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The functional diversity of mammals in coniferous forests of western North America

The ecological knowledge needed to achieve the goals of ecosystem management will not be limited to understanding the influence of habitat manipulations on desired mammal populations; it will also include an understanding of how those mammals contribute to the functioning of the ecosystems they occupy. Examples of the significant influence that mammals may have on the structure and function of ecosystems include the effects of sea otters (*Enhydra lutris*) on the community structure of coastal marine ecosystems (Estes and Palmisano 1974), the effects of American beavers (*Castor canadensis*) on the hydrology and ecology of temperate riparian ecosystems (Naiman et al. 1986, Anthony et al. 2003), the effects of burrowing mammals on soil fertility and stability (Meadows and Meadows 1991, Ayarbe and Kieft 2000), and the effects of large ungulates on successional processes and the structure of plant communities in a variety of ecosystems (Hobbs 1996). Each of these species or species groups has been described as a potential keystone species (Mills et al. 1993) in the ecosystems they occupy. Because most species of mammals may not influence ecosystem processes to the extent that keystone species do, their ecological contributions are often overlooked. We propose, however, that the collective importance of terrestrial mammals to ecosystem structure and function is substantial and that the decline or loss of forest mammal species could have detrimental effects on ecosystem diversity, productivity, or sustainability.

To determine how management actions may influence ecological conditions, managers must be able to characterize and quantify the contributions of resident organisms to ecosystem function. Here, we refer to the roles played by an organism that directly affect other species or strongly influence environmental conditions in a given ecosystem, as *key ecological functions* (KEFs). A classification system and database of KEFs was first developed for plant, invertebrate, and vertebrate species of the interior West (Marcot et al. 1997; also see Morrison et al. 1998) and later for vertebrates of Washington and Oregon (Marcot and Vander Heyden 2001; see Appendix at the end of this chapter). In these projects, the ecological roles of species were identified by expert panels, organized into hierarchical classifications, and coded into relational databases (primarily as categorical data). By querying the database, one can determine the array of KEFs associated with a given species or species group, the array of species sharing a given KEF category, information about the species' habitat requirements and life history patterns, the potential influence of management activities on key habitat elements and KEFs, and other environmental relations.

In this chapter, we evaluate the contributions of mammals to an array of ecological processes in coniferous forests of western North America using the wildlife–habitat relations and KEF databases from the Species-Habitat Project in Washington and Oregon (Johnson and O'Neil 2001). These databases relate wildlife species to forest types, structural conditions, key environmental correlates (KECs), and KEFs; and KECs to

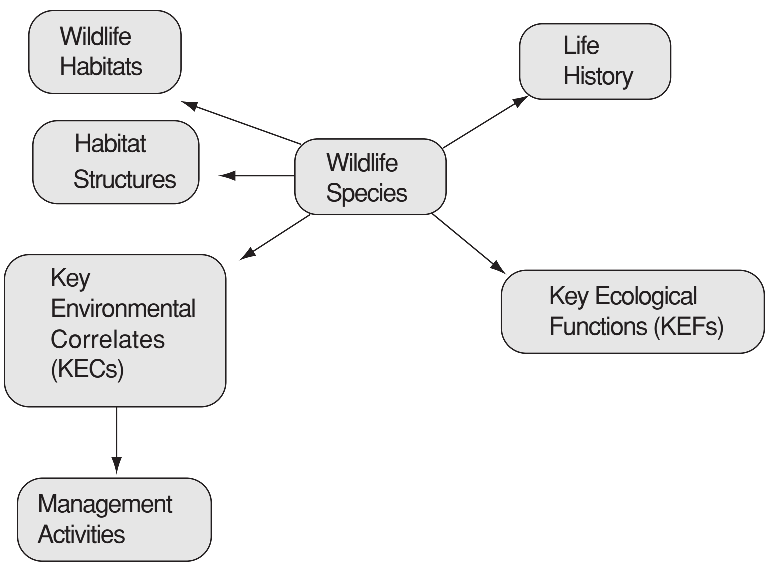


Fig. 19.1. Components of the wildlife–habitat relations database from the Species-Habitat Project in Washington and Oregon (Johnson and O'Neil 2001) used in our functional analyses.

management activities (Fig. 19.1). We present a process to: (1) describe the ecological roles of forest-dwelling mammals; (2) depict the "web of ecological functions" and other parameters associated with various functional groups; (3) link KEFs for each mammal species to forest types, vegetation structure, and KECs; and (4) quantify the potential effects of management actions on forest habitats, the mammals associated with those habitats, and the ecological functions they perform. The manager can use this approach to determine how forest mammals contribute to the functioning of a given ecosystem and estimate the extent to which that ecosystem will retain its functional integrity in response to management actions. The results of such assessments can be treated as repeatable and testable hypotheses of the effects of management activities on forested ecosystems.

Methods

We compared the list of mammals in the Species-Habitat Project database to the list of mammals occurring in forested habitats of western North America and identified the subset of forest-dwelling mammals that occur in Washington and Oregon (hereafter referred to as "forest mammals"). We then queried the databases to evaluate functional roles for various forest mammal assemblages. Because the KEF database consists mostly of categorical data, we used species counts as a unit of measure. We used the taxonomy of functional patterns in KEFs presented by Marcot and Vander Heyden (2001) to structure our investigation. These included community patterns (i.e., functional richness, redundancy, profiles, webs, and homologies), geographic patterns, ecological roles of species (i.e., critical links and functions, and functional breadth and specialization), and the functional responses of species assemblages (i.e., functional resilience and resistance). Definitions of each component of this taxonomy are presented in Results (also see Marcot and Vander Heyden 2001). We also used literature on the ecological roles of mammals to interpret the results of database queries. The information presented here should be viewed as working hypotheses because the specific rates and details of many of the functional relationships we discuss in this chapter have been poorly studied for most forest mammals.

Results

Ecological roles of forest mammals

Some of the ecological functions performed by forest mammals are unique. Mammals are the only vertebrates in western North American forests that feed on bark and cambium (seven species) or that create snags from live trees (three species). These activities add to the structural complexity of forests and provide habitat for a wide array of microorganisms, invertebrates, and cavity-using birds and mammals. Forest mammals are also key players in the dispersal of mushrooms and truffles, including the ectomycorrhizal fungi that play a critical role in the uptake of nutrients by conifer trees (Li et al. 1986, Maser and Maser 1988, Loeb et al. 2000; see Aubry et al. 2003 and Luoma et al. 2003); 11 species of forest mammals (Roosevelt elk (*Cervus elaphus roosevelti*), American pika (*Ochotona princeps*), two of voles, two of mice, and five of squirrels) and only one non-forest mammal (feral pig (*Sus scrofa*)) perform this fungi-dispersal function. In addition, recent work on the food habits of fishers suggests that forest carnivores may also serve as long-distance dispersal agents for fungal spores (see Aubry et al. 2003).

There are several other ecological functions for which forest mammals play a significant role. These include several categories of primary consumption, such as browsing on leaves or stems, eating mushrooms and truffles, eating feces and other excreta, dispersing lichens, excavating rabbit-sized or larger burrows, creating runways or trails, using runways created by other species, impounding water by creating diversions or dams, and altering vegetation structure and composition by browsing on trees or shrubs.

There are also a number of ecological roles, however, for which forest mammals participate the least; these include eating aquatic plants, eating aquatic macroinvertebrates, eating fish, eating fruits, dispersing insects and other invertebrates, dispersing propagules of vascular plants, and excavating cavities. There are an additional 12 KEFs that are not performed at all by forest mammals, including eating sap, creating sapwells in trees, eating freshwater zooplankton, pollinating plants, and serving as nest parasites or hosts. Thus, the array of ecological functions of forest mammals, as an assemblage, is unique and complementary to that of other taxonomic groups.

Community functional patterns

Functional richness and mean functional redundancy

The Species-Habitat Project database listed 733 species of amphibians, reptiles, birds, and mammals that occur in Washington and Oregon, of which 116 (16%) are mammals that inhabit forests, and 58 (8%) are forest mammals closely associated with coniferous forests. Forest mammals

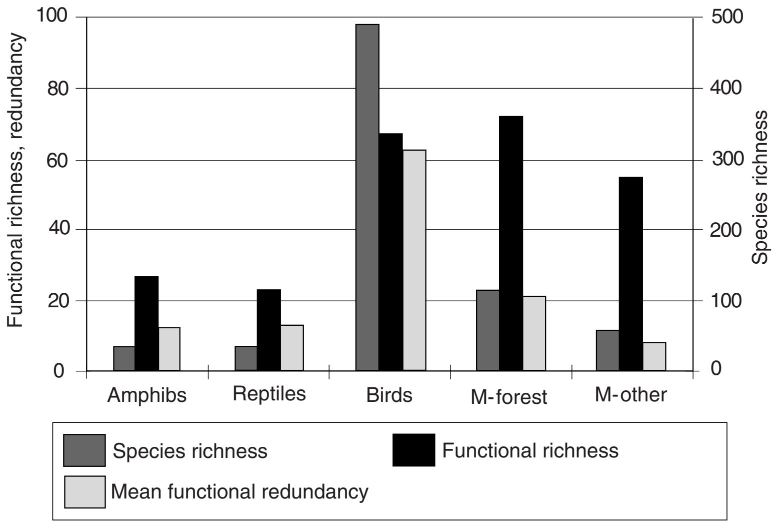


Fig. 19.2. Species richness, functional richness (number of categories of key ecological functions among all species), and mean functional redundancy (average number of categories of key ecological functions/species) of amphibians, reptiles, birds, forest mammals (M-forest), and non-forest mammals (M-other) in Washington and Oregon. Note that forest mammals have relative low species richness but high functional richness.

comprise 67% of mammal species in this region. There are 72 KEFs pertaining to at least one of the 116 forest mammals; this value represents the *total functional richness* (the number of KEF categories) of the forest mammal species assemblage (there is some redundancy in this value, because it includes both categories and subcategories of KEFs; see Appendix). This value is higher than the total functional richness of amphibians, reptiles, birds, and non-forest mammals, even though the total *species* richness of forest mammals is far less than that of birds and only slightly higher than those of each of the other taxonomic groups (Fig. 19.2). Thus, forest mammals fill a disproportionately broad array of ecological roles compared to other terrestrial vertebrate species groups.

On a per-KEF basis, however, the functional diversity represented by forest mammals is relatively low. For each species group (taxonomic group or assemblage), the average number of species performing each KEF is the *mean functional redundancy* of that group, and *functional diversity* is functional richness weighted by mean functional redundancy, analogous to species diversity, species richness, and species abundance (Brown 1995). Forest mammals average a functional redundancy of 21 species per KEF, which exceeds values for non-forest mammals, amphibians, and reptiles, but is much lower than the average value for birds (63 species per KEF; Fig. 19.2). In other words, forest mammals perform a more diverse array of ecological functions than amphibians, reptiles, or non-forest mammals, but contribute less to the functional diversity of forest ecosystems than do birds. Understanding patterns of functional diversity is important, because forest ecosystems with high levels of functional redundancy probably have a higher resilience to perturbations, stresses, and environmental changes (Peterson et al. 1998, Fonseca and Ganade 2001).

Functional profiles

A histogram that compares the functional redundancy among a set of habitats is a *functional profile.* These graphs can be useful for identifying habitats that are particularly rich or poor in specific functions (Marcot and Vander Heyden 2001). Nine forest habitats are described in the Species-Habitat Project database for Washington and Oregon (Chappell et al. 2001). Among these, Eastside Mixed Conifer, Montane Mixed Conifer, and Westside Lowlands Conifer-Hardwood Forests have the highest number of forest mammal species, whereas Western Juniper and Mountain Mahogany Woodlands, and Upland Aspen Forest have the lowest.

The highest functional redundancy in burrow excavation is found in Montane and Eastside Mixed Conifer Forests, whereas the lowest occurs in Western Juniper Forests (Fig. 19.3). However, digging species, which contribute to soil aeration and turnover of soil organic matter (Meadows and Meadows 1991, Butler 1995, Jones et al. 1996), are most numerous in Ponderosa Pine Forests and least numerous in Lodgepole Pine Forests. For dispersers of plant propagules, Montane and Eastside Mixed Conifer forests tend to be most species-rich. Western Juniper and Upland Aspen Forests have the fewest dispersers, which may be related to the relatively simple floras of those forest types compared with mixed-conifer forest types. The objective of comparing such functional profiles among habitats is to determine the habitats that support specific functions the most or the least. Knowing when only a few species provide a specific function in a given habitat may help managers design prescriptions that will reduce the likelihood that these species' ecological functions will be lost from the system.

Functional webs

The array of KEFs performed by an assemblage of species associated with a particular habitat element or structure is a *functional web.* For example, Marcot (2002) and Rose et al. (2001) identified functional webs of

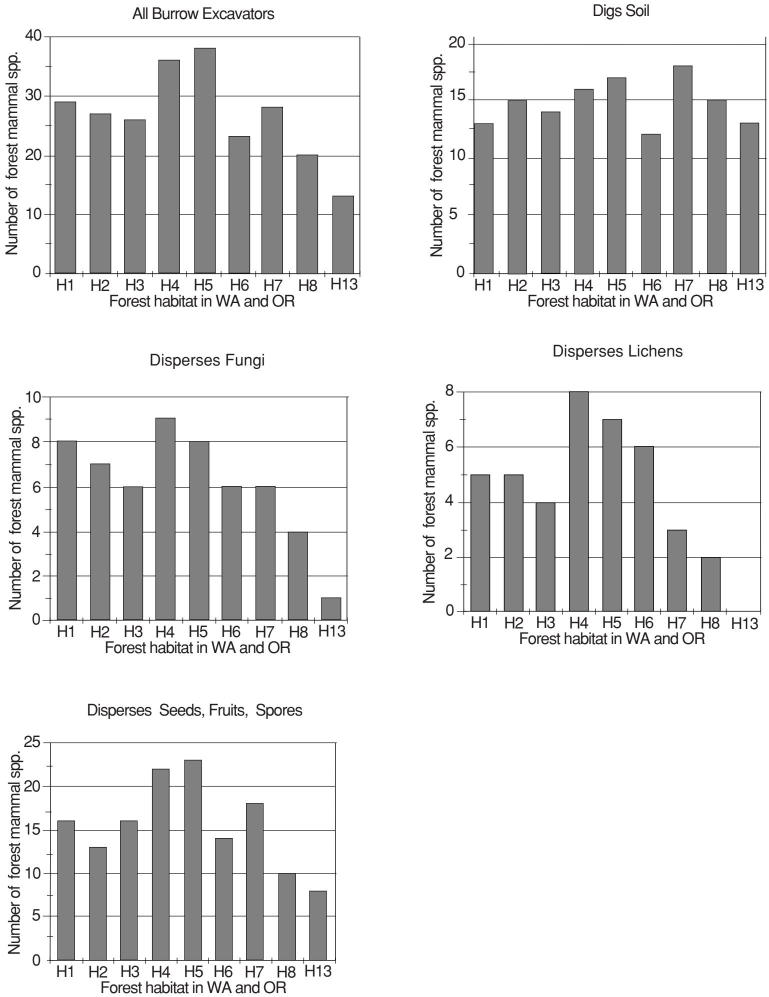


Fig. 19.3. Functional profiles for five selected categories of key ecological functions of forest mammals in Washington (WA) and Oregon (OR). H1 = Westside Lowlands Conifer-Hardwood Forest, H2 = Westside Oak (*Quercus garryana*) and Dry Douglas-fir (*Pseudotsuga menziesii*) Forest and Woodlands, H3 = Southwest Oregon Mixed Conifer-Hardwood Forest, H4 = Montane Mixed Conifer Forest, H5 = Eastside Mixed Conifer Forest, H6 = Lodgepole Pine (*Pinus contorta*) Forest and Woodlands, H7 = Ponderosa Pine (*Pinus ponderosa*) and Eastside White Oak Forests and Woodlands, H8 = Upland Aspen (*Populus tremuloides*) Forest, H13 = Western Juniper (*Juniperus occidentalis*) and Mountain Mahogany (*Cercocarpus montanus*) Woodlands.

forest species (including mammals) that are associated with down wood and snags in forests of Washington and Oregon. Results suggested that down wood was a habitat component for 86 wildlife species, 51 of which are forest mammals, and snags provided habitat for 95 wildlife species including 24 forest mammals. Collectively, these down wood- and snag-using species perform a rather surprisingly broad array of KEFs that could be maintained in the ecosystem by providing adequate amounts of snags and coarse woody debris for the wildlife species that are associated with such structures. Forest mammals play a key role especially in the down wood functional web; all nine wildlife species that are associated with down wood and that disperse fungal spores are forest mammals. Down wood also supports other species of small mammals that are prey for carnivores, disperse plant propagules, and provide an array of other ecological functions (McComb, 2003).

Forest mammals associated with down wood in Westside Lowlands Conifer-Hardwood Forest perform an array of at least 26 ecological functions (Fig. 19.4). Such functional webs can be described for any forest condition or habitat element by querying the databases to determine the array of associated species and the KEFs they perform. By doing so, managers can assess the ecological "value" of providing for a specific habitat element, and gain an understanding of how such structures help support the complex web of ecological functions that characterize coniferous forested ecosystems.

Functional homologies

When different habitats have a similar number of species performing the same KEFs, the habitats can be said to be *functionally homologous.* That is, although species composition may differ, the habitats have similar levels of functional redundancy for the same KEFs (Marcot and Vander Heyden 2001). To what extent are the nine forested habitats in Washington and Oregon functionally homologous? This can be answered by inspecting the functional profile graphs and comparing the number of forest mammal species that perform each KEF across the nine forest types. Results (Fig. 19.5A) indicate that these habitats are not highly homologous for all functions. That is, for some KEFs, the number of forest mammal species (the functional redundancy) varies considerably among forest types. In particular, they vary the most for forest-mammalian functions pertaining to primary excavation of burrows, secondary use of excavated burrows, and dispersal of seeds, fruits, and fungal spores. This means that, at least

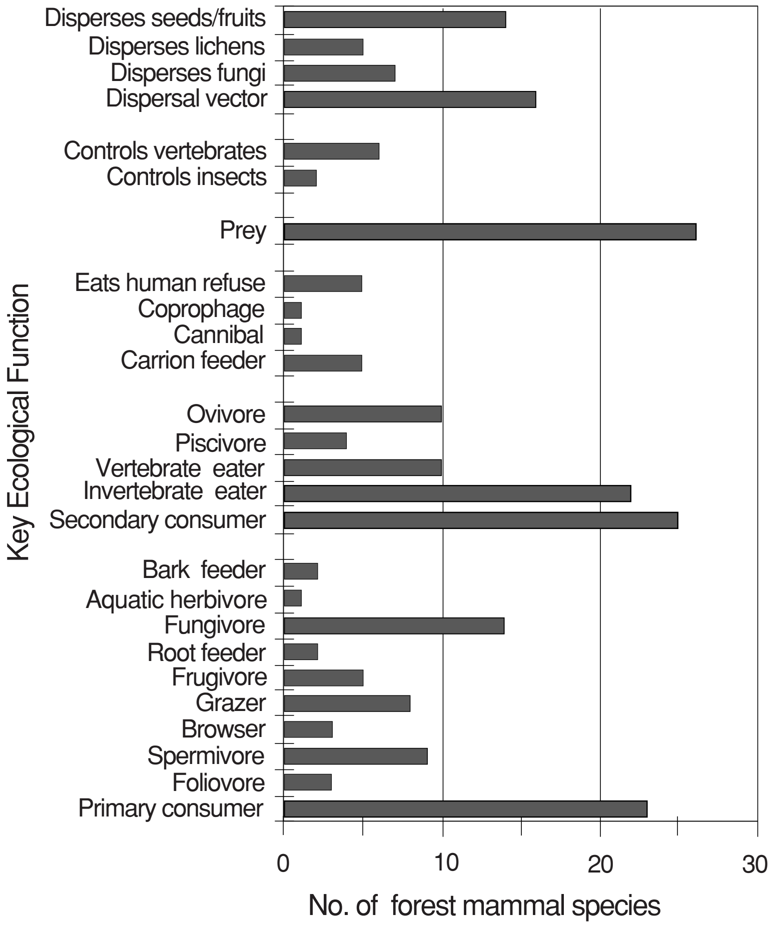


Fig. 19.4. Functional web of forest mammals associated with down wood in Westside Lowlands Conifer-Hardwood Forest. For example, ten species eat eggs (ovivore) as part of their functions within the forested ecosystem.

for forest mammals, the forest types are not strictly the same in terms of their arrays of ecological functions.

Functional homology can also be evaluated by comparing the similarity in the number (functional redundancy) of species per KEF in a cluster classification. Such a comparison (Fig. 19.5B) suggests that Westside Oak and Dry Douglas-fir Forest and Woodlands, and Southwest Oregon Mixed Conifer-Hardwood Forest are quite similar, as are Montane Mixed Conifer Forest, and Eastside Mixed Conifer Forest. The forest type Western

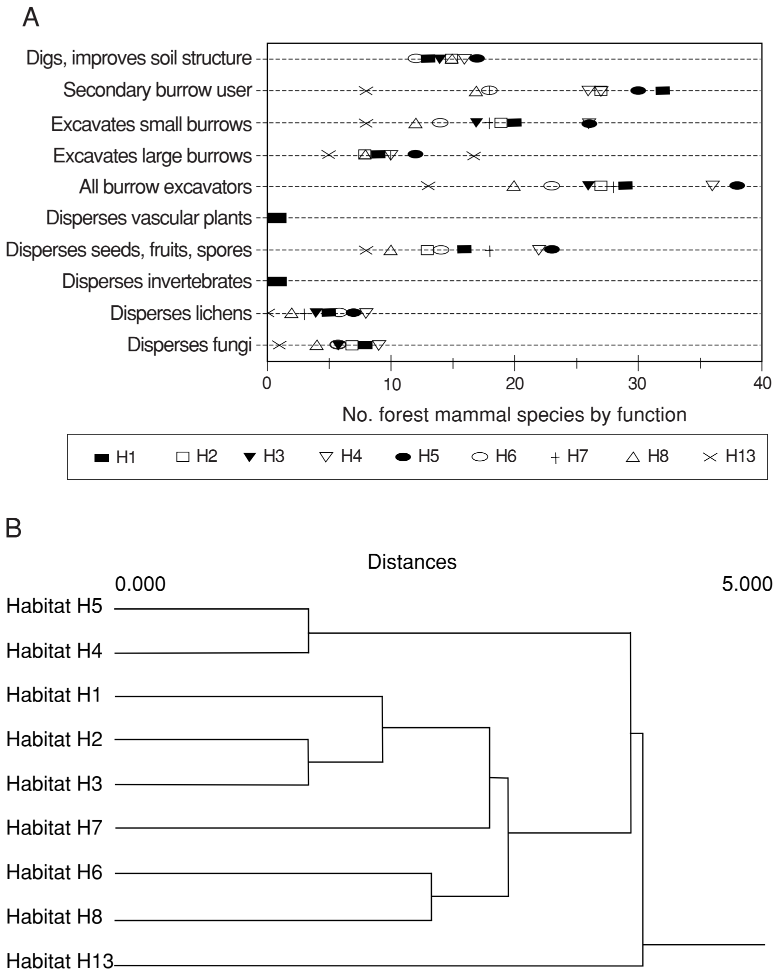


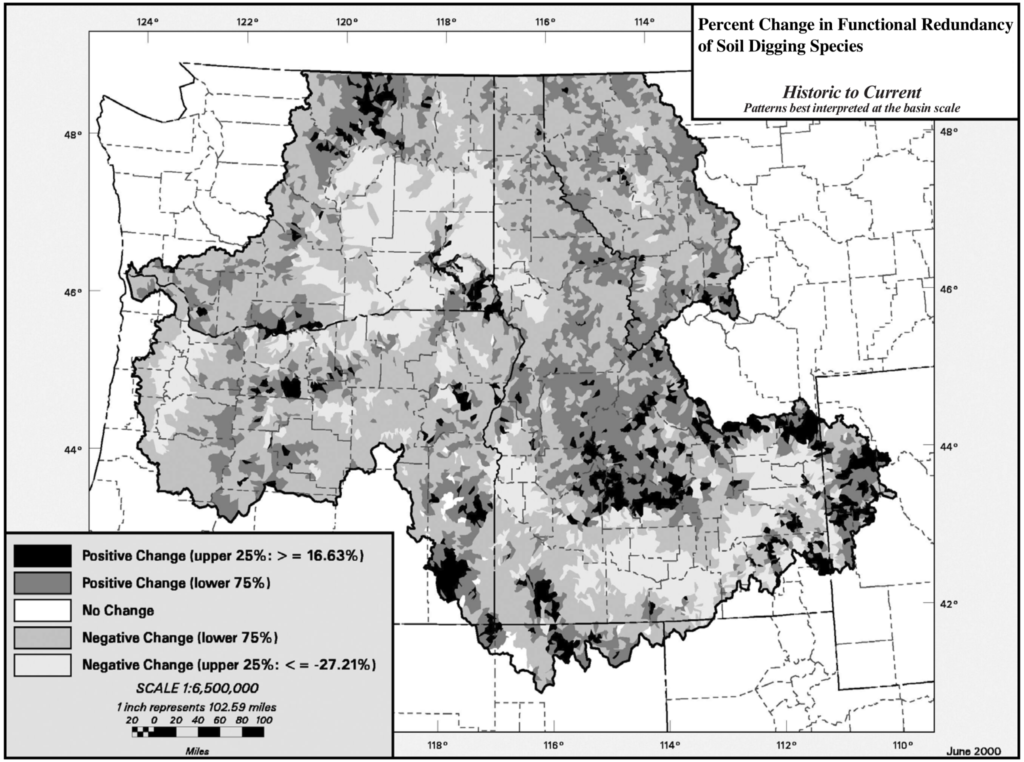
Fig. 19.5. (A) Functional homologies for selected key ecological functions, among nine forest wildlife habitats in Washington and Oregon (see Fig. 19.3 for forest habitat codes). Functional homology is a comparison of numbers of forest mammal species (or functional redundancy) with various key ecological functions (vertical axis) among habitats. (B) Hierarchical cluster classification of the nine forested wildlife habitats in Washington and Oregon, based on the number (functional redundancy) of forest-dwelling mammal species among the ten categories of key ecological functions (KEFs) listed in (A). Clustering was based on single linkage and Euclidean distance metrics. Note that wildlife habitats H2 and H3, and H4 and H5 are the most functionally homologous in terms of number of species performing these KEFs. The most dissimilar (least homologous) habitat functionally is H13.

Juniper and Mountain Mahogany Woodlands is most dissimilar, that is, least functionally homologous to the other forested habitats in Washington and Oregon. (The specific composition of forest mammal species also differs among the nine forested habitats analyzed here, somewhat but not fully paralleling the similarity in functional redundancy, with the least similar species composition occurring in Western Juniper and Mountain Mahogany Woodlands.) Thus, if managers wish to provide for the full array of ecological functions provided by forest mammals in all forested habitats of Washington and Oregon, they would need to provide for conditions that support such functions across the variety of forested habitats.

Geographic functional patterns

Once species' distributions and habitat conditions are accurately mapped, geographic patterns of functional redundancy for any given KEF or set of KEFs can be displayed and analyzed spatially (as has been done for some abiotic functions; see Noronha and Goodchild 1992). For example (Fig. 19.6), the functional redundancy of species that dig soil (most of whom are mammals) can be related to important contributions to soil structure and aeration within the Columbia River Basin in the U.S., and this can be mapped. One type of functional map can depict changes in functional redundancy for this KEF by comparing historic (early 1800's) to current (2000) conditions, showing that there has been a significant decline in functional redundancy of this KEF in many inland valley and basin systems including the Willamette Valley of Oregon, the Columbia Basin of Washington, and the Snake River Basin of Idaho. These are geographic areas where native grasslands and shrublands have been largely converted to agriculture, creating mostly inhospitable conditions for many native soil-digging mammals. Consequently, the soil-digging function currently is not well represented in these locations as compared to historic conditions.

Further, there do not seem to be any corridors of increased redundancy linking these areas. These areas are therefore *functional bottlenecks* that restrict the degree to which this function could operate across the landscape. Managers may wish to know where the geographic weakening or severing of functions might set the stage for further degradation of interacting functional ecosystems (Marcot and Vander Heyden 2001). This may be of particular interest because restoring or maintaining interacting functional ecosystems has been stated as a potential objective for ecosystem management (Strange et al. 1999). In one non-mammal example,


Percent Change in Functional Redundancy of Soil Digging Species
Historic to Current
Patterns best interpreted at the basin scale
124°
122°
120°
118°
116°
114°
112°
110°
48°
46°
44°
42°
Positive Change (upper 25%: > = 16.63%)
Positive Change (lower 75%)
No Change
Negative Change (lower 75%)
Negative Change (upper 25%: < = -27.21%)
SCALE 1:6,500,000
1 inch represents 102.59 miles
20 0 20 40 60 80 100
Miles
June 2000

Nabhan (2001) identified important habitat corridors for 300 species of nectar-feeding pollinators that migrate between Mexico and North America.

In contrast, some of the mountain areas show a significant increase in functional redundancy of the soil-digging and burrowing KEF, including parts of the North Cascades and Blue Mountains in Washington, the Rocky Mountains of southern Idaho, and some of the mountains in the Greater Yellowstone ecosystem of southeastern Idaho and western Wyoming. In these regions, many forested areas have undergone extensive timber harvesting since historic times, reverting them to earlier successional stages that support more wildlife species that dig soil, especially forest mammals. As described previously, communities with higher levels of functional redundancy may be more resilient to stressors and disturbances. However, as viewed throughout the entire Columbia River Basin, the total area of decrease in redundancy of this function (Fig. 19.6) is far greater than the total area of increase, indicating that the Columbia River Basin in the U.S. has suffered an overall decline in redundancy for the soil-digging function.

Such a map could be produced for any KEF, for use by managers to locate specific areas of lowered or lost redundancy or of functional bottlenecks, to help prioritize areas for restoration or maintenance of conditions for specific functions. For example, Dale et al. (2000) noted that "Particular species and networks of interacting species have key, broad-scale ecosystem-level effects." In the Columbia River Basin, patterns of change in other KEFs also vary geographically (Fig. 19.6). Change also can be compared between current and predicted future conditions under various land-planning alternatives (Marcot et al. 2002). In this way, managers can project future geographic effects on ecological functions and, by mapping KEFs, identify land areas needing special attention to avoid significant declines in one or more KEFs. Such an approach can help managers

Fig. 19.6. Map of functional redundancies of soil-digging animals in the Columbia River Basin, showing high and low areas of change in functional redundancy from historic conditions. Although the map depicts terrestrial wildlife of all taxonomic classes, most of the species shown here are mammals (of both forested and non-forested habitats). The map was produced based on wildlife habitats and associated species by sub-watershed, and the different shading denotes quartiles of change categories. For example, the category of highest positive change is shown as the top 25% of sub-watersheds having the highest value in change in functional redundancy, and this represents a change of 16.6% increase in functional redundancy values. (Source: Tom O'Neil, Northwest Habitat Institute, Corvallis, Oregon; used by permission.)

select planning alternatives that best match stated goals for maintaining intact forest mammal communities in specific ecosystems.

Species' functional roles

Critical functions and critical functional link species

When only one or a few species perform a particular ecological function and their removal would signal a serious decline or loss of that *critical function*, such species are designated as *critical functional link species* (Marcot and Vander Heyden 2001). For example, among forest mammals in the Westside Lowlands Conifer-Hardwood Forests of coastal Washington and Oregon, the KEF of creating snags (girdling or killing live trees) is provided by the American beaver, black bear (*Ursus americanus*), and common porcupine (*Erethizon dorsatum*). Insect species and fungal pathogens, along with fire, also provide this function. These forest mammals are the only three vertebrate wildlife species that provide this function in western forests, making this KEF a moderately "critical function" and these species critical functional link species for this particular function.

Although relatively few forest mammals can be considered critical functional link species, several species do provide critical functions in the ecosystems they occupy. In Westside Lowlands Conifer-Hardwood Forests of Washington and Oregon, critical functions include creating ground structures used by other species (bushy-tailed woodrat (*Neotoma cinerea*), Douglas squirrel (*Tamiasciurus douglasii*)), creating aquatic structures and impounding water (American beaver), secondary use of aquatic structures created by other species (fisher (*Martes pennanti*), mink (*Mustela vison*)), and creating wet swales and small ponds by wallowing (Roosevelt elk). No other species than these few forest mammals perform these functions in this particular forest type.

These patterns contrast to those in another forest type, Western Juniper and Mountain Mahogany Woodlands, an arid environment of eastern Washington and Oregon. In this forest type, at least eight KEFs are performed by only a few vertebrates, all of which are forest mammals. These critical functions include eating bark and cambium and creating snags (American beaver, common porcupine), browsing (American beaver, common porcupine, a few ungulates), eating feces (Nuttall's or mountain cottontail (*Sylvilagus nuttallii*)), creating aquatic structures and impounding water (American beaver), secondary use of aquatic structures (mink), and changing vegetation structure or successional stage through intensive herbivory (common porcupine, golden-mantled ground squirrel

(*Spermophilus lateralis*)). However, none of the functions associated with forest mammals in this forest type is an *imperiled function*, that is, the forest mammals listed here are not scarce, greatly declining, or extirpated, so these functions can be reasonably expected to continue. However, in some areas where American beavers have been trapped out, their critical functions listed above may have suffered. Managers could use such information to identify and prioritize functions that may depend on only one or a few forest mammal species. Habitat conditions for these species could then be provided to help maintain high-priority functions that may be in danger of being lost from the system.

Functional breadth and functional specialization of species

The array of functions performed by a species is its *functional breadth*. Species performing very few functions (e.g., fewer than eight associated KEFs) are *functional specialists*, whereas those performing many (e.g., >20 KEFs) are *functional generalists* (Marcot and Vander Heyden 2001). For example, among forest mammals in Westside Lowlands Conifer-Hardwood Forest of Washington and Oregon, functional specialists include the fog shrew (*Sorex sonomae*; five KEFs), Baird's shrew (*Sorex bairdi*; six KEFs), and masked shrew (*Sorex cinereus*), ermine (*Mustela erminea*), long-eared myotis (*Myotis volans*), and Pacific shrew (*Sorex pacificus*) (seven KEFs each). Functional specialists in this forest type tend to be insectivores and some are secondary predators. Functional generalists tend to be omnivorous or herbivorous, and include the black bear (33 KEFs), raccoon (*Procyon lotor*; 27 KEFs), deer mouse (*Peromyscus maniculatus*; 26 KEFs), American beaver (24 KEFs), Douglas squirrel (*Tamiasciurus douglasii*; 23 KEFs), striped skunk (*Mephitis mephitis*; 22 KEFs), and Roosevelt elk (21 KEFs). In contrast, there are only two forest mammals that are functional specialists in Western Juniper and Mountain Mahogany Woodlands of eastern Washington and Oregon: the long-eared myotis and western pipistrelle (*Pipistrellus hesperus*), both of which are insectivorous bats with only seven KEFs each. Functional generalists are limited to the deer mouse (26 KEFs), golden-mantled ground squirrel, and American beaver (24 KEFs each).

Functional specialists in other forest types of Washington and Oregon include wolverine (*Gulo gulo*; five KEFs), lynx (*Lynx canadensis*), northern bog lemming (*Synaptomys borealis*) (six KEFs each), mountain goat (*Oreamnos americanus*), Preble's shrew (*Sorex preblei*), and spotted bat (*Euderma maculatum*) (seven KEFs each); and functional generalists include red squirrel (*Tamiasciurus hudsonicus*; 23 KEFs), black-tailed jackrabbit

(*Lepus californicus*), and grizzly bear (*Ursus arctos*) (22 KEFs each). Although not necessarily a forest-dwelling species, humans (*Homo sapiens*) are the greatest functional generalists of all; our impressive array of 35 KEFs (Appendix) exceeds that of any other vertebrate species. This may explain, in part, why humans have had such an overwhelming influence on so many habitats and wildlife communities (Marcot and Vander Heyden 2001).

Functional responses of species assemblages

Functional resilience and resistance among forest structural classes

Maintaining the biodiversity and productivity of communities or ecosystems may require that they remain resilient or resistant to disturbances (Walker 1992, 1995). The capacity of an ecosystem to rebound to its initial functional pattern following a change from disturbance is its *functional resilience* (Reice et al. 1990, Carpenter and Cottingham 1997, Ludwig et al. 1997, Gunderson 2000, Marcot and Vander Heyden 2001), and *functional resistance* is the capacity of a community to maintain its functional patterns in response to a disturbance (Halpern 1988, Brang 2001, Marcot and Vander Heyden 2001).

Few studies have been conducted on these parameters for individual species or assemblages of forest mammals, although Weaver et al. (1996) discussed the importance of functional resilience to the conservation of large carnivores. These concepts may be useful considerations for managers who want to maintain the functional roles of forest mammals in the presence of disturbance events, especially forest-management activities. Here, we explore the potential changes in functional redundancy of forest mammals among structural and successional stages of Westside Lowlands Conifer-Hardwood Forest as an example of how these concepts can be applied to management. The degree to which forest mammal communities would be able to respond to changes in these forest stages remains to be studied in the field. We intend for this analysis to generate hypotheses regarding the influence of forest management on patterns of functional redundancies in mammals that could be tested empirically.

We compared patterns of functional redundancies among selected KEFs among successional stages and canopy structure conditions in Westside Lowlands Conifer-Hardwood Forest using the Species-Habitat Project database for Washington and Oregon (O'Neil et al. 2001). Successional stages included grass/forb, shrub/seedling, sapling/pole, small tree, medium tree, large tree, and giant tree stages of single-story, closed-canopy forests. Mammal species composition varied among these successional stages. Overall trends in species richness suggested that most forest mammals and most secondary consumers occur in the medium to giant tree stages, with fewest in the sapling/pole and small tree stages (Fig. 19.7A). Functional redundancy of grazing is highest in the grass/forb-closed stage, whereas that of spermivory (seed-eating) is highest in the medium and large tree-single story-closed stages (Fig. 19.7B). Thus, to ensure that the full set of all ecological functions is present, with their highest redundancies, the forest manager may wish to provide for the full array of successional stages. Note that mammal species composition typically varies among successional stages, even for the same ecological function.

The number of forest mammals that are primary consumers tends to be more evenly distributed among the seven stages than are secondary consumers (Fig. 19.7A). KEFs with higher functional redundancies in grass/forb and shrub/seedling stages than in later stages included bark and cambium eaters, grazers, and diggers of small burrows. KEFs with higher functional redundancies in medium, large, and giant tree stages than in earlier stages included seed eaters, fungi eaters, egg eaters, carrion eaters, secondary burrow users, and dispersers of lichens, fungi, seeds, and fruits. KEFs with nearly equal functional redundancies among all seven stages included browsers, root eaters, fruit eaters, cannibals, fish eaters, and diggers of large burrows (Fig. 19.7B–F).

We ran one-way analysis of variance (ANOVAs) with post-hoc Bonferroni multiple comparison tests to determine if levels of functional redundancies among selected KEF categories varied significantly among successional stages, canopy-closure classes (open, moderate, or closed canopy), or number of canopy layers (single or multiple canopies) in Westside Lowlands Conifer-Hardwood Forest (Table 19.1). Results of ANOVA tests suggested that there were no significant effects of successional stage or the number of canopies on the total number of forest mammal species in this forest type (although there was a trend in the means for successional stage as noted above). There was a significant effect of canopy closure, however, with the highest number of species occurring in open-canopy conditions.

Among specific KEF categories, the functional redundancies of carrion eaters were significantly influenced by successional stage and number of canopies, and marginally influenced by canopy closure. The number of large-burrow excavators was influenced significantly by canopy closure but not by successional stage or the number of canopies. The number of small-burrow excavators showed reverse trends, being significantly

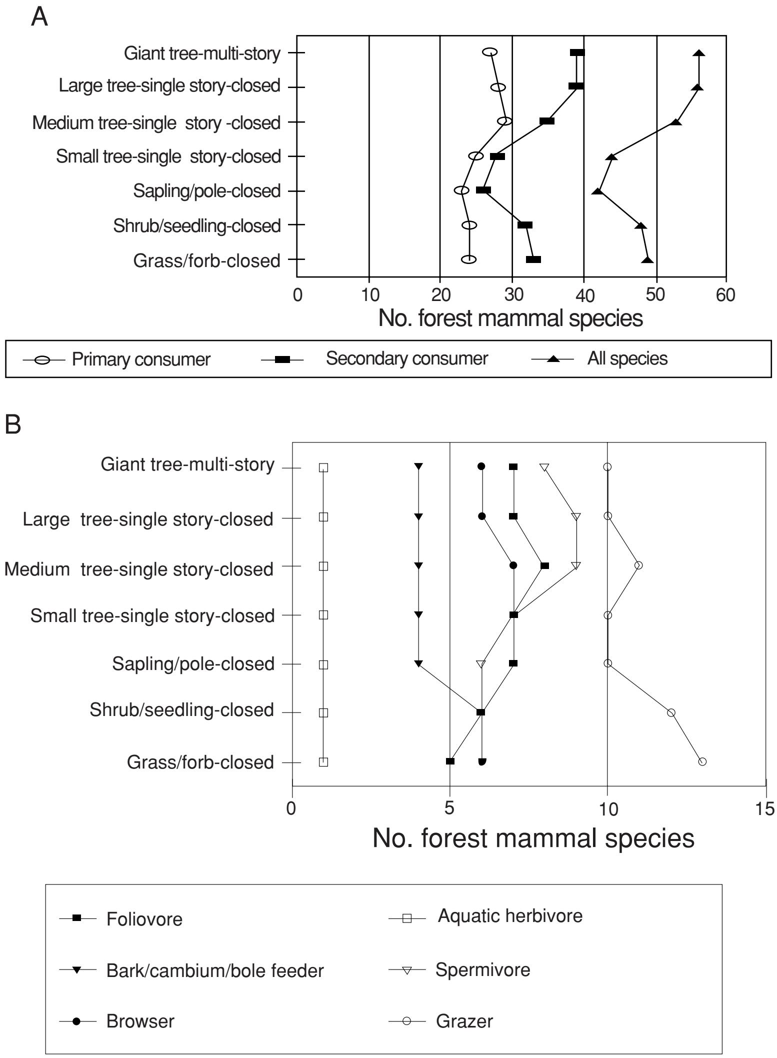
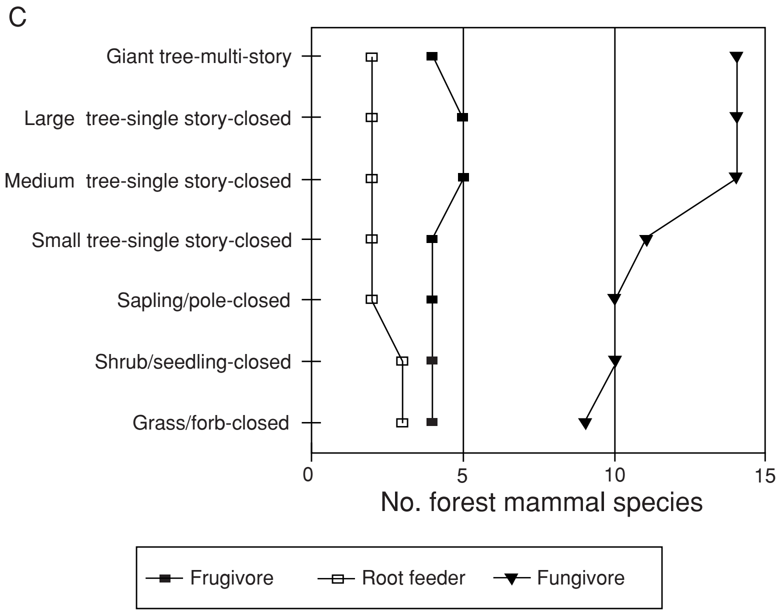


Fig. 19.7A–F. Number of forest mammal species in Westside Lowlands Conifer-Hardwood Forest of Washington and Oregon by seven successional stages of forest growth and selected categories of key ecological functions. Some functions reach their highest number of associated wildlife species (functional redundancy) in early successional stages, whereas other functions reach their highest functional redundancy in late successional stages.



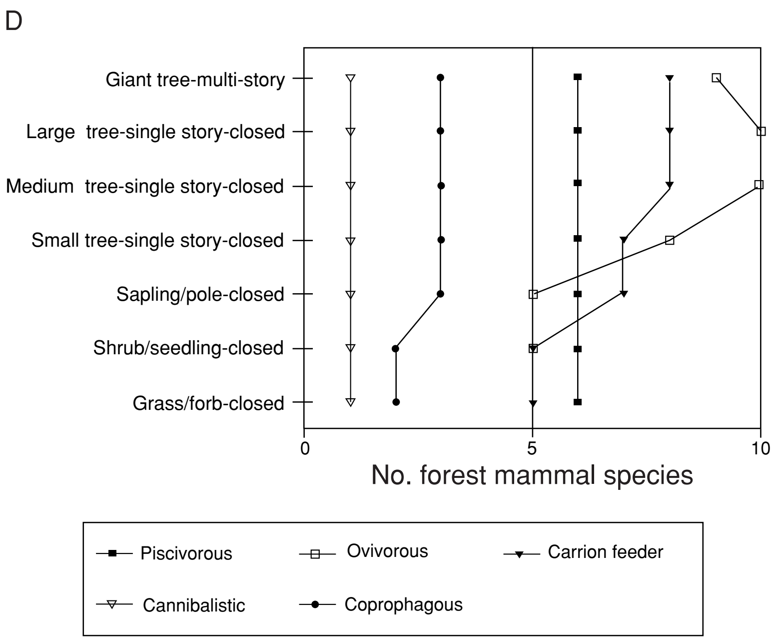


Fig. 19.7A–F. (*cont.*)

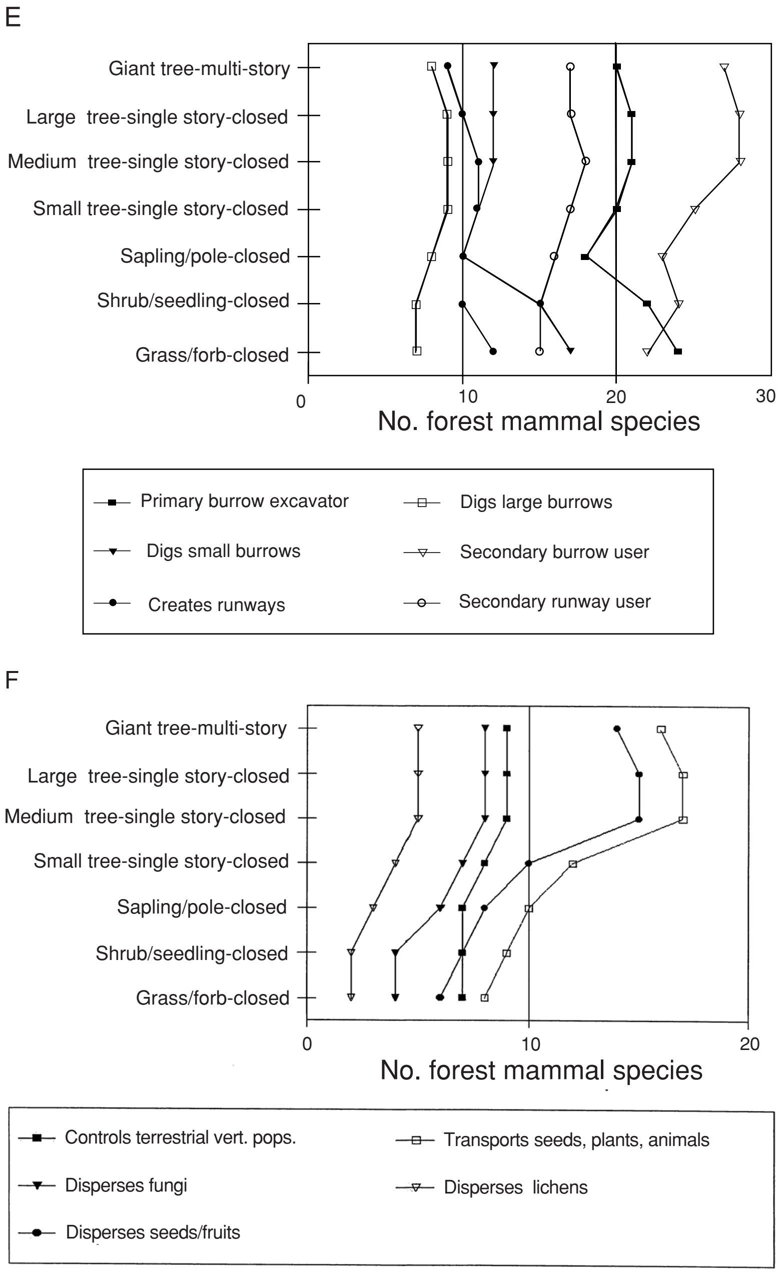


Fig. 19.7A–F. (*cont.*)

Table 19.1. *One-way analysis of variance tests with post-hoc Bonferroni multiple comparisons, on numbers of species (functional redundancies) of forest mammals in Westside Lowland Conifer-Hardwood Forests, for selected categories of key ecological functions (KEF) across successional stage (tree size) and canopy-closure classes, and number of canopies*

KEF category	*F* value	df	*P* value
By successional stage (tree size) class[a]			
All species	1.945	5	0.132
Feeds on carrion	22.034	5	<0.001**
Excavates large (>rabbit-sized) burrows	1.446	5	0.251
Excavates small (rabbit-sized) burrows	18.920	5	<0.001**
Disperses fungi	28.384	5	<0.001**
Digs soil	2.085	5	0.110
By canopy closure class (open, moderate, closed canopy)			
All species	11.471	2	<0.001**
Feeds on carrion	2.924	2	0.074+
Excavates large (>rabbit-sized) burrows	10.866	2	<0.001**
Excavates small (rabbit-sized) burrows	0.526	2	0.598
Disperses fungi	2.085	2	0.147
Digs soil	13.881	2	<0.001**
By number of canopies (single, multiple canopies)[b]			
All species	0.048	1	0.829
Feeds on carrion	6.317	1	0.019*
Excavates large (>rabbit-sized) burrows	2.665	1	0.116
Excavates small (rabbit-sized) burrows	3.546	1	0.072+
Disperses fungi	8.848	1	0.007**
Digs soil	0.476	1	0.497

[a] Successional stage (tree size) classes: grass/forb, shrub/seedling, sapling/pole, small tree, medium tree, large tree, and giant tree. Large tree and giant tree classes were combined in the ANOVAs to reduce number of classes. Tests focused on single-story, closed-canopy conditions of these stages.
[b] ANOVA tests reduce to unpaired Student *t*-tests.
$+\,0.05 \le P \le 0.10$.
$^{*}\,P < 0.05$.
$^{**}\,P < 0.01$.

influenced by successional stage but not canopy-closure class, and only marginally by the number of canopies. The number of fungi dispersers was influenced significantly by successional stage and number of canopies, but not by canopy closure, and the number of soil diggers was influenced by canopy closure but not successional stage or the number of canopies (Table 19.1).

It is clear that the functional redundancies of different KEFs are influenced by different forest structural attributes. Also, at least for Westside

Lowlands Conifer-Hardwood Forest, no single forest condition (e.g., open, multi-canopy, large-tree forest) provides maximum redundancy of all associated forest mammal KEFs; nor is there a single condition that accounts or provides for all maximum KEF levels of all forest mammals. Thus, a mix of successional stages, canopy-closure classes, and canopy densities would be required to provide for the highest number of forest mammals for the KEFs included in these analyses.

Influence of forest management on ecological functions of forest mammals

The functional redundancy of forest mammals is not only influenced by successional stage, canopy closure, and the number of canopies, but also by the presence of microhabitat elements or substrates. This was discussed previously in the section on functional webs of species associated with down wood and snags in coniferous forests.

Additionally, the size of live trees and snags can have varying influences on different KEFs. For example, some fungi-eating (and therefore potential spore-dispersing) forest mammals in Westside Lowland Conifer-Hardwood Forest are also associated with large trees or large snags (Fig. 19.8), especially trees or snags >36 cm (14 in.) in diameter at breast height (dbh). Thus, if the forest manager wishes to provide for

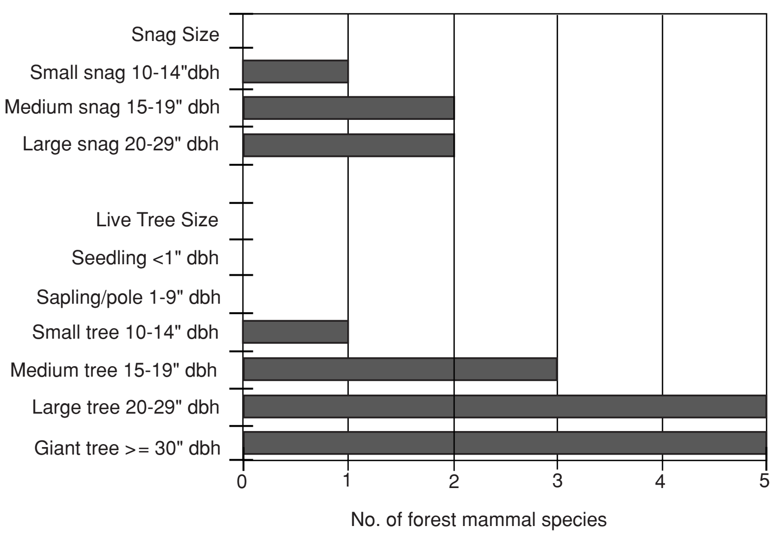


Fig. 19.8. Number (functional redundancy) of forest mammal fungivores that are associated with live tree and snag size classes. dbh stands for diameter at breast height.

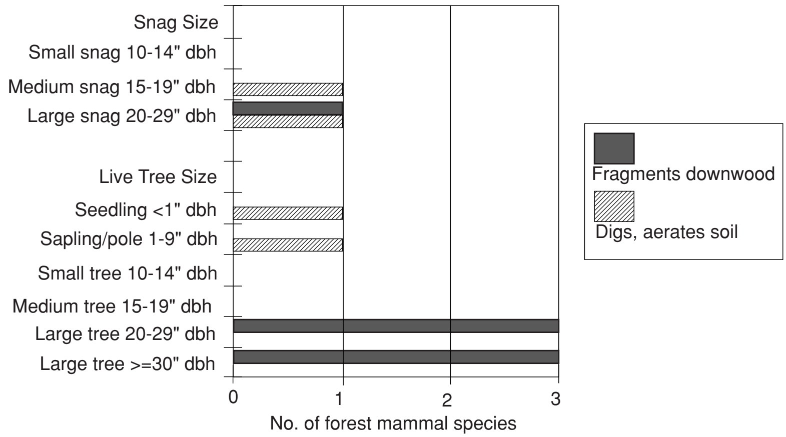


Fig. 19.9. Number of forest mammals that fragment down wood and dig soil and are associated with live tree and snag size classes. Fragmenting down wood and digging soil are natural ecological roles that provide habitat for a variety of fungi, invertebrates, and other organisms, likely speed the uptake of organic matter into soil, and maintain soil productivity. More forest mammals that fragment down wood are associated with large snags and with large and giant live trees, than with smaller snags or live trees, because forest mammals that fragment down wood are largely associated with late successional stages. More forest mammals that turn over soil are associated with medium and large snags than with small snags, and with seedling and sapling/pole size trees than with larger trees, because soil-digging forest mammals are associated with early successional stages. Thus, to maintain the full set of forest mammal species with these two ecological functions pertinent to soil productivity, the manager may provide for large snags in both early- and late-successional stages.

maximum functional redundancy of fungivory, which may be important for dispersal of spores of beneficial fungi, management guidelines could include specifically providing large snags and large live trees.

In another example, only a few forest mammal species provide the function of fragmenting down wood, and these species tend to be associated with large trees and snags >51 cm (20 in.) dbh (Fig. 19.9). On the other hand, forest mammals that dig and aerate soil and are associated with a particular tree or snag size tend to be associated with small, live trees <25 cm (10 in.) dbh, but are also associated with large snags >36 cm dbh.

Managers may want to know the array of microhabitat and substrate elements used by forest mammal species having desired KEFs and ensure that they are provided for in forest-management plans. Most of these habitat elements could be provided relatively easily by ensuring adequate retention of large live trees, snags, down wood, truffle patches, and other elements of older forests (Franklin et al. 2000).

Discussion

Caveats and assumptions of the functional approach

The analyses presented above should not be viewed in isolation from empirical data on the autecology and demography of individual species. Simply because a particular category of KEF is present or maintained in a faunal community does not mean that all native species associated with that habitat are equally well conserved or even present. We intend the kinds of functional assessments we present here to complement, not replace, species-specific conservation.

Marcot and Vander Heyden (2001) listed a number of caveats pertaining to the types of functional assessments presented in this chapter, including the following:

1. In the Species-Habitat Project and Interior Columbia River Basin databases, assignment of KEFs to each species was determined at least as much by the collective judgment of expert panels, as by results of empirical studies. Results should be viewed as testable working hypotheses and should be validated and refined through new field research.
2. Some KEFs are incompletely represented in these databases, especially those relating to nutrient cycling and disease transmission.
3. Results of functional assessments are best interpreted at the level of broad geographic areas, such as ecoprovinces or sub-basins, rather than at the scale of project areas or forest stands. Applying these findings to small geographic areas is likely to lead to overestimations in the number of ecological functions present, unless finer resolution information and local knowledge are applied.
4. Existing databases do not consider how KEFs for a given species might vary in different habitats or with the presence or absence of specific environmental conditions or elements, such as particular prey items. Empirical data on the KEFs for most species, including forest mammals in western coniferous forests and their variation, are generally lacking (Marcot 1997).

For some functions, such as the creation of snags or various influences on soil structure and productivity, other taxonomic groups may have a far greater influence on ecosystem conditions than forest mammals. Thus, the user should have a basic understanding of the relative importance of forest mammals compared to other faunal groups (including invertebrates) for performing various ecological functions.

For example, infestations of bark-feeding cerambicid beetles and some foliage-feeding larval lepidoptera (e.g., spruce budworms) can have far greater influences on the structure of coniferous forests of western North America than the few forest mammals that girdle trees or fragment standing wood (van Hees and Holsten 1994, Williams and Liebhold 2000). Earthworms and other burrowing invertebrates can process soil, enhance uptake of soil organic matter, and engage in soil nutrient cycling at far greater rates than burrowing forest mammals (Hendrix 1995).

One of the basic tenets of the functional assessment approach presented here is that of functional redundancy. However, by definition, each species defines its own niche. Simply because two species share a general category of ecological function does not mean they are completely interchangeable in the ecosystem, that is, define the exact same niche. Each will perform its function in different ways and will interact with different species, use different substrates, and exert its influence at varying intensities or rates. In a sense, the unique attributes of individual species can be depicted by including specific key environmental correlates, habitats, vegetation structural conditions, and even species' life history attributes in queries of wildlife-habitat databases. Ultimately, the notion of one species = one niche becomes that of one species = one or more KEFs. The extent to which sets of forest mammals (or any species assemblage) can provide redundant functions that influence community or ecosystem diversity and stability in equivalent ways is poorly known and needs further study.

Some KEFs may be dependent on the involvement of other species, such as relations involving predators and prey, pollination, and the dispersal of propagules. An example we discussed previously is that of forest rodents that feed on and disperse mycorrhizal fungi, a KEF that in turn aids nitrogen cycling in forests and uptake by trees having obligate symbiotic relations with the fungi (Li et al. 1986). Another example was the relation of beaver to willow and aspen. We speculate that there are probably other co-evolved relations that are mediated by forest mammals but remain undiscovered.

Implications for management

We have described a number of ways that managers might use functional assessments of forest mammals (or other taxa) to guide ecosystem management. Managers may wish to know the influence of historic, current, or potential management actions on ecological functions of organisms, and they may wish to set explicit objectives for conserving or restoring ecological functions to meet the goal of managing for fully functional ecosystems. They could use historic conditions or reference landscapes to assess the extent to which altered landscapes have maintained their functionality. However, managing for ecological functions and functional groups is unlikely to provide for species- or other issue-specific conservation needs.

Because these concepts are new, it may be difficult for some managers to consider a functional assessment approach to forest management and species conservation. However, the impetus of such change is in some existing state and federal mandates for land and wildlife management. For example, 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 ..." (US Endangered Species Act, Sec. 2b). Ensuring that ecosystems remain fully functional may be integral to meeting these objectives.

Implications for research

As others have argued in defense of the keystone species concept (Simberloff 1998), one of the primary advantages of a functional approach to management is that it involves explicit consideration of the mechanisms that underlie ecosystem structure and function. We believe that an important byproduct of the functional approach to forest mammal conservation is the generation of new understandings about ecosystem linkages, new insights about the ecology of individual species, and new research questions. Many of the "findings" described in this chapter can be re-stated as testable hypotheses for future research.

Although studying and conserving forest mammals from the perspective of ecological functionality is a relatively new concept, several recent studies have employed this approach. For example, Kunkel and Pletscher (1999) found that predation was the primary factor limiting deer and elk populations in Montana, and their research findings suggested that managers may therefore be able to enhance other prey populations by changing ungulate densities. Henke and Bryant (1999) found that coyotes may function as keystone predators in some ecosystems because removal of coyotes changed faunal community structure. McShea and Rappole (2000) suggested that breeding bird populations can be managed by controlling the influence of herbivory by deer populations on plant cover. Sirotnak and Huntly (2000) reported that herbivory by voles in riparian areas influenced nitrogen cycling.

Smallwood et al. (1998) found that burrowing by mammals is not only important to soil formation and intermixing of geologic materials and organic matter, it can also influence the environmental exposure of buried hazardous wastes. Among the key burrowing parameters that might influence such exposures are: the catalog of resident burrowing species and their abundances, typical burrow volumes (void space created by soil displacement), burrow depth profiles, maximum depth of excavation, constituents and structural qualities of excavated soil mounds, and proportion of the ground covered by excavated soil. Other important parameters included the rate of mound construction, depth of den chambers, and volume of burrow backfills.

The new insights these and other studies have generated demonstrate the heuristic value of quantitative autecological research on the functional roles of mammals. Research is also needed on how ecological functions of forest mammals vary among individuals, populations, geographic locations, and habitats, and in different successional stages. Through such studies, functional assessments can begin to be framed in quantitative terms that are based on empirical data, not just informed judgments. Quantitative models can provide a scientific basis for the implementation of ecosystem management. Categories of KEFs explored in our functional assessment can be quantified with rates (e.g., numbers of fungal spores dispersed per unit area per time period, or volume of soil dug per unit area per time period). Process models could be devised to initially hypothesize and, through empirical validation, ultimately explain how functional roles of mammals (and other taxonomic groups) quantitatively influence biodiversity, productivity, and the sustainability of ecosystems.

Summary and conclusions

Understanding and quantifying the ecological roles of mammals in forested ecosystems remain important management and research needs. Much recent literature has addressed this topic. We have built upon this work and offered a practical framework and a set of example assessments that can be done with existing databases. Explicitly considering the functional roles of mammals in ecosystems can complement species-specific conservation of forest mammals and generate new understandings of the contributions that forest mammals make to ecosystem function.

Woodward (1994) asked "How many species are required for a functional ecosystem?" We can now begin to answer this in ways of use to land managers. Analyzing the functional richness (number of KEFs), functional diversity (number of KEFs weighted by number of species per KEF), functional web (interactions among species and KEFs), and other KEF patterns of undisturbed or native forests can essentially define a "fully-functional ecosystem." In turn, this can serve as a baseline from which to clearly and repeatably measure the expected influence on ecosystem function from alternative forest-management actions. Such analyses are already being used to characterize the functional patterns of fish and wildlife communities across broad landscapes (Marcot et al. 2002).

We urge forest managers to consider some of the further questions we raise and to pursue a more functional approach to the management and conservation of forest mammals and the habitats they occupy and, in turn, influence.

Acknowledgments

We thank Larry Irwin, Tom O'Neil, and Cindy Zabel for reviews of the manuscript.

Appendix

Categories of key ecological functions as coded for the Wildlife-Habitat Relationships database for Washington and Oregon (Johnson and O'Neil 2001). Not all of these categories pertain to forest mammals.

1. Trophic relationships*
    - 1.1 Heterotrophic consumer*
        - 1.1.1 Primary consumer (herbivore)*
            - 1.1.1.1 Foliovore (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 feeder*
            - 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
            - 1.1.1.13 Bark/cambium/bole feeder

1.1.2 Secondary consumer (primary predator or primary carnivore)*
1.1.2.1 Invertebrate eater
1.1.2.1.1 Terrestrial invertebrates
1.1.2.1.2 Aquatic macroinvertebrates
1.1.2.1.3 Freshwater or marine zooplankton
1.1.2.2 Vertebrate eater (consumer or predator of herbivorous 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)
1.1.4 Carrion feeder
1.1.5 Cannibalistic
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., 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*
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
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 sapwells 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*
3.6.2 Ground structures*
3.6.3 Aquatic structures*

- 3.7 User of structures created by other species
  - 3.7.1 Aerial structures
  - 3.7.2 Ground structures
  - 3.7.3 Aquatic structures
- 3.8 Nest parasite
  - 3.8.1 Inter-species parasite
  - 3.8.2 Common inter-specific host
- 3.9 Primary cavity excavator in snags or live trees
- 3.10 Secondary cavity user
- 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)
- 3.14 Uses runways created by other species
- 3.15 Pirates food from other species
- 3.16 Inter-specific hybridization

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*.

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