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ANALYZING KEY ECOLOGICAL FUNCTIONS FOR TRANSBOUNDARY SUBBASIN ASSESSMENTS[1]

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ABSTRACT: *We present an evaluation of the ecological roles ("key ecological functions" or KEFs) of 618 wildlife species as one facet of subbasin assessment in the Columbia River Basin (CRB) of USA and Canada. Using a wildlife-habitat relationships database (IBIS) and GIS, we have mapped KEFs as levels of functional redundancy (numbers of species with particular KEF categories) that may occur within subbasins and subwatersheds historically and at present. Natural levels of functional redundancy are presumed to be desirable for contributing to resilient ecosystems. Our "functional analyses" complement analyses of habitats and species, and serve to inform on the degree to which wildlife communities are "fully functional" and how that functionality can be influenced by changes in habitats. The focus of the paper is on the use of KEFs but we also have provided, for the first time, the analysis in a transboundary CRB context by merging data on US and Canada. The analysis depicts historic, current, and changes in functional redundancy for selected KEF categories; total functional richness (number of KEF categories performed by all wildlife species in an area); and functional diversity (functional richness weighted by functional redundancy). The maps denote parts of the subbasin that are strong or deficient in specific ecological functions. Land managers could use the maps to guide restoration or conservation priorities for ecological functions of fish and wildlife.*

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INTRODUCTION

For many years now, ecosystem management has incorporated consideration for effects of mostly abiotic ecosystem processes and disturbance regimes such as hydrology (e.g., flooding), climate and meteorological phenomena (e.g., wind storm, ice storms), fire, mass wasting (e.g., slope failure), and other such topics (e.g., Campbell et al. 1996, Gorte 1995, Strange et al. 1999). However, with a few exceptions, the ecological roles of organisms serving to shape environmental conditions for themselves and other species have been largely ignored. Such biotic "key ecological functions" (KEFs) of organisms refer to the major ecological roles that organisms play in their ecosystem that can influence system diversity, productivity, and eventually sustainability of resource use and production (Marcot and Vander Heyden 2001).

In this paper, we explore the use of wildlife-habitat relationships (WHR) databases, that incorporate categorical information on KEFs, to assess the degree of ecosystem function. While the focus of this paper is on KEFs, we also want to note that we have, for the first time, depicted transboundary conditions of ecological functions in the CRB (CRB) by assessing and displaying ecological functional conditions the US and British Columbia (BC), Canada. Wildlife-habitat and KEF databases have already been developed and used for such "functional assessments" in the interior CRB, US (Marcot 1997) and in Washington and Oregon (O'Neil et al. 2001). We report here on how such databases and assessments have been expanded to include all wildlife species and their KEFs in the entire CRB in USA and Canada, an area of 260,000 mi^2 (673,400 km^2). Our objectives are to summarize and present preliminary results of our assessments of patterns of species' KEFs, to illustrate how to map and interpret patterns of KEFs over space and time, and to discuss implications for transboundary ecosystem management.

METHODS

To create the transboundary WHR database, we built upon and synthesized existing WHR databases developed in the US and British Columbia, Canada. Specifically, during 1998-2002, the Northwest Habitat Institute (NHI, Corvallis, Oregon, www.nwhi.org), with additional input from US and B.C. experts, expanded the existing WHR databases cited above to include all wildlife (non-fish vertebrate) and selected fish species. The expanded database has been named IBIS – Interactive Biodiversity Information System – which is housed by NHI. IBIS contains data tables on fish and wildlife species and their habitats, interactions, and ecological functions (Fig. 1).

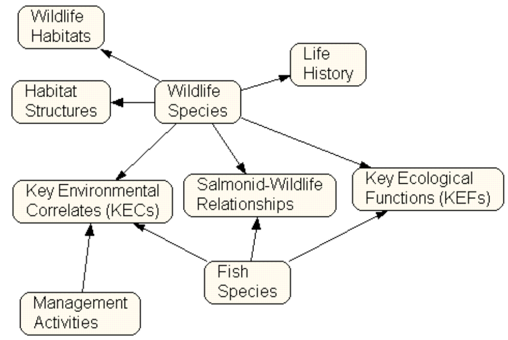

Figure 1. Categories of species information in the IBIS database.

The IBIS database, like its predecessors, was built from a synthesis of ecological literature and expert opinion. Information in IBIS on habitat associations, KEFs, and fish-wildlife relations are mostly categorical and qualitative, and data on some of the life history attributes are quantitative. In this report, we focus on the wildlife portion.

In IBIS, KEFs are depicted for each of the 618 wildlife species categorically. A hierarchical classification system of KEF categories for wildlife was developed (Marcot and Vander Heyden 2001) which codes some 87 categories of KEFs (including headings and subheadings in the classification). The 8 major headings are nutrient cycling, disease transmission, and trophic, organismal, soil, wood structure, water, and vegetation structure and composition relationships.

In IBIS, each species is assigned appropriate KEF codes. For example, Northern Flying Squirrel (*Glaucomys sabrinus*) is coded for 16 KEF categories including fungivory (fungus feeder), prey for predators, secondary cavity user, disperser of fungi, lichens, and seeds, primary creator of tree canopy nests possibly used by other species, and other functions. With such a database, one can determine the set of ecological roles (KEFs) played by a species or group of species, or, alternatively, the species occurring in a particular habitat that play a particular ecological role. For example, there are 11 wildlife species that disperse fungi (elk, 2 voles, 2 mice, 5 squirrels, and pika); in particular habitats, a subset of these species may help distribute mychorrizal fungi that benefits growth of conifer trees which in turn are desired for wood fiber or for contributing to overall ecosystem health.

We queried the IBIS database to determine the number of wildlife species in specific wildlife habitats that associate with each KEF category. We then mapped those numbers in subbasins (4th-code HUCs or hydrologic unit codes, in the USA hydrologic mapping system; Seaber et al. 1987). Such maps were produced for a variety of individual KEF categories across the US-Canada border in the CRB. In this report, we present results of 3 KEF categories which we selected to illustrate the mapping and assessment procedure:

3. Organismal relationships
    - 3.4 Transports viable seeds, spores, plants, or animals
    - 3.9 Primary cavity excavation in snags or live trees
5. Soil relationships
    - 5.1 Soil digging or burrowing (improves soil structure and aeration)

The numbers (3.4, 3.9, and 5.1) refer to the KEF codes as they appear in the IBIS database.

As we manage for healthy systems, we are actually managing for the healthy functions within those systems. The question is, what are the functions, and how can we represent and measure them? A basic tenet of our functional assessment is that patterns of KEFs can be depicted with *functional redundancy* (the number of wildlife species performing a specific KEF) and that greater functional redundancy may be desirable in that it imparts a greater resilience of the ecosystem to adverse perturbations and disturbances (Naeem 1998, Rosenfeld 2002). We color-ramped the KEF maps to depict quartiles of functional redundancy levels, making it easy to pick out geographic areas with high and low redundancy, which may be interpreted as areas with high and low ecosystem resilience.

We also calculated *total functional richness* (number of KEF categories performed by all wildlife species in a habitat and area) to produce a map of *total functional diversity* (functional richness weighted by functional redundancy; Brown 1995), which is analogous to species diversity but for KEFs. These composite indices summarize functional patterns across species and KEF categories, and in a way denote the total functional capacity of a community. High total functional richness and functional diversity imply the presence of many ecological functions, even levels of redundancy across functions, and functionally resilient ecological communities. We related patterns and changes in specific KEFs, total functional richness, and functional diversity, to human activities such as conversion of native wildlife habitats to anthropogenic environments.

The mapping of KEFs is based on 32 wildlife-habitat types that were defined based on 119 plant associations that were identified for the Pacific Northwest and the similarity of wildlife species related with each association (Johnson and O'Neil 2001). Wildlife-habitat types for the US were developed using the National Biodiversity Gap Analysis GIS mapping data layers as a base (with some modifications). Canada mapping was done by establishing relationships within the knowledge tables of the Terrestrial Ecosystem Mapping (TEM), Predictive Ecosystem Mapping (PEM) and Terrestrial Resource Information Mapping (TRIM) GIS data layers. Using the maps of wildlife-habitat types, a wildlife species list was generated for the entire CRB. Then the numbers of wildlife species were related to each habitat type and to each KEF category, and were weighted based on the area of wildlife habitat within each subwatershed. This resulted in a weighted estimate of functional redundancy (number of wildlife species) for each KEF category, within each subwatershed. This was done for historic and current conditions and the percent differences were then mapped. The Canadian portion followed a similar methodology.

Hydrologic unit maps in the US and BC were not available at the same resolution, which resulted in greater map detail in the US portion of the Basin. We also used changes in vegetation conditions in the US portion of the Basin from early historic (ca. 1850) to current times to map changes in functional patterns. We developed a map of historic to current changes in functional redundancy of one function -- KEF 5.1 (soil digging or burrowing) – as an example, and we related results to anthropogenic alterations of vegetation conditions.

RESULTS: KEY ECOLOGICAL FUNCTIONS ACROSS BOUNDARIES

Here, we present results on queries of wildlife ecological functions for the three KEF categories of transporting (dispersing) viable seeds, spores, plants, or animals; primary cavity excavation in snags or live trees; and digging or burrowing in soil that potentially improves soil structure and aeration.

Levels of Functional Redundancy

In the CRB, there is a greater functional redundancy (number of wildlife species) of the ecological role of transporting viable seeds, spores, plants, or animals, and of digging soil to improve structure and aeration, in the US than in Canada, but slightly greater redundancy of primary cavity excavators in Canada than in the US (Table 1).

Some of these differences in functional redundancy may be due to latitudinal effects, with fewer wildlife species occurring further north in general, but the influences of local habitats as well as geography are important factors as well, as is explored next.

Maps of Functional Redundancy of Selected KEFs

Maps of current levels of functional redundancy of these three KEF categories show some striking similarities as well as differences that illustrate how the distribution of habitats influence species and functions. For example, KEF 3.4 (transportation of seeds, spores, plants, and animals) has its greatest current redundancy in mountainous habitats, including the Columbia Gorge, Cascade Mountains, Blue

Table 1. Functional redundancy (number of wildlife species) in three categories of key ecological functions (KEFs).

KEF	Category	Functional redundancy U.S.	Functional redundancy Canada
3.4	Transports viable seeds, spores, plants, or animals	200	150
3.9	Primary cavity excavator in snags or live trees	17	18
5.1	Digs soil, improves structure & aeration	81	29

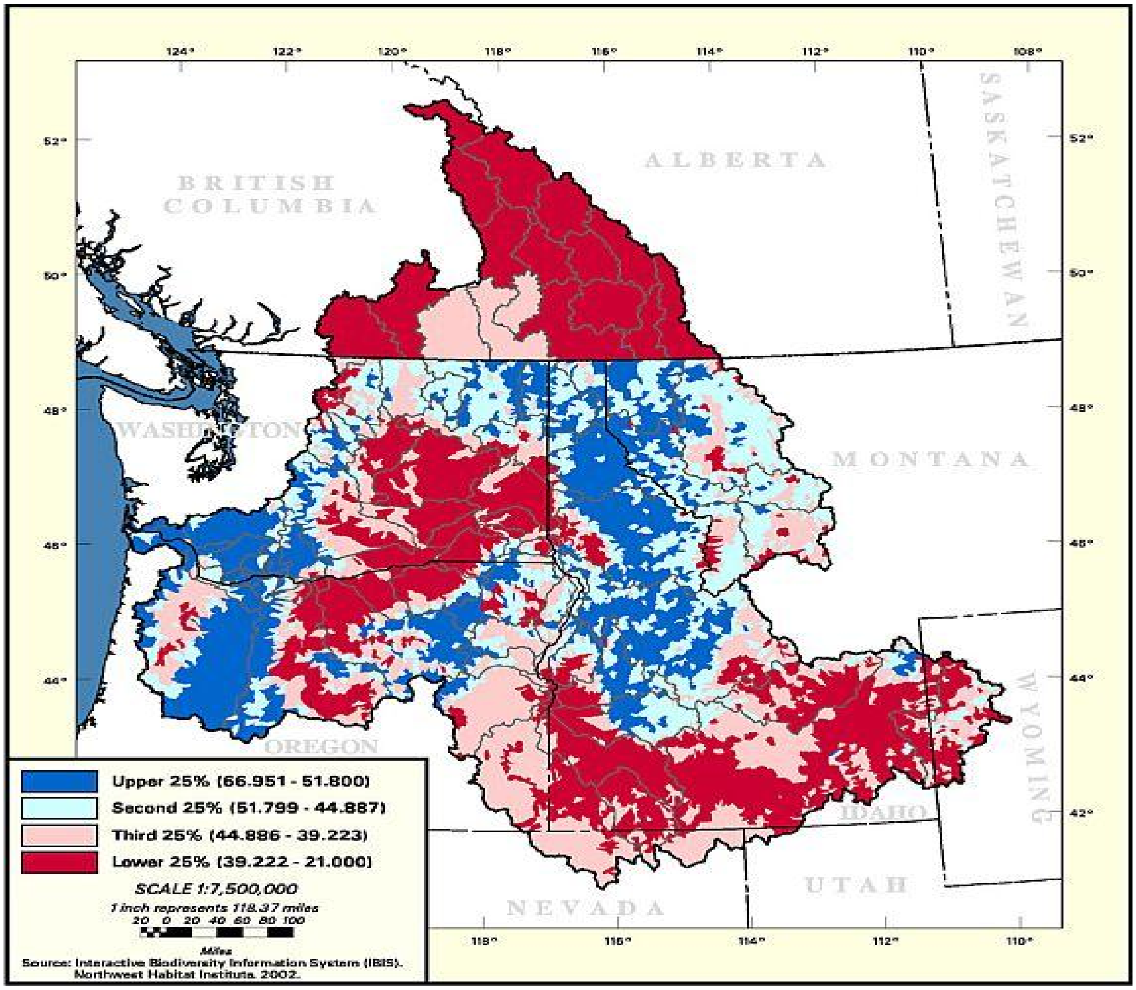

Figure 2. Current functional redundancy (number of wildlife species) of key ecological function 3.4 - transports viable seeds, spores, plants, or animals

Mountains, and the Rocky Mountains. It is least redundantly represented in interior lowlands including the Columbia Plateau and Snake River Basins in the US, and much of the north including the Okanagan River valley in Canada (Fig. 2).

The current functional redundancy levels of EF 3.9 (primary cavity excavator) shows very similar patterns to that of KEF 3.4 in the US, with somewhat lower levels in the Cascade Mountains but higher overall levels in Canada (Fig. 3.).

On the other hand, patterns of current functional redundancy of KEF 5.1 (digs soil, improving structure and aeration) are quite different, showing highest levels in the interior grasslands, sagebrush steppe, and agricultural lands of the Columbia Basin, eastern Oregon, and Snake River Basin. Lowest levels are found in the Willamette Valley, Cascade Mountains, Rocky Mountains, and throughout Canada (Fig. 4).

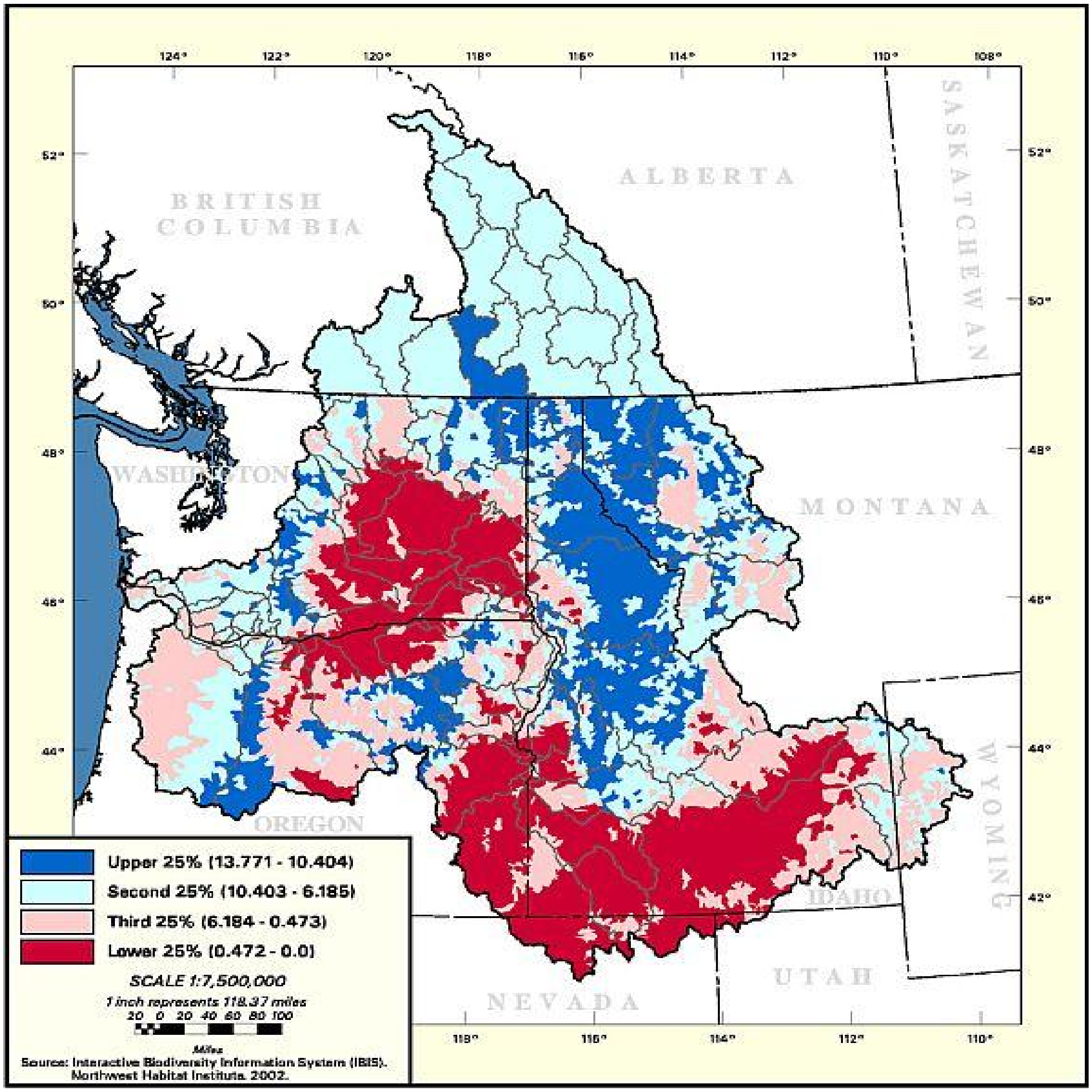

Figure 3. Current functional redundancy (number of wildlife species) of key ecological function 3.9 – primary cavity excavator in snags or live trees.

The differences in patterns of current functional redundancy of these three KEF categories can be explained by the different sets of wildlife species with these KEFs, and the different habitats and geographic areas occupied by these species. Very simply, all else being equal, one would expect to find more wildlife species that excavate trees in forest (montane) environments than in non-forest (inland valley) environments. However, not all KEF categories are this straight-forward, and patterns of KEFs less clearly tied to specific habitats or habitat elements become very useful indicators of far more subtle conditions and changes. For instance, we could not have predicted *a priori* the patterns of KEF 3.4 (transports seeds, etc.).

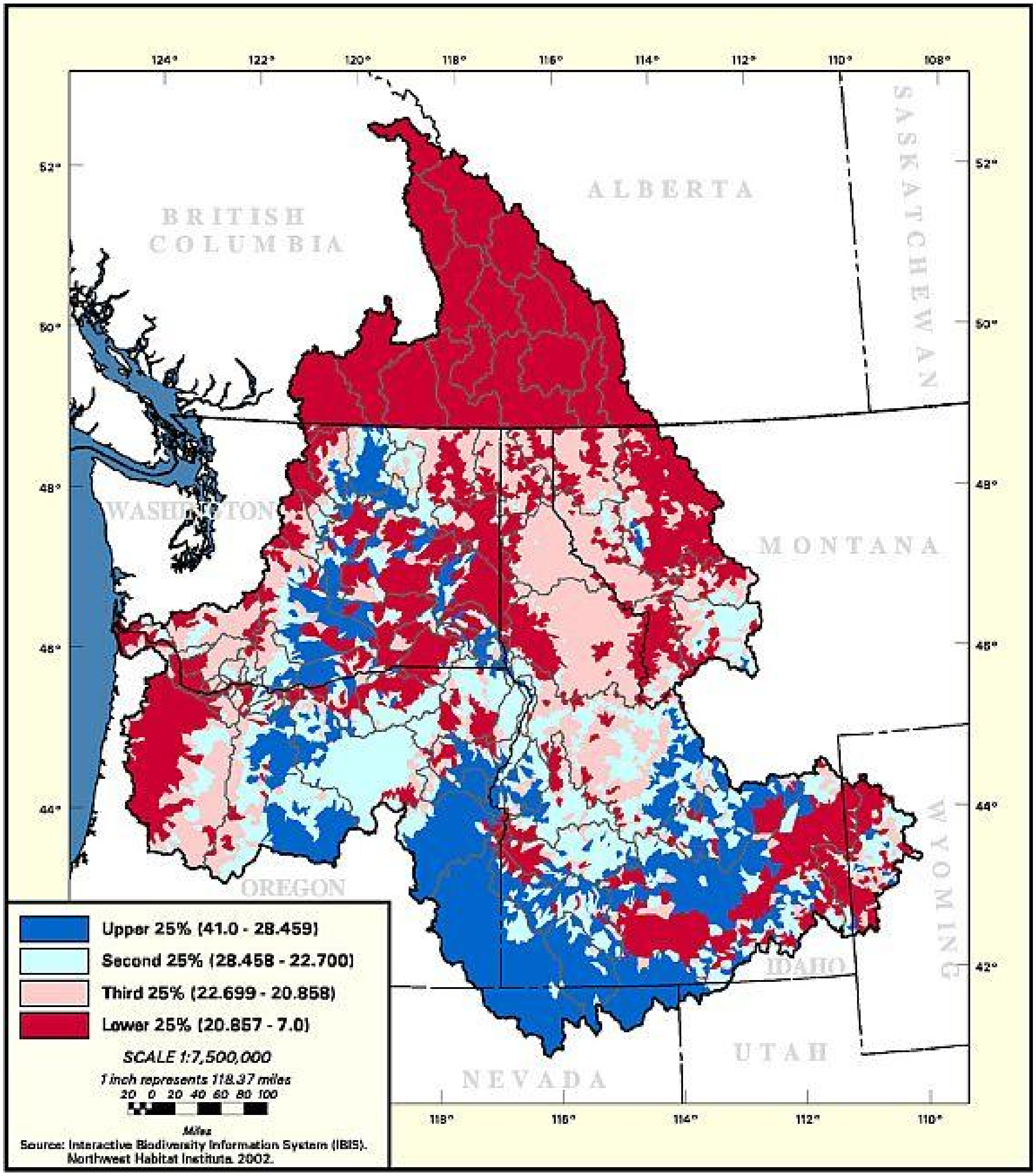

Figure 4. Current functional redundancy (number of wildlife species) of key ecological function 5.1 - digs soil, improving structure and aeration.

Summary Map of Total Functional Diversity

The map of total functional diversity depicts, at a glance, the overall levels of the functional capacity of wildlife communities and ecosystems (Fig. 5). In general, with local exceptions, total functional diversity is lowest in the inland valleys (Willamette, Columbia Basin, Snake River Basin) and in BC, and highest in montane environments (Cascade Mountains, Rocky Mountains, Blue Mountains, Okanagan Highlands, and South Selkirks) of the US.

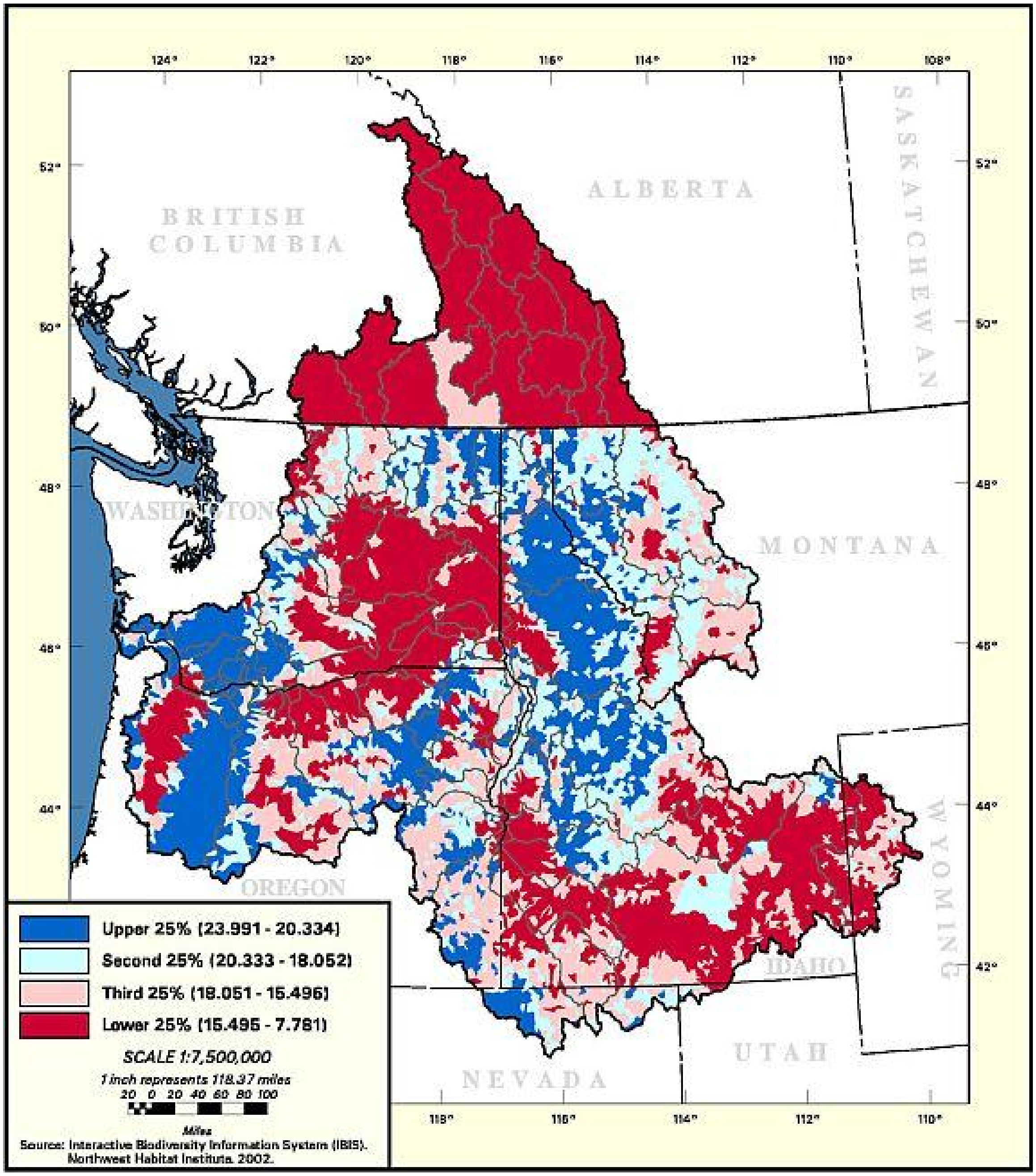

Figure 5. Current total functional diversity (functional richness weighted by functional redundancy) across all wildlife species and their categories of key ecological functions.

This overall pattern is because of patterns of species richness and total functional richness – there are more wildlife species and more total number of their KEFs in montane environments than in lowland environments, and fewer species in higher latitudes.

These patterns are also explained by so much of the interior valley systems having been drastically simplified and altered from their historic, native grassland and sagebrush steppe condition, to their current agricultural and urban uses. Such changes have sacrificed the number of species and functions in these areas. For example, 48 species are closely associated with interior shrub steppe, and these species perform a collective 58 KEFs. Compare this with urban environments, which have on 20 closely-associated species with a collective 46 KEFs.

Historic Changes in Functional Patterns

Quite salient were the patterns of historic to current changes in functional redundancy levels of KEF 5.1 (soil digging or burrowing) in the US (Fig. 6). This soil-digging ecological function has suffered losses throughout most of the CRB in the US except in some of the more remote montane environments. The greatest declines have been in the inland valleys with much conversion to agriculture. This is because wildlife species with this soil-digging function that are associated with native grassland and sagebrush steppe habitats are generally not associated with agriculture, cropland, or urban environments.

Other KEF categories may have very different patterns of change between historic and current conditions. For example, the KEFs of primary cavity excavation and secondary cavity use have increased in areas where conifer trees have invaded grassland, sagebrush, or even agricultural environments.

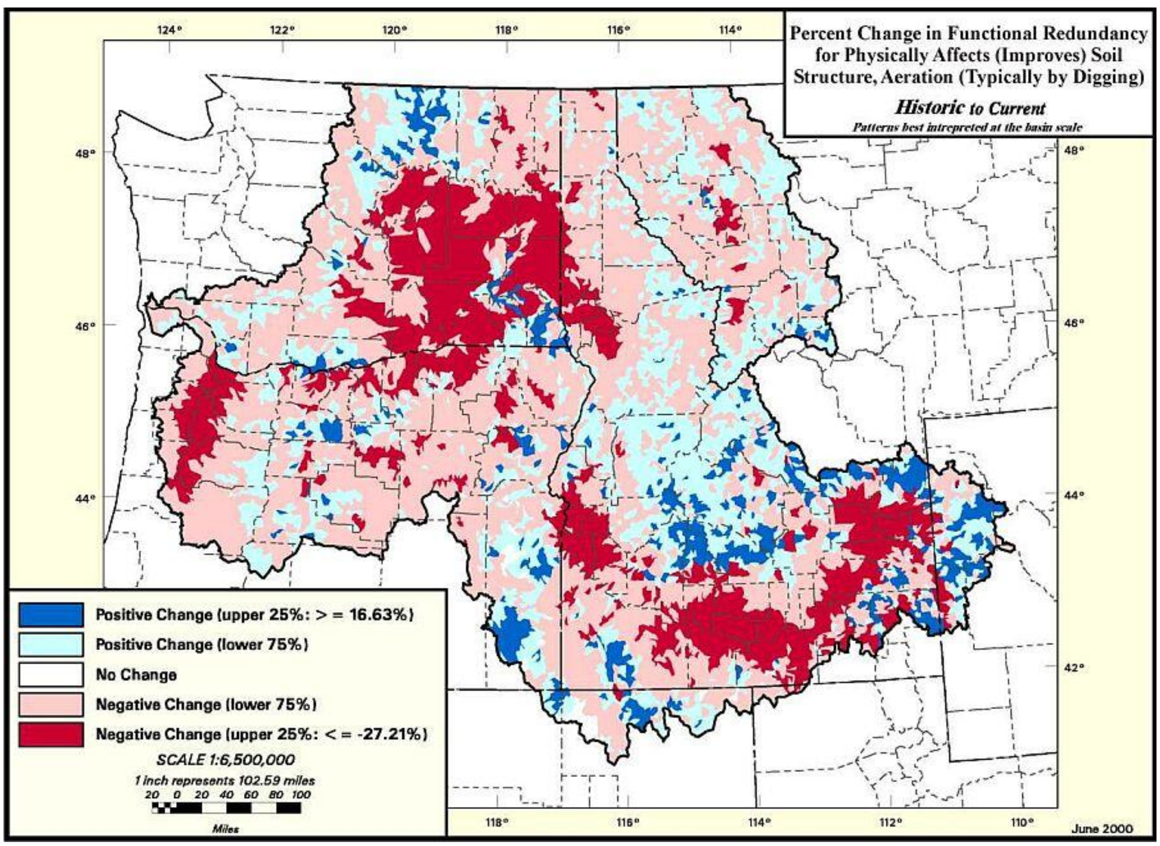

Figure 6. Changes from historic to current levels in functional redundancy (number of wildlife species) of key ecological function 5.1 - digs soil, improving structure and aeration. Historic maps were unavailable for the Canadian portion of the CRB.

DISCUSSION

This likely is the first time that patterns of functional redundancy, richness, and diversity have been mapped for the transboundary area of the CRB in US and

Canada. While the level of mapping is coarse-grained, with a somewhat uneven mapping resolution in the US and Canada, it marks a major advance in visualizing the functionality of wildlife communities across very broad areas as influenced by human activities over time.

Who might use such analyses? The analysis approach and the databases on species ecology and KEFs are currently being incorporated into subbasin assessment procedures for CRB, and will be used to inform subbasin planning for fish and wildlife through the Northwest Power Planning Council, Portland, Oregon. The analysis methods, databases, and results will be made available to subbasin analysts and planners throughout the CRB.

Surely, the maps could be presented differently, and our specific use of quartiles of functional redundancy levels resulted in only one set of possible patterns. We encourage the land planning analyst to explore other, perhaps more useful or appropriate, ways to map patterns of ecological functions.

Functions, Habitats, and Species: An Assessment Triad

We also strongly emphasize that our *functional assessments* should be viewed only as a complement to additional assessments of specific *habitats* and *species* of management interest. Our experience suggests that patterns of habitats, species, and functions provide complementary information. For example, a diversity of abiotic substrates, conditions, and processes likely lends to greater biodiversity, just as greater levels of functional redundancy among organisms lends to greater ecosystem resilience to perturbations.

We strongly suggest that patterns of KEFs be matched with knowledge of which specific habitats and species contribute to those functions. Under different habitat conditions, the same function may be represented by fewer or different species. An example of a decline in species is with the KEF pertaining to species that build nests and other structures in trees, that in turn can be used by other species. In Medium and Large Tree structural conditions of Eastside Mixed Conifer Forest in Washington and Oregon, 4 species closely associated with this condition perform this function, including Northern Goshawk, Northern Flying Squirrel, and two other more common squirrels. Now, if a fire were to reduce such a forest to early Grass/forb and Shrub/seedling structural conditions, only Northern Goshawk would occur, closely associated with these conditions and, in this case, but only for foraging and not for nest-building (so this function is effectively lost in these structural conditions). If one considers less closely-associated species, others with this function may also occur in these conditions. But the lesson here is on the specific influence of vegetation structural conditions on resulting species composition.

Often, following common disturbances such as conversion of native grasslands to agriculture, some of the same functions may be represented by far more common – and sometimes less desirable -- wildlife species, with the more rare species lost. For instance, some 9 wildlife species that dig burrows (KEF 5.1) are closely associated with native interior grasslands (Burrowing Owl, Montane Vole, Deer Mouse, American Badger, 3 squirrels, and 2 pocket gophers). As this habitat type is converted to agriculture, there are still 9 closely-associated species with this KEF, but they constitute a somewhat different composition (Table 2).

Table 2. Wildlife species closely associated with interior grassland or with agriculture, with key ecological function 5.1 – soil digging or burrowing.

Species	Interior grassland	Agriculture
Burrowing owl	X	
Montane vole	X	X
California vole		X
Gray-tailed vole		X
Deer mouse	X	X
House mouse		X
Belding's ground squirrel	X	X
Columbian ground squirrel	X	
Washington ground squirrel	X	
American badger	X	
Northern pocket gopher	X	X
Townsend's pocket gopher	X	
Botta's pocket gopher		X
Camas pocket gopher		X

There are only 4 species in common that are closely associated with native interior grasslands and agriculture. Note the loss of the Burrowing Owl, a species of high interest and special status in western states and provinces (although we acknowledge that Burrowing Owl likely is more of a secondary burrow occupier, although it will also actively reshape or enlarge existing burrows). Also lost would be two ground squirrels, badger, and a pocket gopher, and gained would be two relatively common species of vole, house mouse (an exotic pest species), and two other pocket gophers. Is this an acceptable change? That depends on the overall management goals. If the goal is to provide this soil-digging function at the same level of functional redundancy, the trade is equable, at least at this simple level of analysis that ignores differences in density and behavior of the species, among other factors. If the goal is *also* to provide for specific species of management interest, such as Burrowing Owl, then the change would require further attention to restoration of native grasslands.

Overall, functional patterns may be rather robust to disturbances, whereas specific habitats and species may be more sensitive. In a further example, fire can change vegetation, altering some structural conditions and habitat elements for wildlife. In a forest setting, fire can decrease tree canopy cover and increase the number of snags, and wildlife species associated with such structural conditions and habitat elements may differ markedly before and after fire disturbance. Whether it is an acceptable change is a question of policy, as informed by science, and depends on specific management goals and objectives for wildlife, ecological functions, and other conditions and resources.

Key Management Hypotheses

Ideally, we would want entirely empirically-based data on actual rates of each KEF performed by each species in each habitat, such as number of viable fungi spores dispersed per unit time and unit area by individual fungivorous organisms. Such data are difficult to obtain and will not be available for most species and KEF categories. We propose that the IBIS database can be used meantime to develop useful maps of KEF patterns showing functional redundancy as a crude surrogate for actual rates of functional roles.

In general, if such maps are compared to historically normative conditions or a desired level of functional redundancy, then they depict the degree to which systems are fully ecologically functional, which is often touted as one major goal of ecosystem management (e.g., Dale et al. 2000, DeLeo and Levin 1997). The power of such an assessment comes from mapping temporal changes in functional redundancy of specific KEF categories and total functional diversity, such by comparing historic to current conditions and current to future states under alternative management scenarios.

Maps of KEF patterns should be viewed as management hypotheses. Where such maps are used to guide critical decisions on land management -- e.g., land acquisition, management allocations, and decisions on conservation, preservation, or restoration activities – specific KEF patterns could be verified in the field through applied research studies.

Several main hypotheses can be listed pertaining to functional assessments, including the following (from Marcot and Vander Heyden 2001):

- Functional redundancy imparts resilience to perturbations.
- Functional redundancy provides for greater levels of sustainability.
- Total functional diversity imparts greater productivity and biological diversity.

The research task would be to test, refine, and quantify these hypotheses and relations, to provide the ecosystem manager with greater power to predict effects on ecosystem function from management activities. As noted earlier, it will be important to recognize differences in kind as well as amount of redundancy, so that changes in species and habitat composition are considered in research and in management planning.

Challenges of Transboundary Mapping

The biggest challenge in conducting this mapping evaluation was the difference in the scale of mapping hydrologic boundaries and wildlife habitats in Canada and the US. Lining up the habitat coverage boundaries within GIS across the border required much time to produce a more or less seamless coverage. Differences remain, however, in the level of resolution of the hydrologic units used in the two countries, but this is soon to be resolved as well.

KEFs and Ecosystem Processes

Our approach pointedly focuses on the ecological roles of organisms, that is, the influence of biotic functions of wildlife. The watershed analyst and land manager might also want to map and address abiotic ecosystem processes as mentioned in the Introduction, to determine how human activities influence those as well, and how such ecosystem processes and disturbance regimes affect environments for wildlife habitats, species, and functions.

As well, we recognize that the categories of KEFs in the IBIS database are rather basic descriptions of the ecological roles of organisms. Our analyses provide mostly qualitative insights into functional patterns and do not recognize differences among population sizes and spatial distributions of individuals. Furthermore, we have yet to learn, and depict in databases, how the same general functions may vary in different habitats and ecosystems. This too may become a research agenda particularly for those functions that are seen to guide management the most.

CONCLUSIONS

We conclude that it is possible to produce maps, for the first time across the US-Canada border, of key ecological functions of organisms, depicting levels of functional redundancy of specific KEFs, total functional richness, and functional diversity. Such maps can depict historic, current, or future functional patterns. They may be useful to land managers to help guide land use planning and help decide and prioritize appropriate conservation and restoration activities to maintain ecosystem function.

We hope this prompts the ecosystem manager to think functionally and to set specific objectives for maintaining or restoring ecological functions of wildlife. Much work remains, however, to validate the KEF databases and maps of functional redundancy, richness, and diversity, and to quantify the relations of these functional parameters to measures of overall ecosystem health, integrity, diversity, productivity, and sustainability.

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