Ecological Indicators 82 (2017) 94–105

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Original Articles

Nation-wide indicators of ecological integrity in Mexico: The status of mammalian apex-predators and their habitat

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ARTICLE INFO

Keywords:
Apex predators
Ecological integrity
Spatial indicators

ABSTRACT

Ecological indicators that evaluate the status and trends of mammalian apex predators are necessary for monitoring the ecological integrity of landscapes. Several nation-wide spatial indicators that describe the status of apex predators after habitat transformation have been developed for México. These spatial indicators show the condition of the remnant natural landscape for maintaining the complexity of predator-prey interactions and habitat selection and use. The indicators were obtained using the concept of ecological integrity, that characterize the landscape based upon manifest and latent variables of naturalness, stability and self-organization, according with the measures of spatial distribution of species and natural habitat. When the current status is evaluated for individual species of apex predators, all species showed less than 50% of their distribution areas with a high degree of ecological integrity. Neotropical predators (such as jaguars and ocelots) are more threatened by the transformation of natural habitat, than their counterparts in Nearctic regions (e.g., bears, cougars, bobcats, and coyotes), which showed nonetheless, a high amount of their distribution areas with a high proportion of degraded habitat. The indicators allowed evaluating the status of still extant top predators in the landscape and their habitat condition within major ecoregions in the country.

1. Introduction

An ecological evaluation of the integrity condition in remnant habitats is necessary for long-term conservation goals and sustainability in areas that support viable populations of predators in natural conditions. Nowadays, the human transformation of natural landscapes is the main threat for sustaining the prevalence of apex predators worldwide due to their high dependency of natural conditions (Estes et al., 2011; Hoffmann et al., 2010; Ripple et al., 2014). With the increasing loss of natural areas, ecological integrity is a pre-requisite for maintaining a collection of ecosystems that support a community of organisms with similar species composition and functional organization as found in adjacent natural systems (Parrish et al., 2003). Therefore, adjacent natural areas might play a significant role in restoring ecological conditions, particularly trophic interactions for degraded and transformed surrounding areas. However, ecological indicators that evaluate the integrity of the ecosystem are limited by the information available on their structure and function (Dale and Beyeler, 2001). For that reason, new approaches for developing spatial information derived from existent data about the status and trends of species and their habitat are necessary for making ecological integrity evaluations.

From a theoretical framework, ecological integrity (EI) in the landscape of apex predators can only be observed when some properties, associated with self-regulation, stability and naturalness are manifested (Mora, 2017). Then a set of observable characteristics (associated with species interaction and the condition of their habitat) can be used to derive latent properties associated with ecological integrity. Therefore, EI is a latent, complex variable that stems from the complexity of ecological processes and from mechanisms that sustain ecological interactions resulting from the complexity of biodiversity. Unfortunately, information on ecological integrity can only be indirectly measured; and therefore, basic data describing manifestations of ecological integrity in ecosystems are seldom available. As an alternative, spatial information describing the current patterns of species distributions can be used as manifest information about species, their potential interactions and their habitat condition. Nowadays, new approaches for deriving multi-species geographic information are currently available which are often associated with biodiversity information (Carignan and Villard, 2002; Tierney et al., 2009).

In recent years, spatial biodiversity information based on these new

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http://dx.doi.org/10.1016/j.ecolind.2017.06.030
Received 9 March 2017; Received in revised form 7 June 2017; Accepted 14 June 2017
1470-160X/

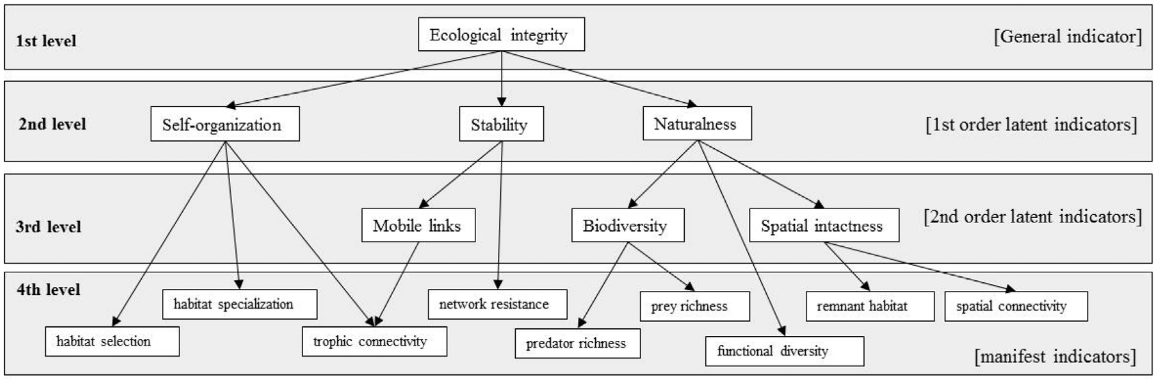

Fig. 1. The ecological integrity hierarchy framework for evaluating the condition in natural ecosystems based on landscape characteristics that sustain predator-prey interactions.

approaches has become increasingly available. The information derived from Species Distribution Models (SDMs) is particularly suitable for ecological integrity analysis. The SDMs integrate the information contained in scientific collections and sampling efforts with expert knowledge and modeling techniques to better represent, according to the best knowledge and data available, the patterns of biodiversity. The SDMs are, to date, one of the most important sources of spatial species distribution information, which is currently used to indirectly analyze the role of species in maintaining ecological processes. Usually, the identity and role of species within ecosystems are used as primary sources of information in ecological modeling efforts because they can be measured directly by recording species' presence and evaluating their abiotic and biotic interactions. Furthermore, the role of species in maintaining ecosystem function requires adequate evaluation and monitoring of key components that are then used as information variables. At present, geographic distribution patterns of species depicted by SDMs are widely used to infer species' composition within ecosystems (Austin, 2007; Cord et al., 2014; Dunstan et al., 2011; Guisan et al., 2006). Therefore, several SDMs can be used as information variables that can describe the ecological integrity condition of processes of interest and derived from species interactions, and, in addition, they can also identify the role of biodiversity in contributing to ecological integrity.

In addition to the current spatial data availability, a collection of artificial intelligence methods are available for building and formalizing ecological concepts associated with ecological integrity that potentially serve as ecological indicators. For example, methods such as structural equation models (SEM) provide a framework that allows statistical testing regarding whether complex notions or concepts can be "*confirmed*" by ecological observations. Then, the ecological integrity concept can be successfully obtained from manifestations of structural and functional attributes using SEM. Therefore, SEM involves more than a way to simply estimate model parameters. It provides a methodological approach in which theoretical ideas are translated into a model for evaluation (or *model specification*) and are then tested for mathematical validity. Additionally, SEM have allowed estimating latent variables that can be then spatially represented as spatial indicators within a GIS for analysis and evaluation (Mora, 2017). Both manifest and latent indicators can be then used for decision making within a spatial decision support system.

The purpose of this research is to show practical applications of stacked-SDMs as manifest variables, or observable landscape characteristics indicating ecological integrity, and later on, their potential for deriving latent spatial indicators of emergent ecosystem properties associated with the concept of ecological integrity. Spatial indicators of ecological integrity are derived from analysis techniques that help formalize the ecological concept within a quantitative framework. It also aims to define a set of observable measures that support a latent analysis, and define several sources of information that can be used to build the concept of ecological integrity within a hierarchical analysis framework. All manifest and latent spatial information is then used to characterize the potential of natural landscapes to support ecological integrity in maintaining biotic and abiotic apex predators' interactions among species and their habitats.

As manifest indicators of ecological integrity, the spatial indicators developed here serve as a way to summarize and describe the status of predator and prey species and their habitat. They can serve to diagnose current habitat conditions, and to monitor significant changes that jeopardize the sustainability of viable populations. Latent indicators serve to monitor the landscape condition to sustain ecological mechanisms that promote the prevalence of species in the long run, and to identify the trends of habitat modification due to human impacts. As a combination, both sources of information (manifest and latent) may be useful for implementing plans towards the conservation and use of biodiversity, as well as implementing land-use plans and programs to sustain viable populations of apex predators.

2. Methods

The overall approach for deriving a set of ecological variables that can be used as indicators of ecosystem integrity is based on an ecological hierarchical network (EHN) as a framework that evaluates changes that occur at several levels in an ecological hierarchy (Fig. 1). The approach includes: (a) the development of spatial indicators that can be used as manifest indicators for ecological integrity as the foundation for the evaluation system; (b) the application of structural equation models (SEM) for deriving a set of latent concepts that build the notion of ecological integrity at two consecutive levels of generalized ecological information (1st and 2nd order latent indicators); and finally, (c) a general indicator that summarizes the integrity in the ecological condition.

Later on, the set of manifest and latent variables are used as properties which characterize the ecological integrity condition of different landscapes and thus, their capability to sustain viable populations of top predators. The set of ecological indicators (latent and manifest) are used as variables to characterize the eco-regions described for Mexico (INEGI, CONABIO, INE. 2007). The evaluation is presented for species (apex predators) and at two scales of geographic evaluation: (a) landscape (nation-wide); and (b) ecoregions.

2.1. Manifest ecological integrity measures as change indicators

Ecological integrity is a complex concept, where some of its emergent properties can be inferred as latent concepts from a hierarchy of manifest (or observed) variables. The emergent properties that the ecological integrity concept conveys are often identified from a reference state or reference dynamics in the ecosystem, and therefore, ecological integrity is essentially an indicator of changing reference

Table 1
Description of the metrics used for manifest ecological integrity indicators. These are derived from SDMs of all species identified in the predator-prey interaction networks on a cell-by cell basis, at 1 km^2 resolution.

Metric	Formula	Description and interpretation	References
Functional diversity	$FD = \frac{FG}{\sqrt{S}}$	Functional diversity (FD) is a concept used to describe the variety of functional characters, complexity of food webs and functional groups present in a community. As used here, functional diversity indicates the number of species groups that perform different functions within ecosystem (FG), or show similar responses to the environment. For predator-prey interactions, all 232 mammal species (plus 7 top-predators) were categorized into seventeen functional groups (5 spp. as big carnivores; 5 spp. as medium carnivores; 1 sp. as small carnivore; 8 spp. as medium frugivores; 5 spp. as small frugivores; 3 spp. as medium granivorous; 82 spp. as small granivorous; 4 spp. as big herbivores; 21 spp. as medium herbivores; 45 spp. as small herbivores; 8 spp. as medium insectivores; 28 spp. as small insectivores; 3 spp. as big omnivores; 7 spp. as medium omnivores; 1 sp. as small omnivore and 6 spp. as ruminants). The FD indicator represents the spatial variation of the relationship between the number of functional groups, and the number of species within groups	(Mason et al., 2005)
Predator and prey richness	Number of species (S)	Predator and prey diversity is expressed as species richness (S). Prey richness is an indicator of the number of prey species present from the species' pool; i.e., 140 species for *C. latrans*; 95 species for *P. yagouaroundi*; 103 species for *L. pardalis*; 102 species for *L. wieddi*; 137 species for *L. rufus*; 45 species for *P. onca*; and 137 species for *P. concolor*; as identified with the predator-prey interaction networks. Predator richness is the number of predators present as described by the stack-SDMs	
Ecological (habitat) specialization	$SSI = \left[\left(\frac{H}{h}\right) - 1\right]^{\frac{1}{2}}$ $CSSI = \sum SSI/S$	Ecological specialization is a measure of the variety of ecological conditions (habitats) where species occur. Here, the term specialization is a manifestation of the tendency of species to occur in different landscapes composed of different species. As a geo-indicator, it provides a similarity measure of the geographic co-occurrence of local species, as compared to large-scale occurrence data (SSI). The level of ecological specialization for predators and prey as they occur in the landscape was calculated as a compound of the specialization index for all species occurring in a location (CSSI)	(Devictor et al., 2010; Julliard et al., 2006; Vimal and Devictor, 2015)
Habitat selection	$HS = \frac{HVr}{HVc}$	The habitat selection (HS) indicator integrates a measure of the species' ability to select all remaining available habitats (HVr) as a function of total number of habitats contained in their potential spatial distribution (HVc). As such, it is an indirect measure of the prevalence of species in the habitat. This indicator is calculated as the variety of different habitats occupied within home ranges by all species described in the interaction networks	
Remnant habitat	Proportion of remnant habitat	The amount of remnant habitat is associated with the spatial requirements of species which allows a viable population to persist as a meta-population. Remnant habitat is defined here as the proportion (within specieś home range) of viable habitat that is not transformed from its natural condition. Therefore, the amount of remnant habitat is an inverse indication of habitat loss	(Hendriks et al., 2009; Riitters et al., 2002)
Habitat connectivity	Probability of habitat adjacency	Habitat connectivity is calculated as the probability of having similar adjacent habitat types within the home-range for each species in the interaction network. Therefore, along with the amount of remnant habitat, it is an indication of habitat fragmentation for top predators	(Riitters et al., 2002)
Trophic connectivity	Probability of habitat adjacency (for apex predators)	Trophic connectivity is the mobility among different habitats for mobile (in this case trophic) links. Mobile links here are organisms that spread the predator function (i.e., apex predators). Trophic connectivity is defined here as the probability that a top predator can visit similar adjacent habitats and perform its ecological role within their surrounding landscape. Trophic connectivity is associated with predator's mobility by analyzing the spatial heterogeneity within its home range. The trophic connectivity is calculated as the probability of adjacency of similar habitats for apex predators, based on the model developed for evaluating habitat fragmentation at the landscape scale	(Lundberg and Moberg, 2003; Riitters et al., 2002)
Network resistance	$C = \frac{L}{S^2}$	Here, network resistance (within an species' interaction network) is an indicator that shows the capacity of the trophic network to resist changes due to species loss by measuring species connectivity (C) as an indirect measure of resistance; i.e., resistance increases as connectivity increases. Therefore, connectivity integrates the information about number of species (S), and number of interactions or links (L) within an interaction network	(Dunne et al., 2002)

conditions (Andreasen et al., 2001; Dale and Beyeler, 2001). Therefore, the several ecological indicators (EI_i) used here as manifest variables are obtained as spatial indicators (or spatial information) from a set of observable ecological metrics (see Table 1). The spatial indicators show ecological conditions in the specific ecological metrics that result from habitat loss relative to reference conditions.

As change indicators, reference conditions show the integrity in their spatial patterns; i.e., without habitat loss effects, using as a baseline the information that describe the potential distribution of species without human effects. This potential distribution (or baseline) is attained from species distribution models (SDMs) obtained from ecological niche modeling for all species associated with interaction networks (in this case, predator-prey interactions for 239 mammal species) and available in CONABIÓs geolibrary of biodiversity information (SNIB-CONABIO; http://www.conabio.gob.mx/informacion/gis/). The current condition (EI_c) is established when the information of habitat loss and landscape transformation (INEGI series 4.0, circa 2010) is combined with the niche models to produce information about the current distribution of species.

Data presentation is based upon a series of ecological metrics that can be easily obtained with quantitative spatial GIS analytical methods, which in turn, summarize expert knowledge within cartographical models that facilitate data automation (Table 1). Furthermore, ecological indicators are in a standardized form so they can be compared (as ecological metrics show different units) and easily aggregated into different scales. The finest scale available is determined by original data sources (1 km^2 resolution), although the cartographic modeling procedure can be implemented at different scales, as different sources of ancillary and satellite data become available. As standardized change indicators, all spatial indicators (EI_i) are expressed as a deviation of reference conditions (EI_r) as:

$$EI_i = 1 - \frac{EI_c}{EI_r}$$

Where, EI_i is the geo-indicator measured with the $_{ith}$ metric; EI_r is the reference condition for the indicator $_i$ and EI_c is the current condition. Then, the standardized indicator shows the proportion of change if $EI_r < EI_c$; otherwise the $EI = 1$; when $EI_r = EI_c$. Current conditions are evaluated when habitat loss is considered from a set of ecological characteristics described in the following sections.

2.2. SEM latent variables as spatial indicators

High order indicators of ecological integrity can be obtained when manifest observations (or, manifest spatial indicators) are used for modeling the concept of ecological integrity with latent variables within a Structural Equation Modeling (SEM) framework (Mora, 2017). As a latent variable, ecological integrity is an emergent property that stems from complex interactions among ecological processes. As such, previous studies coincide in the impossibility to measure ecological integrity directly (Rempel et al., 2016). However, latent indicators can be obtained by applying a SEM approach for developing a set of concepts associated with ecological integrity. Latent indicators that evaluate the ecological integrity for mammalian apex predators and their habitat relate some observable key ecological processes (e.g., predator-prey interactions) to some measurable patterns of ecosystems structure (e.g., habitat fragmentation and habitat loss) (Fig. 2). Therefore, latent indicators of ecological integrity describe the ecosystems' condition based upon manifestations of stability, self-organization, and naturalness. In addition, latent indicators show also the functional value of remnant habitat to support the functional role of apex predators (e.g., mobile links, trophic connectivity) as a response of structural habitat characteristics (e.g., spatial intactness).

For the analysis presented here, all latent spatial indicators were obtained by applying a SEM framework that integrates all manifest spatial indicators in a set of 1,937,913 cases (which represent the total number of pixels contained in a spatial indicator raster map at 1 km^2 resolution) which were then used for model estimation on pixel-by-pixel basis. The SEM parameter and latent variables estimation was obtained using a maximum likelihood procedure in the Onyx software (1.0–872 versions, July 2014), which is graphical software that is used to create and estimate SEM (von Oertzen et al., 2015). Hypothesis tests for model-data consistency were performed using the Chi-square test (χ^2) and its associated confidence levels (*p*-values) as a measure of correspondence between the observed and model-implied covariance matrix. Additional statistical indicators were used to test the model fit using the Root Mean Square Error Approximation (RMSEA) and the Standardized Root Mean Square Residual for covariance matrices (SRMR) to test for significant differences between the observed covariance and those implied by the model. All of the results and interpretations presented in the results section were based on the judgments of better data; i.e., information representation contained within spatial indicators and fit tests obtained for the SEM models (Mora, 2017).

2.3. Abstract indicators of ecological integrity

The status of ecological integrity can be described also as an interaction of high-order conditions described with latent indicators (1st level latent spatial indicators). As qualitative measures of ecological integrity, the emergent conditions of integrity are associated with the different qualitative levels of stability, self-organization, and naturalness. A qualitative description of these three properties also facilitates their interpretation. Therefore, a set of abstract indicators can be derived for guiding a decision-making process, based on the identification of different states or qualitative conditions (e.g., non-desirable to desirable conditions) expressed as a nominal intervals or classes (Fig. 3).

While ecological indicators are calculated as continuous values, discretization of continuous variables may help to a better representation and to facilitate the visualization of the ecological integrity condition as categorical maps. In addition, qualitative representations of EI allow to identify meaningful condition states as well as to gain the ability to use qualitative reasoning, especially when it is represented for data analysis and machine learning (Nuttle et al., 2009). Also, qualitative representations are particularly efficient when describing relationships among variables that are non-linear and complex (Uusitalo, 2007). As compared with continuous data, discrete classes or intervals are easier to understand, use and explain, and are closer to knowledge-level representation (Liu et al., 2002).

However, data discretization is a non-trivial process. Although automatic data discretization methods are available (Cao et al., 2014; Geaur Rahman and Zahidul Islam, 2016; Nojavan et al., 2017), there is always a subjective component associated with the process of identifying meaningful classes. In practice, ecological continuous data is usually discretized in a few classes or intervals per variable (usually from 2 to 10 categories) to make ecological information easy to interpret and use. Here, latent indicators were discretized into four levels that describe a qualitative (abstract) condition of several ecological attributes (Fig. 4).

In order to obtain qualitative abstract indicators, a segmentation procedure based on the Jenks optimization method was applied to continuous data to produce a qualitative representation of the latent concepts. The Jenks natural breaks classification method is a data clustering procedure designed to determine the best arrangement of values into different classes. This is done by seeking to minimize each class's average deviation from the class mean, while maximizing each class's deviation from the means of the other groups. In other words, the method seeks to reduce the variance within classes and maximize the variance between classes (Jenks, 1967; Jiang, 2013). The segmentation approach allowed expressing qualitatively the information content within each latent variable in four different levels, as described in the definition of the concepts (Table 2). The qualitative form of the concepts also allowed the combination of high-latent information in several

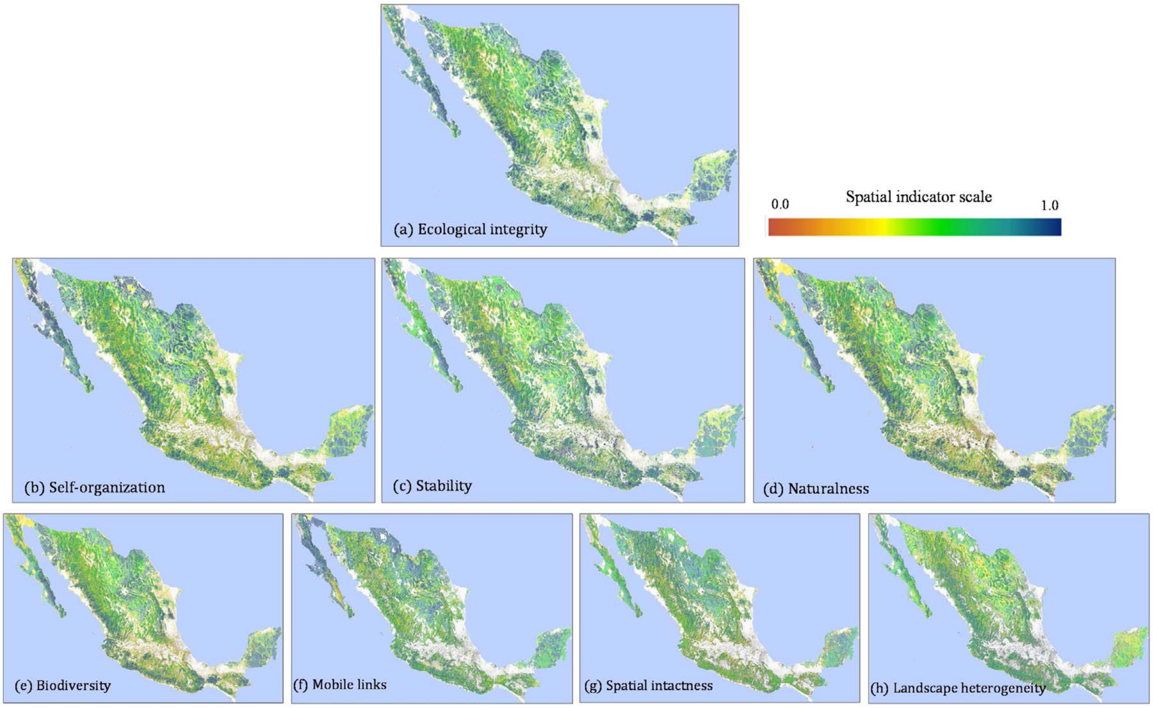

Fig. 2. Latent spatial indicators for evaluating the ecological integrity condition of the predator-prey interaction in Mexico. The latent variables show the emergent properties derived from the interaction among observed spatial indicators of the ecological integrity condition.

composited indicators. The resulting segmented grids were combined using spatial combination functions and conditional rules in Arc/info GRID spatial analyses routines.

The interaction between abstract indicators can also be expressed as a quantitative integrated measure by weighting the amount of natural landscape that pertains to all conditions observed. Therefore a combined score of all possible conditions in a remnant landscape is obtained as an additive index based on cumulative scores of all attributes. As an additive index, the resulting score is integrative, assuming that each state is compensatory and independent, so a reduction or absence of one state may be balanced by an increase in another (McElhinny et al., 2005). Therefore, the integrated score for the interaction between abstract indicators (Fig. 3) can be obtained as:

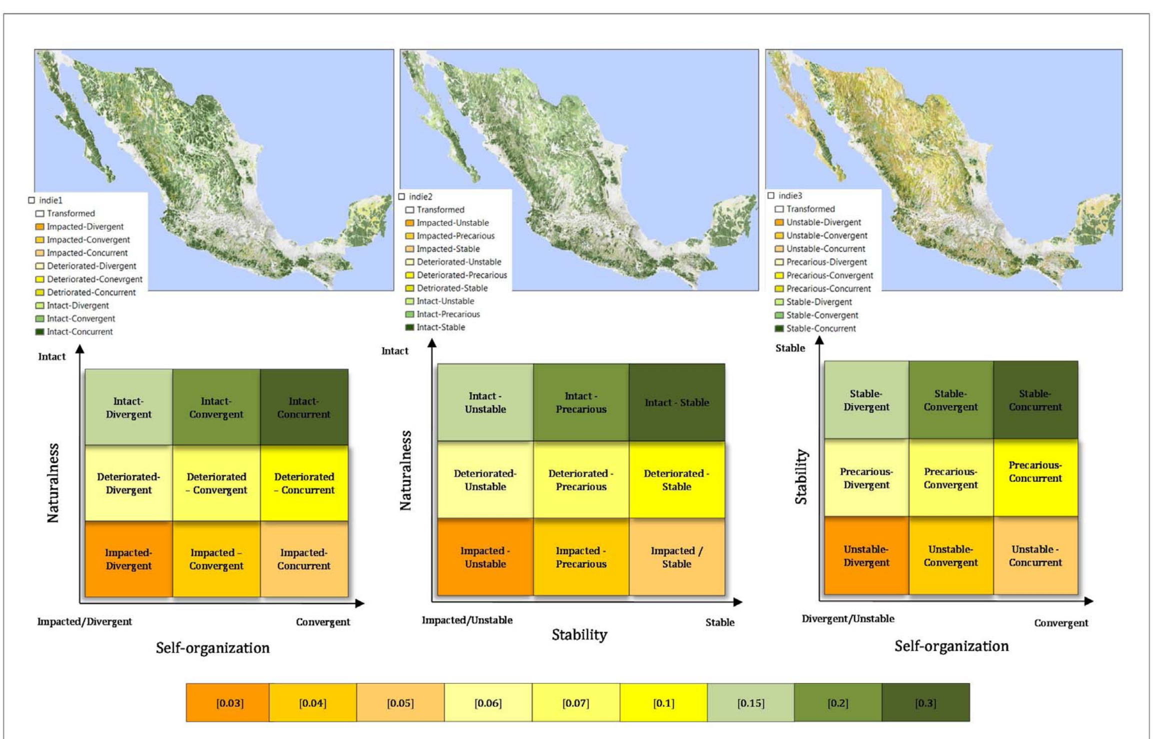

Fig. 3. Abstract spatial indicators for evaluating the relationship between emergent properties of the ecological integrity condition for predator-prey interactions. Interaction conditions are labeled within each box, and weights for obtaining the interaction score are indicated in brackets.

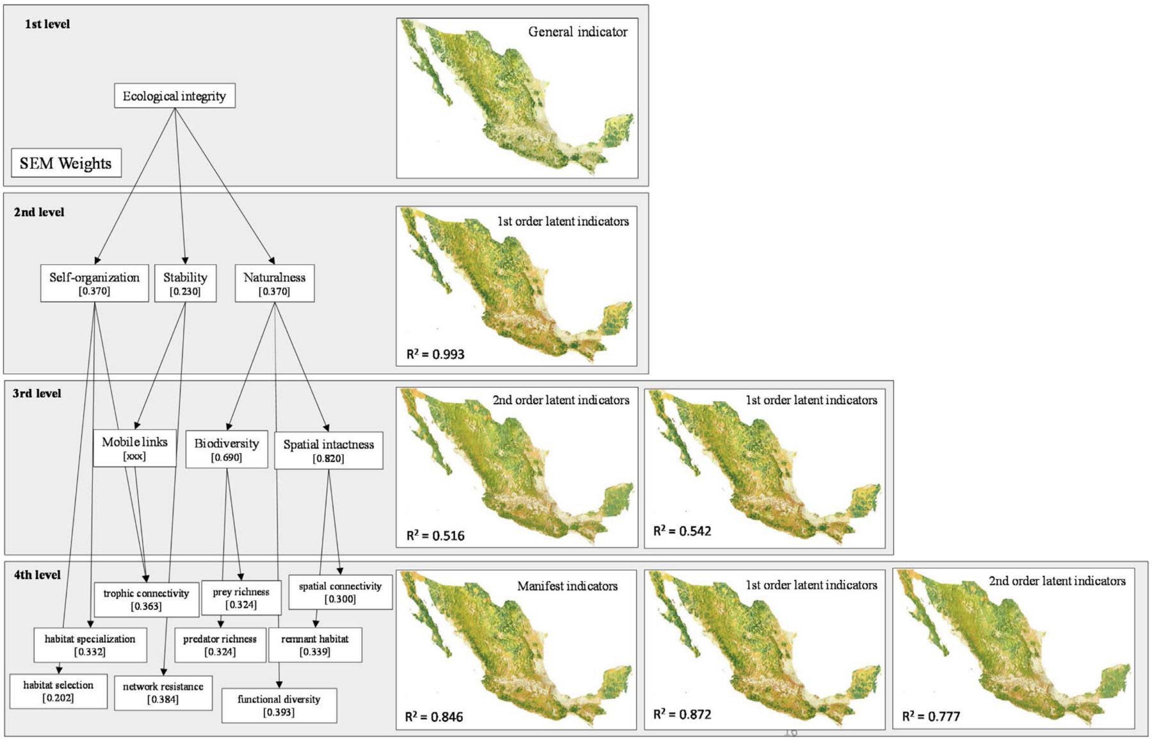

Fig. 4. The hierarchical framework for assigning indicators' weights to ecological variables that sustain ecological integrity. The weights for each variable within a hierarchical level are obtained with SEM analysis. The weights among hierarchical levels were obtained by applying PCA on the set of manifest and latent variables (at each level) to obtain a combined indicator that resembles the general indicator obtained with SEM (the R^2 indicates the variance amount explained between the first principal component obtained at each level, as compared with the general indicator obtained with SEM).

$$EII_{ij} = \sum_{1}^{n} \left[W_n * \frac{AEC_{ij}}{AN_{ij}} \right], \ \text{i} = 1, 2, \ldots \text{n}$$

Where EII_{ij} is the ecological integrity indicator for the interaction between the abstract indicator i_{th} and the abstract indicator j_{th}; W_n is the weight for the n_{th} ecological condition resulting from the interaction between the abstract indicator i_{th} and the abstract indicator j_{th} [from 1 to 9]; AEC_{ij} refers to the area (km^2) of the n_{th} ecological condition of the interaction between the abstract indicator i_{th} and the abstract indicator j_{th}.; and ANij is the total remnant natural area. The resultant EII value represents the mean ecological value for a single region, with a higher EII generally representing higher ecological integrity.

The human impact index (HII_{ij}) is the proportion between the area that has been transformed from natural to non-natural (HT_a), according with the total distribution area of each apex predator (APD_a); so:

$$HII_{ij} = \frac{HT_a}{APD_a}$$

The ecological degradation index is the difference between the actual score EII_{ij} and the potential EII_{ij} score if all remnant natural area was equal to the best ecological condition [1-HII_{ij}]. Therefore, EDI_{ij} is calculated as:

$$EDI_{ij} = [1 - HII_{ij} - EII_{ij}]$$

2.4. Integrated indicators: weights assignment to the ecological integrity indicators within the hierarchical network

A system that evaluates the condition of mammalian apex predators and the status of their habitat requires an integrated value or general indicator, which is, in turn, derived from multiple layers of quantitative indicators (Fig. 1). Here, the overall evaluation is an indication of the integrity in the ecological structure that maintains the ecological conditions for sustaining viable populations of apex predators. With SEM, the general indicator is obtained as a linear combination of latent variables, where regression parameters weight the contribution of each (latent) variable for obtaining the final scores of ecological integrity (Mora, 2017).

In the hierarchical framework, the goal is to evaluate the amount of information (contained in manifest and latent indicators) that is needed for making an evaluation using a subset of indicators. Therefore, in order to maintain the ecological integrity, the total weight of both selected manifest and latent indicators should reach the total proportion of the general indicator (always equal to 1). Then, the weights can be obtained by applying principal component analysis (PCA) on a set of manifest variables of ecological integrity (i.e., within each hierarchical level), so that the individual weights will represent the contribution of each indicator to maintain the ecological integrity. Therefore, the hierarchical framework helps to decide which information is relevant for doing a similar evaluation based on the general indicator.

3. Results

3.1. Hierarchical structure network in ecological integrity

The results of applying structural equation modeling (SEM) to build the concept of ecological integrity as a general indicator, and applying PCA to the selected set of both manifest and latent indicators to maintain the hierarchical network structure (HNS) in ecological integrity is shown in Fig. 4. The goal is to produce information similar to the general indicator (SEM) with a hierarchical structure. Also, the hierarchical structure shows the importance of making an integrated evaluation through the entire HNS. If the evaluation of ecological integrity is only based upon indicators at each specific level of the hierarchy, the proportion of variance explained for by each level is indicated as the R^2 parameter. The best surrogate evaluation is made upon the 1st order latent indicators (R^2 = 0.993), indicating that an evaluation based upon self-organization, naturalness, and stability is

Table 2
Description of the latent ecological integrity indicators obtained with SEM (Mora, 2017).

Latent indicator	Description and interpretation
Stability (1st order indicator)	Stability is an emergent condition that describes the consistency and permanence in predator-prey interactions. As a spatial indicator, stability varies from unstable to stable conditions. Therefore, stability is described here at three levels: (1) unstable, (2) precarious; and (3) stable. An unstable condition shows a lack of key elements in maintaining species interactions as a result of trophic downgrading or biotic homogenization (by losing specialist or generalist species) and the disruption of habitat occupation mechanisms (such as habitat selection), all of which may produce potential non-desirable effects, such as the loss of horizontal biodiversity (functional diversity) and possible "cascade" effects (Duffy, 2002; Duffy et al., 2007). A precarious condition describes the ecosystemś tendency towards a stable condition, by implementing the mechanisms of ecological memory that allow recovering unity and cohesion. Finally, a stable condition describes a state of organization in ecosystems, in which all structural (habitat functions such as connectivity and spatial integrity) and functional elements (interaction networks for predators and preys) remain unchanged due to perturbations and human impact
Self-organization (1st order indicator)	Self-organization is an indication of an ecosystem's ability to self-regulate and self-maintain the organization of several components and their occurrence in the landscape (interaction networks and habitat use). For trophic relationships, it assumes the presence of key components for species interactions (e.g., apex predators, meso-predators and preys), which are, in turn, organized hierarchically as interaction networks. As a latent variable, self-organization describes ecosystem condition at three levels: (1) divergent; (2) convergent; and (3) concurrent conditions. A divergent condition shows that human impact has removed some or all possible elements for habitat use and distribution (e.g., top predators or prey connectivity) in such a way that the ecosystem reflects a loss of the functional balance of trophic connectivity and ecological memory. A convergent condition is present when some of the elements that sustain a species interaction are lost, but they remain in neighboring habitats, allowing their recuperation or re-colonization (depending upon habitat connectivity, ecological memory and mobile links) once the human impact decreases or is removed. A concurrent condition shows that all elements that allow a balance between convergence and divergence processes are maintained throughout evolutionary and ecological processes (e.g., the presence of apex predators regulates prey patterns in addition to other bottom-up effects)
Naturalness (1st order indicator)	As another latent variable, naturalness, qualifies the human ecological impact in a gradient from intact to impacted. As a qualitative indicator, it can be described at three levels: (1) intact, (2) deteriorated and (3) impacted. An impacted condition reflects a strong modification of ecological processes and species interactions due to a heavy human presence (i.e., thru the loss of species and interactions as well as their habitat transformation). A deteriorated condition reflects certain level of human footprint, but mechanisms of self-regulation and self-organization allow the ecosystem to recover without human influence. An intact condition reflects a null (or almost imperceptible) human impact on species interactions and their habitat; i.e., assumes that enough suitable habitats are available to sustain viable populations. The main components for naturalness integrate the modifications of prey and predator diversity indicators, as well as functional diversity, measured as the number of functional groups. Naturalness is also an indication of spatial intactness (i.e., the inverse of habitat fragmentation) in the landscape when the human impact on habitats is considered
Mobile links (2nd order indicator)	Trophic mobile links are a measure of the buffer capacity and opportunity for reorganization after environmental impacts (Lundberg and Moberg, 2003). Therefore, the functional role of predators in maintaining landscape functional unity is accounted by the mobile link indicator. As developed here, trophic links increase positively with landscape heterogeneity and trophic (habitat) connectivity. Apex predators, as process linkers, also play a role in stability since stable conditions are directly affected by mobile links. Mobile links can be associated with some other properties, including predation risk (as trait-mediated effects), and control effects in prey and meso-predators (as density-mediated effects), and the landscape of fear (Coleman and Hill, 2014; Estes et al., 2011)
Biodiversity (2nd order indicator)	Biodiversity represents the richness in the pool of species (i.e., 239 mammal species) identified within interaction networks for extant top predators (Puma *concolor, Panthera onca, Ursus americanus, Leopardus pardalis, Leopardus wiedii, Canis latrans, Puma yagouaroundi* and *Lynx rufus*). The spatial indicators associated with biodiversity integrate the measures of prey and predators' richness, and their spatial distribution in the landscape
Spatial (habitat) intactness (2nd order indicator)	Spatial intactness is an attribute of the natural remnant landscape. As a measure of the amount of natural remnant habitat and connectivity, is an inverse measure of habitat fragmentation. As such, it combines the measures of habitat (remnant) amount and habitat connectivity

highly similar to that based on the general indicator alone. In addition, the evaluation based on 1st order indicators offers more information regarding the spatial heterogeneity of the remnant integrity conditions, as presented in Section 3.3.

On the other hand, an evaluation based on the linear combination of manifest indicators (i.e., 4th level) alone captures almost 85% of the variability in ecological integrity (Fig. 4). This is also supported by the weights obtained among hierarchical levels, where the highest weight ($R^2 = 0.846$) is identified for manifest variables. Therefore, although incomplete, an evaluation based on manifest indicators will be a good surrogate for the general indicator evaluation. Finally, an evaluation based on 2nd order indicators alone is clearly not sufficient for a similar evaluation based on the general indicator ($R^2 = 0.516$). Therefore, the status for all predator species is evaluated with the 1st order ecological integrity indicators, in addition to the general indicator. The results of the evaluation are presented in the following sections.

3.2. The status of ecological integrity (general indicator) for apex predators

The nation-wide ecological integrity status for apex predators is shown in Fig. 5. Overall, more than 50% of the remnant natural landscape in Mexico shows "high" (~27%) or "medium" (~29%) levels of ecological integrity combined, only ~7% showed "low" values; and nearly 36% has been human transformed resulting in areas with null integrity for apex predators. Due to the pattern of habitat transformation, there are several differences among the resulting ecological integrity conditions for Nearctic and Neotropical predator species.

Nearctic extant predator species like black bears (*Ursus americanus*), bobcats *(Lynx rufus*), coyotes (*Canis latrans*), and cougars (*Puma concolor*) showed the highest values for high ecological integrity conditions, with values still greater than habitat transformed within their distribution areas. In contrast, Neotropical predators like jaguarondi (*Puma yagouarondi*), margay (*Leopardus wiedii*), jaguar (*Panthera onca*), and ocelot (*Leopardus pardalis*) showed values of habitat transformed greater than the amount of habitat with high ecological integrity. The average amount of habitat with high ecological integrity conditions for all predators is ~37% ± 5.1% for both Nearctic and Neotropical predators. The condition for extinct predators like Mexican wolf and grizzly bears in natural habitats (*Canis lupus* and *Ursus arctos*) showed a different pattern. While the habitat for grizzly bears maintains better ecological conditions ($IE_{high} = 41\%$); natural habitat for Mexican wolf showed only 29% of its habitat with high ecological condition, and ~38% completely transformed.

The best remnant ecological integrity condition for Nearctic

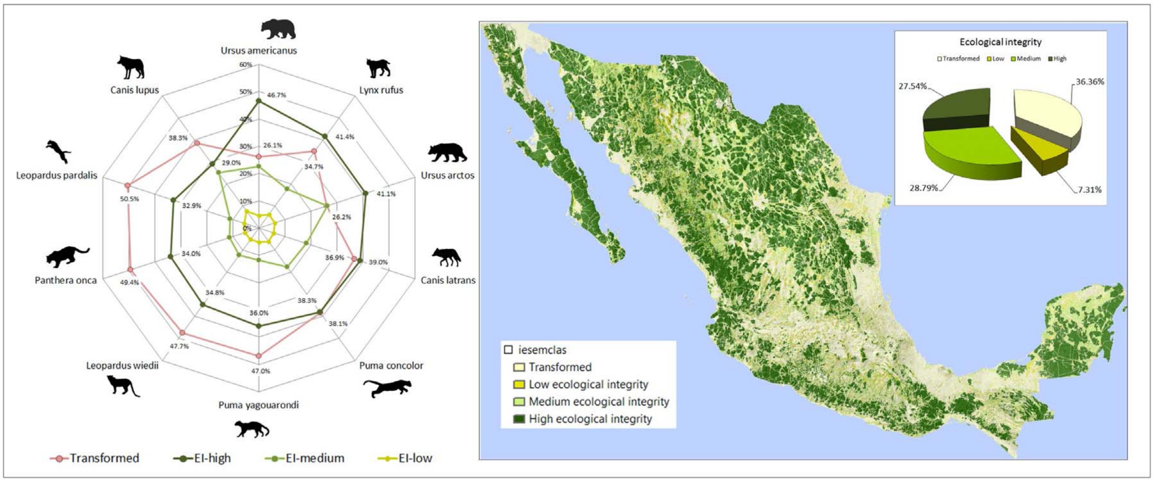

Fig. 5. The status of apex predators in Mexico according with the ecological integrity (general indicator). The general indicator was classified into four different levels of ecological integrity ("high", "medium", "low" and "transformed") in order to evaluate the status for each top- predator within their distribution areas.

predators is observed for black bears, which showed a ~47% of their potential geographic distribution with a "high" ecological integrity status. On the contrary, the Mexican wolf showed only ~29% of its remnant habitat with high ecological integrity in its geographic distribution. All remaining Nearctic species showed values ~41% ± 3.3% of their potential geographic distribution with high ecological integrity. The Neotropical feline apex predators showed a more imperiled situation, which only have, in average ~34% ± 1.3% of their potential distribution with high levels of ecological integrity. The best condition is observed for jaguarondi with 36% of their remnant distribution showing "high" levels of ecological integrity.

For Neotropical predators, the average amount of habitat transformed for each predator (48.6% ± 1.6%) is higher than the remnant natural habitat with any level of ecological integrity in their condition. The average amount of habitat transformed (32.4% ± 5.9%) for Neotropical species is less than the remnant habitat with high ecological integrity. This suggests a mosaic of ecological integrity conditions for individual species which are analyzed in the section describing the status for abstract ecological integrity indicators (Section 3.3).

3.3. The status of abstract indicator conditions for the habitat of apex predators

The status of abstract indicators for extant mammalian apex predators is calculated as a combination of the values obtained for the ecological integrity index (EII_i); the human impact index (HII_i); and the ecological degradation index (EDI_i). The overall status is calculated from the values obtained for all three combinations of 1st order latent indicators of ecological integrity, corresponding to the second level in the hierarchy (Table 3; Fig. 6).

When the status of abstract indicators for all species is compared, a differential pattern between the Neotropical and Nearctic predators emerged (Table 3; Fig. 6). For all species of predators, the ecological integrity index is very low (EII = 0.18 ± 0.03). However, Nearctic species have an ecological integrity index (EII = 0.16 ± 0.01) lower than Neotropical species (EII = 0.21 ± 0.002). Also, ecological degradation is considerably greater for Nearctic predators (EDI = 0.49 ± 0.06) than for Neotropical predators (EDI = 0.28 ± 0.02); although the human impact index is always less for Nearctic species than for Neotropical species. Additionally, the status of human impact for Neotropical predators is characterized with high values (HHI = 0.50; ± 0.02); while Nearctic predators are characterized with lesser values (HHI = 0.35; ± 0.06). However, considering both EDI and HII values, it seems that the effect of "degradation" and "human impact" is greater on Neartic predator species, by showing lower ecological integrity values (EII = 0.16 ± 0.02) than those for Neotropical predator species (EII = 0.215 ± 0.002) within their distribution areas. The highest value for habitat degradation is observed for *Ursus americanus* (EDI = 0.57); while the lowest value is observed for *Panthera onca* (EDI = 0.27). The predators most affected by the human impact is *Leopardus pardalis* (HHI = 0.52) and the least affected is *Ursus americanus* (HHI = 0.27).

3.4. The status of the habitat of apex predators based upon manifest indicators

The status of all apex predators (extant and extinct) within their distribution areas are presented in Fig. 7. Overall, the main effects of

Table 3
Mean abstract indicator values for apex predators in Mexico. *Extinct, ** probably extinct in its natural habitat.

Apex predator	Nearctic	Neotropical	EIIm	HIIm	EDIm	Transformed	EI-low	EI-medium	EI-high
Canis latrans	✓		0.170	0.378	0.452	36.9%	5.8%	18.3%	39.0%
Canis lupus**	✓		0.380	0.396	0.466	38.3%	7.6%	25.1%	29.0%
Lynx rufus	✓		0.171	0.359	0.470	34.7%	6.2%	17.7%	41.4%
Puma concolor	✓		0.175	0.395	0.430	38.3%	6.0%	17.6%	38.1%
Ursus americanus	✓		0.159	0.269	0.572	26.1%	4.6%	22.7%	46.7%
Ursus arctos*	✓		0.145	0.280	0.575	26.2%	6.2%	26.5%	41.1%
Leopardus pardalis		✓	0.215	0.523	0.262	50.5%	5.6%	11.0%	32.9%
Leopardus wiedii		✓	0.212	0.492	0.296	47.7%	5.2%	12.4%	34.8%
Panthera onca		✓	0.217	0.512	0.272	49.4%	5.4%	11.2%	34.0%
Puma yagouarundi		✓	0.217	0.489	0.294	47.0%	5.2%	11.8%	36.0%
Neotropical			0.215	0.504	0.281	48.6%	5.3%	11.6%	34.4%
Nearctic			0.160	0.346	0.494	33.4%	6.1%	21.3%	39.2%

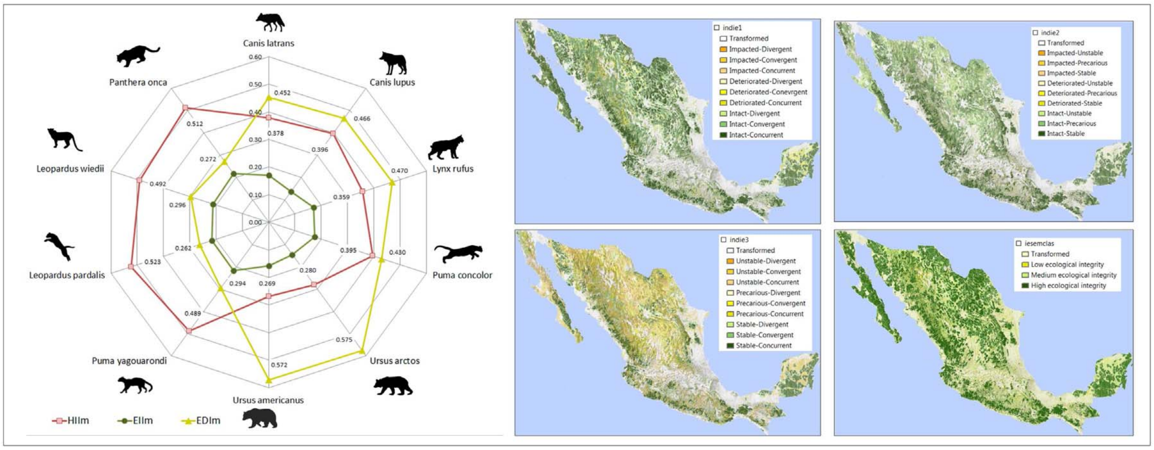

Fig. 6. Status of Nearctic and Neotropical apex predators in Mexico based on abstract ecological integrity indicators. The final scores for HII, EII and EDI are obtained as the average value for each of the combinations among the 1st order latent indicator scores (Self-regulation, Stability and Naturalness) indicated in Fig. 4.

habitat transformation are observed in the decrease of values for the mobile link indicator, as a direct effect of modifying the trophic connectivity and as a result of habitat loss and fragmentation and the interaction of landscape heterogeneity. Additionally, habitat selection is also greatly affected by habitat loss which also directly affects self-organization (Fig. 7). The combined effects of reducing the trophic connectivity and habitat selection have greater effects on self-organization and stability as depicted in the HNS (Fig. 1). The effects of having a reduced capacity for selecting habitats and to perform the trophic link seemed to have greater effects on the resulting ecological integrity, and could be another indication of habitat degradation.

For all Nearctic apex predators, the North American Deserts presented the best ecological conditions in their distribution areas. The Mediterranean California also presented the best ecological conditions for coyotes (*Canis latrans*) and bobcats (*Lynx rufus*); while Temperate Sierras also presented good conditions for cougars (*Puma concolor*) and American bears (*Ursus americanus*). Contrastingly, Neotropical apex predators showed a notable transformation in their original habitat (e.g., tropical rainforests), resulting in better conditions for non-typical habitats (temperate sierras).

4. Discussion

The use of geographical information, describing the species distribution of apex predators and associated prey, has been useful for deriving a set of spatial indicators that characterize the remnant ecological integrity in the landscape of Mexico. When used in a framework that integrates ecological theory, along with latent concept modeling, several spatial indicators of ecological integrity evaluate the capacities of remnant natural landscape to support viability in top predators, as well as to support important ecological functions such as trophic connectivity. Ecological integrity is evaluated here as the capacity to sustain viable apex predator populations, as a response of spatial habitat requirements, and ecological conditions (naturalness, stability and self-organization) and for maintaining predator-prey interactions. However, the results obtained in this study show that only a small area of the country can support such ecological processes. Ecological integrity for apex predators is a feature that disappears when habitat loss and fragmentation prevails as a print of human activity and transformation.

Within an ecological monitoring system framework, ecological integrity indicators are oriented towards a holistic evaluation of the landscape conditions that may sustain ecological attributes needed for supporting key ecological processes such as predator-prey interactions. Here, a surrogate evaluation of landscape conditions is presented when high-cost information for individual species is scanty or non-existent. The information derived here, as a source for characterizing remnant habitat, represents an alternative to individual species' monitoring programs. The information contained in the manifest and latent variables are an indication of the theoretical landscape capacity to sustain viable populations and species interactions. The spatial indicators primarily inform about the landscape status; and within a monitoring system, they may provide a description of the habitat degradation trends for each species when used in a multi-temporal framework.

The ecological integrity hierarchical framework (EHN) (Lin et al., 2009) is used here to represent and preserve the complexity in the ecological integrity concept, and as an aid to select relevant indicators (Fig. 1). With these indicators, the characterization of the ecological condition for natural landscapes describes the status of ecological integrity within a hierarchy of ecological information for all extant mammalian apex predators in the natural landscape of Mexico (viz., *Puma concolor*, *Panthera onca*, *Ursus americanus*, *Leopardus pardalis*, *Leopardus wiedii*, *Canis latrans*, *Puma yagouaroundi* and *Lynx rufus*) as well as for species currently being reintroduced (*Canis lupus*) and one locally extinct apex predator (*Ursus arctos*). All these predators are considered key components for extant predator-prey interactions, and their geographical distributions are considered in the current and reference conditions. A characterization based on the ecologically hierarchy network describes the changes in ecological integrity at various levels of the ecological condition (Lin et al., 2009). The hierarchy describing ecological integrity includes compositional functional and structural elements, which when combined, define the status of the ecological system (Dale and Beyeler, 2001). Altogether, all indicators summarize the current conditions for apex predators, according with the viability for maintaining their interactions and the status of their habitat.

The general indicator (ecological integrity) summarize the current status for top predators, identifying which species showed the best and worst conditions prevailing in their natural remnant habitat. Nearctic predators showed higher levels of ecological integrity in their remnant habitats, particularly for North American deserts and Temperate Sierras, when these are evaluated with the general indicator. In contrast, Neotropical predators showed the highest amount of habitat transformation. This has resulted in the loss of original habitat of the species, leading to a valorization of other habitats (e.g., temperate sierras) as a source to maintain apex predator viability. Nevertheless, the function of apex predators is highly imperiled by habitat loss and fragmentation, which significantly reduce trophic links and habitat selection in their home ranges, and which have direct effects on stability and self-organization, and ultimately in ecological integrity.

Latent indicators showed a higher habitat transformation for Neotropical predators than Nearctic predators. However, the combined effects of habitat degradation and transformation have greater effects in

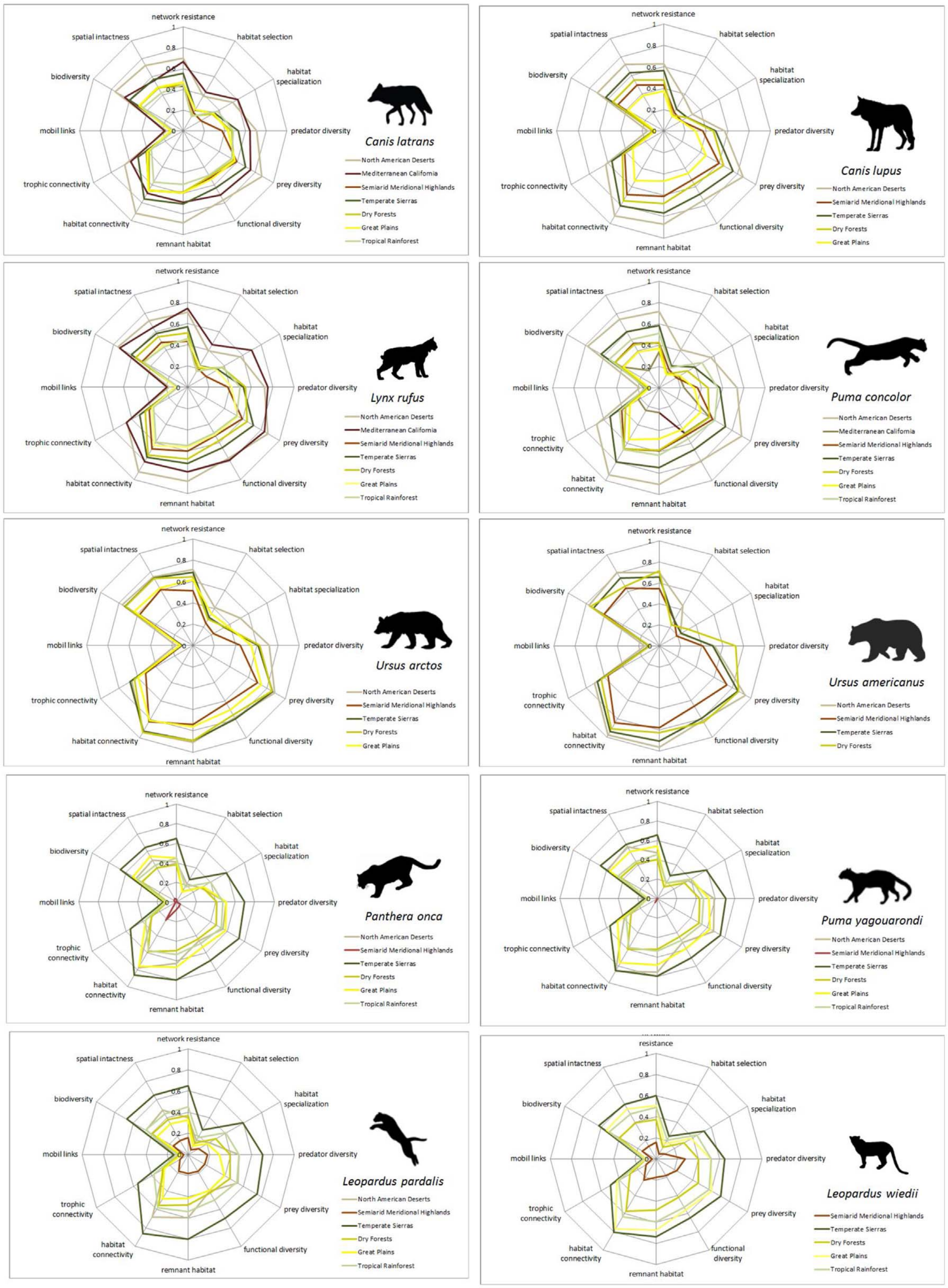

Fig. 7. The status of manifest and 2nd order latent indicators within ecoregions in Mexico, for Nearctic apex predators (coyotes, Mexican wolf, bobcat, cougars, grizzly bear and black bear); and Neotropical apex predators (jaguar, jaguarondi, ocelot and margay).

ecological integrity in Nearctic predators than for Neotropical predators. This has resulted in less areas with intact-concurrent, intact-stable, and stable-concurrent conditions for Nearctic predators (such as cougars, bobcats, and coyotes), than those observed for Neotropical predators (e.g., jaguars and ocelots). Certainly, this situation calls for conservation and restoration programs with different objectives. The main threat for Neotropical species is habitat loss and transformation of natural habitat, while habitat degradation is the main threat for Nearctic species.

The resulting pattern observed for the differences between Nearctic and Neotropical predators is primarily the result of the historical process of land use and land cover transformation in the country. Tropical areas have been continuously deforested as a result of policies oriented towards agricultural production (e.g., crops and cattle) since the 1970s, and evidence has shown that is a continuing process without being diminished (Rosete-Verges et al., 2014). In the Mexican Neotropics, increasing land use and land cover change (LULC), as well as a strong deforestation trend, have characterized the second half of the 20th century, which has resulted in habitat degradation and habitat loss (Kolb and Galicia, 2012). Deforestation process concentrate in particular areas, which showed major forest conversions to grasslands and slash-burning (Díaz-Gallegos et al., 2010). However, recent estimates (1993–2007) showed that forest degradation surpasses tropical deforestation by a 1.7 factor (Kolb and Galicia, 2012), making habitat restoration to intact conditions for large predators practically impossible. Since Neotropical top-predator species showed a high amount of transformed habitat, it seems logical to associate the amount of remnant habitat to LULC trends. However, the low values in the degradation indicators can be more associated to the complete loss of areas with secondary vegetation and degraded lands, since the subsistence of economic activities along with federal and regional land use related policies leads first to forest degradation (through extraction of timber and non-timber products) before forest areas are eventually deforested (Kolb and Galicia, 2012).

Contrastingly, Nearctic areas in Mexico have shown less LULC changes because these are primarily arid and semi-arid landscapes non suitable for agriculture, and some arid forest lands. Therefore, the Nearctic landscape in Mexico shows virtually no deforestation rates, as compared with tropical regions. Habitat transformation can only be explained by land cover changes to urban areas and some agricultural conversions (which are rare, because their low potential for agriculture). However, habitat degradation may play a factor for reducing areas with high ecological integrity, particularly those in which the extension for population viability has been reduced by roads and other changes that lead to habitat fragmentation. Then, spatial intactness and mobile links are the indicators most affected as a result of habitat and trophic fragmentation.

Due to landscape changes and LULC dynamics in the country, naturalness in habitat conditions might be also a misleading indicator of ecological integrity if stability and self-organization are not also considered in an evaluation. All indicators associated with natural conditions (biodiversity, spatial intactness, predator and prey richness) are among the indicator with the highest values of integrity for all species and for all ecoregions. Degradation in the natural landscape, particularly when habitat selection, trophic connectivity, and mobile links are considered, is the condition resulting from the modification of these indicators that have a greater effect on self-organization and stability in the predator-prey interaction networks. Predator functions can be highly modified even if "natural" areas remain with apparently low human impact.

5. Conclusions

The current status of ecological integrity for apex predators in Mexico is at peril. The ecological integrity index (EII) for remnant habitats is very low (EII = 0.18 ± 0.03) for all top predators, with an extension of less than 40%, except for *Ursus americanus* which is ~47%, of their remaining natural habitat with high integrity values. The ecological degradation index (EDI = 0.49 ± 0.06) is greater for Nearctic species than for Neotropical species (EDI = 0.28 ± 0.02), indicating that habitat restoration activities may be a priority for areas with predators such as cougars (*P. concolor*) bobcats (*L. rufus*) and coyotes (*C. latrans*), particularly to improve trophic connectivity and their function as mobile links. The human impact index (HII) indicates that Neotropical species (*P. onca, P. yagouarondi, L. pardalis* and *L. wiedii*) still have the major impacts of habitat transformation and loss (HII = 0.5 ± 0.02), as compared with Nearctic species (HII = 0.35 ± 0.06); which also present values of transformed habitat close to 50%.

The major impacts of habitat loss and transformation are indicated by low integrity values in habitat selection and mobile links. While intact conditions seemed to prevail when naturalness indicators are analyzed, the major effects of habitat loss and transformation are mainly observed in stability and self-organization. Therefore, indicators of biodiversity and even spatial intactness can be misleading of other emergent properties such as stability and self-organization in trophic interactions.

Finally, the ecological hierarchy framework is proven to be a useful tool for selecting adequate geographic information that can be translated to spatial indicators to monitor and evaluate the status of ecological integrity. All spatial indicators are currently used to integrate a spatial decision support system for the evaluation of human impacts on ecological integrity.

Acknowledgements

I would like to thank Dr. Esther Quintero (CONABIO), and Dr. Louis R. Iverson (USFS) and two anonymous reviewers for insightful comments on previous manuscripts. This research was supported by CONABIO and is part of the Spatial Decision Support System for evaluating Human Impacts on Biodiversity (SIESDIB).

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