



6

Key Ecological Functions of Wildlife Species

Bruce G. Marcot & Madeleine Vander Heyden

Introduction

An ecosystem is the set of all its component organisms and populations and their ecological interactions with each other and with the abiotic world. Traditionally, wildlife-habitat relationships (WHR) programs, models, and databases have focused on how the presence of terrestrial vertebrates is influenced by environmental conditions, and have mostly ignored ecological interactions. WHR approaches have assumed that wildlife (W) basically is a function of habitat (H), or $W = f(H)$. Further, most evaluations of biodiversity patterns and of imperiled or scarce species have focused only on mapping species counts or evaluating the role of habitat on species' presence and abundance.

In most of these worthy pursuits, community interactions and ecological roles of species—how organisms change their environments by what they do—have been largely absent. That is, as much as organisms are a function of their habitat, environmental conditions, including habitat and resources available for other species, are influenced by the ecological roles of organisms. This chapter provides a foundation for explicitly considering the ecological roles and interactions of vertebrate wildlife and for integrating those roles with the more traditional habitat-based WHR focus.

The Functional Foundation of Sustainable Ecosystems

Much has been written on sustainable management of natural resources and conservation of wildlife populations and natural ecosystems.⁶ Sustainability may be defined as resource use habits that do not outstrip the capacity of an ecosystem to produce desirable conditions and commodities, and often has been seen as a de facto conservation goal. But what influences sustainability? Sustainable use of resources is made possible by ensuring that rates of production are not exceeded by rates of loss plus extraction.⁴³ Further, natural ecosystems are sustainable only when their native biodiversity (the variety of life and its processes) and the functional basis of productivity are maintained. Ultimately, it is the set of ecological roles played by its component organisms, including humans, that influences ecosystem biodiversity, productivity, and sustainability.

To ensure sustainable wildlife populations, conserving threatened or endangered species should not stop at addressing only their individual habitat needs, that is, the $W = f(H)$ relation. In fact, a primary purpose of the Endangered Species Act is “. . . to provide a means whereby the ecosystems upon which endangered species and threatened species depend may be conserved . . .” (Sec. 2[b]). As well, the U.S. Forest Service has moved to an “ecosystem management” basis for planning and management on national forests and grasslands.³⁴ To conserve and manage ecosystems means understanding their dynamics and processes, including the ecological functions of species.

Key Ecological Functions of Wildlife Species

The term key ecological functions (KEFs) refers to the principal set of ecological roles performed by each species in its ecosystem. KEFs refer to the main ways organisms use, influence, and alter their biotic and abiotic environments. “Key” refers to the main roles played by each species. As we show in this chapter, categories of KEFs can be depicted for each species and used in multiple-species planning, biodiversity conservation, and other facets of ecosystem analysis and management.

Background and Theory

Expanding the WHR Paradigm

The explicit use of functional categories for evaluating effects of land use planning on ecological communities appeared in the terrestrial ecology science assessments of the Interior Columbia Basin Ecosystem Management Project.^{23, 24, 28} In that work, the traditional WHR paradigm was expanded by depicting the environmental and functional influences on a species in a “species influence diagram” (Figure 1). The species influence diagram illustrates how the distribution and abundance of a species (or species group) are influenced by key environmental correlates; that a species performs specific KEFs; that KEFs in turn influence the biodiversity, productivity, and sustainability (BPS) of the ecosystem; that management

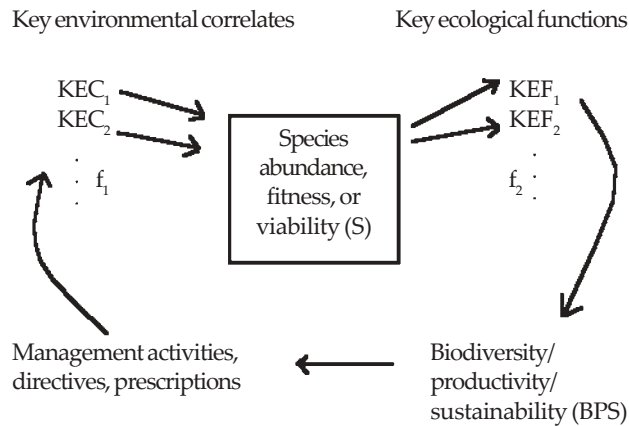


Figure 1. A generalized species influence diagram, showing (1) the relations of species (S) to their key environmental correlates (KECs or habitat elements; f_1 functions) and key ecological functions (KEFs); (2) that species' KEFs influence ecosystem biodiversity, productivity, and sustainability (BPS; f_2 functions); and (3) that management activities can be based on BPS and can influence KECs and habitats, in turn influencing the viability of species. The matrices on the CD-ROM provide data on each of these diagram elements. Arrows represent rates of influence among the elements.

goals for BPS can help establish management guidelines; and that management activities influence species' key environmental correlates. The term "key environmental correlate" refers to wildlife habitats, habitat elements, and other nonhabitat influences on the distribution and abundance of organisms.

We distinguish KEFs of species, which are the biotic and ecological roles of organisms, from abiotic ecosystem processes, which include weather disturbance events and geochemical cycles. In this chapter we focus on the link between species and their environments through KEFs and demonstrate how other components in this overall species influence diagram can be used in evaluations.

Ecological Functions of Vertebrates

It has long been recognized that the ecological roles of vertebrate species influence ecosystems. Only recently, however, has this been integrated into theory and practice.^{7, 42, 44} Examples of some ecological functions of vertebrate species include how:

- browsing or grazing by ungulates can change plant communities;^{1, 3, 14, 41}
- animals can act as "environmental engineers" and influence geomorphology⁵ and ecosystem processes;¹⁷
- frugivores can support viable fruit-bearing plants;²⁵
- pollinators can support plant diversity;³⁶
- seed dispersers⁸ and frugivores¹³ can influence forest succession and regeneration;
- carrion feeding can support the trophic structure of a community;¹²
- carnivore predation can influence populations of ungulate prey species;⁴⁸

- rodents can serve to disseminate beneficial mycorrhizal fungi in western U.S. forests;¹⁸ and
- reptilian primary burrow excavators can provide for avian secondary burrow users.⁴⁶

Many other examples can be found in the literature, especially on ecological functions of plants and invertebrates.

What is the manager to do with all this information? The types and ramifications of ecological functions and interactions in an ecosystem can be overwhelming. This is why we have developed a structured classification of KEFs and provide here a way of considering functions when formulating and evaluating effects of land use management actions. Through the species influence diagram and use of the matrixes on the CD-ROM, management activities can be linked to habitat elements and structures, and thence to species, their KEFs, and their influence on ecosystem BPS.

Ecological Functions Central to the Trophic Structure of Wildlife Communities

Ecological functions of organisms support the trophic structure of ecosystems, that is, energy flows, food webs, and nutrient cycling. More biodiverse systems support wider arrays of ecological functions,^{16, 37} and thus might support a broader or deeper trophic structure. Ecosystems differ in their rates and patterns of primary production (photosynthesis by plants), which largely supports vertebrate primary consumers and much of the rest of the food web and trophic pyramid. Trophic structures differ among ecosystems in that different sets of vertebrate species participate in various ways in providing major standing crop biomass, types and rates of consumption and decay or recycling functions, energy transfer and nutrient cycling, and interspecific interactions including competition and predation. We provide some examples below.

Building a Database of Species' Key Ecological Functions

Purpose

The purpose of building a matrix of KEFs of vertebrates is to provide a consistent framework from which to consider the ecological roles of wildlife in the management of populations, habitats, and ecosystems. A related purpose is to provide a means of posing working hypotheses of the ecological roles of wildlife and effects of management actions on those roles.

Methods

We developed the KEF matrix by first refining the existing hierarchical classification system of KEFs developed by Marcot et al.,²³ and then populating the KEF matrix by denoting the pertinent KEF categories for each species. Marcot et al.'s KEF classification was developed for use with soil microorganism groups, lichens, bryophytes, vascular plants, and invertebrates, as well as vertebrates. To maintain some similarity, we retained their major KEF

categories and numbering system, trimmed out subcategories not pertinent to vertebrates, and expanded some subcategories. As with the original system, our revised KEF classification is strictly hierarchical so that one can query the matrix at various levels of specificity.

In populating the KEF species matrix, we started with that of the Interior Columbia Basin Ecosystem Management Project.²¹ We added pertinent wildlife species not included in that database, including coastal and marine birds and mammals, and deleted species not found in Washington and Oregon. We also reviewed published literature, used our own experience and professional judgment, and sought peer review of the species or KEF categories we added. We lacked data by which to describe KEFs for a species for each wildlife habitat, habitat element, or habitat structure individually.

Database Results

The KEF classification system includes some 85 categories of ecological functions, including major headings and subheadings (Table 1). The 8 major headings are trophic relations, nutrient cycling, organismal relations, disease vectors, soil relations, wood structure relations, water relations, and vegetation relations.

The KEF matrix on the CD-ROM includes 598 wildlife species out of the 755 species identified for the project area. The 157 species not included are considered “accidental” or are subspecies of KEF-coded species. The KEF matrix has 7,319 records, each record being a specific KEF category for a species. Thus, species average 12 KEF categories each (including KEF categories and subcategories, so there is some duplication in this count) and range from 3 (California condor and turkey vulture, both carrion-feeder specialists, the former of only historical occurrence), to 30 (American black bear) KEF categories.

As might be expected, the frequency of species by number of KEF categories roughly follows a normal

distribution that is slightly skewed to the right (Figure 2). That is, few species are coded with very few, or very many, KEF categories, and there are slightly more species with many KEF categories than predicted by a normal distribution. The species with few KEF categories are functional specialists; like the condor and vulture, they perform only a very few functions within their ecosystems. The species with many KEF categories tend to be functional generalists; they perform many functions. We discuss the ecological implications of such functional patterns below.

Patterns of Key Ecological Functions of Vertebrate Species in Washington and Oregon

Following are some examples of various functional patterns of wildlife communities in Washington and Oregon.

Trophic Structure of Wildlife Communities

The KEF matrix can be used to depict general trophic structures of communities by summing number of species according to their trophic and diet relations. In Washington and Oregon as a whole, 50% of all wildlife species are primary consumers (herbivores), 87% are secondary consumers (primary predators), and only 1% are tertiary consumers (secondary predators), with bird species playing a proportionally greater role across this spectrum (Figure 3). Other minor trophic categories include carrion-feeders (6%, mostly birds and mammals), cannibalistic feeders (1%, amphibians, birds, and mammals), and coprophagous feeders (2%, all mammals).

The main (>50 species) primary-consumer categories are spermivores (seed-eaters), frugivores (fruit-eaters), grazers (grass/forb-eaters), foliovores (leaf-eaters), and aquatic herbivores (Figure 4). Amphibians play the main role of feeding on plant material in water on decomposing

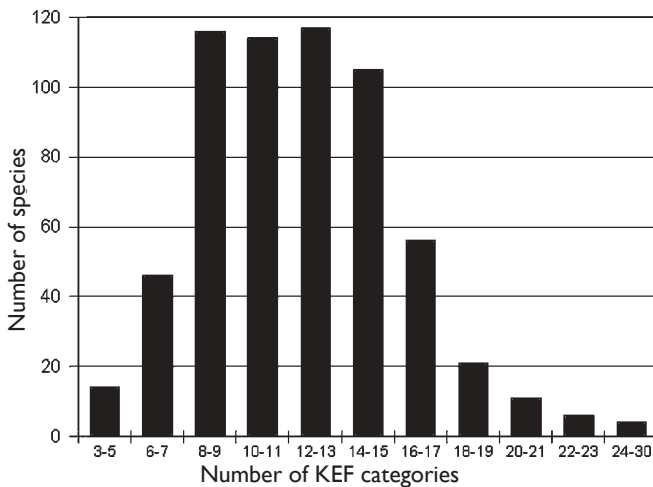


Figure 2. Frequency histogram of number of vertebrate wildlife species in Washington and Oregon by number of categories of key ecological functions (KEFs) they perform, as denoted in the KEF matrix.

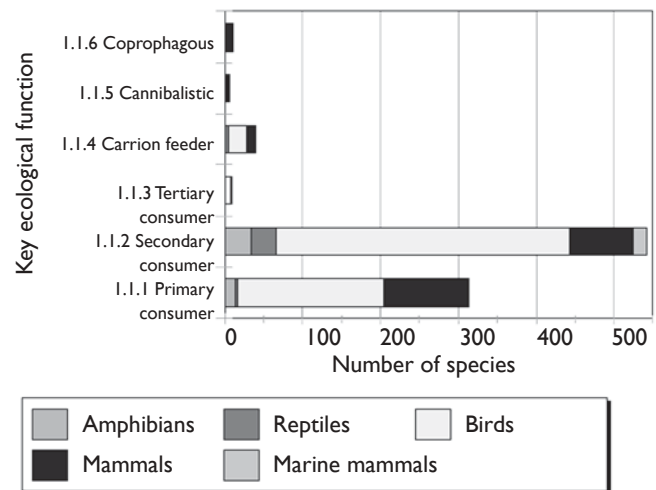


Figure 3. Trophic level functions of wildlife in Oregon and Washington.

Table 1. The classification of key ecological functions of wildlife in Washington and Oregon.

- I Trophic relationships *
 - 1.1 heterotrophic consumer (an organism that is unable to manufacture its own food and must feed on other organisms)*
 - 1.1.1 primary consumer (herbivore; an organism that feeds primarily on plant material) (also see below under Herbivory) *
 - 1.1.1.1 folivore (leaf eater) *
 - 1.1.1.2 spermivore (seed eater) *
 - 1.1.1.3 browser (leaf, stem eater)
 - 1.1.1.4 grazer (grass, forb eater)
 - 1.1.1.5 frugivore (fruit eater) *
 - 1.1.1.6 sap feeder
 - 1.1.1.7 root feeders *
 - 1.1.1.8 nectivore (nectar feeder)
 - 1.1.1.9 fungivore (fungus feeder) *
 - 1.1.1.10 flower/bud/catkin feeder
 - 1.1.1.11 aquatic herbivore
 - 1.1.1.12 feeds in water on decomposing benthic substrate (benthic is the lowermost zone of a water body)
 - 1.1.1.13 bark/cambium/bole feeder
 - 1.1.2 secondary consumer (primary predator or primary carnivore; a carnivore that preys on other vertebrate or invertebrate animals, primarily herbivores) *
 - 1.1.2.1 invertebrate eater
 - 1.1.2.1.1 terrestrial invertebrates
 - 1.1.2.1.2 aquatic macroinvertebrates (e.g., not plankton)
 - 1.1.2.1.3 freshwater or marine zooplankton
 - 1.1.2.2 vertebrate eater (consumer or predator of herbivorous or carnivorous vertebrates) *
 - 1.1.2.2.1 piscivorous (fish eater) *
 - 1.1.2.3 ovivorous (egg eater)
 - 1.1.3 tertiary consumer (secondary predator or secondary carnivore; a carnivore that preys on other carnivores)
 - 1.1.4 carrion feeder (feeds on dead animals)
 - 1.1.5 cannibalistic (eats members of its own species)
 - 1.1.6 coprophagous (feeds on fecal material)
 - 1.1.7 feeds on human garbage/refuse
 - 1.1.7.1 aquatic (e.g., offal and bycatch of fishing boats)
 - 1.1.7.2 terrestrial (e.g., garbage cans, landfills)
 - 1.2 prey relationships
 - 1.2.1 prey for secondary or tertiary consumer (primary or secondary predator)
- 2 Aids in physical transfer of substances for nutrient cycling (C,N,P, etc.) *
- 3 Organismal relationships *
 - 3.1 controls or depresses insect population peaks *
 - 3.2 controls terrestrial vertebrate populations (through predation or displacement) *
 - 3.3 pollination vector
 - 3.4 transportation of viable seeds, spores, plants, or animals (through ingestion, caching, caught in hair or mud on feet, etc.) *
 - 3.4.1 disperses fungi
 - 3.4.2 disperses lichens
 - 3.4.3 disperses bryophytes, including mosses
 - 3.4.4 disperses insects and other invertebrates (phoresis)
 - 3.4.5 disperses seeds/fruits (through ingestion or caching)
 - 3.4.6 disperses vascular plants *
 - 3.5 creates feeding, roosting, denning, or nesting opportunities for other organisms *
 - 3.5.1 creates feeding opportunities (other than direct prey relations) *
 - 3.5.1.1 creates sawwells in trees
 - 3.5.2 creates roosting, denning, or nesting opportunities *
 - 3.6 primary creation of structures (possibly used by other organisms) *
 - 3.6.1 aerial structures (typically large raptor or squirrel stick or leaf nests in trees or on platforms, or barn swallow/cliff swallow nests)*
 - 3.6.2 ground structures (above-ground, non-aquatic nests and ends and other substrates, such as woodrat middens, nesting mounds of swans, for example)*
 - 3.6.3 aquatic structures (muskrat lodges, beaver dams)*
 - 3.7 user of structures created by other species
 - 3.7.1 aerial structures (typically large raptor or squirrel stick or leaf nests in trees or on platforms, or barn swallow/cliff swallow nests)

- 3.7.2 ground structures (above-ground, non-aquatic nests and ends and other substrates, such as woodrat middens, nesting mounds of swans, for example)
- 3.7.3 aquatic structures (muskrat lodges, beaver dams)
- 3.8 nest parasite
 - 3.8.1 interspecies parasite (commonly lays eggs in nests of other species)
 - 3.8.2 common interspecific host (parasitized by other species)
- 3.9 primary cavity excavator in snags or live trees (organisms able to excavate their own cavities)
- 3.10 secondary cavity user (organisms that do not excavate their own cavities and depend on primary cavity excavators or natural cavities)
- 3.11 primary burrow excavator (fossorial or underground burrows)
 - 3.11.1 creates large burrows (rabbit-sized or larger)
 - 3.11.2 creates small burrows (less than rabbit-sized)
- 3.12 uses burrows dug by other species (secondary burrow user)
- 3.13 creates runways (possibly used by other species; runways typically are worn paths in dense vegetation)
- 3.14 uses runways created by other species
- 3.15 pirates food from other species
- 3.16 interspecific hybridization (species known to regularly interbreed)
- 4 Carrier, transmitter, or reservoir of vertebrate diseases
 - 4.1 diseases that affect humans *
 - 4.2 diseases that affect domestic animals
 - 4.3 diseases that affect other wildlife species
- 5 Soil relationships *
 - 5.1 physically affects (improves) soil structure, aeration (typically by digging) *
 - 5.2 physically affects (degrades) soil structure, aeration (typically by trampling) *
- 6 Wood structure relationships (either living or dead wood) *
 - 6.1 physically fragments down wood *
 - 6.2 physically fragments standing wood *
- 7 Water relationships *
 - 7.1 impounds water by creating diversions or dams *
 - 7.2 creates ponds or wetlands through wallowing
- 8 Vegetation structure and composition relationships *
 - 8.1 creates standing dead trees (snags) *
 - 8.2 herbivory on trees or shrubs that may alter vegetation structure and composition (browsers)
 - 8.3 herbivory on grasses or forbs that may alter vegetation structure and composition (grazers)

* Key ecological functions of *Homo sapiens*.

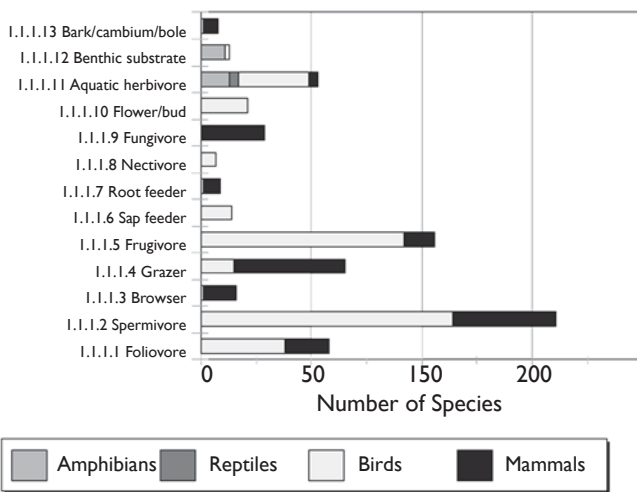


Figure 4. Primary consumption (herbivory) functions of wildlife in Washington and Oregon.

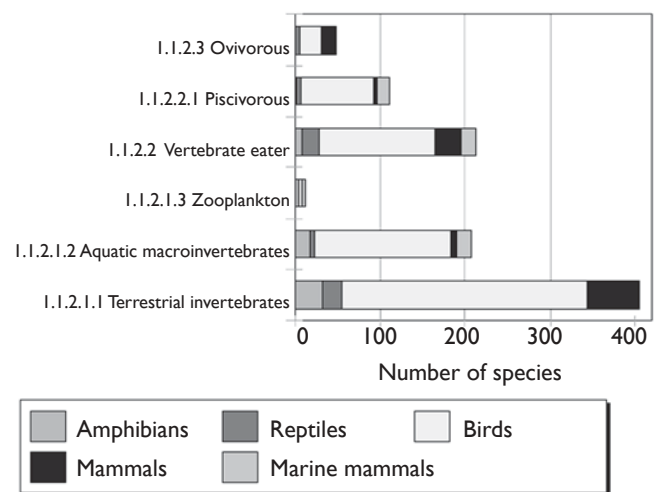


Figure 5. Secondary consumption (carnivory) functions of wildlife in Washington and Oregon.

benthic substrates. Birds play main roles as frugivores, sap feeders, nectivores (nectar-feeders), and flower, bud, and catkin feeders. Mammals play main roles as browsers, grazers, root feeders, and fungivores (fungus-feeders). Both birds and mammals participate more equally as folivores and spermivores.

The main (>100 species) secondary consumer categories are feeders on terrestrial invertebrates, vertebrates, aquatic macroinvertebrates, and fish (piscivores) (Figure 5). Amphibians participate in all secondary consumer categories, but proportionally are the greatest consumers of freshwater invertebrates. Birds proportionately dominate all categories except that of consuming freshwater invertebrates. Mammals participate in most categories with their greatest proportionate representation as terrestrial invertebrate-feeders, vertebrate feeders, and ovivores (vertebrate egg-eaters). Tertiary consumers include a few birds and mammals only.

These patterns differ among native wildlife habitats. For example, avian primary consumers tend to be most numerous (total number of species and proportion of all species) in both eastside (east of the Cascade Mountains crest) and westside wetlands and in dry forest types, whereas avian secondary consumers are most numerous in westside (wetland, forest, woodland, and riparian) types. Mammalian primary consumers are most numerous in higher elevation or eastside grassland, shrubland, or forest types, whereas mammalian secondary consumers are most numerous in westside types (riparian, wetland, grassland, woodland, and forest types alike). Much of this can be explained by the kinds of climates and vegetation physiognomies present in various geographic locations, such as the dry eastside rainshadow effects where grasslands, shrublands, and grazing and browsing mammals (mammalian primary consumers) are more common.

Understanding such trophic patterns and their biogeographic relations may be important to managers at a broad scale, as land ownership patterns and management activities might affect habitats differently, favoring one trophic category over another in different areas. For example, the two anthropogenic (human-created) habitats—Agriculture, Pastures, and Mixed Environments, and Urban and Mixed Environments—provide poorly for mammalian secondary consumers. Comparing historical to current habitat patterns may reveal broad-scale and longer-term shifts in trophic structures of wildlife communities, which in turn can disclose differential repercussions on other ecosystem functions and biodiversity patterns. It may be of interest to compare current and potential future conditions to extrapolated historical conditions, to see if and how wildlife communities have changed in terms of their trophic patterns and to help set broad-scale planning objectives. Such objectives might include restoring or maintaining all historical trophic categories by geographic area or habitat, or mitigating the adverse reduction of trophic categories in anthropogenically disturbed environments.

Organismal Relations Within Wildlife Communities

Some 26 categories of organismal relations within wildlife communities can be evaluated with the KEF matrix. Patterns presented here are for all communities in Washington and Oregon (Figures 6-8); patterns among specific wildlife habitats may differ.

A number of examples of symbiosis can be demonstrated. Seven species of birds (hummingbirds and orioles) serve as pollination vectors for plants. Among terrestrial vertebrates, mammals are the sole dispersers of fungi and lichens; among terrestrial vertebrates, primarily birds disperse invertebrates and vascular plant parts; and both birds and mammals disperse seeds and fruits (Figure 6). Birds create sapwells for feeding by other species. Both birds and mammals create roosting, denning, or nesting structures in aerial, ground, and aquatic situations that other amphibian, reptile, bird, and mammal species also use (Figure 7).

Three bird species act as nest (brood) parasites (although only the brown-headed cowbird regularly parasitizes nests of other species within the Oregon-Washington area) and 58 bird species serve as their hosts. Eighteen birds and 1 mammal species act as primary cavity excavators, serving 32 bird and 24 mammal secondary cavity-using species. Twenty-one mammal species dig large (rabbit size) burrows and 9 bird and 53 mammal species dig small burrows, which also provide for 7 amphibian, 14 reptile, 1 bird, and 59 mammal secondary burrow-using species. Forty-six mammal species create runways in terrestrial vegetation that also can be used by 2 amphibian and 41 other mammal species (Figure 8).

Managers might wish to determine which species of such symbiotic, organismal relations occur in the wildlife habitats and communities under their charge to ensure that the habitat requirements of all members are duly addressed, and that full ramifications of modifying habitat for one set of species on their symbiotic partners are acknowledged.

Soil, Wood, Water, and Vegetation Relations

Some examples of soil, wood, water, and vegetation relations are shown in Figure 9. Seventy-five species of amphibians, reptiles, birds, and mammals may help improve or maintain soil structure and aeration through tunneling, digging, and turning over soil. This also has the benefit of increasing aerobic bacterial decay in soils and incorporating coarse decaying wood as organic matter into the soil. One bird and 20 mammal species physically help fragment down wood, and 1 bird and 1 mammal species fragment standing wood; these functions, too, help hasten the wood decay process.

Seven mammal species, including 2 elk subspecies, impound water by creating diversions or dams, or create ponds or wetlands through wallowing. Such ponds and wetlands can then provide for a wide array of other wildlife species; the habitat elements database lists 242 species of amphibians, reptiles, birds, and mammals as being associated with ponds and wetlands. Three

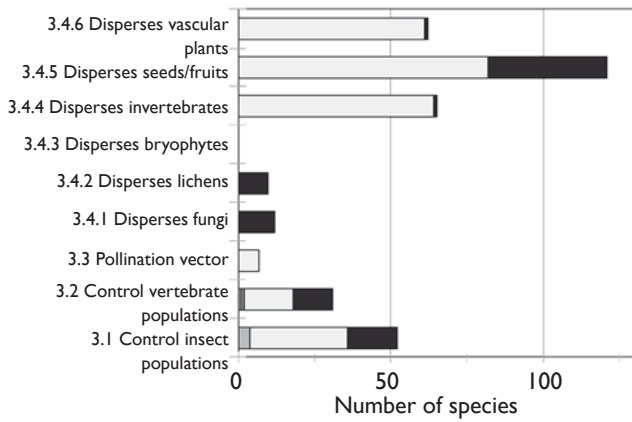


Figure 6. Organismal functional relations of wildlife in Washington and Oregon: population control, and pollination and dispersal vectors.

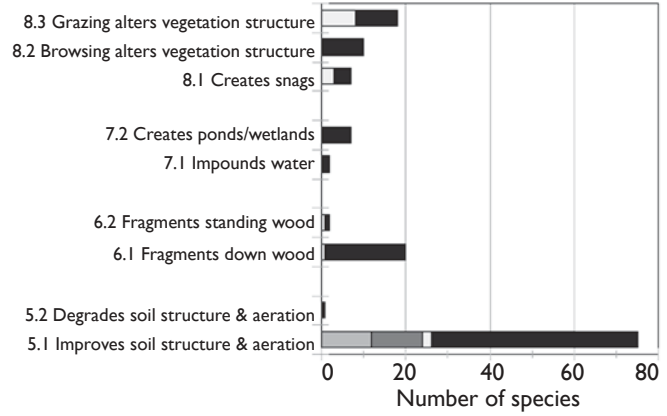


Figure 9. Soil, wood, water, and vegetation functional relations of wildlife in Washington and Oregon.

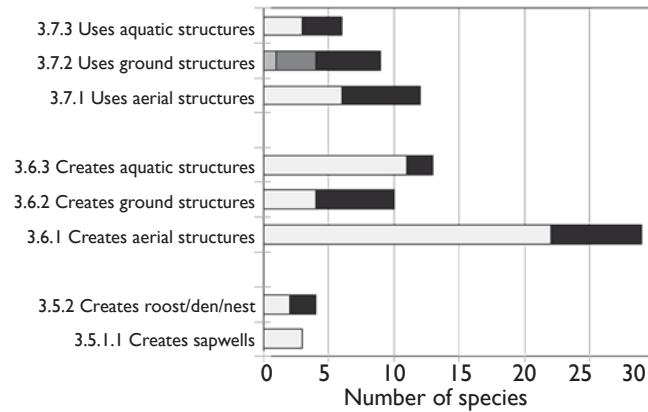


Figure 7. Organismal functional relations of wildlife in Washington and Oregon: creation and use of feeding, breeding, and resting structures.

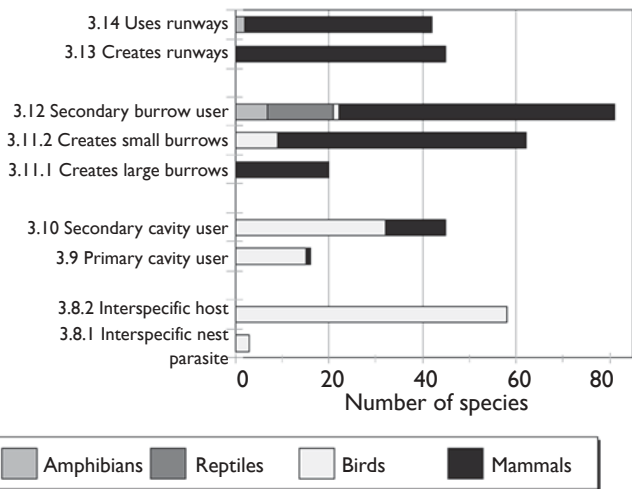


Figure 8. Organismal functional relations of wildlife in Washington and Oregon: nest parasitism and hosts, and cavity, burrow, and runway excavation and use.

mammal species create snags through shredding, digging into, or girdling of trees. The habitat elements matrix lists 131 species of amphibians, birds, and mammals as being associated with snags. Browsing by 10 mammal species and grazing by 1 bird and 7 mammal species can alter vegetation structure and composition. This in turn can change habitat conditions for a wide array of other wildlife associated with grass, forb, and shrub species and cover.

Taxonomy and Definitions of Functional Patterns

Beyond the simple species tallies discussed above, what are the functional characteristics of ecosystems that can be evaluated by using the KEF matrix? We suggest a taxonomy of 15 types of patterns of ecological functions (Table 2, follows Literature Cited at end of chapter) and provide some examples here of using the matrix for evaluating them. Some of these patterns are discussed in the literature but many we pose here for the first time as working hypotheses of how wildlife communities operate and can be evaluated. All of the types of patterns need empirical study to determine actual rates of influence of the functional roles of animals.

Patterns to Watch

Community patterns. Community patterns of KEFs in wildlife communities include functional redundancy, functional richness, total functional diversity, functional webs, functional profiles, and functional homologies.

Functional redundancy is the number of wildlife species performing a specific ecological function, and is determined by tallying species in the KEF matrix for specific KEF categories for specific habitats conditions. Functional richness is the number of KEF categories in a community. Total functional diversity is functional richness weighted by functional redundancy,⁴ analogous to species diversity.

A number of wildlife habitats in Washington and Oregon are more or less equally functionally rich except

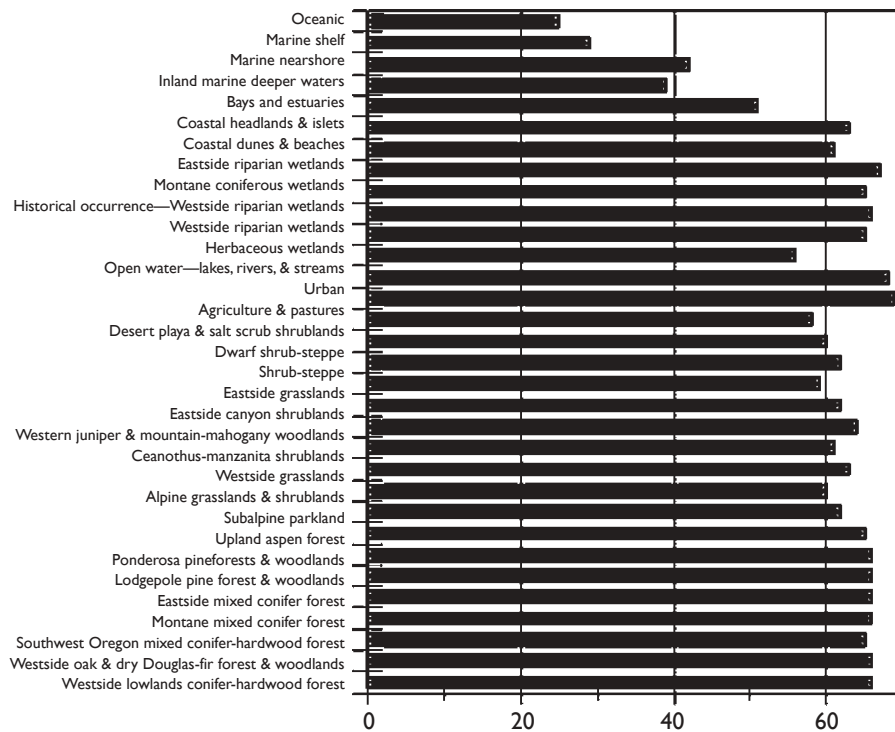


Figure 10. Total functional richness (number of key ecological function categories) by wildlife habitat in Washington and Oregon.

for the less rich marine and coastal habitats (Figure 10). Agriculture, Pastures, and Mixed Environments, and Urban and Mixed Environments are the most functionally rich, but the matrixes might overstate the viability of wildlife species within these anthropogenic environments. Among native wildlife habitats, a number of forest, woodland, and wetland environments rank as the most functionally rich.

Total functional diversity differs more among wildlife habitats in Washington and Oregon than does functional richness, although it follows much of the same ordinal pattern (Figure 11). An exception is with various alpine and shrubland wildlife habitats that have low functional diversity. This means that even though a relatively high number of categories of KEFs are represented in alpine and shrubland wildlife communities, there is lower functional redundancy (fewer wildlife species) performing many of those functions than found in forest, woodland, and wetland communities; there are far fewer still in marine and coastal communities. This may imply a greater sensitivity of alpine, shrubland, coastal, and marine communities to change than with forest, woodland, and wetland communities.

This illustrates the premise that functionally redundant, rich, and diverse communities may be more resistant or resilient to perturbations^{20, 29, 33} and can support greater levels of biodiversity⁴⁵ than less functionally redundant, rich, or diverse communities. Managers may wish to develop functional profiles (see below) not just of local wildlife habitats but also of structural stages and combinations of habitat elements. Then they can identify those communities that are naturally rich, diverse, and redundant in their ecological functions, and those that are not, to help prioritize further evaluations and to focus

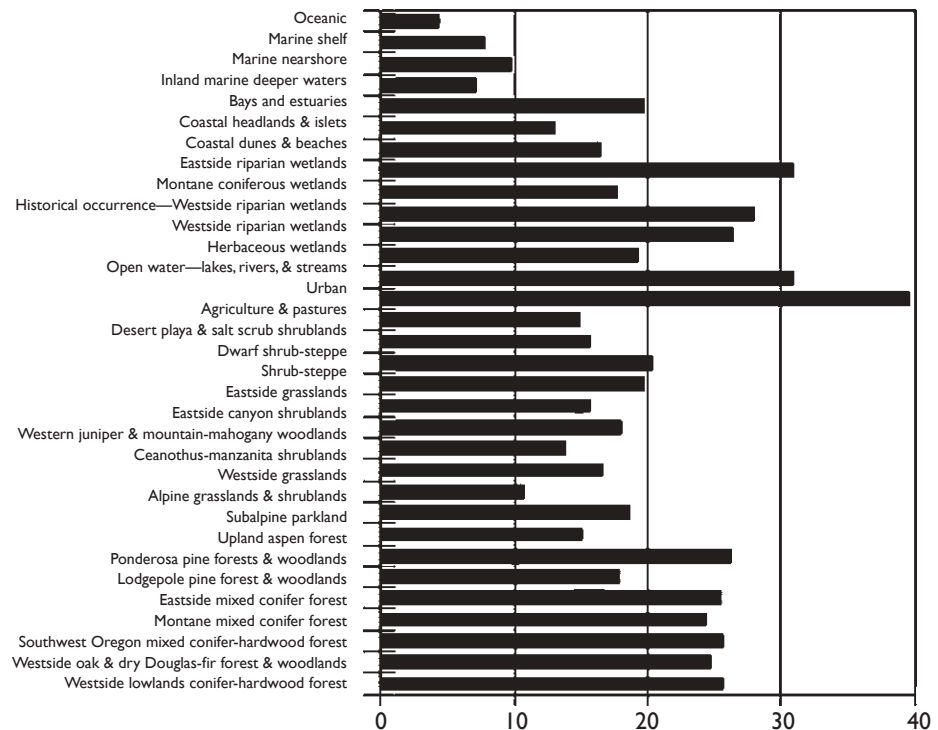
conservation attention on the latter and ensure the continued integrity of the former.

A functional web is the full array of all KEFs associated with a set of species that may be specified by some habitat element or structure. An example given in Morrison et al.²⁸ from the interior Columbia Basin illustrates an array of 22 KEF categories just of mammals associated with down wood in eastside ponderosa pine forest communities. Many of these functions, such as dispersal of fungi or primary burrow excavation, extend well beyond the confines of down wood substrates per se. This demonstrates the concept of how functions supported in part by specific habitat elements can influence parts of the ecosystem well beyond those habitat elements.

Marcot et al.²⁴ provided functional profiles, or graphs showing functional redundancy for each KEF category, and of total functional diversity of all KEF categories, across all vegetation communities of the interior Columbia Basin. The concept of functional homologies, or how communities compare in their functional categories and redundancies, is new but can be easily evaluated using the KEF database (Table 2) and similarity analyses. Managers may wish to evaluate functional webs, profiles, and homologies to help describe the unique functional roles of communities in their charge.

Geographic Patterns. Species' range maps or distributions by wildlife habitats can be used to depict geographically many of the functional patterns discussed here. This opens the door to a new way to display functional patterns spatially, and may be termed "geographic functional ecology". For example, stacking the range maps of species with a particular KEF category produces a map of functional redundancy. Areas of lowest redundancy that serve to link areas of high redundancy can be delineated

Figure 11. Total functional diversity (functional richness times mean number of species per function) by wildlife habitat in Washington and Oregon.



as functional bottlenecks or cold spots, just as areas of highest redundancy can be identified as functional linkages or hot spots. In this way, many other aspects of KEFs can be mapped. It may be of interest and importance to managers to map such geographic functional patterns, to identify areas and communities worthy of greater conservation attention.

Species' Functional Roles. Two major patterns of the functional roles of species are functional keystones and functional specialization. Functional keystones are species whose removal would most alter and degrade the structure or function of the community. If the species is the only one that performs a particular ecological function within a community, it is a critical functional link species. The function it performs is then a critical function. Functional breadth is the number of ecological functions performed by a species. When a species performs very few functions, it is a functional specialist.

Functional keystones, functional link species, and functional specialists can be identified by querying the KEF database. For example, the turkey vulture was identified above as being an extreme functional specialist (it performs the fewest total functions). Its function is KEF category 1.1.4 (see Table 1), which means that it is a heterotrophic consumer and, more specifically, a carrion feeder. It has no other trophic categories, which means that it is a specialist in this function. Loss of carrion means loss of this species.

But is the reverse also true, that is, is the turkey vulture critical to the carrion-feeding function? This is determined by identifying the functional redundancy of that function. Querying the KEF database shows that there are 39 other wildlife species also coded as carrion feeders in Washington and Oregon. Granted, many of these species

feed on different kinds of carrion in different habitats and on different substrates than does the turkey vulture. Also, there may be fewer carrion-feeding wildlife species in any given wildlife habitat; this is determined by linking the KEF database to the wildlife habitats database. For example, there are only 17 carrion-feeding species found in Westside Lowland Conifer-Hardwood Forest. In fact, the fewest number (8 species) occurs in Inland Marine Deeper Waters and Marine Nearshore habitats, but the turkey vulture does not occur in either of these habitats. Where it does occur, the carrion-feeding function is shared by other species. Therefore, although the turkey vulture is a functional specialist, its function is usually performed by at least some other species, so, although specialized, its carrion-feeding role, in general, is not entirely a keystone role. It may be a keystone role, however, for specific kinds of carrion on specific substrates or in specific seasons; there are many dimensions to a species' niche.

Some KEFs, however, have few participants, even if the associated species are not functional specialists. An example is the American beaver, which is the only species coded in the database with KEF code 7.1. "impounds water by creating diversions or dams". So for this function, this species is a critical functional link and a keystone. American beaver is also coded with 24 other KEF categories (these include subcategories as well), so it is not much of a functional specialist. However, it is the only species that performs KEF 7.1, which is a function that influences many other species. In fact, the habitat elements database lists 49 other wildlife species directly and positively associated with habitat element 2.3, "Beaver/muskrat activity, including dams, lodges, and ponds" in Washington and Oregon.

The lesson for the manager here is to pay attention to both the array of functions by species, as well as the array

of species by function. The concept of a keystone species or keystone function has many dimensions and potential management implications. We caution against careless use of the general term “keystone” without clarifying its context and significance.²⁶ For example, species that are functional specialists are probably highly vulnerable to changes in their environment if they depend on that function for survival. A species that is a functional generalist with broad functional breadth, that is, that performs the widest array of functions—might greatly influence an ecosystem upon its removal, but this depends on what and how other species also perform such functions. A function with one or few species may itself be vulnerable and of management interest for ensuring its continuance in an ecosystem.

Functional Responses of Communities. The categories discussed above can be used to characterize the functional responses of communities. Community functional responses refer to how communities respond functionally to disturbances. Responses can be categorized as functional resilience, resistance, attenuation, and shifting, and imperiled functions.

Functional resilience is the capacity of a community to rebound to a starting functional state after a perturbation, such as a natural or human-caused disturbance event. Functional resistance is the degree of inertia of a community to retain its initial functional state and not change under stressors. Functional attenuation is the degree to which a community loses functions after a disturbance, and functional shifting is the difference in functions before and after disturbance when the community has finally stabilized in species composition. Imperiled functions are those functions that are represented by few species that are themselves at risk.

Some Hypotheses on Ecological Functions

Ecological implications of functional patterns of species and communities, as discussed above, can be taken as testable hypotheses about the roles of wildlife and how ecosystems work (Table 1). Some additional hypotheses include the following:

1. Functional switching imparts functional resistance: a greater degree of functional switching by species imparts a greater functional resistance to the community.
2. Functional redundancy imparts resilience: for a particular function, the higher the functional redundancy, the greater is the functional resilience (or resistance) for that function.
2. Functional diversity imparts low attenuation: the greater the functional richness and diversity of a community, the lower is the degree of functional attenuation (loss of functions).
3. The more functionally diverse a community, the greater is its productivity and its biodiversity.
4. The greater the functional redundancy, the more sustainable is the set of resources that the function provides.
5. Functional breadth is not necessarily related to critical functional links. That is, species, which are the sole (or few) performer(s) of a given function in a community might also perform very few, or many other, functions.
6. Critical functional links cannot be predicted from functional breadth.

Of course, working hypotheses also can be stated as null hypotheses for the purpose of critical testing of their veracity. For example, the first working hypothesis can be stated as the following null hypothesis: there is no influence on functional resistance of a community from degree of functional switching of its component species. Then, an appropriate research study can be devised that compares the functional constitution of communities before and after a disturbance, for communities that differ in their degree of functional switching of their component species.

Lost Functions of Extirpated Species

Thirteen species are recognized in this effort as extirpated from either Oregon and/or Washington (see Chapter 18). Extirpated species performed 49 ecological functions (including subcategories) that were potentially reduced or eliminated as a result of extirpation. Because ecosystem sustainability is dependent on the maintenance of biodiversity and native ecological functions, the loss of these species may have affected the functional integrity of the communities in which they formerly occurred. The degree of such influence, however, is largely unstudied.

Key Ecological Functions of Extirpated Species in Oregon and Washington

Trophic Relations. The 13 extirpated species varied widely in their degree of functional specialization, with most species performing >1 trophic-related KEF. The grizzly bear, for example, had the widest functional breadth of trophic KEFs (7) among the extirpated species, whereas California condor was a functional specialist (1), feeding exclusively on carrion. The upland sandpiper and yellow-billed cuckoo also were narrow in their trophic relations, feeding solely on terrestrial invertebrates and serving as prey for secondary or tertiary consumers. Overall, trophic relations of extirpated species included spermivores (grizzly bear, Wyoming ground squirrel, trumpeter swan, and sharp-tailed grouse), grazers (pronghorn, bison, bighorn sheep, and trumpeter swan) frugivores (gray wolf, grizzly bear, and sharp-tailed grouse), root-feeders (grizzly bear), and foliovores (trumpeter swan and sharp-tailed grouse). Eight species were secondary consumers, including 4 species that consumed vertebrates; 1 species was a tertiary consumer (gray wolf); 2 were carrion-feeders; 1 was cannibalistic, and 9 were prey for other species.

Organismal Relations. The 13 extirpated species performed 6 categories of KEFs related to organismal relations. Three mammal species were primary burrow excavators; 3 mammals were creators or users of runways;

2 mammals potentially controlled vertebrate populations; 2 birds and 3 mammals dispersed insects and/or seeds; and 2 mammals created feeding opportunities for other species. Other functions of extirpated species included carriers of disease (4 mammals), and functions related to soil (1 mammal), wood (3 mammals), and water relations (1 mammal).

To assess the potential impact of losing these functions, we calculated functional redundancy by tallying the number of species with selected KEFs by wildlife habitat. These species function profiles depict the degree of functional redundancy among habitats, thus serving to identify imperiled or lost functions. From among the set of KEFs performed by each extirpated species, we selected for analysis those functions that might be expected to vary among communities, as we discuss next.

Carrion-feeding. Feeding exclusively on carrion, the California condor was an extreme functional specialist. Historically, it inhabited the Westside Grasslands, Westside Riparian-Wetlands, and Coastal Dunes and Beaches of Oregon and Washington. Querying the matrices shows that 24 individual species perform this function in these 3 habitats. Twelve species perform this function in Westside Grasslands, 20 in Westside Riparian-Wetlands, and 16 in Coastal Dunes and Beaches. Similar to the turkey vulture, the condor was not a keystone species for the maintenance of the carrion-feeding function. Nonetheless, functional specialists may be highly sensitive to changes in their environment, thus increasing their vulnerability to extinction or extirpation.³¹ The extreme degree of specialization (for carrion as well as perhaps other needs) of the California condor may have contributed to its demise.

Control of Vertebrate Populations. This KEF was examined for redundancy within the range of habitats historically inhabited by gray wolves in Oregon. Thirty other species potentially perform this function, including 1 amphibian, 1 reptile, 16 birds, and 11 mammals (excluding the grizzly bear, also extirpated from Oregon). Obviously, not all of these species perform this KEF in comparable ways. Among the assemblage of mammals associated with this function, coyotes, mountain lions, and black bears might perform this KEF similarly to gray wolves, although they may selectively prey on other species.

Importantly, the loss of top predators from a community may have reverberating effects on the rest of the community. Predators lost from a complex food web “release” their herbivore prey, thus potentially leading to significant changes in vegetation structure, cover, and species from increases of the prey population.³¹ In the Greater Yellowstone Ecosystem, for example, the extirpation of wolves led to an unprecedented growth in the moose population, which had profound effects on willow communities, and consequently, on neotropical migrants associated with those communities (Berger et al., unpubl. data). Furthermore, wolves are dominant over coyotes and aggressively exclude or displace them. With

the extirpation of wolves, coyotes increased dramatically.²⁷ Studies currently are assessing the impacts and dynamics of wolf recolonization on coyotes in the Greater Yellowstone Ecosystem.

Provision of Feeding Opportunities. The grizzly bear, now rare in Washington and extirpated from Oregon, performed the function of providing carrion in 11 habitats. The species function profile for the KEF “provides feeding opportunities” revealed that 6 other species (minus the gray wolf, which was also extirpated from Oregon) also perform this function. However, only 1, the mountain lion performs this KEF in essentially the same manner, by providing carrion. It does so in all 12 of the habitats that the grizzly bear once occupied. This is an example of a potentially imperiled function. Although this function was not completely lost, the elimination of grizzly bears and gray wolves from their historical range may have greatly constricted the occurrence and rate of this carrion-providing function. Because providing carrion is a symbiotic, organismal relation, other species that use carrion might be affected by the scarcity of this function.

Creation of Ponds or Wetlands Through Wallowing. Wallowing bison likely once created small ponds and wetlands in 8 habitats in Oregon and Washington. Four ungulate species currently perform this function in subsets of these habitats. Of the 4 species, the Rocky Mountain elk is the only ungulate that can create small ponds and wetlands in all 8 of the habitats formerly occupied by bison, and it is the only ungulate that performs this function in Lodgepole Pine Forests and Woodlands. Although not imminent, extirpation of the Rocky Mountain elk from this habitat would result in the loss of this potentially imperiled function.

The Rocky Mountain elk, therefore, is a critical functional link species for the critical function of creating small ponds and wetlands in Lodgepole Pine Forests and Woodlands. Twenty wildlife species that occur in this habitat are associated with ephemeral pools, including 8 species of amphibians. Interestingly, 4 species of frogs that occur in Brazil breed only in peccary wallows and other small permanent ponds; conserving these amphibians necessitates preserving the wallowing function of peccaries.⁴⁰ This is an example of how the loss of one species (bison or peccary) can influence the distribution of another.

We found no evidence that the extirpation of the pronghorn, Wyoming ground squirrel, sea otter, or upland sandpiper resulted in the loss or imperilment of any specific ecological function in their former habitats. The trophic KEF categories of these species (e.g., grazer, spermivore, invertebrate-eater) were and are shared by other species; thus the habitats they occupied were highly redundant for these functions. However, we recognize that the level of specificity in our database is insufficient to characterize the complete set of ecological functions for every species; simply performing the same general KEF in the same habitat does not necessarily confer substitutability. At some level, one species is never

completely interchangeable with another, regardless of functional similarity.

Evaluating the KEFs of extirpated species may help land managers understand the influences that historically contributed to ecosystem function. From this understanding, restoration goals can then be formulated to restore lost functions and to protect rare ones. Species that perform functions with low functional redundancy in a particular habitat could receive priority to ensure perpetuation of that function in the community. Because most species are involved in several to many trophic, organismal, and symbiotic relations, the conservation of overall biodiversity can surely lend to community stability. By minimizing species loss, the integrity of ecosystem function may be maintained.⁴⁵ Understanding how species contribute to community function therefore may be imperative to crafting “ecosystem management” guidelines and defining ecosystem restoration objectives. Also, KEF analyses can be used to formulate and test hypotheses related to the effects of function loss on community stability and ecosystem integrity. The manager can apply this approach at a variety of scales. That is, a species need not go extinct in a two-state area before its more local reduction or extirpation of its populations and associated functions are addressed.

Competing Functions of Exotic Species

Thirty-one non-native (exotic) species occur in Oregon and Washington, including 2 amphibians, 3 reptiles, 14 birds, and 12 mammals (see Chapter 16). Collectively, they perform 54 KEFs in 30 wildlife habitats, and thus exotic species are able to exploit niches occupied by native animals. The most successful non-native species have KEFs that confer a competitive advantage, often to the detriment of native species. Exotic species threaten biodiversity by displacing native species either directly through predation or displacement, or indirectly through the alteration of ecosystems, and have been described as one of the greatest threats to native species and human-disturbed ecosystems in the world.³⁵

The exotic species found in Oregon and Washington compete with native species through trophic and organismal relations; soil, wood, and water relations; and by altering vegetation structure, and composition. Trophic relations involve competition for food or predation. Most exotic primary consumers are foliovores (9 bird species and 2 mammals), spermivores (12 bird species and 6 mammals), and frugivores (8 bird species and 5 mammals). Seven exotic species are grazers, including the wild burro and feral horse, which compete with native ungulates for forage. Seven exotic species are aquatic herbivores, and a few are root feeders, browsers, flower feeders, and decomposing benthic substrate feeders (2 species each). None of the exotic species consumes sap, nectar, or bark. Of the 25 exotic species that are secondary consumers, most consume invertebrates (24 species) and 12 prey on vertebrates, including 3 exotic species that feed on fish (bullfrog and 2 reptiles) and 2 species that are ovivorous (Eastern fox squirrel and Virginia opossum). Three species

feed on carrion (2 reptiles and Virginia opossum), 2 mammals are coprophagous, and 23 are prey for secondary or tertiary consumers.

Twenty-three exotic species participate in organismal relationships including the potential control of terrestrial vertebrate populations (bullfrog), and transportation of seeds (9 birds and 4 mammals). Two exotic squirrel species create structures that are used by other species, and 3 exotic species use structures created by other species. Exotic secondary cavity users, the eastern fox squirrel, eastern gray squirrel, English or house sparrow, and European starling, compete for cavities in their respective habitats with up to 40 native species. Declines of Lewis’ woodpecker and purple martin have been attributed, in part, to competition with starlings for cavities. Three exotic mammals are primary burrow excavators and 7 are secondary burrow users, with 2 exotic rats (Norway rat and black rat) alone competing with up to 51 native secondary burrow users. Five exotic mammal species create runways and 5 other exotic mammal species use runways created by others.

Exotic species can affect gene pools (e.g., eastern cottontail hybridizes with native species) and spread disease (at least 5 exotic mammal species carry diseases that may affect humans). Soil-related KEFs include potentially physically improving soil structure by digging or burrowing (4 exotic mammals and 1 exotic reptile) and physically degrading soil structure by compaction (wild burro, feral horse). Three exotic species fragment down wood (wild burro, feral horse, and feral pig) and the same 3 species can create small ponds or wetlands through wallowing. Lastly, the eastern cottontail, feral pig, and wild burro can alter vegetation structure and composition through grazing.

Understanding how exotic species compete with native wildlife may help land managers predict which native species are most likely to be affected, and in which habitats. Although the mechanisms by which systems resist introductions are not well understood, they seem to be related, in part, to trophic complexity.³¹ Introductions of more trophically generalized mammals to species-poor, trophically simple systems (e.g., islands) have had extreme effects on the native species. Conversely, trophically complex, species-rich systems may be more resilient. Maintaining the functional web, or full set of KEFs, within a community may, therefore, increase resistance or resilience to the effects of exotic species whether introduced intentionally or not.

The Functional Roles of Marine Species

Marine Birds

There are 83 species of coastal and pelagic birds associated with the 4 oceanic wildlife habitats: Inland Marine Deeper Waters, Marine Nearshore, Marine Shelf, and Oceanic habitats. Collectively, they comprise 53 KEF categories. They are all secondary consumers; 13 are also primary consumers, mostly including aquatic herbivores, but a few (mostly waterfowl) are also foliovores, spermivores,

browsers, and grazers. Many consume invertebrates (76 bird species) and/or vertebrates (63 bird species), including fish (60 bird species) and eggs (12 bird species). Seventeen bird species (skua, eagle, gulls, and jaegers) pirate food from other species, an adaptation found much less in terrestrial habitats; 13 species (waterfowl, fulmar, eagle, gulls, storm-petrels, and shearwaters) are carrion feeders; and 12 species (skua, fulmar, gulls, albatrosses, shearwaters, and jaegers) feed on human garbage or refuse in the ocean, principally offal and bycatch of fishing boats. Some help disperse invertebrates (28 bird species) or plants (25 bird species).

Because most coastal and pelagic bird species nest on stacks, sea cliffs, and other coastal substrates, and some are fossorial and nocturnal, there are 7 species (guillemot, auklets, kingfisher, puffin, and storm-petrels) that are primary excavators of small burrows and 11 species (grebes, 1 eagle, 1 gull, 1 tern, 1 pelican, and osprey) that create structures used by other species. There are even 4 secondary cavity users (waterfowl) and 3 species (cormorants) that can kill trees and create snags. Again, many of these are examples of how species' ecological roles extend beyond just the realm of their primary habitat, in this case, coastal and open ocean.

Marine Mammals

The matrix includes 18 species of marine mammals. Collectively, they comprise some 20 KEF categories. All 18 species consume aquatic invertebrates and 3 (whales) consume marine zooplankton. Seventeen species consume vertebrates (15 of these eat fish) and 7 serve as prey for other predators. Four whale species create feeding opportunities for other species, and a number of species aid in nutrient cycling and carry or transmit disease, although these functions are poorly studied in marine environments.

The Functional Roles of Humans

Although not explicitly included in the KEF matrix, *Homo sapiens* nonetheless is one of the most effective ecological change agents that can adversely affect BPS.^{9, 19} Anthropogenic change of habitats is a major disturbance event in native ecosystems of Washington and Oregon (see chapter 20 on Management Activities).

Humans perform some 35 categories of KEFs (Table 1) (this tally includes category headings and subheadings, so there is some repetition in this value). This exceeds the influence of the two most functionally broad native wildlife species, the American black bear (30 KEF categories) and the American beaver (24), and helps explain how humans have so greatly altered ecosystem functions and processes. Humans certainly rate as a functional keystone species, in that their removal from a system would likely result in major redistributions of other species and their functions. However, none of the ecological functions performed by humans are necessarily critical link functions, which are not performed in at least some general way by other wildlife species.

So, what is it about the ecological functions of humans that so greatly influence native ecosystems and wildlife communities? It is not that humans play any critical functional roles, or that humans are functional specialists. Rather, it seems to be our amazing functional breadth—that is, the number of functions we perform and our resounding influence on the rest of the functional web of natural communities. Such functional influences should be considered when evaluating effects of human activities. Managers, in fact, may wish explicitly to include the KEF categories of humans in their evaluations of functional patterns of wildlife species and communities.

Management Implications

Throughout the text above, we have offered some ideas on how managers might use this new approach to describe the functional patterns of wildlife species and communities and influences of human activities. More specifically, the manager can link the KEF matrix with the other matrixes, especially those depicting wildlife habitats, habitat elements, habitat structures, and management activities.

For example, one could begin by specifying a particular management activity, such as using herbicides in shrubland or grassland management (Management Activities 5c; see Chapter 20) within a particular wildlife habitat such as Eastside Grasslands (Wildlife Habitat 15; see Chapter 20). Linking the management activities, wildlife habitats, and habitat elements matrixes, one can determine which wildlife species are potentially influenced by this activity in this habitat, that is, which species are coded for using habitat elements that are affected by this activity in this wildlife habitat. In this case, it is a set of 2 amphibians, 7 reptiles, 75 birds, and 44 mammals.

Next, one can link this species set to their KEFs and determine which KEF categories might be most influenced by this management activity by comparing their functional redundancies to those of all wildlife species in this habitat. For example, the ecological function of fungi dispersal is performed overall by two wildlife species in Eastside Grasslands: the deer mouse and Rocky Mountain elk. These two species both are also potentially influenced by use of herbicides in this habitat, because herbicide use is linked to at least one habitat element used by each of these species, namely the habitat elements of herbaceous layer (Habitat Element code 1.2.1), fruits/seeds (1.2.2), shrubs (1.2.6), fungi (1.2.7), forbs (1.2.8), grasses (1.2.10), and plants (2.1.1). Herbicide use may have a less salient influence on some other KEFs depending on how many wildlife species perform the functions that are not influenced by the activity. In this and other ways, the manager can use the matrixes to evaluate the potential influence of specific management activities on ecological functions and determine the functions that may be most sensitive to the activities, and perhaps those worthy of special mitigation or conservation attention. We suggest using the categories and analysis procedures listed in Table 2 to address this and other patterns of ecological function.

Ultimately, a goal of wildlife conservation may be to help ensure fully functional ecosystems. To this end, the manager could use the approaches we offer in this chapter to determine, for individual wildlife habitats:

1. the full set of native ecological functions,
2. the full functional redundancy of each KEF category and total functional diversity,
3. habitat elements contributing to maintaining functional diversity of wildlife communities, and
4. which management activities simplify, extirpate, or restore functions.

The manager can use functional profiles to compare among communities, or a community over time under different management scenarios, to determine: (1) which scenario would provide for the fullest array of native KEF categories; (2) the degree to which full functionality of an ecosystem can be maintained; (3) which functions might be at higher risk; and (4) which species, habitat elements and structures, and management activities account for reduction or loss of specific functions. This provides a basis for identifying threats to KEFs as influenced by human (or other) disturbance events. Linking to maps of species and functions as discussed above, the manager can then determine spatially where such threats might occur.

Caveats

We emphasize that the information in the KEF database largely represents a collective expert judgment and is mostly not based on scientific field studies. As well, the KEF information is coded largely as categorical data and not quantified as rates of influence. Thus, patterns generated by querying the KEF matrix should be considered as tentative working hypotheses requiring empirical validation and refinement. We view the major value of the KEF matrix as providing (1) a way of explicitly and repeatably evaluating the functional patterns of species and communities and the potential influences from human activities, and (2) generating working hypotheses on such influences for management consideration and testing.

Following Marcot,²² we offer the following caveats when using the KEF matrix:

Completeness of the KEF Database

Although all vertebrate species are included, there may be many ways to represent their ecological functions, and some functions likely are incompletely depicted. An example is KEF category 2 on nutrient cycling relations. This category was originally developed more for plants and invertebrates²³ but could be more fully developed for vertebrates. Some KEF categories require additional attention. An example is KEF category 4, disease vector. Species listed under this category need review and refinement by wildlife disease experts. There are likely to be other errors of omission and commission in the matrix and other needs to revise or expand the KEF classification system (Table 1).

Need for Validation and Primary Field Studies

Ecological implications of the KEF pattern categories discussed in this chapter should be viewed as working hypotheses. Further, the relations depicted among the elements in the species-influence diagram may be quantified as specific rates (e.g., rates of soil digging and turnover, rates of pollination, etc.). To do this for the entire set of species, KECs, KEFs, and their relations to BPS and management activities would entail a major research program. Thus, the matrixes can be used to prioritize critical relations and identify functions most in need of empirical, quantitative study.

Scientific knowledge of some functions and species is more complete than for other functions or species. We did not denote this variation in the database per se, but wildlife specialists or systems ecologists should be able to determine areas needing further, or primary, empirical study.

Resolution of the KEF Categories

Some KEF categories are broadly generalized whereas others are very specific. This is inevitable, given the variation in scientific knowledge and understanding across species and functional categories. The user of the KEF matrix should not expect it to accurately predict ecological functions within small or local geographic areas such as single forest stands; if linked to the wildlife habitats and habitat elements matrixes, the KEF matrix will likely err on the side of commission of functions rather than omission. The KEF matrix might serve the manager better at broader geographic scales.

Ecological Functions of Other Taxonomic Groups

The user needs to integrate the information provided in the KEF matrix with some understanding of the functions of other taxonomic groups, namely algae, plankton, plants, plant allies (cryptogams), and invertebrates. The user should not expect to be able fully to describe (and prescribe!) ecosystem processes only in terms of vertebrate wildlife species. This is especially true with ecological functions that are poorly represented by vertebrates, such as those pertaining to soil productivity, wood decay, carbon sequestration, filtering of xenobiotics, and many other functions.²³

When managing wildlife in an ecosystem context, it is important not to ignore the functional influence of plants and invertebrates, which really perform most ecological functions in ecosystems. For example, plants and their allies—including algae, fungi, lichens, bryophytes (mosses and liverworts), and cryptogamic soil crusts, as well as vascular plants—provide the foundation of net primary production, and trophic and physical structures of ecosystems (except for rare autotrophic, chemosynthetic and other extremophile-based systems found in a few locations). Invertebrates, including soil microorganisms such as mites, springtails, nematodes, rotifers, protozoa, and bacteria, also play central functional roles in

ecosystems, especially in soil and decaying wood; E.O. Wilson called invertebrates the "little things that run the world."⁴⁷

Ecological functions of plants and invertebrates may best be addressed in functional groups of species,^{10, 30, 32} for example, as suggested for wetland plants,² exotic plant species,^{11, 15} plants central to ecosystem process and global change,³⁹ and invertebrates that play ecological roles in managed forests.³⁸

Vertebrates also take a back seat to other organisms in terms of species richness. In the interior Columbia River Basin in the U.S., vertebrates constituted only 4% of all known species and 1% of all expected (known and unknown) species of macroorganisms, and even far less if microorganisms are included.²³ Nonetheless, the relation of plants, plant allies, and invertebrates to vertebrate species is pertinent and may be of interest to managers for maintaining overall ecological functions and ecosystem processes. Plants support vertebrate primary consumers including browsers and grazers; invertebrates support insectivores and other secondary consumers. Plants and plant allies provide many kinds of physical habitat structures, help filter water and detoxify soils, support soil structures for burrowing, and many other functions of use to vertebrates. Invertebrates or their byproducts (e.g., honey) serve as a food source; they also foster wood decay, create snags and down wood, serve as disease transmission vectors, and play many other ecological roles affecting vertebrates.

Conclusion

Ecosystem managers can address the biotic component of ecosystems by explicitly including key ecological functions of species (including humans) in assessments and in formulating management direction. Many ecosystem management approaches to wildlife and land use planning are already considering ecosystem processes of disturbance events (e.g., fire, wind, drought, and flooding). The picture needs to be made complete by also considering the functional role of organisms, and the influence of those functions on overall ecosystem biodiversity, productivity, and sustainability. The framework we offer here provides a rigorous, repeatable means of evaluating at least the qualitative influence of wildlife on their ecosystems, and should be viewed as starting hypotheses from which to focus conservation or research attention. We fully expect that many KEF categories and even their qualitative relations with wildlife species may change given empirical study.

Acknowledgments

We thank Tom O'Neil, Kelly Bettinger, and Sally Olsen-Edge for helpful comment on the manuscript. We gratefully acknowledge the contributions of Marla Trevithick in developing the databases. We benefited from ecological discussions with Mikell O'Mealy and Susan Tank.

Literature Cited

1. Augustine, D. J., and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *Journal of Wildlife Management* 62: 1165-1183.
2. Boutin, C., and P.A. Keddy. 1993. A functional classification of wetland plants. *Journal of Vegetation Science* 4: 591-600.
3. Brelsford, M. J., J. M. Peek, and G. A. Murray. 1998. Effects of grazing by wapiti on winter wheat in northern Idaho. *Wildlife Society Bulletin* 26: 203-208.
4. Brown, J. H. 1995. *Macroecology*. The University of Chicago Press, Chicago, IL.
5. Butler, D. R. 1995. *Zoogeomorphology: animals as geomorphic agents*. Cambridge University Press, New York, NY.
6. Callicott, J. B., L. B. Crowder, and K. Mumford. 1999. Current normative concepts in conservation. *Conservation Biology* 13: 22-35.
7. Chapin, F. S., III, and others. 1996. The functional role of species in terrestrial ecosystems. In B. Walker and W. Steffen, editors. *Global change and terrestrial ecosystems*. Cambridge University Press, New York, NY.
8. Duncan, R. S., and C. A. Chapman. 1999. Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. *Ecological Applications* 9: 998-1008.
9. Forester, D. J., and G. E. Machlis. 1996. Modeling human factors that affect the loss of biodiversity. *Conservation Biology* 10: 1253-1263.
10. Golluscio, R. A., and O. E. Sala. 1993. Plant functional types and ecological strategies in Patagonian forbs. *Journal of Vegetation Science* 4: 839-846.
11. Gordon, D. R. 1998. Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. *Ecological Applications* 8: 975-989.
12. Green, G. I., D. J. Mattson, and J. M. Peek. 1997. Spring feeding on ungulate carcasses by grizzly bears in Yellowstone National Park. *Journal of Wildlife Management* 61: 1040-1055.
13. Green, R. J. 1995. Using frugivores for regeneration: a survey of knowledge and problems in Australia. Pages 651-657 in J. A. Bissonette and P. R. Krausman, editors. *Integrating people and wildlife for a sustainable future*. The Wildlife Society, Bethesda, MD.
14. Hobbs, N. T. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management* 60: 695-713.
15. Horvitz, C. C., J. B. Pascarella, S. McMann, A. Freedman, and R. H. Hofstetter. 1998. Functional roles of invasive non-indigenous plants in hurricane-affected subtropical hardwood forests. *Ecological Applications* 8: 947-974.
16. Huston, M. A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* 110: 449-460.
17. Jones, C. G., J. H. Lawton, and M. Shachak. 1996. Organisms as ecosystem engineers. Pages 130-147 in F. B. Samson and F. L. Knopf, editors. *Ecosystem management: selected readings*. Springer, New York, NY.
18. Li, C. Y., C. Maser, Z. Maser, and B. A. Caldwell. 1986. Role of three rodents in forest nitrogen fixation in western Oregon: another aspect of mammal-mycorrhizal fungus-tree mutualism. *Great Basin Naturalist* 46: 411-414.
19. Mack, M. C., and C. M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evolution* 13: 195-198.
20. MacNally, R. C. 1995. *Ecological versatility and community ecology*. Cambridge University Press, New York, NY.
21. Marcot, B. G. 1997. Species-environment relations (SER) database. U.S. Forest Service, Pacific Northwest Research Station, Portland, OR. Interior Columbia Basin Ecosystem Management Project database available on-line at URL: <http://www.icbemp.gov/spatial/metadata/databases/dbase.html>

22. Marcot, B. G. 1997. The species-environment relations (SER) database: an overview and some cautions in its use. U.S. Forest Service, Pacific Northwest Research Station, Portland, OR. Interior Columbia Basin Ecosystem Management Project database documentation available online at URL: <http://www.icbemp.gov/spatial/metadata/databases/792aux2.html>
23. Marcot, B. G., M. A. Castellano, J. A. Christy, L. K. Croft, J. F. Lehmkuhl, R. H. Naney, K. Nelson, C. G. Niwa, R. E. Rosentreter, R. E. Sandquist, B. C. Wales, and E. Zieroth. 1997. Terrestrial ecology assessment. Pages 1497-1713 in: T. M. Quigley and S. J. Arbelbide, editors. An assessment of ecosystem components in the interior Columbia Basin and portions of the Klamath and Great Basins. Volume III. U.S. Forest Service General Technical Report PNW-GTR-405.
24. Marcot, B. G., L. K. Croft, J. F. Lehmkuhl, R. H. Naney, C. G. Niwa, W. R. Owen, and R. E. Sandquist. 1998. Macroecology, paleoecology, and ecological integrity of terrestrial species and communities of the interior Columbia River Basin and portions of the Klamath and Great Basins. U.S. Forest Service, General Technical Report PNW-GTR-410.
25. Mawdsley, N. A., S. G. Compton, and R. J. Whittaker. 1998. Population persistence, pollination mutualisms, and figs in fragmented tropical landscapes. *Conservation Biology* 12: 1416-1420.
26. Mills, L. S., M. E. Soule, and D. F. Doak. 1993. The keystone-species concept in ecology and conservation. *BioScience* 43: 219-224.
27. Moore, G. C., and G. R. Parker. 1992. Colonization by the eastern coyote (*Canis latrans*). Pages 23-37 in A. H. Boer, editor. Ecology and management of the eastern coyote. Wildlife Research Unit, University of New Brunswick, Fredericton, New Brunswick, Canada.
28. Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1998. Wildlife-habitat relationships: concepts and applications. Second edition. University of Wisconsin Press, Madison, WI.
29. Naeem, S. 1998. Species redundancy and ecosystem reliability. *Conservation Biology* 12: 39-45.
30. Paruelo, J. M., and W. K. Lauenroth. 1996. Relative abundance of plant functional types in grasslands and shrublands of North America. *Ecological Applications* 6: 1212-1224.
31. Pimm, S. L. 1994. Biodiversity and the balance of nature. Pages 347-359 in E. D. Schulze and H. A. Mooney, editors. Biodiversity and ecosystem function. Springer-Verlag, Berlin, Heidelberg, Germany.
32. Pugnaire, F. I., and F. Valladares, editors. 1999. Handbook of functional plant ecology. Marcel Dekker, New York, NY.
33. Rastetter, E. B., L. Gough, A. E. Hartley, D. A. Herbert, K. J. Nadelhoffer, and M. Williams. 1999. A revised assessment of species redundancy and ecosystem reliability. *Conservation Biology* 13: 440-443.
34. Rauscher, H. M. 1999. Ecosystem management decision support for federal forests in the United States: a review. *Forest Ecology and Management* 114: 173-198.
35. Reid, W. V., and K. R. Miller. 1989. Keeping options alive-the scientific basis for conserving biodiversity. World Resources Institute, Washington, D.C.
36. Robertson, A. V., D. Kelly, J. J. Ladley, and A. D. Sparrow. 1999. Effects of pollinator loss on endemic New Zealand mistletoes (Loranthaceae). *Conservation Biology* 13: 499-508.
37. Schlapfer, F., and B. Schmid. 1999. Ecosystem effects of biodiversity: a classification of hypotheses and exploration of empirical results. *Ecological Applications* 9: 893-912.
38. Schowalter, T., E. Hansen, R. Molina, and Y. Zhang. 1997. Integrating the ecological roles of phytophagous insects, plant pathogens, and mycorrhizae in managed forests. Pages 171-189 in K. A. Kohm and J. F. Franklin, editors. Creating a forestry for the 21st century: the science of ecosystem management. Island Press, Washington, D.C.
39. Smith, T. M., H. H. Shugart, and F. I. Woodward, editors. 1997. Plant functional types: their relevance to ecosystem properties and global change. Cambridge University Press, New York, NY.
40. Soule, M. and K. A. Kohm. 1989. Research Priorities for Conservation Biology. Island Press, Washington, D.C.
41. Stohlgren, T. J., L. D. Schell, and B. Vanden Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. *Ecological Applications* 9: 45-64.
42. Stone, R. 1995. Taking a new look at life through a functional lens. *Science* 269: 316.
43. Urbanska, K., N. Webb, and P. Edwards, editors. 1998. Restoration ecology and sustainable development. Cambridge University Press, New York, NY.
44. van Gardingen, P. R., G. M. Foody, and P. J. Curran, eds. 1997. Scaling-up: from cell to landscape. Cambridge University Press, New York, NY.
45. Walker, B. H. 1992. Biodiversity and ecological redundancy. *Conservation Biology* 6: 18-23.
46. Williams, J. B., B. E. Tieleman, and M. Shobrak. 1999. Lizard burrows provide thermal refugia for larks in the Arabian desert. *Condor* 101: 714-717.
47. Wilson, E. O. 1987. The little things that run the world (the importance and conservation of invertebrates). *Conservation Biology* 1: 344-346.
48. Young, D. D., Jr, and T. R. McCabe. 1997. Grizzly bear predation rates on caribou calves in northeastern Alaska. *Journal of Wildlife Management* 61: 1056-1066.

Table 2. A taxonomy of patterns of key ecological functions (KEFs) of wildlife species and communities, and how to evaluate them using the KEF database.*

Functional pattern	Definition	Ecological implications	How to evaluate
Community patterns			
Functional redundancy	The number of species performing the same ecological function in a community.	High redundancy imparts greater resistance of the community to changes in its overall functional integrity. Low redundancy suggests critical functions to watch.	Tally number of species by KEF category for specific wildlife habitats, comparing changes over time or among habitats.
Functional richness	The total number of KEF categories in a community.	Denotes degree of functional complexity; greater functional richness means more functionally diverse systems. Also denotes the degree to which the full “functional web” of a community would be provided or conserved.	Tally number of KEF categories among all species present in a wildlife habitat and, optionally, habitat structure. Compare such tallies resulting from changes in habitats and structures.
Total functional diversity	The total array of KEF categories weighted by their redundancy, i.e., the number of functions times the mean functional redundancy across all functions.	Denotes total functional capacity of a community. High functional diversity means many functions and even redundancy among functions; low functional diversity means few functions and skewed redundancy (some functions with few species).	Tally number of species by KEF category for a given wildlife habitat; calculate mean number of species per KEF category. Can assign weights to some KEF categories if they pertain to specific management objectives.
Functional web	The set of all KEFs within a community and their connections among species and thence to habitat elements.	Depicts how habitat elements provide for species, and the array of ecological functions performed by those species. Functions typically extend well beyond the specific habitat elements.	Identify habitat elements of management interest; list all species within a wildlife habitat that are associated with those habitat elements; list all KEF categories associated with those species. Compare changes in habitat elements.
Functional profile	The degree of functional redundancy compared across communities.	Identifies communities with low (or high) redundancy of particular KEF categories. This can help prioritize habitat management, e.g., to ensure continuance of low-redundancy functions.	Tally number of species by KEF category and by wildlife habitat. Identify wildlife habitats with lowest tallies for each KEF category.
Functional homologies	The functional similarity of communities even if species composition differs.	Two communities are functionally homologous if they have similar functional profiles and patterns of functional redundancy, even if the species performing the functions differ. Functionally homologous communities can be expected to operate in similar ecological ways.	Produce functional profiles across all KEF categories for several communities or for a community over time based on its expected changes in habitat elements, habitat structures, etc. Compare the profiles (e.g., via contingency analysis) and identify statistically similar (functionally homologous) communities.

* Many of these categories are unstudied in wildlife communities of Washington and Oregon; thus, ecological implications should be viewed as working hypotheses. (See Table 1 for KEF categories.)

Functional pattern	Definition	Ecological implications	How to evaluate
Geographic patterns			
Functional bottlenecks or cold spots	Geographic locations with very low functional redundancy of an otherwise widely-distributed functional category.	Functional bottlenecks denote areas of higher risk of severing functionally connected communities across the landscape. Severing functions might set the stage for degradation of functional ecosystems.	Map wildlife habitats and/or distributional ranges of wildlife species. For a given KEF category, map the number of wildlife species in each habitat or overlay their range maps. Identify locations with lowest species richness bordering higher richness on each side; these are geographic functional bottlenecks (“cold spots”).
Functional linkages or hot spots	Geographic locations with very high functional redundancy.	Functional hot spots denote areas where many species provide a specific ecological function; such communities may be more resilient to changes in environment or habitat for that function.	Map species richness for a particular KEF category as above. Identify locations with highest species richness; these are functional linkages (“hot spots”). Determine which species occur in a given hot spot and their wildlife habitats, habitat elements, and habitat structures, and how changes might influence the persistence of the species and thus the redundancy of the function.
Species’ functional roles			
Functional keystone species, critical functional link species, and critical functions	Functional keystone species are species whose removal would most alter the structure or function of the community. One form of this may be critical functional links, which are species that are the only ones that perform a specific ecological function in a community. A critical function therefore is the associated functional category represented by only 1 (or very few) species within a community.	Reduction or extirpation of populations of functional keystone species and critical functional links may have a ripple effect in their ecosystem, causing unexpected or undue changes in biodiversity, biotic processes, and the functional web of a community.	For a given wildlife habitat, tally the number of species for each KEF category (functional redundancy). For KEF categories with only 1 species, determine which species performs this function. This is a critical functional link species for this particular function in this habitat.
Functional breadth and functional specialization of species	The number of ecological functions performed by a species.	Species with the narrowest functional breadth (i.e., fewest functions) are functional specialists and may be more vulnerable to extirpation from changes in conditions supporting that function.	For a given wildlife habitat, tally the number of KEF categories for each species. Identify the species with the fewest number of categories. These are functional specialists. Determine their habitat elements and structures and thus their potential vulnerability to changes thereof. Functional specialists that are also functional keystones may be of high priority for conservation attention.

Functional pattern	Definition	Ecological implications	How to evaluate
Functional responses of communities			
Functional resilience	The capacity of a community to return to a starting pattern of total functional diversity, richness, and redundancy, following a disturbance event.	Functionally resilient communities are better able to maintain their biotic processes in the face of disturbances. Conversely, it is important to know how far a community can be changed by some anthropogenic disturbance event and still be able to return to its starting functional pattern.	Determine the total functional diversity, functional richness, and functional redundancy of a pre-disturbance community. Then determine the types and rates of recovery of its wildlife habitats, habitat elements, and habitat structures following some disturbance; the wildlife species associated with such recovery stages; and the species' KEF categories and functional diversity, richness, and redundancy for each recovery stage. Compare stages for functional similarity and thus resilience.
Functional resistance	The ability of a community to resist changing its functional diversity, richness, and redundancy, following a disturbance event.	Functionally resistant communities can be counted on to continue to provide specific ecological functions in spite of and during disturbances. They may provide a bastion for a specific desired function in a disturbed or managed landscape.	Analyze as above and determine the degree to which functional diversity, richness, and redundancy do not change for each post-disturbance stage. This is a measure of functional resistance.
Functional attenuation	The degree to which the set of ecological functions within a community simplify following a disturbance event.	Functionally attenuated communities provide fewer or lower redundancies of ecological functions. It may be particularly important to know the degree of functional attenuation to be expected following anthropogenic disturbances.	Analyze as above and determine which KEF categories likely drop out and which remain over post-disturbance recovery stages as compared with initial conditions. Calculate functional diversity, richness, and redundancy for each stage to determine the rate of functional attenuation. Compare final stage to initial conditions to determine overall functional attenuation.
Functional shifting	The degree to which a community changes to a new, stable, functional constitution following a disturbance event.	Communities with low functional resilience or resistance may end up with a new array of functions and a new pattern of functional diversity, richness, and redundancy. It may be particularly important to know how a community might functionally shift following anthropogenic disturbances and thus which functions might be weakened, strengthened, lost, or gained.	Analyze as above and compare KEF categories and functional diversity, richness, and redundancy between pre-disturbance and final, stable stages. Identify which functions are lost or gained, and which change in redundancy.
Imperiled functions	A function that is represented by very few species (critical functional link species) or by species that are themselves scarce, declining, or moribund, where extirpation of the species would mean loss of the function. Imperiled functions also can be identified geographically.	Loss of imperiled functions serve to degrade overall ecosystem integrity. Even seldom-performed ecological functions might be critical to maintaining ecosystems, such as occasional dispersal of plant seeds in the face of shifting climates.	For a given wildlife habitat, determine KEF categories with the lowest functional redundancy, and the risk level of the associated species. Imperiled functions are those with 1 or few species which are themselves at risk.