands, in the North; soil types with pAspen at 0 or 1 in the South). These predictions are the expected relative abundance of the species in that footprint or ecosystem type. Exceptions are soft and hard linear footprint, where there is never 100% of that one type. For these linear features, we instead use the models to predict the effect of converting 10% of an average site to these linear features. Confidence intervals are estimated directly from the models. These values are graphed and exported as tables to allow review of the habitat models for each species, or to allow the models to be used by others for other applications.

2. For the models of the effects of surrounding footprint, we predict the change in abundance of a species at a site that has an intermediate level of the species as surrounding human footprint varies from 0 to 100%. This is graphed to illustrate the additional effects of surrounding human footprint.

3. We use climate and location information from each quarter section in the analysis region to plot the residual effects of climate and location across the region. These maps show how much a site in a particular location with a particular set of climate variables would differ from the average site for that species.

4. We combine the climate and location information for quarter sections with information on the human footprint and ecosystem composition of each quarter section to map the predicted abundance of each species based on the habitat models and residual effects of location, climate and surrounding human footprint. This is the predicted current abundance of the species.

5. We repeat 4., but using a map in which all human footprint has been "back-filled" – replaced by the vegetation type that was most likely to have occurred prior to footprint. Back-filling in the North is based on the vegetation types immediately surrounding the human footprint, as well as rules about which footprint types are restricted to certain vegetation types (e.g., forestry is only in mature upland forest, agriculture is only on upland sites). The resulting map is the predicted reference abundance of the species – the abundance it would have had if there was no footprint in the area. In the South, the ecosystem variables soil type and pAspen are mapped for

all areas, including in human footprint, and therefore we do not need to back-fill human footprint to get reference conditions in this region.

2.4 Using sites with more than one visit

Some sites have been surveyed more than once. These repeat samples are included in intactness models but weighted by the number of repeats (1/n; in other words, each site has the same overall weighting even if some sites include data from more than one survey). During bootstrap analysis (section 3.3), the site is treated as the unit of resampling, such that data from all surveys at a site are resampled together.

Once data from the planned re-surveys of sites become available in the future, additional terms will be added to the models to allow the species abundance to differ between initial and subsequent sampling periods. The predicted abundance for the second (or later) measurement cycle could therefore be greater or less than the abundance predicted from footprint alone. Intactness calculations after a second set of samples is begun will include both the footprint effect and any additional changes in the species. This will allow us to attribute changes in species abundances to both the effects of changes in human footprint and other changes unrelated to footprint.

2.5 "Off-grid" sites

In addition to the 1656 sites on the systematic grid across the province, ABMI samples many "off-grid" sites. These sites are chosen to complement the systematic sites for the purpose of addressing specific short-term questions, and are sampled with the same protocols as the main sites. A main objective of off-grid sites surveyed to date has been to improve sampling coverage along the gradient of human footprint levels, and thus to improve estimation of species-footprint relationships. Off-grid sites have therefore been focused on the end of the footprint gradient that is less common in a region: high footprint sites in the boreal and foothills region, and low footprint sites in the grasslands and parklands. Effort is made to find sites satisfying these conditions while also being widely distributed and representative of the ecosystem types in a particular region (although this is not always possible). Some off-grid sites are chosen to target underrepresented footprint types, such as large industrial sites, or address specific management questions, such as the rate of species recovery in older cutblocks. Because we calculate reference and current abundances of species using complete maps of the region of interest rather than just our sampled sites (section 3), our intactness results are not affected by the fact that the off-grid sites are not a representative sample of the footprint in the region.

3. Intactness

3.1 Species Intactness

ABMI's intactness index compares the predicted current abundance of each species to its predicted reference abundance (product 4 in section 2.3 versus product 5). Our reference condition is therefore the current abundance with the effects of human footprint statistically removed using our habitat models (Nielsen et al. 2007). Alternative definitions of reference conditions have been used elsewhere, but these are problematic: 1) Abundances in protected areas cannot be used, because protected areas are rarely representative of all ecosystems. In Alberta, many protected areas are in remote or high elevation regions with low productivity. 2)

Time-zero approaches set the reference condition as abundance in a certain year. However, human footprint has affected parts of Alberta for over a century, and many areas had extensive development when systematic monitoring began in 2003. 3) Desired or target abundances of species are sometimes used as references, but these are social values that differ for different people, and it is infeasible to set targets for thousands of species. Using a reference condition based on statistically removing the effects of human footprint overcomes these problems. However, this "de-footprinted" reference condition cannot account for any past changes in the species' abundance that are not due to local footprints, including historical exploitation, effects of diseases or introduced species that are not associated with footprint, climate change or past effects outside the province for migratory species.

The species intactness index compares the predicted relative abundance of each species across the reporting region to the predicted abundance for that species under zero human footprint in the same region. This measure of intactness is scaled between 0 and 100, with 100 representing current abundance equal to that expected under reference conditions, and 0 representing species abundance as far from reference condition as possible. Both over- and under-abundances are viewed as deviations from intact conditions. The index is estimated as:

Current / Reference × 100%, when Current<Reference, or

Reference / Current × 100%, when Reference<Current

A value of 50%, for example, means that the species is either half as abundant as the reference condition, or twice as abundant. Because the intactness index for individual species decreases from 100% with either downwards or upwards differences from reference conditions, an "increaser" species does not cancel out a "decreaser" species. Instead, both contribute to lowering the average intactness.

The reference and current abundances of a species in a reporting region are calculated by applying the habitat models and models of residual climate/location/surrounding footprint to landbase data from every quarter section in the region. The landbase data comes from province-wide maps of vegetation, soils and human footprint produced by ABMI. Compiling and updating the human footprint information for the whole province is time-consuming, so regional intactness results usually represent human footprint levels 2 or 3 years prior to reporting.

The intactness index uses the predicted current abundance for each quarter section when the footprint variables are set to their current levels, rather than directly using the counts at surveyed sites, for 3 reasons:

1) This approach allows us to do the calculations using quarter sections that cover the entire area of the region, rather than just the small subsample of the area where we have ABMI sites with the direct counts. That is particularly important for reporting on small subregions.
2) Measurement error is large for single counts, and substantial even across multiple sites in a subregion. We do not want to compound true changes in species caused by footprint and the effects of measurement error.
3) The reference condition is calculated using regression models with a link function (log or logit). The current condition also needs to be calculated with this link function, to avoid

differences due simply to different types of scaling (parallel to the difference between arithmetic and geometric means).

When we report on changes in intactness over time in a region, we use a subset of 3x7km areas overlaying ABMI sites (i.e., on a 20km x 20km grid) in which human footprint has been mapped from satellite images for most years from 1999 to present. These 3x7 areas are a 5.25% sample of the whole region. Because they are a sample of a region, rather than a complete inventory, they add sampling error to the intactness estimates. Our analyses show that this sampling error adds 2-3% additional error to the intactness estimates for species, which is small compared to the uncertainty in the models generating the current and reference predictions.

In areas with low footprint, such as much of northern Alberta, species that increase with human footprint tend to have lower intactness than species that decrease. With 5% footprint in a region, for example, it is rare to have a species that decreases more than 5%. To do so, the species would have to have a strong negative response to footprint and footprint would have to be concentrated in preferred habitat for that species. In contrast, it is more common for some species to increase several-fold as soon as any footprint occurs in a region, because several species associated with footprint are expected to be extremely rare under no-footprint reference conditions – the proportional increase when they show up in footprint is therefore large. Although species that increase with footprint can be an ecological concern because of negative effects on other species, species that decrease with footprint are usually a greater priority. For this reason, we often report intactness of decreaser and increaser species separately, or highlight decreaser species or groups of species.

Non-native plants: A different approach is used for non-native plants. We assume that the reference condition is 0 for these species, then calculate a species' intactness as: SI_s = 100% - percent occurrence of the species. Percent occurrence is calculated at the quadrat (50m x 50m) level. For example, a non-native species that occurred in 20% of quadrats would have an intactness value of 80%.

3.2 Intactness for groups, taxa and overall biodiversity

Intactness for groups of species within a taxon, such as old-forest birds or berry-producing shrubs, is simply the average intactness of species in the group. Similarly, intactness for a taxon like bryophytes or mites is the average intactness of all analysed species in that taxon.

Overall biodiversity intactness is the average of the intactness for each of the included taxa (birds, mammals, vascular plants, bryophytes, mites, lichens). Each taxon is weighted equally, regardless of how many species it contains.

We considered many other ways of combining species intactness results, but decided that a simple mean is the most appropriate. Geometric, harmonic or other types of averages have undesirable properties, including giving excessive weight to individual species with extreme values, which were often the most poorly estimated results (for rare or highly aggregated species). Alternatives that weighted species by the precision of their intactness estimate are biased toward common species. More complicated methods that statistically correct for the expected relationship between abundance and precision could be used to remove this bias with precision-weighted averages. However, the loss of transparency and ease of understanding the results was considered to outweigh any possible statistical benefits of such a procedure.

Non-native plants: For non-native species, it does not make sense to calculate an average intactness, because the more rare non-native plant species that are included, the higher the intactness. For example a non-native species that is observed once in a region with 100 sites sampled has an intactness of 99%, and another non-native that is observed at 50 sites has an intactness of 50%. If these intactness values were simply averaged, the first record of a newly invading non-native species would raise the mean intactness, which is not a sensible result. For that matter, potential non-native species that have not yet been detected would have an intactness of 100%, and would raise the average intactness for the overall group even higher. Instead, we calculate the overall intactness of all non-native plants as 100% - percent occurrence of any non-native species on a quadrat. This value is simply the percent of quadrats on which no non-native species was detected in a region.

3.3 Bootstrapping and confidence intervals

The sampling distribution of species intactness indices are estimated using bootstrapping, in which the original data are resampled with replacement and the entire analysis repeated 100 times. The bootstrap replicates are used to calculate the median reference condition and confidence intervals (based on percentiles of the 100 resampled values). Bootstrapping is required, rather than an analytical formula, because the current abundances and reference conditions are not independent, and the intactness calculation is complicated for the multi-stage, multi-model approach with different weighting of revisited sites. A blocked bootstrap is used, in which the resampling is done within pre-defined spatial blocks to preserve some of the spatial structure of the sample design. For mammal snow-tracking, the transect or triangle is used as the unit of resampling. When we are using the 3x7km areas to estimate intactness changes over time, the 3x7 areas in the reporting region are also resampled during the bootstrapping to include the additional error due to these areas being a sample of the region, rather than a complete inventory.

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