Review of Conservation Science Produced Since 1997 and Its Relationship to the Tongass National Forest Land and Resource Management Plan

Report Prepared For:

**Tetra Tech and the
Tongass National Forest**

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INTRODUCTION

The Tongass National Forest is reviewing the status of its National Forest Land and Resource Management Plan that was prepared in the 1990's with the Record of Decision released in 1997. A question of importance to the Forest Service is whether the conservation science used in the plan is still applicable given advances that have been made in the intervening years. Specifically, the Forest was interested in identifying new findings in the areas of conservation strategies, conservation planning, population and species viability, and landscape ecology that have been reported in the literature since the plan was released, and evaluating and relating this new information to the conservation strategy used in the Tongass Forest Plan. The potential implication of new information to the Plan was to be reviewed, and recommendations suggested for possible updates to the plan. In addition, a bibliography of new information on conservation planning generated since 1996 was prepared.

OBJECTIVES

The objectives to be addressed in this report include the following:

1. a summary of the relevant scientific information and professional knowledge that has been developed since completion of the Tongass conservation strategy;

2. an evaluation of the relationship of the recent scientific information to the Tongass conservation strategy, and

3. Recommendations for possible changes or updates to the plan relative to an identified new conservation science.

METHODS AND SCOPE OF PROPOSED PROJECT

LITERATURE SEARCH

A literature search was conducted to identify new information relating to conservation planning generated since 1996. This literature search was conducted in several ways. Computer searches of the literature were used to identify articles containing appropriate key words. Web of Science was a primary search engine used to conduct the search, but we also used Science Direct, Blackwell Synergy, and Agricola search engines. Key words used in the literature searches included: conservation planning, conservation strategies, species viability, population viability, island biogeography, landscape ecology, ecological representation, landscape connectivity, corridors, and landscape scale. In addition, a number of key articles in the primary literature that had particular relevance to these topics were worked forward using Web of Knowledge/Web of Science citation index. Citations identified in the search were screened for appropriateness to the specific topics and applicability to the Tongass conservation strategy. Abstracts of all potentially pertinent articles were reviewed to identify the literature with specific relevance to this review. Full articles were then obtained through JSTOR or directly from the journals. In addition, recent books on the topics identified above were evaluated for relevancy to the topic. We obtained a number of relevant books and reviewed them for pertinent information. An internet search for "gray" publications on the appropriate subjects was also conducted. Identified sources of information pertinent to the subjects of interest were only included in this reporting if they appeared to be of credible science and without any particular advocacy stance.

In addition, we identified a number of recently completed or on-going conservation planning initiatives to identify approaches and strategies being actively used by agencies, conservation organizations, or companies in addressing conservation planning needs. While a complete review of such initiatives was not conducted, prominent and informative initiatives were identified and included in this report as examples of various conservation approaches and strategies.

LITERATURE REVIEW

CONSERVATION STRATEGIES

Conservation strategies refer to the framework and the underlying basis and assumptions used in planning to maintain or enhance biological diversity. A wide range of strategies exist, each with advantages and disadvantages. Some are narrowly focused, only striving to address a subset of biodiversity. Most state an objective of conserving biodiversity, but many have not been clear in describing what they meant by this objective, as biodiversity may have different meanings to different people. Therefore, to discuss conservation strategies for biodiversity, it is first important to define what is meant by biodiversity. Baydack and Campa (1999) reviewed the range of definitions that have been applied to biodiversity. While a large number of specific definitions exist, virtually all recognize that biodiversity includes multiple levels of organization. Perhaps a definition that describes this succinctly is that of the United Nations Environment Programme (1991) which defined biodiversity as: "The variety of and variability within and among living organisms and the ecological complexes of which they are part; this includes diversity within species, between species, and of ecosystems." Many discussions of biodiversity revolve around the maintenance of species, but it must be emphasized that conserving biodiversity is about maintaining genetic, species, community or ecosystem, and landscape levels of biological organization.

For a conservation strategy targeting biodiversity to be truly effective, it should have the following characteristics or expected outcomes:

- It should include the conservation of all levels or scales of biodiversity in the planning area (Schwartz 1999, Poiana et al. 2000),
- It should be comprehensive in its inclusion of all elements (Lambeck and Hobbs 2002, Groves 2003),
- It should address the concept of adequacy (Lambeck and Hobbs 2002, Tear et al. 2005)
- It should provide a framework for monitoring (Haufler et al. 2002, Tear et al. 2005), and
- It should anticipate change (Tear et al. 2005).

While many conservation efforts may contribute to various aspects of biodiversity conservation, the focus of this discussion is on those strategies that have the objective of addressing all biodiversity.

Numerous publications have appeared between 1997 and 2006 that discuss strategies for biodiversity conservation. Advances to the general science of conservation have been made in many areas, and further synthesis of information has occurred that has helped to more clearly focus objectives and methods. Various principles for conservation planning have been suggested. For example, Shaffer and Stein (2000) identified and articulated that conservation initiatives should emphasize representation, resiliency, and redundancy in the selection of conservation areas. To be representative, conservation areas need to address the range of environmental conditions within the planning area. To be resilient, conservation areas must be of sufficient quality and maintain appropriate processes to withstand expected natural and human perturbations. To safe guard against unpredictable events, conservation areas should be redundant, with sufficient number of areas to insure that all will not be affected by a major perturbation event. Allen et al. (2005) addressed the concept of resiliency, and stressed that primary determinants of resiliency are functions and processes, not necessarily species, so that understanding the role of these factors is a critical component in designing reserve networks. The concepts of scale, landscape effects, and habitat networks (Opdam 2002), primarily a focus of landscape ecology discussed below, have received considerable attention in recent years, and have added to the complexity of conservation planning. A related topic that has received considerable attention is that of conservation design within landscapes to address concerns for animal movements and thresholds of fragmentation (Flather et al. 2002).

In order to organize a discussion of new findings related to conservation strategies, those strategies that target biodiversity conservation will be classified into various types. One basic classification of strategies is the distinction between coarse and fine filters, terms that have been widely used, although often incorrectly, in the literature. Coarse filter strategies focus on providing an appropriate mix of ecosystems or ecological communities across a planning landscape, while fine filter strategies focus on providing for the needs of individual or multiple species within a landscape (The Nature Conservancy 1982, Marcot et al. 1994, Haufler 1999a, Schwartz 1999). While many conservation planning efforts blend the two strategies, there is a fundamental difference in whether the primary basis of a strategy is focused on ecosystems or species. In addition to this basic classification of types of strategies, another division of strategies is between a focus on protection status of areas in reserves versus a focus on functional provision of ecosystems or species habitat, a distinction described by Callicott et. al. (1999) as stemming from the difference between a compositionalism viewpoint versus a functionalism viewpoint. A final dichotomy of strategies relates to those that attempt to maintain biodiversity by focusing on rare or declining elements (species or ecosystems) versus those that attempt to provide representation of all elements through either a coarse or fine filter strategy. Each type of strategy is based on various assumptions as to how it can provide for biodiversity conservation (Haufler 1999a), with each having its associated advantages and disadvantages (Haufler 1999b). A number of publications have appeared in the literature since 1996 that address these topics.

Coarse Filter Strategies

Coarse filter strategies have the goal of maintaining enough diversity of ecosystems or ecological communities to maintain the ecological integrity of these ecosystems and to provide for the habitat needs of all species and their genetic diversity inherent to a landscape. A key to the success of this strategy is to have an appropriate classification of ecosystem diversity that is applied at an appropriate scale (Schwartz 1999, Mayer and Cameron 2003) and with adequate precision or grain (Mayer and Cameron 2003) to address biodiversity objectives. Few coarse filter strategies have assessed these important components to their effective use. Most coarse filter efforts simply use whatever classification happens to be available, without evaluating the appropriateness or effectiveness of these classifications for the objectives of their strategy. Numerous authors have identified the importance of ensuring that both the variety of ecosystems and their environmental variation is represented in conservation areas within a planning region (Pressey 1998, Schwartz 1999, Shaffer and Stein 2000, Lambeck and Hobbs 2002, Groves 2003). Both biotic and abiotic factors should be included in identifying conservation areas (Groves 2003, Saxon 2003). De Blois et al. (2002), Haufler et al. (1996, 1999a) and Poiana et al. (2000) identified the importance of understanding both the role of abiotic factors that create different types of ecological sites within a planning landscape, and how ecosystems react temporally following disturbance across these different ecological sites. These suggestions parallel the importance of a planning consideration termed the time principle identified by Dale et al. (2000) in discussing guidelines for managing land uses.

The World Commission on Protected Areas proposed various criteria for the identification of conservation areas (Davey 1998). These included the following:

- Representativeness, comprehensiveness, and balance: assuring that the full range of biodiversity is represented in a balanced manner,
- Adequacy: that sufficient amounts are included in conservation areas,
- Coherence and complementarity: that areas complement each other and add to the composite set of conservation areas,
- Consistency: uniform application of decision processes in selecting areas, and
- Cost effectiveness, efficiency and equity: balancing the needs of other objectives of the landscape with conservation needs.

Another important consideration of coarse filter approaches is that in addition to determining the types and amounts of ecosystems to maintain or restore within a planning landscape, the composition and structure of representative ecosystems must be appropriate for that specific ecosystem (Poiana 2000, Haufler et al. 2002). This addresses the concern for resiliency identified in numerous publications (i.e., Shafer 1999, Shaffer and Stein 2000, Groves 2003) For example, if a particular area has an infestation of exotic species that may exceed an appropriate threshold level, then this area should not be considered as representative of the target ecosystem conditions. However, few coarse filter approaches have addressed more than landscape level measures of amounts of different ecosystems. Schwartz (1999) discussed coarse filter strategies and identified many of their advantages as well as some of the challenges to their use. Hughes et al. (2000) and Vos et al. (2002) discussed how use of ecosystem (habitat) approaches is the direction in which conservation planning is generally heading, with Hughes et al. (2000) noting the complexities of addressing insect diversity as one example of why this is occurring. Various tests of coarse filter strategies have shown that they can be effective for biodiversity conservation (Nichols et al. 1998, Wessels et al. 1999, BenWu and Smeins 2000, Kintsch and Urban 2002, Oliver et al. 2004). However, Lindenmayer et al. (2002) and Noon et al. (2003) have questioned the use of landscape surrogates for addressing species needs and distributions. The new Forest Service Planning Regulations and associated Directives stress a coarse filter approach to forest planning and environmental monitoring.

It should be noted that relatively few coarse filter approaches have been developed in detail or applied in a systematic manner. However, such approaches can be effectively implemented. South Dakota recently used a coarse filter approach to characterize ecosystem diversity across the state as a primary focus of their Comprehensive Wildlife Conservation Plan (SDGFP 2005), demonstrating the ability to use such approaches as effective planning tools.

Haufler (1999a, 1999b, 2000) discussed strategies for biodiversity conservation and identified several types of coarse filter strategies. One type of strategy, that can be termed a habitat diversity approach, has an objective of maintaining or restoring adequate amounts of existing vegetation communities. The Nature Conservancy has used an approach that partially addresses ecosystem diversity in their ecoregional planning efforts (Groves 2003). Their approach strives to identify rare elements including ecosystems defined by the National Vegetation Classification System (Grossman et al. 1998), and to represent these ecosystems in reserves within each planning ecoregion (The Nature Conservancy 2001, Groves 2003). Similarly, Sierra et al. (2002) utilized an existing vegetation classification to prioritize ecosystems in need of representation in Ecuador.

A fundamental question for all habitat diversity approaches is how does one know if the existing vegetation communities are the right communities to maintain within a planning landscape? In many landscapes, human activities have altered disturbance regimes, and have caused a change or loss of many ecosystems. Without a perspective or reference, how does an initiative address the question whether their classification is appropriate. A separate question for all coarse filter strategies is how much of any specific ecosystem is adequate to meet the objectives of biodiversity conservation? Thus the question of representation and adequacy can be challenges to the habitat diversity approach.

Because of the question about the appropriateness of including an ecosystems in the habitat diversity approach, two other coarse filter strategies, termed the historical range of variability approach and the historical reference approach (historical range of variability-based approach) (Haufler 1999a), have been proposed or utilized in various planning efforts. Both of these approaches are based on the premise that the ecosystem diversity that occurred in an area over the past hundreds to thousand years defined biodiversity at the ecosystem and landscape levels, and that provided the habitat that supported the species and genetic diversity of a landscape (Poiana 2000, Haufler et al. 2002). These approaches have as their objective the maintenance of all historically occurring ecosystems at some level of representation. The historical range of variability approach sets its objective as maintaining the landscape within historical ranges of variability, as discussed in various draft Forest Service revisions to their planning regulations and by Aplet and Keeton (1999). This approach is unrealistic in most, if not all planning landscapes where human activities have altered amounts, distributions, and types of ecosystems as well as the compositions, structures, and functions of specific ecosystems (Haufler et al. 2002), however it may be possible to apply this approach specifically to one type of ownership, such as U.S. Forest Service lands, contained within a broader planning landscape. The historical reference approach strives to understand, characterize, and quantify the historical ecosystem diversity that occurred within a planning landscape, and then attempts to maintain suitable representation of these ecosystems within the landscape factoring in the historical reference at both landscape and ecosystem levels (Haufler et al. 2002). The goal is not to return or maintain a landscape in historical conditions, but to use this understanding as a baseline or reference for providing representation of ecosystems at both the landscape and ecosystem levels. Use of either of these approaches requires the development of information on historical ecosystem diversity (Morgan et al. 1994, Landres et al. 1999). These approaches generally have a focus on understanding how historical ecosystem disturbances and processes combined with different ecological sites within planning landscapes to produce the dynamics of historical ecosystem diversity, and to determine how and to what extent these have been changed by recent human activities.

Palik et al. (2000) used a hierarchical classification system of ecosystems to develop, evaluate, and prioritize needed ecosystem restoration in the Southeastern U.S. They used estimates of the amounts of each ecosystem that occurred historically to prioritize ecosystem restoration needs. Haufler et al. (1996, 1999a, 2000) described a coarse filter process based on historical reference to characterize forest ecosystem diversity in Idaho. Their method quantified historical amounts of ecosystems based on historical disturbance regimes and compared these amounts to current conditions. These comparisons allowed for a prioritization of those ecosystems with the greatest need for conservation based on a deviation from historical amounts. Poiani et al. (2000) applied an historical analysis to a classification of ecosystems along the Yampa River in Colorado, and were able to identify focal ecosystems for setting restoration and maintenance goals, based on historical flood events and their influences on riparian ecosystems. Hemstrom et al. (2001) used an historical reference approach to assess ecosystem conditions in the Upper Columbia River planning landscape, using conditions described in the mid-1900's as the historical reference. Another example of analyzing current and historical ecosystem conditions for conservation planning was described by van Wyngaaden and Fandino-Lozano (2005) for Columbia. They mapped existing conditions with satellite imagery, investigated abiotic factors, and determined what historical ecosystems were present. This allowed them to conduct comparisons of historical to existing conditions and to prioritize conservation efforts to most efficiently use limited conservation funds. All of these examples identified the feasibility of implementing coarse filter approaches based on historical references.

Redford et al. (2003) discussed various conservation approaches being used by 13 different conservation organizations. This description included a number of coarse filter approaches that they identified under various labels including ecosystem approach, landscape approach, land and resource management planning, biodiversity action plans, site conservation planning, and ecoregional conservation planning.

Fine Filter Strategies

A large number of publications relating to conservation planning produced after 1996 report on various topics concerning fine filter strategies. These strategies have a primary focus on planning for single or multiple species. Related topics in many publications addressed such measures as species richness or species diversity, and the use of hotspots for identifying conservation areas. A majority of the recent publications on fine filter strategies have been focused on reserve planning, and use species as a basis for identifying the most appropriate places to locate reserves.

Fine filter strategies have the advantage of having a legal basis for their use in conservation planning in the United States and other countries through provisions of endangered species legislation (Schwartz 1999). Proponents who favor fine filter strategies over coarse filter strategies argue that species are the fundamental parts of ecosystems (although geneticists might argue that genes are the fundamental parts), and that using coarse filter analyses to represent species needs is inaccurate and inadequate (Noon et al. 2003). Lindenmayer et al. (2002) reported on the use of landscape surrogates for predicting species locations and found that those they analyzed for arboreal marsupials in Australia did not work to describe or explain the observed distribution of these species in remnant forest patches, suggesting that a focus on the species was needed. Goldstein (1999) argued that inclusion of species in conservation planning is essential in order to understand the interaction of organisms with processes meaning that conservation strategies that focus on abiotic parameters as surrogates will be ineffective.

Fine filter strategies have numerous limitations (Schwartz 1999, Groves 2003). A primary concern is that the number of species occurring in any area is so large that they cannot all be accounted for in fine filter approaches. Attempts to simplify this complexity through the use of surrogates have not been effective, as discussed below. Further, most fine filter strategies fail to consider the landscape and ecosystem levels of biodiversity, so their ability to represent all levels of biodiversity is questionable.

Most recent publications on fine filter strategies focus on specific methods for addressing how to conserve species with the typical goal of finding ways of identifying efficient surrogates for simplifying a process of accounting for all species, especially the use of one or more types of indicator species. Lambeck (1997), Noon and Dale (2002) and Groves (2003) provided descriptions of different types of species classifications that have been proposed for conservation planning. Groves (2003) listed the following categories of species that have been suggested for conservation focus: declining species (threatened, endangered, and imperiled), at-risk species, endemic species, flagship species, umbrella species, focal species, keystone species, and indicator species. Noon and Dale (2002) added ecological engineers, link species, and phylogenetically distinct species to this list, while Carignan and Villard (2002) also listed dispersal-limited species, resource-limited species, and process-limited species, and species that are closely linked with specific habitat features. Each category of species classification has advantages and disadvantages to its use.

Numerous publications point out the difficulty and limitations of using species groupings as surrogates for conservation planning (Flather et al. 1997, Niemi et al. 1997, Pearson and Carroll 1998, van Jaarsveld et al. 1998, Carroll et al. 2001, Fleishman et al. 2001, 2002, Lawler et al. 2003, Su et al. 2004). Regarding use of indicator species, Carignan and Villard (2002) provided a good discussion of the problems associated with species selected to indicate conditions for other species including the fact that no two species have the same niche (Gauze 1934), and even species within a guild will have substantially different habitat requirements (Block et al. 1987). Lindenmayer (1999) discussed indicator species and reported on poor relationships between a selected species and other species. He stated (1999:279) that: "Indeed from an evolutionary perspective, it should be expected that functionally similar or closely related taxa will have developed strategies that allow them to co-exist. Therefore, different responses to processes like human disturbances also should be expected." Groves (2003) discussed studies on the use of indicator species and stated that the resounding conclusion was that they did not work as surrogates, citing the work of Kershaw et al. (1995), Williams et al. (1996), Kerr (1997), Pimm and Lawton (1998), van Jaarsveld et al. (1998), and Pharo et al. 1999). Redak (2000) reported that there are an estimated 163,487 species of arthropods in North America, only 66% of which have been estimated to have been described taxonomically. Given this lack of information on just one taxon, how can use of indicator species provide for biodiversity?

A number of fine filter approaches have been proposed. One type of approach is the use of umbrella species. Umbrella species are defined as species whose conservation should provide broader protective status to numerous co-occurring species (Lambeck 1997, Simberloff 1997, Lambeck and Hobbs 2002, Groves 2003). For example, the Idaho Partners in Flight Bird Conservation Plan (http://www.blm.gov/wildlife/plan/ppl_id_10.pdf) used sage grouse as an umbrella species to address needs of other sagebrush associated species. Fleishman et al. (2001) evaluated the use of a set of umbrella species for selection of conservation areas. They found that use of a number of umbrella species within two taxa could reduce the number of required conservation areas to obtain 75% coverage of the taxa compared to a random selection of surrogate species. They also found that umbrella species were no more effective than random species when used as surrogates for cross-taxon representation. They cautioned about the utility of the umbrella species. Other publications came to the same conclusions. Lambeck and Hobbs (2002:373) stated the following: "The foundations for using particular species as surrogates for other components of an ecosystem remains problematic. Although the concepts of keystone and umbrella species have been widely accepted, their use in planning is not straightforward (Simberloff 1997). There are no clear criteria for selecting such species and no rationale for predicting the extent of the benefit that would accrue to the ecosystem in which they occur. Most species will respond to changes in their environment and, hence, could be considered an indicator of something. Similarly, many species have requirements that encompass some needs of other species, allowing virtually any taxa to be nominated as umbrella species." Carroll et al. (2001) evaluated the use of one carnivore as an umbrella species for other carnivores, and true to the observations of Lambeck and Hobbs (2002) found that this was not supported by the distributions of this taxonomic group. Kerr (1997) similarly reported that carnivores did not support the umbrella species assumptions. Roberge and Angelstam (2004) examined the umbrella species approach for insects, and did not find support for its use, although they suggested that perhaps a multi-species umbrella approach may have some merits.

Keystone species (Paine 1966, Power et al. 1996, Lambeck 1997, Noon and Dale 2002, Lambeck and Hobbs 2002) are species whose importance in a community is disproportionately large relative to their abundance. Examples include starfish (Paine 1966), prairie dogs (Kotliar 2000), and beaver (Naiman et al. 1988). Two of these examples, prairie dogs and beaver, are also considered ecological engineers, whose actions cause changes that create new ecosystems that support habitat for a number of other species (Naiman 1988, Kotliar 2000). Failure to account for these species and their effects on ecosystem conditions in conservation planning will have significant consequences for other species. For example, a conservation planning effort in eastern Wyoming initiated by the Thunder Basin Grasslands Prairie Ecosystem Association (www.tbgp-eco-assn.org) is primarily focused on a coarse filter approach to providing ecosystem diversity. However, this group recognized the importance of prairie dogs as ecological engineers that produced unique habitat conditions that needed to be maintained in their planning landscape if biodiversity objectives were to be met, and have included a specific prairie dog conservation plan in addition to an ecosystem diversity plan. Keystone species are considered to be a relatively small subset of species (Groves 2003), and ecological engineers are an even smaller subset. While the importance of these species to ecosystem dynamics and other processes and functions is important to include in conservation planning, their use as surrogates for other species in conservation planning appears to be limited (Lambeck and Hobbs 2002).

Species that are particularly sensitive to a particular threat have been termed focal species (Lambeck 1997, Lambeck and Hobbs 2002). If these species can be maintained in a landscape, then species less sensitive to that threat should also be maintained. For complete protection of species, each threat to each specifically defined community would need to have a focal species identified that would address that particular threat. This assumes that each threat can be identified, and that all community types (vegetation type, habitat type, etc.) are correctly accounted for by a focal species. Noon and Dale (2002) reported on a different use of the term focal species, to be species that are indicators of the broader state of the larger ecological system. They included as focal species indicator species, keystone species, ecological engineers, umbrella species, link species and phylogenetically distinct species. Groves (2003) defined focal species as species that will not be properly accounted for by coarse filter strategies because they have very specialized resource use or life history needs. Thus, the concept of focal species has not developed a consistent standard for its definition in the recently reported literature. Given this, evaluation of the use of focal species is difficult, although depending on the definition selected, advantages and problems described for other types of surrogate species groupings would apply.

Indicator species are surrogate species whose status is indicative of the status of a broader group of species (Groves 2003), larger functional group of species (Noon and Dale 2002), key habitat type (Noon and Dale 2002), or an early warning of a stressor to ecological integrity (Noon and Dale 2002). Analysis of the use of indicator species has not received empirical support (van Jaarssveld et al. 1998, Davies et al. 2000, Redak 2000, Fleishman et al. 2002, Lawler et al. 2003). Niemi et al. (1997) investigated management indicator species used by the U.S. Forest Service in Wisconsin, and found that these species did not do a good job of tracking the status of other species. Araujo et al. (2004) examined indicators of species assemblages in Europe to see if this method would track well within group changes or among taxa changes. The assemblage diversity method was not better than chance for describing differences observed either within group or across groups they examined. Carignan and Villard (2002) discussed indicator species and various considerations and challenges to their use. Quayle and Ramsay (2005) reported that using the conservation status of a species (i.e., Red Lists) as a basis for selecting indicator species was a poor method for tracking overall biodiversity. Davies et al. (2000) empirically tested whether taxonomically related species responded similarly to habitat loss and fragmentation compared to non-related species, and determined that they did not respond the same.

Reynolds et al. (1996) developed a fine filter approach that identified the habitat needs of goshawks and Mexican spotted owls for lands in Arizona, and also identified the habitat required by their prey species. They then equated these habitat needs to historical ecosystem conditions in the area, and used the needs of these species to indicate the amounts and types of the historical conditions to provide. In this way, they provide representation of historical ecosystem conditions based on the needs of the food web required to support the two primary species of interest. They stated that this approach assures that management objectives are compatible with ecosystem capabilities and long-term sustainability. This approach has been used to manage U.S. Forest Service lands in Arizona.

A final fine filter strategy is the use of species richness indicators and hotspots in the selection of conservation areas. As discussed by Chaplin et al. (2000), by identifying areas where the greatest number of species exist, efficiency can be gained in conservation planning. However they also noted that a drawback to this approach is that it may do a poor job of representing the full array of biodiversity. Myers et al. (2000) discussed that 44% of the world's identified vascular plants and 35% of 4 vertebrate groups occur within 25 hotspots that comprise only 1.4% of the Earth's surface. Protecting these areas is a way to maintain occurrence of a maximum number of species with limited conservation funding. Kerr (1997) compared endemism and species richness and found a relationship between these two parameters within a taxon. However, he found that areas supporting a richness of one taxon did not conform to richness of other taxa. Pearson and Carroll (1998) looked at the richness of selected taxa in various continents. They found certain relationships between some taxa (i.e., birds and beetles in North America), but did not find congruence among many taxa, and found that relationships for taxa in one continent were not the same as relationships in another continent. Gjerde et al. (2004) looked at the relationship of species richness at a fine scale (1ha plots) in northern forests, and did not find good relationships among taxa. Pimm and Lawton (1998) concluded that the majority of studies conducted found that areas rich in one taxon do not overlap with areas rich in another taxon. An additional concern with the use of hotspots is that areas that maximize the number of species may occur in environmental transition zones, and may have more species but place them at the margins of their ranges. Araujo and Williams (2001) investigated this and found that species were more likely to be at the edge of their range in identified hotspots. Lesica and Allendorf (1995) suggested that this may be desirable as populations at the periphery of their range may be genetically more diverse than those in the center of a range. However, individuals at the edge of the range may be in lower quality habitat, and not be representative of the primary fitness of the population. Groves (2003) indicated that hotspots seemed to have little conservation value unless they represented concentrations of endemic or threatened or endangered species. Thus, while the idea of hotspots to maximize conservation efficiency is appealing, the empirical evidence suggests that it has very limited utility in effective conservation planning.

A number of publications have addressed the use of various algorithms for conservation planning, such as those that weight level of species representation (Arponen et al. 2005), weighting of endangered species (Arthur et al. 2004), and biodiversity indices (Benayas and de la Montana 2003). Cabeza and Moilanen (2001) discussed how the effectiveness of the use of reserve selection models has been limited by the lack of available data and the choice of suitable surrogates for biodiversity. Marxan (http://www.ecology.uq.edu.au/index.html?page=27710&pid=20497) is a conservation planning tool used to identify reserve designs that maximize the number of species or vegetation communities contained within a designated level of representation. The methodology behind this approach is described by Possingham et al. (2000), and it has been incorporated into various planning efforts of The Nature Conservancy (http://www.biogeog.ucsb.edu/projects/tnc/overview.html) .

Protection Versus Functional Emphasis

As indicated previously, a basic difference in the assumption of many strategies is the necessity of the protection status of a conservation area versus an emphasis on its functional capabilities. Conservation planning has as its primary focus the identification and delineation of conservation areas. Conservation areas can be generally defined as areas in which the primary concern is with the conservation of biotic or environmental features (Groves 2003). Reserves can be defined in a similar manner, but typically imply a level of protection from various human activities. Many efforts, such as the gap analysis initiative (Scott et al. 1993) and ecoregional planning by The Nature Conservancy (Groves 2003) only consider an area as providing representation for biodiversity if it is in a wilderness area, national park, or similar protected status. Other efforts, such as many collaborative planning efforts (Haufler 2004) emphasize the maintenance, enhancement, and restoration of conservation areas based on their functional attributes, regardless of ownership or protection status. Such efforts may address long-term objectives through use of such tools as conservation agreements or incentive programs. Callicott et al. (1999) discussed some of these differences and attributed them to the difference between a compositionalism viewpoint versus a functionalism viewpoint. The compositionalism approach, stemming largely from an evolutionary focus, views humans as separate from nature, and attempts to protect nature in reserves. The functionalism view stems largely from ecosystem ecology, and strives to balance human and conservation needs, seeking solutions in working landscapes. While both views recognize that wild areas and strict reserves are an important tool for some components of biodiversity, and working landscapes and their management can make important contributions to biodiversity conservation, the basic philosophical differences between the two divide many specific conservation efforts. Haufler et al. (1996, 1999a, 2000) identified a functional-based approach to conservation planning with a primary focus on representing functional ecosystems at landscape and ecosystem levels, without regard to specific protection status. Haufler (1999b) and Kernohan and Haufler (2000) discussed how a focus on the protection status of reserves isolates humans from biodiversity, and can make it difficult for private landowners to get engaged in and supportive of biodiversity conservation initiatives. However, the main body of conservation biology literature is based more in the compositionalism camp than in the functionalism camp.

Reserves and reserve networks have received review in the recent literature. Much of it has related to a focus on the distribution of protected areas, and the types of conditions included in protected areas (Scott 1999, Scott et al. 2001a, 2001b). Margules and Pressey (2000) reported that reserves are primarily located in remote areas, while they need to also occur in all areas including areas productive of natural resource commodities. Scott et al. (2001a, 2001b) emphasized that the protected areas in the United States contain a disproportionate amount of rock and ice, and not enough of more highly productive ecosystems. Sierra et al. (2002) discussed that reserve systems in Ecuador currently don't adequately represent ecosystems occurring in the drier environments.

A final finding relative to reserves was work reported by Bengtsson et al. (2003). They discussed the "static" view of reserves- that protected reserves largely assume maintaining the same conditions as when they were established. They emphasized the dynamic nature of ecosystems, and how conservation planning needs to accommodate these dynamics in the location of specific conditions needed for conservation purposes.

Thus, the different assumptions behind various strategies for conservation of biodiversity can have a major influence on the application or implementation of these strategies. Basing conservation planning on a compositionalism view, while important for some components of biodiversity, can lead to alienation of some potential contributors, such as private landowners in many working landscapes.

Rarity Strategies Versus Representative Strategies

An additional major distinction among many conservation strategies can be identified based on the primary focus of the strategy. Specifically, many strategies have a different emphasis and design based on whether they are primarily concerned with rare or declining species or ecosystems, or with representation of all species or ecosystems.
A number of approaches, such as The Nature Conservancy's ecoregional planning (Groves 2003) have a primary focus on identifying rare or declining elements, either ecosystems or species, and to represent these elements in protected reserves. A basic assumption of this approach is that these elements are in the greatest conservation need, are where conservation funds and efforts are most important, and by maintaining these elements, biodiversity conservation will be achieved. This is substantially different than an approach that strives to maintain representation of all elements in either reserves or functionally defined areas. For example, in forested areas, the rarity focus for a coarse filter approach would typically identify old growth conditions as the most in need of conservation, and set up reserve selection to protect this element. Early successional forests typically would be assumed to be present in sufficient amounts, and would not be specifically addressed in the conservation plan. A representative coarse filter approach would characterize all ecosystems (such as through use of an ecosystem diversity matrix (Haufler et al. 1996, 2000) that characterized all historically occurring ecosystems as influenced by abiotic drivers and disturbance regimes), and would then seek to represent adequate amounts and distributions of functional areas of each ecosystem within the planning landscape. This latter approach would insure that early successional conditions were present with the appropriate compositions, structures, functions, and processes to support species and ecological integrity of these ecosystems, as well as the old growth ecosystems. It may not be concerned if these areas were within protected reserves, and could potentially have representative areas move around in the landscape over a planned timeframe.

Thus, as with protection versus functional-based approaches, rarity and representative approaches differ in the assumptions for their implementation, and in their practical application. Conservation organizations, with an interest in focusing their funding and efforts on the elements of greatest concern, have largely focused on rarity approaches. Efforts at conservation planning that span both wild and working landscapes often address representation of all components or elements. Recent interest and attention in rangeland ecosystems have emphasized the need to understand the functional aspects of ecosystem representation and to provide for full representation of historically occurring ecosystems (Fuhlendorf and Engle 2004).

Combination Strategies

The above discussion separated out each type of approach, and noted findings related to its use, advantages, and disadvantages. Many, if not most, conservation planning initiatives use a combination of approaches to address their objectives. Many coarse filter approaches combine in some way with fine filter approaches. The Nature Conservancy approach (Groves 2003) combined a rarity focus in identifying both fine and coarse filter elements for representation in reserves. Haufler et al. (1996, 1999a, 2000) used a coarse filter approach based on an historical reference, but then suggested that this be checked through use of species assessments for indicator species selected to test the effectiveness of the coarse filter. As mentioned above, the Thunder Basin Grasslands Prairie Ecosystem Association is using a coarse filter approach with plans to check this with assessments of selected indicator species, as well as developing a prairie dog conservation plan to specifically address this non-habitat limited species.

Combination approaches have the capability of addressing many of the concerns identified with individual strategies. The goal of any specific initiative should be to develop a comprehensive and cohesive conservation planning approach, and to carefully review the approach to identify any holes in coverage where elements of biodiversity might not be sufficiently addressed. As noted by many including Haufler et al. (2002) and Groves (2003), much is unknown about conservation planning, so monitoring and adaptive management designs are important considerations.

LANDSCAPE ECOLOGY

Landscape ecology is a field that has seen considerable attention in the recent literature. It is primarily concerned with the influences of spatial amounts and arrangements of landscape mosaics (Wiens 2002). It addresses the relationships of landscape patterns with ecological processes (Turner 2005a). Information generated by this field has significant relevance to biodiversity conservation, as most conservation planning must address issues of sizes, shapes, and distributions of conservation areas, and relate these to processes, ecological integrity, and species persistence. Gutzwiller (2002) edited a book specifically focusing on landscape ecology and biological conservation. Turner (2005b) discussed the past, present, and future directions of landscape ecology. Her abstract concluded by stating: "Landscape ecology should continue to push the limits of understanding of the reciprocal interactions between spatial patterns and ecological processes and seek opportunities to test the generality of its concepts across systems and scales."

One of the key concepts addressed in landscape ecology is that of scale, and its influence on ecological interactions and relationships. Freemark et al. (2002) reviewed 25 documents related to application of scale issues. They reported that at the landscape scale, a number of concepts, principles, and emerging ideas relative to conservation planning were identified including:

- Need for higher levels of connectivity and landscape permeability,
- Greater provision of buffers to habitat patches,
- Creating shorter distances among habitat patches,
- Greater use of corridors, linkage zones, and stepping stones,
- Greater focus on location of habitat patches,
- Consideration of juxtaposition and interspersion requirements of species
- Increased amounts and types of representation
- Maintain, restore, or simulate natural disturbances regimes,
- Decrease the influences of roads and human access,
- Increase variance in the size of habitat patches, and
- Increase mean and provide areas of minimum large patch size.

Many of these relate to the movements of species within landscapes, with an emphasis on maintaining landscapes that are more permeable, and that contain sufficient amounts and distributions of suitable habitat. These topics relate directly to landscape linkages and corridors, and to fragmentation and the question of adequacy, discussed below. They also have direct links to population and species viability, as well as the consideration of metapopulations, both of which are also addressed below.

A number of publications that addressed conservation planning related to landscape ecology were identified. Williams et al. (2005) emphasized the need for spatial analysis to be incorporated in reserve selection models, bringing concepts of landscape ecology into direct application. Hawkins and Selman (2002) discussed the need for incorporating spatial land use strategies into conservation planning so that conservation plans are more applicable to a wider countryside. They stressed the importance of factors such as connectivity and shape of reserves which are often overlooked in reserve selection methods. Opdam et al. (2001) identified the need for landscape ecologists to increase their emphasis on developing guidelines and standards for landscape conditions, and to increase the amount of interdisciplinary work. Similarly, Antrop (2001) discussed the need for landscape ecologists and planners to work more closely, so that the information on processes, scales, and patterns generated by landscape ecologists can be applied by planners.

Scale issues are a central focus of both landscape ecologists and conservation planners. Conservation planning must identify appropriate delineations and boundaries for planning areas, and identify both the grain and extent to be used (Caraher et al. 1999, Haufler et al. 1999b, Wiens 2000, Mayer and Cameron 2003). Bassett and Edwards (2003) analyzed how the selection of landscapes at different scales (EMAP hexagons, watershed, and county) influenced the number of species and ecosystems included in a selected area, and the implications of this for reserve selection models. Johnson et al. (2004) modeled habitat for wolves and grizzly bears at different scales, and reported that patch-based models and landscape-based models produced different results, and suggested that both levels need to be integrated in conservation planning.

Many publications appeared between 1996 and 2006 that addressed the use of landscape metrics. Release of the landscape metrics tool Fragstats (McGarigal and Marks 1995) encouraged a flurry of studies that calculated numerous landscape metrics and related these to various ecological variables. Many of the resulting studies lacked rigor or proper review of causative relationships. Li and Wu (2004) prepared a perspective paper that reviewed landscape analysis, and discussed how the potential of these analyses have been largely unfilled. One problem they noted that has contributed to this lack of progress has been improper use of landscape metrics. They identified that many landscape analyses have treated the analysis of landscape pattern as an end in itself, without properly examining the cause and effect relationships. They further noted that many landscape indices and mapped data are used without any consideration of the ecological relevancy. Leitao and Ahern (2002) reviewed studies on landscape metrics, and developed a set of metrics that they recommended for use in ecological landscape planning. O'Neill et al. (1999) discussed the current availability of remote imagery data, GIS tools, and landscape metrics that can be applied to landscape analyses for monitoring changes in patch sizes and configurations. They developed recommendations of how to use landscape metrics to reach environmental endpoints such as analyses of wildlife habitat.

While this review of advances in landscape ecology does not include sizeable areas of the literature on the subject, it does point out the types of advances relevant to conservation strategies and planning that have occurred. Clearly, work in landscape ecology is helping to better define the roles of scale, pattern, and processes in understanding and quantifying amounts, sizes, and spacing of conservation areas to meet conservation objectives.

LANDSCAPE LINKAGES AND CORRIDORS

Corridors have been a concept for conservation planning that stem from protection or reserve strategies. The premise is that core reserves provide primary areas for biodiversity, but these core areas need to be connected with corridors to allow for population exchange between and among the reserves. Advances in the fields of landscape ecology, habitat fragmentation, and population genetics have led to a broader view of connectivity, with less of a structured focus on corridors, and more of a perspective on landscape linkages (Bennett 1999). This shift has led to more focus on patterns of patches and the role of intervening conditions, discussed below under habitat fragmentation.

A number of studies on corridors appeared in the literature since 1996. Vos et al. (2002) provide a good overview of corridors and species dispersal. Similarly, Tischendorf and Fahrig (2000) reviewed 33 studies relating to landscape connectivity. They discussed how terminology differences can cause confusion, and stressed the importance of understanding the difference between functional connectivity and structural connectivity- analogous to the differences between the concept of corridors and the concept of landscape linkages. Corridors assume habitat continuity. Linkages address movement capabilities, habitat patches, landscape configurations, matrix conditions, barriers, and their relationships in maintaining continuous populations. Similarly, Hess and Fisher (2001) and Rosenburg et al. (1997) discussed corridors and related terminology and stressed the differences between functional and structural expectations. Beier and Noss (1998) reviewed 32 studies that addressed corridors. They reported that only a limited number of these studies were designed to empirically test the use of corridors by species, but that a number of these did show that corridors provided some level of connectivity. Earn et al. (2000) pointed out some concerns with corridors, including that the maintenance of some level of fragmentation may be important to avoid such problems as synchronized outbreaks of diseases. Baum et al. (2004) reported on the importance of matrix conditions that a corridor passes through, with high-resistance matrices reducing corridor effectiveness compared to low-resistance matrices. Similarly, Anderson and Danielson (1997) reported that the reliance upon corridors will be influenced by the surrounding landscape. With (1999) reviewed information on corridors, and reported on a number of studies that documented uses of corridors, but also discussed how, in many other studies, landscape connectivity was not a function of corridors.

A number of empirical studies on corridors and landscape linkages have been published since 1996. Coulon et al. (2004) studied roe deer movements, and determined that corridors of woodlands were utilized as movement areas by this species, supporting the importance of corridors in their landscape. Collinge (1998) found that corridors decreased the rate of species loss, but only in medium-sized patches for insects in grasslands of Colorado, and increased the rate of recolonization of these patches. One in three of the insects investigated preferentially traveled in corridors. Haddad (1999) found that corridors increased interpatch movement of butterflies. Mech and Hallett (2001) demonstrated that corridors provided genetic links in red-backed vole populations in forested patches connected by corridors, but deer mice were not influenced by the presence of corridors.

HABITAT LOSS, FRAGMENTATION, AND THE QUESTION OF ADEQUACY

Habitat loss is acknowledged as one of the greatest threats to biological diversity at the species level (Noss et al. 1995, Wilcove et al. 1998, Stein et al. 2000) and has been identified as a primary cause of extinction for species (Klok and De Roos 1998, Stein et al. 2000). Wilcove et al. (2000) identified various causes of habitat loss, and identified agriculture as the leading cause of species endangerment, followed by land conversion for commercial development, with these two combined contributing to the listing of 73% of the U.S. endangered and threatened species. Logging was identified as contributing to habitat loss associated with 12% of the listed species.

Habitat loss can occur from a wide variety of causes, but generally falls into several types. First is the actual loss or conversion of areas from native ecosystems to human-created conditions that convert habitat to non-habitat for a species. Examples include urban sprawl, agricultural development, or other direct conversions. A second way is through changes to the amounts or types of successional conditions or states of ecosystems. Timber harvest, for example, can change the amounts of late-successional conditions in a landscape, but may still be supporting forested conditions that may be similar to early successional stages of naturally occurring ecosystems (Bunnell 1999), without factoring in the influence of roads. A third type of habitat loss occurs through indirect loss caused by changes to disturbance regimes or other processes that cause alteration of the composition, structure, or function of ecosystems (Wilcove et al. 2000), with disruption of fire regimes estimated to affect 14% of listed species. These disruptions of disturbance regimes can result in changes to amounts of successional stages within a landscape (Agee 1999), and may even result in new conditions being produced that did not historically occur in a landscape (Haufler et al. 2000). A fourth type of habitat loss can occur through changes to ecosystem compositions or structures or species interactions due to invasion by exotic species (Wilcove et al. 2000), with the listing of many species in Hawaii attributed to the invasion of exotics. A final type of habitat loss occurs when changes at a landscape level affect the amounts or occurrence of other species, whether these are predators, parasites, or competitors for resources that can make habitat conditions unsuitable for a species (Stribley and Haufler 1999, Lloyd et al. 2005, Watson et al. 2005). For example, the spread of cowbirds across landscapes with high levels of agricultural conversion has resulted in habitat sinks in remaining forest patches that, without the landscape of agriculture conversions, could be functional habitat for various species of birds (Lloyd et al. 2005). Most considerations of habitat loss focus primarily on the effects of the first types of loss, often with little attention paid to the latter three types.

Habitat loss and fragmentation are often considered together as a combined impact, as loss of habitat typically results in smaller sizes of habitat patches available to a species, increased distances among habitat patches, and increasing amounts of matrix conditions in which habitat patches are embedded. However, Fahrig (1997, 1999, 2002, 2003), Harrison and Bruna (1999), and Bunnell (1999) provide strong evidence that habitat loss and fragmentation are two separate issues, as habitat can be lost resulting in small or large remaining patches that can be distributed in close proximity or that can be spread throughout a landscape. When habitat loss does lead to smaller patches that are at increasing distances from each other, the distribution of a species within a landscape may change from being a single "continuous" population to that of a patchily distributed population with a number of independent subpopulations. These subpopulations may then interact through dispersal of individuals, which can lead to the occurrence of a metapopulation condition within a landscape (Hanski and Gilpin 1997) or lead to discontinuity that cause genetic concerns (Mills and Tallmon 1999).

Habitat for a species can be distributed in varying qualities and sizes across a planning landscape, with each species responding to similar environmental features in potentially different ways as influenced by patch, matrix, scale, and landscape characteristics (Wiens 2002, Fischer et al. 2004). Understanding the historical distribution of the habitat for a species in a landscape is important to its evaluation, as it provides an indication of how habitat of varying quality for a species may have occurred under historical disturbance regimes (Sallabanks et al. 1999). Most species have adapted to interact within patchy environments either spatially within a landscape (Wiens 1997), or temporally as habitat qualities within a landscape shifted over time (Camp et al. 1997, Wiens 1997). These factors add complexity to the evaluation of the effects of habitat loss, and emphasize the importance of an historical reference.

Numerous publications appearing since 1996 have addressed the effects and relationships of habitat loss and fragmentation. A number of studies report on empirical analyses of landscapes and the observed effects of loss of habitat on species. Many evaluations of habitat loss have been based on theoretical models of habitat loss and fragmentation.

Empirical Studies of Habitat Loss and Fragmentation

Various studies have investigated the direct effects of habitat loss and/or fragmentation on species. Freemark et al. (2002) summarized information on habitat loss and concluded that conservation planning should focus first on the amount of habitat provided in a planning area. Fragmentation and distributional questions appear to only be a concern in landscapes with substantial habitat loss, particularly in landscapes where habitat conversion has been due to causes such as agriculture or urban spread where negative edge effects have been documented. Bender et al. (1998) reviewed 25 studies on habitat loss and patch effects and came to similar conclusions. They reported that habitat loss and fragmentation will increase the status of edge species, decrease the status of interior species, and not affect generalist species. They reported that migratory species were less affected by habitat loss and fragmentation than were resident species.

McGarigal and McComb (1999) examined vegetation and birds in 30 landscapes in Oregon and compared effects of habitat loss versus habitat configuration. They found that with the exception of a few edge species, effects of habitat change were strongly influenced by the amounts of habitat and only secondarily affected by habitat configuration. They noted that at the scale of their analysis (300ha watersheds), loss of late successional conditions corresponded to increases in early successional conditions, with some species reduced with loss of late succession and other species favored by this loss. Similarly, Trzcinski et al. (1999) found that the amounts of woodlands in their study areas influenced the occurrence of bird species more than the spatial arrangement of the woodlands. A study conducted by Villard et al. (1999) on a smaller scale then that of Trzcinski et al. (1999) found that both amount and configuration of habitat contributed to the occurrence of bird species. This study also pointed out the importance of scale in addressing habitat loss and fragmentation. Goodsell and Connell (2002) empirically tested the relationship of habitat loss versus fragmentation effects using invertebrates in kelp beds as the study organisms. They found that loss and fragmentation were not independent. Habitat loss was the primary effect, but the proximity of patches also played a role in lessening the effects of habitat loss. Rare species were found to be impacted the most from habitat loss as compared to more common species. Collinge (1998) found that patch size influenced species loss, with small patches losing species of insects at a faster rate than large patches in native grasslands in Colorado.

Davies et al. (2000) tested the relationship of habitat loss and fragmentation to characteristics of various species of beetles in forests of Australia. They found that:

- Rare species declined more than relatively common species,
- Species in isolated patches declined more than those in less isolated patches,
- Predators declined the most of the taxonomic groups examined,
- Body size was not related to responses, and
- Related species did not respond the same to habitat loss or fragmentation.

Davies et al. (2001) reported on within-patch and between-patch responses of beetles in Australia, and found different results than many other empirical studies. They found no effects of fragmentation on extinction rates, with no reduction in species richness or in occurrence of rare species in forest fragments compared to continuous forest. They did report on edge effects that increased the number of species, particularly of detritivores and fungivores in edges of patches, but not to the detriment of the forest-associated species. Between patches, they did not note any effects from fragments on colonization rates, some species utilized the matrix among patches, and the matrix did not serve as a source of invading species. They concluded that fragmentation had an influence on stabilizing community dynamics.

McIntyre and Wiens (1999) conducted a study with beetles in an experimentally manipulated environment of grass patches. They found that habitat loss was a primary driver of beetle occupancy, with fragmentation effects having less influence. They did note that size of patches and their distance away from other patches had more influence on beetle use of a patch than did number of patches or measures of edge. Radford et al. (2005) conducted an empirical study of bird species richness in 100 km^2 landscapes as influenced by the amount and configuration of forest patches. They found significant effects of habitat loss, but not of measures of fragmentation. However, they did find that the shape of the non-linear response curves differed in landscapes with aggregated patches of habitat compared to landscapes with dispersed habitat patches. Overall, they found that 55-60% of the variation in species richness was explained by habitat loss, 10% was explained by the extent of habitat aggregation, and 14% was attributed to other environmental gradients such as elevation. They noted a habitat loss threshold at 10%, where species richness dropped dramatically. Brown and Sullivan (2005) found that bird utilization of isolated forest patches did not show consistent trends, and examined the influence of bird body mass on their abilities to utilize different patches. They concluded that home range requirements come into play in bird use of isolated fragments, and that birds of medium body size may do better in isolated patches than birds with smaller or larger body sizes.

Braden et al. (1997) discussed the importance of habitat quality within patches as compared to more generalized measures of habitat loss. They stressed the need for maintaining or improving high quality habitat for the California gnatcatcher within habitat patches, a factor not addressed by others in examining effects of habitat loss on this species. Klok and De Roos (1998) found that for a shrew, population density was primarily affected by overall amounts of habitat in the landscape, but that the expected time to extinction of a population due to demographic stochasticity was affected much more by habitat quality. Breininger et al. (1999) suggested that increasing the quality of the habitat within patches for the Florida scrub-jay was more critical to the survival of the species than restoring more "habitat".

Several studies have investigated whether habitat patches in terrestrial landscapes follow island biogeography theory. Brotons et al. (2003) compared late successional forest patches in a forest landscape to true islands supporting forests. They found that the true islands displayed expected island biogeography responses, while the silvicultural forest patches did not. Forest specialist species showed responses on the true islands compared to more generalist species. Hill and Curran (2001) examined species areas curves applied to forest fragments in Ghana. They found more species of trees in larger patches than in smaller patches, with rare species increasing with size of patches and common species forming a stable foundation of about two-thirds of all species.

A number of studies have been conducted to determine specific causes or effects of fragmentation in various landscapes, with a primary focus on the edge effects and the responses of specific species to these effects (Kremsater and Bunnell 1999, Marzluff and Restani 1999). Many studies have reported on the effects of fragmentation on bird populations, emphasizing effects on nest success, parasitism, and predation in relation to amounts of forest cover at various scales (e.g., Donovan et al. 1997, Hartley and Hunter 1998, Marzluff and Restani 1999, Lloyd et al. 2005, Watson et al. 2005). These studies have revealed that significant differences in effects were noted among landscapes that had conversion of ecosystems from forests to agriculture as compared to landscapes that were influenced by shifts in the amounts of successional stages or composition of forest ecosystems (Kremsater and Brunnel 1999, Freemark et al. 2002). The same negative effects of fragmentation on vertebrates observed in many studies where ecosystems were converted to agricultural or suburban/urban uses have not been found in landscapes where surrounding land uses have primarily been timber production (Tewksbury et al. 1998, Freemark 2002, Kremsater and Bunnell 1999).

Theoretical Studies of Habitat Loss and Fragmentation

In theoretical modeling, two perspectives on habitat fragmentation have emerged (With 1999). The first, based primarily on the theory of island biogeography (MacArthur and Wilson 1967), attributes habitat patches to being equivalents of islands surrounded by an inhospitable sea or matrix of non-habitat. These models then direct attention on identifying suitable distribution of habitat patches. The second, the landscape mosaic perspective (With 1999) views landscapes as spatially complex, heterogeneous arrangements of habitat conditions. It stresses the need to use an organismal assessment of landscape conditions, and typically uses animal movement models such as percolation models to assess landscape configuration and its effect on species persistence.

A number of modelers have examined the question of habitat loss versus fragmentation effects. These models generally report that the effects of habitat loss have a much greater effect on species populations and persistence probabilities than effects of habitat fragmentation (Fahrig 1997, 1999, 2001, 2002, 2003, Flather et al. 2002), findings that are supported by various empirical studies described in the previous section.

Theoretical models of habitat loss have estimated that if some minimum amount of habitat is maintained in a landscape, that the likelihood of population persistence remains high. Fahrig (1997:608) indicated that when breeding habitat was greater than 20% of a landscape, that survival of a species was "virtually ensured no matter how fragmented the habitat is." Other investigations have estimated slightly higher amounts. Andren (1994) reported that fragmentation was not an issue when habitat levels were above 30% in a landscape. Flather et al. (2002) conducted theoretical modeling of habitat loss and configuration, where a landscape was defined either as areas of habitat or non-habitat, and evaluated for species that were considered to be good dispersers and species that were considered poor dispersers. They found that above 40% habitat, effects of habitat fragmentation were inconsequential, with the amount of habitat explaining 97% of the variance in population persistence. Below 40%, effects of fragmentation were noted, however, habitat loss still accounted for 30% of the simulated effects on population persistence, with fragmentation and the habitat loss/fragmentation interaction variable accounting for only 12% of the variance. Flather et al. (2002) reported that simulation models that left less than 20% old growth habitat produced fragmentation effects on owl persistence in the Pacific Northwest of the U.S.

With (1999) modeled habitat loss and fragmentation, and examined their effects on two types of species, species that had some dispersal ability and species that lacked any dispersal ability. Species that had some dispersal ability were found to not have connectivity concerns until habitat was reduced to below 20%. For species with no dispersal capability, connectivity concerns were found when habitat was reduced below 40%. Soule and Sanjayan (1998) used theoretical models of habitat reduction based on island biogeography theory and linked these to estimated effects on species modeled with use of species-area curves to predict that habitat representation should be 50% of a landscape, and that at a level of 10% representation, massive extinction of species would occur.

These theoretical models provide some insights for understanding how the effects of habitat loss may operate, and can be used in hypothesis generation. However, their relevancy to real landscapes has been questioned (Wiens 1997, Haila 1999, With and King 1999). Haila (1999) discussed how theoretical models that assume an area is 100% habitat and then model loss from this level are completely unrealistic. Models that only discriminate between habitat and non-habitat are also unrealistic. Similarly, use of the island biogeography perspective of habitat fragmentation (With 1999) has drawn criticism. The use of species-area relationships drawn from island biogeography theory, such as used by Soule and Sanjayan (1998), has been criticized (Hanski and Simberloff 1997, Wiens 1997, Brunnel 1999) as the relevancy of real islands as models for terrestrial landscapes is unrealistically simplistic. Habitat patches in terrestrial systems are not surrounded by water, but by habitat of varying quality (Noss 1996, Monkkonen and Reunanen 1999). In addition, habitat patches in most landscapes change over time, allowing for temporal connectivity not available to true islands (Camp et al. 1997, Wiens 1997, Monkkonen and Reunanen 1999). Wiens (1997:45) stated, "In landscape ecology, the 'matrix' is itself spatially structured, and spatial relationships play an active role in determining the dynamics within the 'patches' of interest." Bunnel (1999) compared species distributions and movement capabilities in forested landscapes and concluded that there was little evidence in forests of the Pacific Northwest that vertebrates perceive old forest stands as discrete patches. He felt that connectivity of patches could be important, but that the needed amount of interchange is unknown. Further, he stressed the importance of the matrix conditions to understanding connectivity concerns. Kupfer et al. (2006) demonstrated the influence of different matrix conditions in models of species responses to habitat loss. Fahrig (2001) showed in a simulation experiment that quality of the matrix can influence the requirement for required habitat maintenance by up to 58%. Szacki (1999) studied small mammals in Poland, and found that the matrix conditions were more important to population density and compositions than patch area or isolation. Many studies have documented the occurrence of species-area relationships (e.g., Ambuel and Temple 1983, Hayden et al. 1985, Robbins et al. 1989) supporting that larger-sized habitat patches, up to some level, will support more species. However, the complexities of patch sizes, shapes, surrounding habitat conditions, and the historical relationship of these factors all make a simple application of species-area relationships problematic (Connor et al. 2000). Haig et al. (2000) found that species-area relationships predicted from island biogeography theory did not occur in a study of plant species diversity.

Adequacy and Habitat Thresholds

Modelers have hypothesized that certain thresholds exist (Flather et al. 2002, Huggett 2005, Lindenmayer and Luck 2005), although Lindenmayer and Luck (2005) discussed a number of limitations of the threshold concept. Green (1994) defined critical thresholds as some attribute of landscape structure below which abrupt changes in some attribute, such as species persistence occur. Thresholds have been viewed as occurring rapidly around a certain point (Muradian 2001), or occurring within zones (Wiens et al. 2002) as a more gradual change. Examples of each have been identified. Thresholds relative to extinction probabilities have been examined to determine whether habitat amount influences species extinction (With and King 1999, Flather et al. 2002). Models reveal that habitat loss and reduction of population size are linearly related, up to some threshold. Below this threshold, the added effects of habitat fragmentation increase the rate of population reduction, and in turn, the risk of extinction. Empirical studies provide support for this relationship. Huggett (2005) noted, however, that many factors can influence thresholds including different responses by different species, different responses by the same species due to different combinations of gradients in a landscape, and the effects of wide zones of influence for some species compared to narrower point responses of other species.

Models of habitat loss have found varying results in estimating a threshold level where extinction rates occur. Andren (1994) estimated a threshold at 30% (70% habitat loss). Fahrig (1997) estimated a 20% level of remaining habitat as a threshold where extinction probabilities increased. Flather et al. (2002) estimated a 40% level of remaining habitat as a level where risk started to increase at a higher rate due to compounding fragmentation effects, although in a worse case model, fragmentation effects could begin at a 60% level of remaining habitat. With (1999) modeled connectivity in landscapes, and identified increasing concerns with connectivity when habitat dropped below a 20% threshold. Pearson et al. (1996) identified a "connectivity threshold" using simple grid cell modeling at a 60% level of remaining habitat, below which they determined that connectivity potential can be reduced. This is a different measure than that of extinction probability. Soule and Sanjayan (1998), using species area relationships from island biogeography theory estimated a need for less than 50% loss. All of these models provide interesting insights into how habitat needs, dispersal capabilities, and landscape patterns could affect extinction thresholds. However, none of these modeling approaches were based on empirical data or used real landscapes as the basis for their analysis. Svancara et al. (2005) reported on a review of literature containing recommended levels of representation based on policies compared to empirically or conservation planning generated estimates of adequate levels of representation. They noted that policy generated levels were less than levels reported for conservation planning and empirically determined levels. Their analysis did not evaluate the basis of conservation planning estimates (i.e., opinion versus empirical determination), nor did they differentiate the different types of empirical information (theoretical models of various types versus actual empirical results from field investigations) raising questions about the merit of their findings.

Empirical studies of species responses to habitat loss are far more difficult to quantify than modeling approaches due to the great complexity of factors that operate in real landscapes and the wide range of species responses to these factors. However, a number of studies have attempted to address the question of adequacy of representation. Radford and Bennett (2004) investigated the distribution of white-browed treecreepers in woodland patches in southern Australia. They reported an extinction threshold of between 15 and 25% residual cover, with the amounts varying with the quality of the habitat. Carlson (2000) examined the effects of ecosystem loss compared to historical amounts of deciduous forest on the white-backed woodpecker in Sweden. He reported that the amount of old deciduous forest has decreased from approximately 30% of the forestland to approximately 2-4%. Further, he reported that the amount of dead wood (e.g., snags) in the forests had declined from about 20% of the forest to 1%. The population of the white-backed woodpecker has declined to low levels with only a few areas supporting populations of any size. These data indicate that the reduction of this ecosystem has threatened this species. This study emphasizes the importance of addressing both direct and indirect losses of ecosystems, with the loss of dead wood within forests an equally important consideration to the area of remaining forest. Virkkala and Toivnen (1999) discussed maintenance of biological diversity in Finnish forests and concluded that 10% of forest land in each biogeographic forest zone and section be placed into reserves. They felt that this was necessary because of the intensive nature of forestry practices being applied to virtually all lands not in reserves. Their recommendation was designed to provide representative stands of late successional conditions well dispersed across forest types and areas by distributing reserves among biogeographic zones and units. They did not address the need for other successional stages for maintenance of biological diversity or ecosystem integrity. They based their assessment of the recommended 10% amount on distributional studies of both birds and plants. Virkkala and Toivnen (1999:28) stated for birds that, "for the adequate representation of species in an areal network there is a threshold, which is approximately 10% of the land area." For plants they found that 8% of the land area would provide for adequate representation. They also recommended that the matrix lands among reserves should be managed in a manner to help contribute to biodiversity. Radford et al. (2005) reported a habitat threshold of 10% below which species loss jumped significantly. They noted however, that their measure (species richness) is different than a single species evaluation of extinction probability.

Groves (2003) summarized information relating to adequacy of representation. He concluded that a representation level of 30-40% for ecological communities was a good goal, but that this may not maintain all species. He pointed out the complexity in setting goals with the need for representativeness, with each community distributed appropriately across planning landscapes, redundancy of sites, with minimums for each element, and resiliency expressed in quality of representative areas. Tear et al. (2005) addressed the challenges of adequacy, and discussed the fact that social, political, and legal contexts ultimately determine the probabilities of persistence that are deemed acceptable. Habitat thresholds are difficult to define specifically because of the confounding factors of habitat quality in residual patches, habitat pattern, matrix quality, reproductive and emigration rates of different organisms, and dispersal capabilities of different species (Hill and Caswell 1999, Huggett 2005).

In addition to total amounts of habitat loss that may be thresholds to increased rates of species loss, specific needs of individual species may need to be considered. For example, most species of birds are capable of dispersing across sizable distances. However, in Australia, thresholds of 1500m between woodland patches have been proposed as effective barriers to some sedentary woodland species (Brooker et al. 1999). Also in Australia, van der Ree et al. (2004) suggested that the maximum gliding distance of the squirrel glider, a small marsupial, is about 75m, so that habitat patches separated by more than this amount may not be available to this species. Thus, identification of specific thresholds for habitat retention has multiple considerations, making a generalized recommendation problematic. However, a compilation of available information would indicate that below a 10% level, dramatic losses of species would be expected. Definition of adequate levels of representation will vary, with in general a goal of 10-40% appearing to be a reasonable expectation of providing for species persistence.

POPULATION AND SPECIES VIABILITY

The concept of species viability is not new to science. Ecologists such as Allee (1931) and Leopold (1933) discussed the concept of minimum viable population size. The application of the concept for endangered species analysis received increasing attention since the 1980's. Species viability is a term that emerged largely in the 1980's, with an initial focus on identifying minimum viable population sizes (Beissinger 2002). Population viability also developed in the 1980's, with a focus on tools that addressed population viability analysis (PVA). Population and species viability are topics that have seen considerable publication since 1996. Beissinger and McCullough (2002) compiled an excellent set of review papers on population viability analysis. A component of population viability that received substantial focus during this timeframe has been the development of metapopulation biology (Hanski and Gilpin 1997). This report does not identify or summarize all of the literature that was published since 1996 relating to population viability or metapopulation biology, but attempts to point out some of the significant trends and findings of the work during this timeframe.

Specifically defining what is meant by species viability in a management context as well as determining how to measure or predict species viability has proven to be difficult. Numerous factors influence the viability of any species. However, habitat is the greatest overall factor affecting viability of a species (Wilcove et al. 1998). Reed et al. (2006) identified four broad classes of factors influencing viability of a species; population size and structure, habitat, demography, and relationships between demographic rates and habitat and between demographic rates and population size. Other factors include environmental stressors, natural and introduced competitors, predators, parasites, or diseases, and human stressors including pesticides, pollutants, and domestic animals. Given this myriad of potential influences on the viability of a species, it is not surprising that quantification of species viability has been a difficult task. Consequently, most assessments of species viability in a planning or impact assessment context have been conducted qualitatively, usually with the use of expert opinion in relation to projected future conditions.

Population status of a species in the future must include projections of future habitat conditions, as the population of a species is dependent on the quality and quantity of habitat available to that species. Thus, virtually all assessments of species viability link to projections of habitat assessments. However, how the actual likelihood of persistence is determined can be based on a number of different methods or analysis models.

Habitat-based assessments of species viability have ranged from expert assessments of future population status based on projected habitat conditions to more complex analyses of individual home ranges and their contributions to species persistence in spatially-explicit individually-based population viability models (Noon et al. 1999). Individually-based spatially explicit models may be the most realistic (Breininger et al. 2002), but these approaches also require many model parameters that may not be known with any accuracy, and include various assumptions that may be difficult to test. A number of recent efforts have been linked to GIS for their computations and projections. The spatial description of habitat quality produced from this approach can be used for a variety of habitat-based population viability assessments (Akcakaya and Atwood 1997, Akcakaya 2000). Lawler and Schumaker (2004) evaluated habitat surrogates for population parameters of red-shouldered hawks and goshawks, and found poor relationships between predicted habitat quality and observed habitat quality.

In the 1980's the term population viability assessment (PVA) was introduced (Beissinger 2002). Various models for PVA have been proposed and developed (see review by Akcakaya and Sjogren-Gulve 2000), most involving theoretical relationships of demographic data. The idea behind PVA has been to determine an estimate of the extinction risk to a species based on current demographic conditions and alternative future conditions. Some of these tools have been applied to analyses of populations of threatened or endangered species (e.g. Akcakaya and Atwood 1997, Breininger et al. 1999, McCarthy and Lindenmayer 2000). However, given the complexities of species viability described above, it is not surprising that sufficient data generally do not exist to conduct a thorough population viability analysis. For example, Green and Hirons (1991) reported that data suitable for population modeling were available for only 2% of threatened bird species, taxa about which we know the greatest amount, while Samson (2002) reported that suitable data existed to conduct a PVA for only 3 of 119 species at risk in the Northern Great Plains.

A number of different demographic-based approaches have been proposed for assessing species viability. As with habitat-based approaches, these range from relatively simple approaches to much more complex approaches. Incidence function models are relatively simple models designed to provide an estimate of the risk of extinction (Hanski 1999). They examine occupancy of patches of habitat within a landscape over a time interval (Ralls et al. 2002). With these data, estimates of extinction and colonization rates of habitat patches of different size or distribution can be estimated, and the probability of population extinction evaluated in comparison to various possible changes in sizes or distributions of habitat patches. This approach requires the presence or absence of species of interest to be determined for various habitat patches in a landscape over a time. Appropriate time frames are difficult to estimate, as different populations have different generation times and vulnerability to extinction events. Actual demographic data are not required. This approach assumes relatively static habitat conditions (Ralls et al. 2002), an unlikely condition for management planning or impact assessments, but useful for empirically testing theories relating to island biogeography.

A second demographic-based approach is the use of population trend information (Morris et al. 1999). This approach requires the population of a species to be consistently monitored over time to determine any changes in the population size. Morris et al. (1999) recommended a minimum of 7 years of trend data for accurate analysis. Even with this information, the population trend applies only to that time interval and landscape studied.

A number of population simulation models have been developed that address questions of productivity and survival rates of a population. Most of these models are deterministic single-population models or stochastic single-population models (Ralls et al. 2002). These models require detailed information on the demographics of the population under evaluation, data that are seldom available (Bessinger and Westphal 1998). These models are most effective or accurate when they link demographic information directly to habitat quality (Breininger et al. 1999). With accurate modeling of the relationship of habitat quality to demographic parameters, such models can be used to project risks of extinction with projected changes in habitat amounts. Spatially explicit population models link demographic parameters with the quality and quantity of habitat (Reed et al. 2002). When the species is primarily influenced directly by these two variables, then the spatial arrangement of the habitat is less important than its total amounts and quality. Letcher et al. (1998) used a spatially explicit population model for red-cockaded woodpeckers that provided insights into population management. Carroll et al. (2003) used a spatially explicit population model for carnivores to help identify key areas for reserves and linkage zones. Lindenmayer et al. (2001) used a spatially explicit population model to analyze landscapes for greater gliders in Australia. Individual-based spatially explicit models track the status of individual home ranges and aggregate these for the entire landscape. Such efforts are extremely data hungry (Reed et al. 2002), and require a knowledge of many demographic parameters and their relationship to habitat quality. Melbourne et al. (2004) advocated development and calibration of individually-based spatially explicit models for their potential contributions to understanding species dynamics in fragmented landscapes.

Beissinger and Westphall (1998) discussed use of PVA's in endangered species management. They suggested caution in use of predictions produced from such analyses because of the unreliability of data available for such models as well as the lack of understanding of both periodic fluctuations and density dependent factors, and varying model assumptions that can cause changes in results. They suggested that PVA's consider relative rather than absolute rates of extinction, be limited to short projections, and use models compatible with the available data. Belovsky et al. (2002) emphasized the importance of density dependent factors in PVA's, revealing the problems that the lack of information on these relationships may cause. Reed et al. (2002) presented a number of recommendations relative to use of PVA's. First, they suggested caution in the use of PVA's recognizing that PVA's are only as good as the quality of the data for the model, that measures of confidence should be included, model framework and results should be subject to peer review, and that the model structure, inputs, and results should be treated as hypotheses to be tested. Further, they recommended that PVA's not be used to determine minimum population sizes or estimates of specific probabilities of extinction, but rather be used to compare relative effects of potential management actions on population growth or persistence. Ellner et al. (2002) and Ludwig (1999) reported that the results of PVA analyses may be unbiased, but that they are generally too imprecise to provide meaningful information. Brook et al. (2002) responded to this with the argument that while imprecise, no other methods may exist to produce any better results, so that PVA's should be used, but interpreted cautiously. Brook et al. (2000) took 21 long term data sets and applied PVA analyses to the first half of each time series and then again to the second half and found good congruence of results, leading them to recommend the use of PVA's. Witting et al. (2000) used PVA's from multiple species to evaluate landscape management alternatives, and advocated this methodology for landscape analyses.

Metapopulation models

Certain populations may be limited by the spatial distribution of their habitat, where dispersal among patches is a relatively rare event, so that population demographics within a patch are largely independent of other habitat patches within the landscape. When this arrangement occurs, it is known as a metapopulation (McCullough 1996, Hanski and Gilpin 1997). A number of metapopulation models have been developed that attempt to address population persistence in patches as balanced by dispersal rates among patches. Such models, to be accurate, require information on the status of a population within a habitat patch, including the habitat quality, population size, and internal-patch demographic parameters. In addition, the distribution, and size of other patches in the landscape and rates of successful dispersal among the patches must be known. Dispersal data are one of the least known and most difficult parameters to assess for a population, and small errors in assessment of dispersal can cause large errors in projections of metapopulation models (Reed et al. 2002). In addition, even if these population parameters are collected, as with other demographic parameters, they are usually not transferable to other conditions than those in which they were collected.

Concerns over habitat fragmentation have led many to assume that populations are regularly being converted to metapopulations, and to view any system with a patchy distribution as a metapopulation (Hanski and Simberloff 1997, Harrison and Taylor 1997). However, this is generally not correct, as actual metapopulations are rare (Harrison and Taylor 1997). Various types of metapopulations have been described (Harrison and Taylor 1997), and various modeling approaches have been developed (Hanski and Simberloff 1997). For example, Harrison and Taylor (1997) reported that while fragmentation may cause a previous continuous population to become discontinuous, whether this discontinuity results in separated subpopulations, a metapopulation, or fragmented populations on an extinction trajectory would need to be determined by detailed analyses.

Hanski (1999) discussed the basic parameters that need to be considered to conduct a metapopulation analysis. Metapopulation analyses point out some of the key components of landscapes relative to population distribution and persistence, specifically the degree and effectiveness of dispersal (Doak 2000, Johst et al. 2002), the quality of habitat within each patch (Breininger et al. 1999), the distribution of patches (Johst et al. 2002), and the quality of the matrix conditions for dispersal (Szacki 1999, Lawes et al. 2000). Haydon and Pianka (1999) added the perspective that species responses to fragmentation cannot be predicted from pre-disturbance distributions. Consideration of these factors place metapopulation analysis and studies of habitat fragmentation as parallel efforts.

CLIMATE CHANGE

Global climate change has been a subject of increasing interest and focus in the past 10 years. A number of publications have discussed biodiversity conservation in the face of global warming. Saxon (2003) presented a good discussion of this topic. He recommended that conservation planning occur across ecoregions, and that these ecoregions be identified based on abiotic factors including climate, but also based on other abiotic factors than climate as this factor is likely to change. With climate change expected to have a greater effect on more polar regions, incorporating the potential consequences of global warming relative to conservation planning in Alaska is warranted.

RELEVANCY AND RECOMMENDATIONS FOR THE TONGASS PLAN

ASSESSMENT OF THE TONGASS PLAN

The Tongass National Forest Land and Resource Management Plan (Forest Plan) was described as a "habitat-based wildlife conservation strategy that employed old growth associated umbrella species to design a coarse filter/fine filter approach for species conservation" (Tongass Conservation Strategy Overview). The coarse filter focused on a network of interconnected, variably-sized, old growth reserves distributed throughout the forest. The reserves were established around the habitat requirements of several old growth associated species with large home ranges. The plan further incorporated standards and guidelines to address needs of vertebrates that had additional habitat requirements. Landscape connectivity among old growth reserves was designed to address the needs of species whose dispersal capabilities were considered limited.

Coarse Filter Assessment

The coarse filter strategy was specifically directed at old growth forests, rather than a full consideration of all succesional stages. The reason for this was that analysis of the forest revealed that forest stands in the Tongass received very few disturbances. An extremely low rate of fire was found to occur naturally, and any that did occur were typically very small in size. Some windthrow was stated to occur, but this generally was thought to occur as a gap-phase event, with limited numbers of sizes of larger disturbance events. However, research by Kramer (1997), Nowacki and Kramer (1998) and Kramer et al. (2001) found that in some areas, windthrow damage in the Tongass can be extensive, and can keep up to 30% of forests from progressing to late-seral states. Further, DeGayner et al. (2005) demonstrated that animal populations were sensitive to these types of changes in forest structure, demonstrating that black bears select dens on the basis of the effects of windthrow. These research results raise a question concerning the role of windthrow and the inclusion of sufficient windthrow areas within reserves in the coarse filter strategy of the plan. It is quite conceivable that the designated reserves have sufficient areas occurring in windthrow-prone areas and areas protected from windthrow, particularly given the protection of shoreline forests. However, this was not specifically addressed in the plan, and may be worthy of additional analysis. The work of Caouette and DeGayner (2005) may provide a feasible method for investigating size distributions of trees across the forest, and may allow for a better determination of windthrow effects and inclusions in old growth reserves.

The old growth reserve strategy was designed to allocate various types of old growth forest into the reserve network. Old growth that occurred at both high and low elevations was assigned to the reserve network. Old growth that was on both highly productive and low productivity sites was included in the reserve network. Buffers along riparian areas and buffers along shorelines were protected and included in the old growth network. These designations were designed to ensure that diverse old-growth conditions were maintained.

The FEIS discussed 57 plant associations that have been identified as occurring in the Tongass National Forest. It is assumed that all of these plant associations were either old-growth types, or associated with relatively human-undisturbed settings along shorelines, riparian zones, wetlands, or other areas not subjected to timber harvest. A complete old-growth coarse filter should evaluate whether or not all of these plant associations include old growth conditions are sufficiently represented in the reserve network. For example, are there certain forest types occurring in the more readily accessible areas of the forest that were preferentially targeted in the past for forest harvest, and if so, what percent of their 1954 amounts are still present today? While there is no indication that these areas are not sufficiently represented, neither have data been developed to show that they are all sufficiently represented. A finer scale mapping of forest types should now be available from new remote sensing, such as SPOT 5 satellite imagery that should allow a better assessment of the distribution of the 57 plant associations. What could be more difficult to determine would be the original amounts and distributions of these types, although it should be possible to obtain a reasonable estimate of this through an analysis of abiotic factors associated with the current distribution of the 57 plant associations and then mapping previously-harvested areas to historical conditions based on the distribution of abiotic factors. Hanley and Brady (1997) examined some of the effects of abiotic factors on overstory and understory vegetation in the Tongass National Forest. Additional work along these lines might help identify a set of abiotic factors that could provide an additional analysis layer for coarse filter evaluation. The Alaska vegetation classification system has been mapped for the Tongass National Forest (van Hees and Mead 2005) and could be used as another analysis of the distribution of types within the old growth reserves. However this classification, based primarily on dominant overstory vegetation, may be too coarse in classification to adequately account for an appropriate coarse filter. A focus on the 57 plant associations may be more appropriate.

The old-growth reserve network established in the Forest Plan maintains extensive amounts and distributions of old growth. No studies of ecosystem loss have indicated that this general level of representation should lead to a loss of ecological integrity to the forest's ecosystems. With the exception of the consideration of windthrow effects and a finer scale analysis of the distribution of the 57 identified plant associations, the plan appears to still be consistent with available science on coarse filter strategies. It should be noted that the very long time frame for development of these forests to old growth status generally means that they are a non-renewable resource in all practical terms. Therefore, the relatively extensive reserve network established in the plan appears to be justified for maintaining adequate amounts of this resource.

The Tongass Plan should consider the effects of global warming on its objectives and plans. While the Forest Plan and its network of old growth reserves seems to be as well positioned as possible to address potential negative effects of global warming, review of the plan in light of this new emphasis could be warranted. While it is unlikely that such a review would lead to any changes in the plan, there may be additional ways that global warming might be factored into future plans.

Fine Filter Assessment

Literature relating to fine filter assessments produced since the issuance of the Forest Plan has improved the understanding of various relationships and tools, but does not appear to undermine the information used in the development of the Plan. The forest plan largely relied upon expert panels to evaluate the status of the selected umbrella species. The recent literature is critical of the role of umbrella species as surrogates for biodiversity representation. However, the selection of the species in the plan was based more on a focal species basis to represent and test the coarse filter, rather than a use of umbrella species to provide coverage of biodiversity. In a focal species role, selection of these species appears to be supported.

The use of expert panels has been questioned, but alternative methods such as more detailed population viability analyses (PVAs) have limitations as well. Based on recommendations from Beissinger and Westphal (1998) Ralls et al. (2002), and Reed et al. (2002), PVAs are not recommended to determine specific extinction probabilities but rather to serve as a comparative tool among alternatives. The data available on the selected focal species used in the Tongass Plan were generally lacking to conduct quantitative PVAs, and even had these been possible, using them for comparative purposes would not have yielded results different than expert panels. Clearly, any evaluation of risk to old growth species when the various options differ primarily in the amount of old growth that will be left will rank risk lowest with the alternatives with the largest amounts of remaining old growth. The level of risk evaluated by the panels was questionable, especially given the defined criteria for maintaining a distribution of the population of each species. While PVA and metapopulation modeling techniques have advanced since 1996, they would not appear to provide significant new insights into the status of the selected species analyzed in the plan if conducted today.

The Tongass National Forest is unique in a number of ways (Everest 2005), one of which is that much of its land base is an archipelago. Species occurring in patchy arrangements, as is the case in an archipelago, can have more involved (and evolved) population conditions (Cook and MacDonald 2001). The water matrix of the archipelago effectively limits dispersal and movements of many species, leading to a higher likelihood of having endemic species distributed among the islands. Cook and MacDonald (2001) discussed the importance of understanding and monitoring the status of endemics in islands of the North Pacific Coast. The Tongass National Forest occurs across the Alexander Archipelago, so that additional attention is required to address the potential for important endemics or evolutionary significant units likely to occur within this area. However, cautions in the determination of significant differences in genetic analyses have also emerged as a consideration in recent years (Crandall et al. 2000). At the time of plan development, these concerns were recognized, with specific concerns raised for the northern flying squirrel and red-backed vole populations, suspected old growth-associated species with limited dispersal capabilities. Consequent studies of these two species (Hanley et al. 2005) reported that concerns with these species may be lessened due to use of additional vegetation types by northern flying squirrels and the ability of red-backed voles to move across secondary forest. Additional studies of endemism and genetic distributions applicable to the Tongass National Forest have been reviewed by Smith (2005), and summarized by Szaro et al. (2005). These studies support the importance of the consideration of archipelago effects and their continued evaluation in the Tongass, but have not invalidated the appropriateness of the Tongass Plan.

Recent work (MacDonald and Cook 1996, Conroy et al. 1999, Stone and Cook 2000, Bidlack and Cook 2001, 2002, Cook et al. 2001, Cook and MacDonald 2001) further expounded on the potential for more endemic species occurring within the Alexander Archipelago. In addition to new information on unique genetics of various species, this work has demonstrated various areas of the Archipelago that are functioning to support possible discreet population segments. For example, the Prince of Wales Island complex appears to be an area that is isolated from other parts of the Tongass for a number of species. This new information raises the question of the validity of viability assessments conducted for these species under the Forest Plan that were conducted for the entire forest. These analyses did not find viability concerns for the species at the Forest level, but some questions about the "well distributed" status were raised, although this criterion was determined to be adequately addressed in these analyses. While questions of what subpopulations might need to be maintained remain uncertain at this time, it would appear that population viability assessments, conducted at a finer scale within identified endemism zones of the Tongass, is warranted. This does not imply that the conservation strategy of the Forest Plan is inadequate, but simply that a viability analysis conducted at a finer scale within the Tongass would ensure that concerns about endemics are adequately addressed by the conservation strategy.

Adequacy of Representation

The amount of forest included in old growth reserves in the Tongass Plan varies across the various management units, but in all but one unit exceed 50%, and in some units is at 100%. Information in the literature since 1996 pertaining to the question of how much is enough have generally found that this level of representation should be sufficient to maintain a high probability of species persistence. The finer scale analysis of population viability within endemism zones would further examine this level of representation within smaller management units.

As stated previously, old growth forests in this setting should be viewed as a non-renewable resource in all practical terms. Therefore, a conservative allocation, as included in the Forest Plan, of amounts of forest for harvest is justified. Determining the balance between conservative allocation and adequacy in this case is a value judgment that seems to have been well addressed by the planning team. No new information was reviewed that has changed the science behind this value decision.

RECOMMENDATIONS FOR POTENTIAL CHANGES TO THE TONGASS PLAN

The review of the recent literature supports the appropriateness of the science used in the Tongass Forest Plan. The coarse filter strategy linked with a species assessment remains a supported conservation approach. While some finer scale analysis relative to effects of windthrow and distribution of plant associations is recommended, there is currently no reason to presume that the current reserve system does not adequately address representativeness. This additional analysis is recommended to add specificity to the current reserve network, and to make sure that full representation is included. If any concerns are identified, it is likely that they can be addressed with minor adjustments to the reserve system, particularly with potential changes to the location of the small reserves. However, the need or adequacy of any such adjustments won't be known until the additional analysis is completed.

The assessment of species viability that serves as a focal species check on the appropriateness and adequacy of the coarse filter as a conservation strategy is supported by current science. However, the scale utilized in the viability assessments should be modified in light of new information on species determined since the plan was completed. In particular, recent and on-going research addressing questions of endemism indicate that new viability analyses conducted at a finer scale than those conducted in the original plan may be warranted. Specifically, viability assessments as checks on the coarse filter are recommended to be conducted at the management unit scale consistent with zones of endemism identified in recent research.

While no new information undermines the basic structure of the conservation strategy of the plan, a finer scale analysis of viability for selected species would allow for a better assessment of the status of populations that might be of concern as important endemics. Using selected species that may have distinct subpopulations of concern as checks on the coarse filter, applied at a scale where specific endemics have been reported to occur, will provide a thorough check on the coarse filter and identify if any problems exist at finer scales. It is recommended that additional viability assessments for the various identified endemism zones be conducted for selected species of mammals (and possibly spruce grouse or possible endemics within other taxa) to check that the conservation strategy will maintain viable populations of these species within these zones. Given the home range sizes of the goshawk and its documented movement capabilities within the archipelago, finer scale assessments of viability for this species are not recommended. Rather, a forest-wide assessment for goshawks, with a consideration for its distribution within the forest seems appropriate.

Viability should be assessed for species that are habitat limited, and the future projections of habitat provided through both the coarse filter and management activities should be evaluated. If viability is shown for those species selected to be focal species for the coarse filter, then the conservation strategy will be confirmed. Management concerns for species that are limited by direct human actions (wolves, marten, deer) need to be considered in the Forest Plan, but these are different concerns than those of the conservation strategy to address viability and well-distributed population requirements. The conservation strategy should ensure that the Forest Plan provides for the habitat needs of all species in amounts and distributions sufficient to maintain viable and well-distributed populations. Additional management considerations to address human use of wildlife populations are important to include in the plan, but these should be kept separate from those plan components designed to address the viable and well-distributed requirements.

A possible approach to use in a viability assessment is habitat-based species viability, with one example of this described by Roloff and Haufler (1997, 2002). Similarly, Haight et al. (2001) have utilized a stochastic demographic model based on habitat quality to assess habitat protection options. This approach offers advantages over reliance on expert panels. This approach quantifies habitat information on species of interest, and uses best information to determine the provision of habitat needs of a species based on distributions of varying quality of home ranges across each landscape designated for analysis. While expert opinion is typically needed to help define and quantify habitat needs of each species, the method provides a more consistent and accountable determination of existing and expected future conditions relative to the known requirements of each selected species. While acceptable levels of risk to species are still a value judgment, this method provides a much more rigorous basis for making decisions about acceptable levels of risk. It is also a method that does not require years of demographic information on each species to conduct, but that can be tested and reevaluated as new information on species is generated through research programs, including any new information on demographic responses to specific habitat conditions.

Endemism influenced by the archipelago should continue to be a focus of research. Continuing efforts, especially on the larger islands with higher levels of past timber harvest, makes sense. Understanding the range and distribution of unique genetic developments should be a component of the Forest Service's research missions. However, determination that any newly identified endemics deserve distinct population status should receive broad and intensive scientific review before acceptance of this status.

Standards and guidelines added to the Forest Plan to address concerns of the viability panels for maintaining well distributed populations of specific species may be reexamined in light of new viability assessments at finer scales. By conducting assessments at these finer scales, the well distributed component will be addressed for a focal species if viability within each of the endemism zones is met. With this information, the role of the matrix lands (lands included in various harvest prescriptions) should be examined in relation to their importance to maintaining viable and well-distributed populations. Once this need has been assessed, then the importance of matrix lands to other objectives, including maintaining wildlife populations for human use, can be addressed relative to these desired objectives.

Monitoring of key species is an important component of adaptive management to provide a check on the assumptions used in the assessments of these species. This is not a recommendation for specific survey and monitoring protocols to be added to the plan, but rather support for continuation of the various research programs designed to determine if assumptions concerning species habitat requirements included in the Forest Plan continue to be valid.

This literature review has compiled information that is pertinent to the management of the Tongass National Forest. While the objective of this project was to include all pertinent literature, the timeframe and scope of the project make it likely that some pertinent literature was overlooked. However, the developments in the field of conservation science produced since 1996 indicate that the conservation strategies used in the plan are still valid at the present.

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