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BIODIVERSITY RESPONSE TO STAND STRUCTURAL FEATURES IN SOUTHERN PINE FORESTS: A LITERATURE REVIEW

TECHNICAL BULLETIN NO. 958
DECEMBER 2008

by
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PRESIDENT'S NOTE

Retained stand structural features such as snags, down wood, and green trees are widely perceived to contribute to the support of biological diversity although there is a paucity of information that quantitatively relates benefits to biodiversity from various levels or distributions of these structures. Retention levels are mandated or recommended in some states. Sustainable forestry certification programs such as the Sustainable Forestry Initiative® require the "development and implementation of criteria, as guided by regionally appropriate science, for retention of stand-level wildlife habitat elements (e.g., snags, mast trees, down woody debris, den trees, nest trees)" (SFIS Indicator 4.1.4). Regional standards of the Forest Stewardship Council also require consideration for habitat features at the stand scale.

Because of these considerations, forest managers need more information about the role of retained stand-level structural features in meeting biodiversity-related objectives, the spatial and temporal dynamics of retained structures, quantitative measures of biodiversity response, and cost-effective options for influencing their dynamics. Such information would help managers address indicators in sustainable forestry certification programs and to begin answering the question "How much is enough?" Thus, NCASI supported this literature review to assess the state of knowledge on relationships between retention of selected stand-level habitat features in southern pine forests and response of wildlife communities. Specifically, the report summarizes the state of knowledge related to five habitat features: coarse woody debris, snags, den trees, isolated wetlands, and streamside management zones. These features have demonstrated potential for impacting diversity, though their contributions in pine systems are not always well-documented. The report provides definitions and general characteristics of habitat features considered particularly important to wildlife in southern forests, examines wildlife relationships to each habitat feature, and identifies information gaps and research needs.

The review was developed by Drs. Phil Jones, Brice Hanberry, and Steve Demarais of Mississippi State University. At the time, Drs. Jones and Hanberry were graduate research assistants working under the direction of Dr. Demarais. Dr. Ben Wigley coordinated NCASI involvement in the review.

Ronald A. Yeske

December 2008

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MOT DU PRÉSIDENT

La rétention des éléments structuraux des peuplements forestiers comme les chicots, les billes gisant sur le sol et les arbres verts est largement reconnue comme contribuant à soutenir la diversité biologique, mais très peu de textes scientifiques établissent, de façon quantitative, une relation entre les bénéfices pour la diversité biologique et les différents niveaux ou distributions de ces éléments structuraux. Les niveaux de rétention sont obligatoires ou recommandés dans certains états américains. Les programmes de certification forestière comme le programme d'Initiative pour une forêt durable (*Sustainable Forestry Initiative*®) requièrent que le « développement et l'implantation de critères se fondent sur la science régionale appropriée, pour favoriser la rétention d'éléments structuraux servant d'habitats fauniques à l'échelle du peuplement (par exemple, les chicots, les arbres en forme de mât, les débris ligneux gisant sur le sol, les arbres servant de repaires, les arbres servant de nids) » (SFIS Indicateur 4.1.4)[1]. Les normes régionales du *Forest Stewardship Council* exigent également la prise en compte des caractéristiques des habitats à l'échelle du peuplement.

À la lumière de ce qui a été mentionné précédemment, les gestionnaires de la forêt ont besoin de plus d'information sur le rôle de la rétention des éléments structuraux à l'échelle du peuplement dans l'atteinte des objectifs de biodiversité, sur les dynamiques spatiale et temporelle des structures retenues, sur les mesures quantitatives de la réponse sur la biodiversité et sur les options économiquement viables qui influencent leurs dynamiques. Cette information serait susceptible d'alimenter les gestionnaires quant aux indicateurs contenus dans les programmes de certification des pratiques d'aménagement forestier durable et de les aider à formuler un début de réponse à la question « Quel est le niveau d'effort suffisant ? ». Par conséquent, NCASI a contribué à cette revue de littérature pour évaluer l'état des connaissances sur la relation entre la rétention de certaines caractéristiques d'habitats fauniques à l'échelle du peuplement dans les forêts de pins du sud et la réponse des communautés fauniques. Plus particulièrement, le rapport fait la synthèse de l'état des connaissances reliées à cinq caractéristiques d'habitat : les débris ligneux grossiers, les chicots, les arbres servant de repaire, les milieux humides isolés et les zones d'aménagement des bandes riveraines. Ces caractéristiques sont susceptibles de générer un impact sur la diversité même si leurs contributions aux écosystèmes constitués de pins ne sont pas toujours bien documentées. Le rapport contient les définitions et caractéristiques générales des habitats qui sont considérés particulièrement importants pour la faune des forêts méridionales, il examine les relations entre la faune et chaque caractéristique d'habitat et identifie les besoins en matière d'information et de recherche.

Les Dr Phil Jones, Brice Hanberry et Steve Demarais de l'Université d'état du Mississippi ont effectué cette revue. Lors de la réalisation de la revue, les Dr Jones et Hanberry œuvraient comme assistants de recherche sous la direction de Dr Demarais. Dr Ben Wigley a coordonné la contribution de NCASI à cette revue.

Ronald A. Yeske

Décembre 2008

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[1] NDT : Traduction libre

BIODIVERSITY RESPONSE TO STAND STRUCTURAL FEATURES IN SOUTHERN PINE FORESTS: A LITERATURE REVIEW

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ABSTRACT

The conservation of biological diversity is a high priority in managed forests of the southern United States. Forest certification programs require participants to have biodiversity management programs in place supported by up-to-date science and, in some cases, to have guidelines for retention of important stand-level habitat features important to wildlife. To meet this information need, we reviewed the scientific literature for information on relationships between stand-level habitat features and wildlife communities. Within this report, we give definitions and general characteristics of habitat features considered particularly important to wildlife management in southern forests. Because of the prominence of pine plantation management in the southern U.S., particular attention is paid to research performed in southern pine systems. We follow with a comprehensive examination of wildlife relationships to each habitat feature and an analysis of information gaps and research needs.

We selected five habitat features for review: coarse woody debris (CWD), snags, den trees, isolated wetlands, and streamside management zones (SMZs). These features have demonstrated potential for impacting diversity, though their contributions in pine systems are not always well-documented. There were indications of other features with potential impact (e.g., fork-topped pines, roads), but there was as yet little evidence of their importance.

Coarse woody debris (CWD) is used by a great number of wildlife species; however, few manipulative experiments have been performed in southern pines to determine whether this use is obligatory or facultative. While some species have shown responsiveness to CWD, benefits supplied by pine litter may substantially overlap those supplied by CWD in other forest types.

Snags increase wildlife species diversity and richness by providing nesting and roosting sites for cavity-nesting species and foraging sites for insectivores. The effects of snag density are generally well-documented, at least for avian communities; however, the impact of snag distribution on communities of snag-dependent wildlife, both within stands and across the landscape, has not been adequately investigated.

Den trees are mostly confined to hardwood species, and can contribute multiple habitat values such as mast and vertical structure. Den users are often highly selective, and may take into account features of the den itself, the immediate habitat, or the surrounding landscape. Den tree research in pine-dominated landscapes is almost completely lacking, and study of den trees in SMZs and retention patches could provide much-needed information regarding optimum density, juxtaposition, and distribution.

Isolated wetlands, while individually managed at the stand level, involve definite landscape-scale considerations as well. Species associated with isolated wetlands may spend most of their life cycle in adjacent uplands, requiring knowledgeable management of both wetland and upland to insure their contribution to biodiversity. The impacts of silvicultural practices on communities associated with isolated wetlands are not well known, and most of the research conducted in pine systems is of limited scope. Long-term manipulative experiments, complete with pre-treatment data and adequate replication, are critical to understanding the disturbance regimes to which wildlife communities associated with isolated wetlands in different regions are best suited.

Streamside management zones also involve both stand- and landscape-scale consideration. Because they contain a heterogeneous mix of habitat elements not always found in pine plantations, SMZs have the potential to greatly increase biodiversity in pine-dominated landscapes, to provide refuges for disturbance sensitive species, and to serve as population sources for recolonization of disturbed sites. Studies regarding the impact of SMZ width in pine-dominated landscapes have produced inconsistent and even conflicting results, and it seems unlikely that a single recommended width will suffice for all situations. Management of sites adjacent to SMZs may have as much or greater impact than SMZ width.

We suggest research goals and methodology to address information gaps and research directions in southern pine forests. Long-term manipulative experiments are encouraged both to increase the power of researchers to test hypotheses and to account for long-term variation in wildlife populations. Wildlife responses to habitat manipulations should be measured using demographic characteristics rather than density alone. Statistical methods such as multivariate analyses should be brought to bear on questions of community ecology and response to habitat characteristics. Studies performed in natural pine and pine-hardwood forests can provide baseline material for comparisons with managed pines. There also is a need to improve knowledge of the impact of silvicultural actions, including herbicide use, on the dynamics of snags and CWD, and to develop reliable landscape-scale models to predict the results of management on stand-level habitat features.

KEYWORDS

biodiversity, coarse woody debris, den trees, down woody debris, , isolated wetlands, snags, streamside management zones, structural retention, sustainable forestry

RELATED NCASI PUBLICATIONS

None

CORRÉLATION ENTRE LA BIODIVERSITÉ ET LES CARACTÉRISTIQUES DES ÉLÉMENTS STRUCTURAUX DES PEUPLEMENTS DANS LES FORÊTS DE PINS DU SUD : REVUE DE LITTÉRATURE

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RÉSUMÉ

La conservation de la diversité biologique constitue une priorité élevée dans les forêts aménagées du sud des États-Unis. Les programmes de certification forestière requièrent que les adhérents instaurent des programmes de gestion de la biodiversité, fondés sur les dernières tendances scientifiques. Dans certains cas, ces programmes exigent le développement de lignes directrices portant sur la rétention des caractéristiques des habitats, à l'échelle du peuplement, qui s'avèrent importantes pour la faune. Afin de rencontrer ce besoin en matière de recherche d'information, nous avons revu la littérature scientifique au chapitre des relations entre les caractéristiques des habitats à l'échelle du peuplement et les communautés fauniques. Dans ce rapport, nous présentons les définitions et les caractéristiques générales des habitats qui sont considérés particulièrement importants pour la gestion de la faune des forêts méridionales. Puisqu'il y a une prédominance d'aménagement de plantations de pins dans le sud des États-Unis, nous portons une attention particulière aux textes scientifiques traitant des écosystèmes constitués de pins du sud. Nous complétons cette revue par un examen exhaustif des relations entre la faune et chaque caractéristique d'habitat ainsi qu'avec une analyse des besoins d'information et de recherche.

Nous avons retenu cinq caractéristiques d'habitat : les débris ligneux grossiers (DLG), les chicots, les arbres servant de repaire, les milieux humides isolés et les zones d'aménagement des bandes riveraines (ZABR). Ces caractéristiques sont susceptibles de générer un impact sur la diversité même si leurs contributions aux écosystèmes constitués de pins ne sont pas toujours bien documentées. Les travaux ont montré que d'autres caractéristiques sont susceptibles de produire un impact (par exemple, les pins fourchus, les chemins), mais leur importance reste encore à prouver.

Un nombre considérable d'espèces fauniques utilise les débris ligneux grossiers (DLG). Toutefois, peu d'expériences de manipulation sur les pins du sud ont été réalisées à ce jour pour déterminer si cet usage est nécessaire ou facultatif. Certaines espèces ont présenté une sensibilité aux DLG mais les bénéfices fournis par la litière de pin peuvent dépasser ceux associés aux DLG dans d'autres types de forêts.

Les chicots améliorent la diversité et la richesse des espèces fauniques en fournissant des sites de nidification et des dortoirs pour les espèces nichant dans des cavités ainsi que des sites de recherche de nourriture pour les espèces insectivores. Les effets associés à la densité des chicots sont généralement bien documentés, du moins pour les communautés aviaires. Toutefois, l'impact de la distribution des chicots sur les communautés fauniques dépendantes des chicots, autant à l'intérieur même des peuplements qu'à travers le paysage, n'a pas fait l'objet d'une investigation adéquate.

Les arbres servant de repaires font, pour la plupart, partie des essences de feuillus et ils peuvent contribuer à augmenter la valeur des habitats en tant que mats ou structure verticale. Les utilisateurs de repaires sont souvent hautement sélectifs et peuvent considérer les caractéristiques du repaire lui-même, l'habitat immédiat ou le paysage environnant. La recherche sur les arbres servant de repaire dans les paysages dominés par des pins est pratiquement absente et des études sur les repaires dans les ZABR et les blocs de rétention pourraient dévoiler l'information recherchée au chapitre de la densité optimale, de la juxtaposition et de la distribution. .

Les milieux humides isolés sont aménagés de façon individuelle à l'échelle du peuplement, mais ils doivent être considérés à l'échelle du paysage également. Les espèces associées aux milieux humides isolés peuvent passer la majeure partie de leur cycle reproductif dans les terrains adjacents en amont, ce qui fait qu'il importe de connaître l'aménagement de ces terrains en plus de celui des milieux humides, ceci afin de cerner leur contribution à la biodiversité. Les impacts des pratiques sylvicoles sur les communautés associées aux milieux humides isolés ne sont pas bien connus et l'étendue de la plupart des recherches effectuées dans les écosystèmes constitués de pins est limitée. Pour comprendre les régimes de perturbation qui conviennent le mieux aux communautés fauniques associées aux milieux humides isolés, il est essentiel d'effectuer des expériences de manipulation à long terme, complétées par un pré traitement des données et une réplication adéquate.

Les zones d'aménagement des bandes riveraines doivent aussi être considérées à l'échelle du peuplement et celle du paysage. Étant donné qu'elles contiennent un mélange hétérogène d'éléments d'habitat, atypique des plantations de pins, les ZABR sont susceptibles d'augmenter significativement la biodiversité dans les paysages dominés par des pins. Elles ont également le potentiel de fournir des refuges pour les espèces sensibles aux perturbations et de servir de sources de population lors de la recolonisation des sites perturbés. Les études qui se sont penchées sur l'impact de la largeur de la ZABR dans les paysages dominés par des pins ont révélé des résultats inconsistants et même contradictoires. Il semble peu probable qu'une seule recommandation de largeur pourrait être appliquée dans toutes les situations. L'aménagement des sites adjacents aux ZABR peut avoir un impact comparable si non plus important que la largeur de la ZABR elle-même.

Les auteurs proposent d'établir des buts et des méthodologies de recherche pour répondre aux besoins d'information et diriger les futures recherches dans les forêts de pins du sud. Il est souhaitable de réaliser des expériences de manipulation à long terme pour améliorer la capacité des chercheurs à vérifier les hypothèses et pour tenir compte des variations à long terme des populations fauniques. Les réponses des espèces fauniques aux manipulations d'habitats devraient être mesurées en utilisant des caractéristiques démographiques plutôt que la densité uniquement. Les futures recherches devraient employer des méthodes statistiques comme les analyses à variables multiples pour être en mesure de répondre aux enjeux reliées à l'écologie des communautés et à la réponse des caractéristiques d'habitats. Les études réalisées dans les forêts de pins naturels et les forêts mixtes de pins et de feuillus peuvent donner le matériel de base permettant les comparaisons avec les forêts de pins aménagées. Également, il importe d'améliorer les connaissances de l'impact des pratiques de sylviculture (incluant l'utilisation d'herbicides) sur les dynamiques des chicots et des DLG et de développer des modèles fiables, à l'échelle du paysage, pour prédire les résultats de l'aménagement sur les caractéristiques d'habitats à l'échelle du peuplement.

MOTS CLÉS

biodiversité, débris ligneux grossiers, arbres servant de repaire, débris ligneux gisant sur le sol, chicots, milieux humides isolés, zones d'aménagement des bandes riveraines, foresterie durable, rétention des structures

AUTRES PUBLICATIONS DE NCASI DANS CE DOMAINE

Aucune

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BIODIVERSITY RESPONSE TO STAND STRUCTURAL FEATURES IN SOUTHERN PINE FORESTS: A LITERATURE REVIEW

1.0 INTRODUCTION

Forest management effects on biodiversity are of increasing interest to many segments of the public, especially as management intensity for wood and fiber production increases in some areas. Plantation management in particular is of interest among biologists because of the perception, earned or not, that monocultures managed primarily for wood products lack key components of habitat for some wildlife species. If biodiversity is a legitimate measure of ecosystem state, then intensive management favoring one tree species may be perceived as antithetical.

Recently, sustainable forestry certification systems have emerged to ensure that the ecological impacts of management are studied so that results can be integrated back into improved management models. Certification systems typically contain provisions related to the management and biodiversity contributions of stand-level habitat features. For example, the Forest Stewardship Council's (FSC) Forest Certification Standard for the Southeastern United States (Principle 6.3.c.1) requires managers to provide for a diversity of habitats such as declining trees and snags; vertical and horizontal structural complexity; understory species diversity; well-distributed, large woody debris; habitats and refugia for sedentary species and those with special habitat requirements; and riparian areas on rivers, streams, springs, bogs, and seeps (Principle 6.3.b.2) (Forest Stewardship Council 2005). Similarly, the Sustainable Forestry Initiative® (SFI) standard (2005-2009 edition) requires that "Program Participants shall have programs to promote biological diversity at stand and landscape levels" (Sustainable Forestry Initiative® Sustainable Forestry Board 2004:6). One indicator of meeting this performance measure is the "(d)evelopment and implementation of criteria, as guided by regionally appropriate science, for retention of stand-level wildlife habitat elements (e.g., snags, mast trees, down woody debris, den trees, nest trees)" (Sustainable Forestry Initiative® Sustainable Forestry Board 2004:6).

If managers are to meet expectations such as these in a meaningful way, they must have scientifically credible information regarding the response of species and habitat to the retention of stand-level habitat features. Thus, one objective of this review is to gather and synthesize information in the scientific literature on this topic. This information is especially important for managers in the southern United States because some authors (e.g., Haynes 2002; Prestemon and Abt 2002) have projected that the area in that region under pine plantation management will increase over the next few decades in response to increasing demand for wood products. This review also identifies information gaps specific to pine management and diversity and suggests future research priorities.

While this review is primarily concerned with management of pine forests in the South, it should be noted that we incorporate selected information about wildlife responses to habitat features developed elsewhere, either in terms of geography or ecosystem. We include this information when it provides a more complete image of the state of science regarding each feature, and when results of studies in other regions/systems raise questions that need to be addressed in pine-dominated systems as well. However, while information from other regions/systems is undoubtedly beneficial to our understanding, we caution that its application to southern pine systems may be inappropriate.

1.1 Methods

The scientific literature was computer-searched using a series of databases and key words/phrases to identify and locate publications addressing forest management and diversity in the Southeast. In addition, Wildlife Abstracts was reviewed by hand back to 1980. Pertinent books, reports, and habitat suitability models were perused for possible references. Ongoing and recent studies, perhaps as yet unpublished, were examined for potential contributions.

2.0 COARSE WOODY DEBRIS

2.1 Definition and Characteristics of Coarse Woody Debris

The literature does not agree as to the definition of coarse woody debris (CWD). For example, the term may refer either to both standing snags and fallen dead wood (Sollins 1982; Muller and Liu 1991; McComb and Lindenmayer 1999), or to fallen dead wood only (Brannon 2000; Greenberg 2002). While fallen snags can be substantial contributors to down CWD, windthrown trees, fallen branches, and logging slash account for large portions as well. Furthermore, snags are held to perform ecological functions that may not continue after they fall (e.g., nesting sites). Therefore, we define CWD as fallen logs or branches, stumps, and upturned root systems and consider snags separately from CWD. Minimum size requirements for CWD range from as little as 5 cm diameter (Zollner and Crane 2003) to 20 cm (Muller and Liu 1991). Thus, to insure comprehensive coverage, we have included studies with criteria as low as 5 cm.

Studies from numerous forest types and regions have contributed to a general picture of CWD dynamics. Accumulations of CWD following harvest and stand reestablishment often follow a U-shaped temporal pattern (Tritton 1980; Spies, Franklin, and Thomas 1988; McCarthy and Bailey 1994). Harvest provides a pulse of CWD, mostly as smaller diameter logs from logging slash and unmerchantable trees (McCarthy and Bailey 1994; Grialou, West, and Wilkins 2000), followed by several years of little input as the new stand of growing trees is established. Stands reestablished following catastrophic disturbance, such as wildfire, may initially contain large amounts of large logs and snags (Harmon et al. 1986). Once the new stand is established, competition leading to suppression mortality provides a source of stems from out-competed trees, which are generally small and may not meet minimum CWD diameter requirements (Spies, Franklin, and Thomas 1988). As stands mature, CWD is added in slowly increasing amounts and includes a greater proportion of large pieces (Shifley et al. 1997). A peak is reached as mature trees begin dying (Harmon et al. 1986; Muller and Liu 1991; Waldrop 1996). Because commercially grown pine stands are younger on average than non-commercial stands and are generally harvested before trees become over-mature, commercial stands will likely not reach the higher levels of CWD accumulation found in old-growth stands (McMinn and Hardt 1996).

This background of CWD accumulation is often punctuated by spikes due to stochastic events, such as storm or insect attack (Harmon et al. 1986). Wright and Lauterbach (1958) measured a spike in CWD input of 60 times the “normal” yearly rate of 0.5 Mg/ha in Douglas fir stands following a bark beetle epidemic; a similar spike was found in pitch pine following southern pine beetle attack (Smith 1991). Loeb (1999) found a threefold increase in log and snag density in longleaf and loblolly pine stands following a tornado. Variation in input from stochastic events may be affected by species composition. Rebertus and Shifley (1997) found basswood and American elm to be more susceptible to ice storm damage than white oak, eastern hophornbeam, and shagbark hickory.

Decay rates, which are affected by many factors, play a strong role in CWD dynamics. Logs of larger diameter tend to persist longer than smaller ones (McComb and Lindenmayer 1999); thus, CWD loadings should remain more stable when input comes from larger trees. Tree species express differing rates of decomposition (Harmon et al. 1986), with log mineralization rates varying from 0.007/year for *Pseudotsuga* (Graham 1982) to 0.274/year for loblolly pine and 0.52/year for tulip poplar (Harris 1976). Loblolly pine logging slash in contact with the ground decayed 50% faster than aerial slash, with an average decay coefficient of 0.072 (Barber and Van Lear 1984). Episodic events such as windstorms (Loeb 1999) or harvest (Grialou, West, and Wilkins 2000) create CWD in an earlier stage of decay than that created from snag fragmentation. Climate and elevation may also play a role in CWD persistence, with greater accumulations in cooler climates where decay processes are slower (Harmon 1982; Muller and Yiu 1991).

Site productivity may affect CWD production, with more productive sites capable of producing more CWD (Huston 1996). Waldrop (1996) used site index as one input variable to predict levels of CWD accumulation in hardwood stands.

Stand management actions impact CWD creation and condition McCarthy and Bailey (1994) reported that large logs in reestablishing hardwood stands had often been crushed by logging equipment, thus affecting their ecological function, and that large diameter CWD was rare even in old stands (>100 years), possibly due to the effects of commercial thinning. Mattson, Swank, and Waide (1987) recorded high levels of CWD (91.2 Mg/ha) in cove hardwoods immediately following clearcut operations which declined by 42% over the next 2 years. A pilot study found that North Carolina forests clearcut harvested with a satellite chip mill component contained less new CWD than those harvested without one (Hess and Zimmerman 2001). Prescribed fire reduces the amount of CWD present (Miller and Bigley 1990), though fire may also create snags which act as a future source (Tinker and Knight 2000).

McMinn and Hardt (1996) reported lower CWD accumulations on private industrial lands in Georgia and South Carolina than on either non-industrial private or public lands, which they attributed to industry lands having a higher proportion of pine plantations than other ownership classes. Pine plantations exhibited lower accumulations of CWD than other forest types, and lowland hardwood stands and natural pine stands the highest (McMinn and Hardt 1996).

2.2 Wildlife Relationships with Coarse Woody Debris

2.2.1 *General*

Usefulness of CWD to wildlife varies with species or species group. Whiles and Grubaugh (1996) found evidence in the literature of CWD use in southern forests by every major herpetofaunal group for many vital life processes such as feeding or reproduction. Lanham and Guynn (1996) found that a wide variety of birds in southern forests used CWD for perching, nesting, foraging, and displaying both for territory defense and mating purposes. At least 55 of the 81 southeastern mammal species make some use of CWD (Loeb 1996).

Small mammals use CWD for travel pathways, which may help them avoid predators (McCay 2000; Ucitel, Christian, and Graham 2003; Zollner and Crane 2003). It is possible that the low amount of deciduous leaf litter in pine stands, with a concomitant reduction in movement-related noise, may reduce predation risk to small mammals, therefore reducing their dependence on CWD as travel corridors (Roche, Schulte-Hostedde, and Brooks 1999; McCay 2000). While softer, more decayed logs provide quieter travel surfaces than logs in earlier stages of decay, decay level may (Barnum et al. 1992; Brannon 2000) or may not (Bowman et al. 2000; Loeb 1999; Roche, Schulte-Hostedde, and Brooks 1999; Osbourne and Anderson 2002) be of consequence to small mammals.

Terrestrial salamanders generally make greater use of well-decayed logs as critical microhabitat, with less-decayed logs receiving little or no current use (Herbeck and Larsen 1999; Grialou, West, and Wilkins 2000). Studies in southern hardwood (Herbeck and Larsen 1999; Hicks and Pearson 2003) and northwestern fir-hemlock (Grialou, West, and Wilkins 2000) forests indicate that CWD present after logging is of lower value to terrestrial salamanders than that found in old-growth stands.

2.2.2 *Southern Pine*

Only a few manipulative experiments testing wildlife response to CWD have been performed in southern pine forests. These studies indicate that CWD in pine forests is important for some species of small mammals and breeding bird populations. Studies of herpetofaunal use are more limited. Edwards (2004) presented data from an ongoing study of CWD dynamics in loblolly pine stands in South Carolina. The study addresses CWD recruitment, loading, rates of decomposition, and effects on faunal communities in southern pine forests. Following initial removal of all CWD, treatments were implemented which annually removed 1) all CWD or 2) all CWD and all snags. The study also has control plots on which CWD and snags were not altered. Four of the experiments reviewed below (McCay and Komoroski 2004; Lohr, Gauthreaux, and Kilgo 2002; Mosely, Castleberry, and Ford 2004; Mosely et al. 2005) are related to this study.

Microhabitat use of mole salamanders (all scientific names are listed in Appendix A) was monitored under South Carolina loblolly pine stands in 3m × 3m enclosures manipulated for varying levels of CWD and pine litter (Mosely, Castleberry, and Ford 2004). Salamanders were located nightly using harmonic radar detection. Pine litter appeared to provide adequate microhabitat conditions; locations associated with CWD accounted for only 2.15% of those in enclosures with mean pine litter depth of 2.98 cm, but this increased to 22.73% where litter depth was reduced to an average 0.78 cm. The authors also tested movement rates in enclosures with complete pine litter removal versus unmanipulated controls, finding higher activity levels for salamanders confined to enclosures with no pine litter. The authors conjectured this higher activity level may have indicated dissatisfaction with suboptimal temperature control, humidity, and arthropod abundance in the litter removal plots.

Diet and body measurements of southern toads were examined in South Carolina loblolly pine plantations under conditions of fivefold increase, removal, and unmanipulated levels of CWD (Mosely et al. 2005). No differences in diet, length, body weight, or stomach content were found. The authors found no evidence that Southern toads were dependent on CWD in early decay stages.

Avian response to CWD and snag manipulation was studied in loblolly plantations in South Carolina (Lohr, Gauthreaux, and Kilgo 2002). While wintering birds were unaffected, weak excavators, secondary cavity nesters, neotropical migrants, great-crested flycatchers, and Eastern towhees all declined following CWD removal. Community analysis found that an abundance of breeding-bird territories, species diversity, and species richness were all lower in treatments with CWD removal than in control plots (Table 2.1).

Mengak and Guynn (2003) constructed microhabitat use models for six small mammal species in natural and artificial loblolly pine regeneration areas in the South Carolina Piedmont. They concluded that CWD was a positive factor in determining habitat quality for golden mice and cotton mice, but that it may act as a deterrent to cotton rats (Mengak and Guynn 2003). Loeb (1999) found that small mammals were more abundant in a South Carolina pine forest which retained tornado-caused CWD than in a salvaged stand (Table 2.1). Differences in overall abundance were due mostly to the large response of cotton mice. Adult female cotton mice on unsalvaged plots were more likely to be in reproductive condition and showed greater survival (Loeb 1999). McCay (2000) found that cotton mice used CWD in loblolly pine plantations at greater than expected rates. Daytime refuges were almost exclusively (93%) associated with CWD, showing preference for larger, decayed stumps without regard to tree species. Root boles were also used, with mice preferring larger, more decayed pine boles. Powder-tracked mice exhibited a strong preference for CWD as travel corridors (Table 2.1). The mice used longer logs, and showed a preference for using hardwood stems. Because use of logs was lower in this study than in similar studies for *Peromyscus*, the author theorized that the low amount of deciduous leaf litter in pine stands may decrease the dangers of travel on the forest floor (McCay 2000).

Table 2.1. Wildlife Response to Levels of Coarse Woody Debris from Experiments Performed in Southern Pine Systems

Study	Context	CWD Variable	Response
Loeb (1999)	32- to 36-yr-old managed pines	Logs/ha	Relative abundance of small mammals
		102.0	55.0/trapping grid
		327.5	93.0/trapping grid
McCay (2000)	45-yr-old loblolly plantations	CWD Coverage	Use rate of CWD for movement by cotton mice
		3.3%	24.1%
Lohr et al. (2002)	40- to 50-yr-old loblolly pines	CWD stems/ha	Avian diversity (H`)
		96.3	2.99
		9.3	2.40
			Avian species richness
		96.3	19.9
		9.3	13.4
			Breeding-bird territories/ha
		96.3	3.46
		9.3	2.30

Demographic responses of shrews to CWD manipulation were tested in 45-year-old loblolly pine plantations in the South Carolina Coastal Plain (McCay and Komoroski 2004). Removal of CWD had little or no effect on capture rates; only one of three species (Least shrew) showed a significant reduction in CWD removal plots. A shift in age distribution toward older individuals in removal plots was noted for Southern short-tailed shrew; the authors conjectured that while populations of Southern short-tailed shrew were similar in both plot types, removal plots were acting as a population sink. Additionally, they hypothesized that the relatively low amount of CWD present in control plots may have been below a threshold necessary to show a treatment effect.

2.3 Information Gaps and Research Directions

2.3.1 *Coarse Woody Debris Dynamics*

Standardization of methodology and definition would help make studies directly comparable. Measurements of CWD have been taken using line transects (McCay 2000; Greenberg 2002) and circular plots (Ucitel, Christian, and Graham 2003; Loeb 1999; Fuhrman 2004). Fuhrman (2004) compared the variability of estimates of CWD (including snags) using 0.1-ha circular plots and 71-m transects. Transects led to volume estimates approximately double that of circular plots, and with greater variability. However, similar standard errors were achieved in half the field time using transects. Minimum size of down wood considered as CWD has varied somewhat among studies, but most have used 10.2 cm (4 inches) diameter as a minimum. Harmon and Sexton (1996) recommended setting the separation between coarse and fine woody debris at 10 cm diameter (10 cm at the large end of the piece for fine CWD), and presented methodologies for measuring characteristics of woody detritus which were designed to be applicable over most forest types.

Maser et al. (1979) presented criteria for assigning decay class values to CWD which have been widely used (e.g., McCay 1998; Loeb 1999; Bowman et al. 2000). Some investigators have modified these decay classes, generally by collapsing them into fewer divisions (Grialou, West, and Wilkins 2000; Edwards 2004). We urge investigators to err on the side of more classes than may be strictly necessary, as opposed to reducing categories for convenience. While the response of an individual species might be quantifiable using fewer classes, it is likely that there will be at least some species within any given community for which the greater number of classes is more appropriate. Using the full suite of classes recommended by Maser et al. (1979) also may facilitate comparisons across studies.

Modeling CWD dynamics could lead to helpful management tools. For example, Waldrop (1996) presented CWD loadings from computer simulations of 2 hardwood mixtures on sites in the Cumberland Plateau. Results showed a peak in CWD at about 100 years for both tests, followed by a gradual decline and eventual leveling out by 200 years. The mesic, more productive site projected a peak approximately 63% higher than the xeric site. The author identified limitations of the model, including 1) limbs falling from snags were not included in CWD loadings; 2) decomposition rates for species were assumed to be identical; and 3) snags were not distinguished from down CWD. No pine regeneration occurred in any of the simulations. Additionally, the simulation took into account only natural mortality (i.e., no anthropogenic or catastrophic events) based on the silvics of individual species. Decomposition rates were assumed to be identical between the xeric and mesic sites (6%/year); however, changing the decomposition rate on the mesic site to 8%/year reduced CWD accumulation to levels similar to the xeric site (Waldrop 1996). Where models are developed to simulate CWD loadings in pine forests, we recommend that they address these limitations, as well as include the effects of various silvicultural disturbances, such as intermediate harvest, fire, purposeful creation of snags, and herbicide application. Catastrophic disturbance (e.g., strong winds, disease or pest outbreaks) should also be accounted for so that adjustments in estimates of CWD loading retain some validity following such inevitabilities (Van Lear 1996). Growth and yield models could provide a potential starting point for models useful to pine management.

2.3.2 *Biodiversity*

There are significant opportunities to improve studies of CWD in southern pine forests. The wide range of initial CWD volumes found within treatments in some studies may reduce their power and make conclusive evidence difficult to find (Osbourne and Anderson 2002). The ability to effectively manipulate CWD volume and composition (both species and decay class) makes it possible to reduce variance in treatment plots, effectively increasing the power of statistical tests to detect biologically meaningful differences and relationships. There are many unanswered questions about how relationships between biodiversity and CWD vary depending on CWD species composition, CWD size class, fire effects, decay rates, site productivity, and topography (Carroll 1996), which could be addressed through precise manipulations.

Measurements of abundance and density common to CWD studies are not sufficient to describe the relationship between CWD and fitness (Van Horne 1983). Work in southern pines indicates that similarities in capture rates and trapability of small mammals in treatments and controls may mask important demographic differences among populations (Loeb 1999; McCay and Komoroski 2004). Thus, demographic information as measures of fitness is strongly recommended for all studies of CWD-wildlife relationships.

While it is possible that small mammal use of CWD is more or less correlated to its availability (Loeb 1999; Ucitel, Christian, and Graham 2003), neither presence nor abundance of small mammals has yet been firmly tied to CWD levels (Menzel et al. 1999), and, for at least some small mammal species, CWD may have more impact on distribution within stands than on presence or abundance (Greenberg 2002). Consequently, future research should strive to separate obligatory relationships between CWD and small mammals from preferential ones. In addition, research is needed to determine the functions CWD serves for each species, the characteristics that determine its suitability and utility, and how use and importance of CWD vary with habitat (Loeb 1996).

Whiles and Grubaugh (1996) found an abundance of natural history/observational information regarding CWD use by herpetofauna, but little experimental data. In addition, log use may be obligatory for some life processes and facultative for others, making definitive needs difficult to ascertain. Given potential regional differences in herpetofaunal microhabitat needs (Russell et al. 2004) and the results of experiments in pine systems (Mosely, Castleberry, and Ford 2004; Mosely et al. 2005), we recommend the use of manipulative experiments to determine the level to which herpetofauna in pine forests depend on CWD, and whether pine litter is a viable alternative.

McCay et al. (2002) and Edwards (2004) reported on a long-term manipulative experiment investigating CWD in loblolly pine plantations at the Savannah River National Ecological Laboratory. The ongoing study includes snag and CWD dynamics, and population responses of arthropods, herpetofauna, small mammals, and avifauna; it is slated to run for 10 years. To date it has produced one paper each regarding avifauna (Lohr, Gauthreaux, and Kilgo 2002), soricids (McCay and Komoroski 2004), cotton mice (McCay 2000), toad diet (Mosely et al. 2005), and CWD dynamics (Edwards 2004). This experiment is an example of the kind that should be repeated, with appropriate adjustments, throughout pine forests of the South. In addition to the plantation context of this study, future studies should consider including comparisons with natural pine and/or pine-hardwood stands (Hagan and Grove 1999; McCay and Komoroski 2004), which generally contain higher quantities of CWD than managed even-aged stands (McMinn and Hardt 1996), and may therefore provide a wider range for comparison.

3.0 SNAGS

3.1 Definition and Characteristics of Snags

Snags are defined as standing dead trees (Harmon et al. 1986). Snags shorter than 1.4 m, the height for measurement of diameter at breast height (dbh), are classified as stumps, which we regard as CWD. Researchers variously measure snags with minimum heights of 1.4–4.4 m (Cline, Berg, and White 1980; McComb et al. 1986a) and minimum dbh of 2.5–12.7 cm (Cline, Berg, and White 1980; Brawn, Elder, and Evans 1982; Land, Marion, and O'Meara 1989; Lohr, Gauthreaux, and Kilgo 2002). Snags ≥9 cm dbh have typically been used in studies of nesting habitat (Harlow and Guynn 1983; McComb and Muller 1983); snags <9 cm dbh have been used in some (McComb and Muller 1983; Rosenberg, Fraser, and Stauffer 1988) but not all (Brawn, Elder, and Evans 1982; McComb and Rumsey 1983; Swallow, Howard, and Gutierrez 1988) studies of avian foraging habits.

The dynamics of snag creation, size, and density are subject to numerous influences throughout the life of the stand. Young stands resulting from catastrophic stand replacement events, such as fire or large-scale insect damage, may contain a high density of large snags (Harmon et al. 1986). Stands resulting from harvest and regeneration will have more or fewer snags depending on the structure of the previous stand and the techniques used to establish and manage the new stand. Young stands are dependent on holdovers from the previous stand to provide snags of a size suitable for wildlife use (McComb et al. 1986a; Sabin 1991; Moorman et al. 1999). Suppression mortality following crown closure creates a pulse of small snags (Cline, Berg, and White 1980) which may provide feeding substrate, but such snags fall quickly and are not large enough for creation of cavities useful for nesting (Scott et al. 1977; Evans and Conner 1979; McComb and Muller 1983). In natural stands, senescence of early succession species may provide the first pulse of snags from the new stand which will have value as nesting habitat to cavity-nesting species (Tritton 1980). As the stand ages, background addition of snags decreases, and the size distribution widens to include both small suppressed trees and larger trees killed by disease, insect attack, fire, or wind breakage (Cline, Berg, and White 1980). Overall, snag availability in southern forests increases with stand age across a wide variety of forest types (McComb et al. 1986a). Size distribution of snags in mature uneven-aged stands follows a reverse-J distribution, and species distributions closely follow those of live trees (Shifley et al. 1997), though there is a time lag between introduction of a species into the stand and its recruitment into the snag population (Cline, Berg, and White 1980).

Pulses of snags may be created at any time during stand development through stochastic events such as wildfire (Harmon et al. 1986), insect attack (Showalter and Whitmore 2002), or silvicultural treatment (Paxton, Wilson, and Watts 2004). Such events may drastically increase snag availability for a time, followed by a gradual return to pre-event background levels (Harmon et al. 1986). As an example, defoliation of West Virginia oak-hickory forests by gypsy moths in 1988-1989 resulted in creation of a pulse of snags >23 cm dbh over the next 5 years; snag density peaked in 1989 with a 480% increase over pre-defoliation levels, and was still 300% greater 11 years following attack (Showalter and Whitmore 2002).

Snag abundance differed by land ownership and forest type in Florida (McComb et al. 1986a). Snag densities on industrial pine forests were 48% lower than on publicly owned ones, with non-industrial private forests intermediate (Table 3.1). This was likely related to the fact that industrial pine forests tended to be younger than publicly owned pine forests (22 vs. 36 years), and that plantations tended to be younger than natural stands (14.4 vs. 33.9 years). Among forest types, snags were least abundant in slash, longleaf, and pond pine forests (3.6–4.8/ha). Loblolly, sand pine, oak-pine, and oak forests were intermediate (5.4–10/ha); oak-hickory, oak-tupelo-cypress, and palmetto forests were highest (10.6–17.5/ha).

Non-pine stands on Francis Marion National Forest had greater snag abundance than pine stands (Table 3.1), perhaps due to less intensive management (Harlow and Guynn 1983). Surveys from managed forestland in the South Carolina Piedmont found similar results, though with higher overall densities, with pine plantations containing fewer snags than cove and upland hardwoods (Moorman et al. 1999) (Table 3.1). Intensively managed loblolly stands in eastern North Carolina displayed slightly lower densities (Paxton, Wilson, and Watts 2004) (Table 3.1) than pine stands reported by Harlow and Guynn (1983).

Snag persistence is influenced by size. Larger-diameter snags tend to remain standing longer than smaller ones (Dickson, Conner, and Williamson 1983; Cain 1996; but see Moorman et al. 1999), and may be the only ones to go through all recognized stages of decay before falling (Cline, Berg, and White 1980). Cain (1996) studied the dynamics of hardwood snags created by herbicide injection over a 7-year period in natural, uneven-aged loblolly-shortleaf pine stands in southeastern Arkansas. Diameter was closely correlated with snag persistence; fragmentation rate for snags ≤11 cm dbh was 76%/year, while snags ≥25 cm dbh were lost at a rate of only 5%/year. While initial diameter distribution followed the negative exponential (reverse-J) pattern, the higher fragmentation rate of smaller-diameter snags led to a normal distribution by the sixth year following injection.

Decay rates also differ among species and species groups, causing differences in snag longevity. Among hardwood snags created by 2,4-D injection and girdling in east Texas pine stands, oak snags remained standing longer than sweetgum or mockernut hickory (Dickson, Conner, and Williamson 1983; Dickson, Williamson, and Conner 1995). Decomposition rates of 10 snag species created by fire were examined in Great Smoky Mountains National Park (Harmon 1982), with chestnut oak showing the fastest deterioration (11%/year) and Virginia pine the slowest (3.6%/year). Conifers (*Tsuga* and *Pinus*) tended to decay more slowly than hardwoods. Overall, decay rates in southeastern forests are intermediate between snags in the western USA and the tropics (Harmon 1982).

Table 3.1 Snag Densities Found in Surveys of Southern Pine Forests

Study	Context	Forest Type	Snags/ha
Harlow and Guynn (1983)	Francis Marion National Forest, South Carolina Coastal Plain	Pine basal area >50%	3.48
		Pine basal area <50%	9.68
McComb et al. (1986a)	Commercial forestland in Florida	Industrial pine	3.2
		Private (non-industrial) pine	4.9
		Public pine	6.2
		Naturally regenerated pine	5.1
		Pine plantation	3.1
Land et al. (1989)	17- to 38-yr-old industrial pine in Florida	Slash pine	10.6
Moorman et al. (1999)	South Carolina Piedmont	Upland hardwood	35.6
		Cove hardwood	31.9
		Pine-hardwood	28.0
		Pine plantation	20.2
Paxton et al. (2004)	10- to 26-yr-old industrial pine in North Carolina Coastal Plain	Loblolly pine	1.7-3.2

Snag longevity is also affected by the method used to create the snag. Morrison and Raphael (1993) used long-term data on snag dynamics to build a Leslie matrix predicting future snag resources in pine-fir forests in California, and found the model worked only when it accounted for the factor creating the snag. This conclusion is in agreement with findings of studies from pine forests in Oregon (Bull and Partridge 1986), California (Shea et al. 2002), and east Texas (Conner, Kroll, and Kulhavy 1983), which found snags created by different methods fragmented at different rates.

Snag creation using herbicide has been explored in southern hardwood species (Conner, Dickson, and Locke 1981; Conner, Kroll, and Kulhavy 1983; McComb and Rumsey 1983; Dickson, Williamson, and Conner 1995). Broadcast of picloram pellets in mixed mesophytic forests of eastern Kentucky created an abundance of snags which increased at higher application rates (McComb and Rumsey 1983). Conner, Kroll, and Kulhavy (1983) compared decay rates of injected versus girdled red oaks and found that injected oaks were more extensively decayed 18 months after treatment. Longevity of four hardwood species killed by injection was compared over a 16-year period in a pine-hardwood stand in Texas (Dickson, Williamson, and Conner 1995). Post oak and Southern red oak snags stood an average of 7.0 and 6.3 years, respectively, with sweetgum (3.8 years) and mockernut hickory (3.9 years) snags standing a substantially shorter time (Dickson, Williamson, and Conner 1995).

Silvicultural treatment can influence snag dynamics through removal of suppressed or damaged trees, or by damaging unharvested trees. Group selection harvest and thinning caused an 82% reduction in snag abundance in hardwood stands in Ozark National Forest (Nelson and Lambert 1996). Thinning removed many existing snags but created a small pulse of new ones in intensively managed loblolly pine plantations in coastal North Carolina (Paxton, Wilson, and Watts 2004). Thinning of Douglas fir stands in western Oregon had the overall effect of reducing snag density due to removal of suppressed, decayed, or diseased trees destined to become snags, thereby reducing long-term snag recruitment (Cline, Berg, and White 1980).

3.2 Wildlife Relationships with Snags

3.2.1 *General*

Snags are important for a variety of vertebrates. Forest herpetofauna are known to use snags for basking and foraging (Ernst and Barbour 1989; Mount 1996), and possibly for territorial and/or mating display (Whiles and Grubaugh 1996). Hamel (1992) listed 45 bird species that use snags in southern forests for nesting, foraging, and perching. Twenty-three of 81 mammals found in the Southeast use cavities in or the underside of loose bark on snags for nesting, denning, or roosting (Loeb 1996). Several bat species roost behind sheets of exfoliating bark or in cavities (Lacki and Schwierjohann 2001; Menzel, Carter, et al. 2001; Menzel, Menzel. et al. 2001; Britzke et al. 2003).

Wildlife use changes with the progression of snag deterioration. Woodpeckers typically forage for arthropod prey attracted to newly dead trees before they begin excavating nesting cavities (Swallow, Howard, and Gutierrez 1988). Primary cavity excavators are influenced by tree hardness (Schepps, Lohr, and Martin 1999), and prefer excavating in trees softened by heart rot (Conner, Miller, and Adkisson 1976). As decay advances further, weaker excavators are able to create cavities (Schepps, Lohr, and Martin 1999), which may increase overall availability to both primary and secondary cavity users. However, snag fragmentation associated with advanced decay removes cavities excavated in higher portions of the bole (Maser et al. 1979; DeGraaf and Shigo 1985). Therefore, continuous recruitment of new snags is necessary to maintain cavity density.

Snag diameter limits potential cavity size, and thus limits the size of species that can use the snag for nesting (Thomas et al. 1979). Snags <10 cm in diameter are considered to be of no value as nest sites for primary cavity-nesters (Scott et al. 1977; Evans and Conner 1979). Cavity incidence has been positively correlated with diameter in mixed forests of South Carolina (Sabin 1991), Arkansas hardwoods (Nelson and Lambert 1996), and industrial pine forests of coastal North Carolina (Paxton, Wilson, and Watts 2004). Larger snags increase opportunities for both large and small cavity-nesters, because smaller animals can use cavities in both small and large trees. In addition, snags of larger diameters tend to persist longer than smaller ones (Dickson, Conner, and Williamson 1983; Cain 1996), thus increasing the availability of cavities excavated in them. Data from Ozark National Forest suggest that snags >30 cm dbh and >15 m in height are particularly valuable to wildlife (Nelson and Lambert 1996). Densities of obligate cavity nesters increased with densities of snags ≥24 cm dbh on the Olympic Peninsula (Zarnowitz and Manuwal 1985). Foraging activity is also influenced by diameter, with birds preferring to spend foraging time on larger diameter snags (Brawn, Elder, and Evans 1982; Raphael and White 1984; Rosenberg, Fraser, and Stauffer 1988; Swallow, Howard, and Gutierrez 1988), perhaps for reasons of efficiency. Even so, small diameter snags may be an important component of foraging substrate (Rosenberg, Fraser, and Stauffer 1988).

Snags in recently clearcut stands and subsequent young plantations are shown to increase abundance, species richness, and diversity of avian species (Johnson and Landers 1982; Dickson, Conner, and Williamson 1983; Niemi and Hanowski 1984; Caine and Marion 1991; Hanberry 2005). In mature hardwood forests, abundance of primary and secondary cavity-nesters has been closely correlated with snag abundance (Showalter and Whitmore 2002), while snag retention following timber stand improvement cuts increased species richness and abundance over treatments that removed snags (Stribling, Smith, and Yahner 1990).

Vegetation surrounding snags may affect usage. Brown-headed nuthatch density was positively correlated with groundcover density in commercial loblolly pine stands in eastern North Carolina (Wilson and Watts 1999). Nuthatches in east Texas longleaf pine savannah preferred nesting in snags with little to no mid-story surrounding the nest site (Dornak et al. 2004). Diversity and richness of living trees ≥7 cm dbh within 12.5 m of the snag were significant variables for predicting avian use of snags in New York riparian and second-growth hardwood forests (Swallow, Gutierrez, and Howard 1986).

Wildlife use of artificially created snags may be influenced by creation method. Bull and Partridge (1986) compared six methods of creating snags from ponderosa pine in Oregon. Topped trees and herbicide-treated trees showed nearly complete mortality (88–100%) 2 years following treatment; however, evidence of nesting within five years occurred in only 1% of injected trees, versus 8% for topped trees. Injected trees were also used for foraging at much lower rates than all other methods (13% vs. 38–82%). Shea et al. (2002) found pheromone treatment leading to beetle attack created ponderosa pine snags with greater insect activity and more evidence of woodpecker foraging than on snags created by girdling. Six years after treatment, 44% of beetle-killed trees contained cavities, while no cavities were found in girdled trees. Conversely, Brandeis et al. (2002) found no differences in woodpecker utilization of Douglas fir snags among 10 snag creation methods four years following treatment.

3.2.2 *Southern Pine*

Because snags potentially open an area to an entire guild of users, it is not surprising to find snag abundance in southern pine systems correlated with measures of avian abundance, species richness, and diversity (Table 3.2). Studies of stands ranging from newly established to 50 years old, and geographically spread from eastern Texas to South Carolina, have consistently documented these relationships. The primary questions biologists face are how to determine an appropriate number of snags, and what is the best way to distribute them.

Table 3.2 Breeding Bird Response to Snags in Southern Pine Plantations

Study and Context	Experimental Design	Key Results and Observations	Comments
Hanberry (2005) 1–2-yr-old loblolly in south Mississippi	5 site preparation and release treatments in randomized complete block. One site prep treatment was chemical only; the remaining 4 involved mechanical treatment which removed most snags.	Differences among treatments developed in year 2. Snag density was greater in chemical-only treatment (78.9/ha vs. 4.9-8.5/ha). Mean species richness was 14.8 in chemical only plots, 5.2–7.8 in mechanically treated plots. Relative abundance was 45.5 birds/observation point in chemical-only, 8.3-25.5 in mechanical. Chemical-only sites had higher scores for both total conservation (135.5 vs. 23.0-77.5) and conservation of species of regional concern (59.3 vs. 3.9-34.1). Of birds classified as species of concern, breeding abundance was significantly influenced by habitat variables for 13 of 16 species. Snag density was either the best or was among the best models for 12 of those 13 species for at least one year.	No snag characteristics were recorded. Results are short-term. Study is continuing through crown closure.
Caine and Marion (1991) 2–4-yr-old slash and adjacent 20-25-yr-old stands in north-central Florida	3 paired control and treatment plots consisting of artificial snags with nest boxes (2/ha) added to young plantations. Results considered young plantation only (8 ha), and young and older stands combined (12 ha).	Within the young plantations only, treatments had greater species richness (6.8 vs. 3.5) and abundance (102.7 vs. 53.9 pairs/km^2) in both years, greater diversity in year 1 only (H`=2.1 vs. 1.3). When data from the adjacent older stand were combined with the younger stands, no differences were found. Cavity-nesting birds were practically absent from control plots, but were responsible for 38% of total abundance in treatment plots.	Only study to consider adjacent landscape.
Lohr et al. (2002) 40–50-yr-old loblolly in South Carolina	Treatments in RCBD design were: control, removal of all CWD, and removal of CWD and snags. Snag densities were similar on control and CWD removal plots.	Snag removal reduced snag density from 8.5/ha (control and CWD removal plots) to 1.9/ha. From control to snag removal treatment, species richness declined 46%, number of territories declined 48%, and H` declined from 2.99 to 2.11. CWD removal plots were intermediate between control and snag removal plots for all 3 measurements.	Because there were no plots that removed snags only, results of snag removal are confounded with CWD removal.

(Continued on next page)

Table 3.2 Continued

Study and Context	Experimental Design	Key Results and Observations	Comments
Land et al. (1989) 20–38-yr-old slash in Florida	Surveyed plantations for snags and cavity-nesting birds (CNBs). Developed regression models explaining relationships between CNBs and snag densities and stand characteristics.	Primary CNB density responded positively to increases in stand dbh. Secondary CNBs displayed higher densities in response to shorter snags and more snag clusters (i.e., increased cluster index). Overall CNB density was not linearly related to either snag density or the cluster index. Stand and snag characteristics explained 96% of variation in CNB diversity and density. CNBs had more influence than expected on diversity and species richness of the entire avian community. CNBs accounted for 21% of avian density, 38% of all bird species, and 48% of variance in total density.	
Dickson et al. (1983) 2–6-yr-old loblolly in eastern Texas	Relict hardwoods in a 500 ha cutover were injected to create treatment plots with 5.6-9.4 snags/ha; 4 control plots were snagless. Birds were surveyed each breeding season for 5 years.	Mean species richness (5.10 vs. 4.04), abundance (8.59 vs. 6.93), diversity (H`=1.42 vs. 1.19), and equitability (J`= 0.91 vs 0.85) were all greater on plots with snags. CNBs comprised 8% of birds seen in snag plots and <1% in controls, accounting for most of the difference between treatments.	Study plots were small (2 ha) and may not have been independent. Average snag dbh was large (44 cm).

The impact of snags may be affected by other aspects of vegetation structure. Hanberry (2005) found that differences in bird response to snag density in regenerating loblolly plantations were not apparent until the second year following site preparation, when ground-level vegetation had recovered. Johnson and Landers (1982) found that while diversity and abundance in fallow cutovers and young slash pine stands were closely correlated with residual timber and snags, bird communities changed in a predictable manner with vegetation structure, with diversity and species richness quickly increasing following an overall low in 1-year-old plantations. Caine and Marion (1991) acknowledged that their 2–4-year-old slash pine stands had advanced in seral stage between the years of their study. They theorized that this might explain the change from higher diversity of birds in snag plots during the first year to no difference during the second.

Studies of bird communities in older plantations also show positive responses to snags. Lohr, Gauthreaux, and Kilgo (2002) investigated the importance of snags to avian communities in 40–50-year-old loblolly plantations in South Carolina. During breeding season, removal of snags negatively affected diversity, species richness, overall abundance, and abundance of residents, strong excavators, great crested flycatchers, Carolina wrens, and eastern wood-pewees. It should be noted that neither the wren nor the pewee are obligate cavity nesters; snags may have been important foraging sites for these species. Overall woodpecker abundance was drastically reduced by snag removal. Some cavity-nesting species (red-bellied woodpeckers, tufted titmice, Carolina chickadees, and brown-headed nuthatches) used alternative nesting sites (dead limbs, decomposing stumps, and natural crevasses) and were unaffected by snag removal. Outside of breeding season, no effects of snag removal were detected for any species or species group (Lohr, Gauthreaux, and Kilgo 2002). Densities of cavity-nesting birds ranged widely (5.5–94.7/km^2) in 20–38-year-old slash pine plantations managed for pulpwood production in north Florida, and was explained by models of stand and snag characteristics (Land, Marion, and O’Meara 1989). The contribution of cavity-nesters to overall species richness and diversity was out of proportion with its relatively small impact on overall adundance.

It is unclear whether stand scale responses to snags constitute an addition to diversity at a higher scale. Caine and Marion (1991) found that differences in measures of avian abundance, richness, and diversity between young plantations with and without artificial snags were eliminated when survey data from older adjacent stands was included. Measurements of community overlap might still have found substantial differences between treatments and controls, but were not employed. None of the other studies we reviewed surveyed birds outside treated plots. Overall, while we have substantial documentation on impact of snags within stands, we still do not know how this effect may be altered by snag distribution across the landscape.

Pine stands, especially young plantations, may contain fewer and smaller snags than needed to support average populations of cavity-nesting birds. Harlow and Guynn (1983) determined average population densities of cavity-nesting species common to Francis Marion National Forest from Hamel’s (1982) compilation of Southeastern bird census data, then estimated their snag requirements and compared them with snag availability. For species using snags 12.7-22.9 cm dbh, pine stands provided 20% of the estimated requirement; pine stands provided only 6% of estimated requirements for species requiring snags ≥25.4 cm dbh (Harlow and Guynn 1983). Using similar methodology, McComb et al. (1986a) estimated minimum requirements of snag density by size class to support an average population of cavity-nesting birds in Florida pine stands. They compared their estimates with Forest Inventory and Analysis data to determine the levels of habitat among forest types. With the exception of stands ≤30 years old, pine forests had sufficient snag availability for cavity nesters requiring snags 12.7–24.9 cm dbh. For species requiring snags 25.0–49.9 cm dbh, pine and pine-hardwood forests ≤30 years old would have supported 20–30% of average populations. Pileated woodpeckers, which require snags ≥50 cm dbh, would have been limited to about 20% of average population levels in Florida pine forests (McComb et al. 1986a). These results indicate a need to consider snag availability and distribution in pine stands, in adjacent habitats, or both, in order to conserve avian species richness.

Because of their role in cavity excavation, woodpecker presence is important to cavity-dependent wildlife. Shackelford and Conner (1997) determined woodpecker abundance and habitat associations in mature forests in east Texas. Eight woodpecker species were recorded in longleaf savannah, 7 in bottomland hardwood and 7 in mixed pine-hardwood forests. Longleaf savannahs supported similar overall numbers of individuals as mixed pine-hardwood forests; both supported fewer individuals than bottomland hardwoods. Factors influencing overall abundance included presence and numbers of live hardwood trees, snags, and logs.

Paxton Wilson, and Watts (2004) surveyed bird communities and snag density in industrial loblolly pine plantations during a 2-year study in coastal North Carolina. Plantations were managed on a 30–35-year rotation, with commercial thinning at approximately 10 and 20 years. Overall densities of snags ≥12 cm dbh ranged from 1.7–3.2/ha. Densities were lowest in pre-thinned plantations and in plantations following second thinning, and highest 2 years after first thinning; snag dbh increased following second thinning. Bird species richness and total bird density were positively influenced by stand age. Evidence of nesting was found only in the first year, with 12 nests in 166 cavity-bearing snags; cavity nesting was not observed in the pre-thin and 1–2-year post-thin age classes, but was observed in all older age classes. None of the 44 available cavities were used for nesting in the second year of this study.

Southern flying squirrels preferred cavities in snags over living hardwoods for diurnal nesting in mature pine-hardwood forests and greenbelts in Ouachita National Forest (Taulman 1999). All decay classes of snags were used for diurnal nesting more than expected. Because squirrels selected against nesting in 1–40-year-old pine plantations and harvested areas, the author recommended providing refuge for displaced squirrels through retention of mature forest adjacent to harvest areas, and use of retention patches and SMZs within harvest areas (Taulman 1999).

Brown-headed nuthatches in commercial loblolly pine stands in eastern North Carolina were 3× more likely to be observed within survey points containing snags than in those without (Wilson and Watts 1999). While nuthatch abundance was positively correlated with ground cover density, the authors surmised that snags influenced nuthatch distribution within stands. In east Texas, nuthatches preferred nesting in older, more decayed snags with little to no midstory surrounding the nest site, but nest success and fledging rate were not correlated with either snag characteristics or habitat variables (Dornak et al. 2004).

3.3 Information Gaps and Research Directions

Experimental manipulation has been recommended for determining the relationship between snags and species diversity for herpetofaunal (Whiles and Grubaugh 1996), and avian (Lanham and Guynn 1996) communities. Miller, Arnett, and Lacki (2003) emphasized the need for manipulative experiments to determine bat responses to varied levels of forest resources, including snags. McComb and Lindenmayer (1999) found that the available models for estimating wildlife response to dead wood abundance were based mostly on correlative studies rather than experiments. They also suggested that secondary cavity nesters may be better candidates for monitoring the effects of forest management on dead wood than primary cavity nesters, because of their reliance on both primary cavity nesters and wood decay processes to supply their needs.

Snag use may be opportunistic rather than obligatory, and thus may not necessarily equate with dependence. Thus, there is a need to characterize animal abundance and dead wood dynamics in order to clarify functional relationships (McComb and Lindenmayer 1999). Research that correlates snag use and function with measures of fitness is necessary to place wildlife-snag relationships along a gradient from obligatory to facultative (Swallow, Howard, and Gutierrez 1988; Loeb 1996). Experimental manipulations would help elucidate the level of snag density at which competitive interactions might be reduced and habitat partitioning increased (Loeb 1996). Because intensive management practices may decrease snag availability, snag densities and recruitment rates from natural pine or pine/hardwood forests are needed for comparisons with more intensively managed forests.

The dynamics of hardwood snags created using a wide variety of methods are still lacking for southern pine systems. In particular, cost-benefit analysis of various creation methods could be coupled with studies of wildlife usage to provide managers with cost-efficient methods for maintaining snags of maximum utility to wildlife. Both direct and opportunity costs should be included.

Multivariate statistical procedures provide opportunity to study the entire spectrum of services provided by snags rather than focusing on a single arbitrarily chosen attribute (Swallow, Howard, and Gutierrez 1988). Study of wildlife/snag interactions over a broad range of snag community characteristics would provide suitable data for developing predictive models of snag creation, longevity, and use. For example, Swallow, Gutierrez, and Howard (1986) predicted avian use of snags as nest sites in central New York riparian and second-growth hardwood forest using a multiple logistic regression model based on total snag basal area, and diversity and species richness of living trees ≥7 cm. The model had a correct prediction rate of 80.5% for unused sites and 85.0% for used sites. Cain (1996) was able to derive multiple regression equations to predict snag density, minimum snag dbh, maximum total height, the proportion of snags with crowns, maximum crown width, and minimum height of bole cavities for hardwood snags created by herbicide injection. These studies suggest that researchers can develop models useful for identifying stands and individual snags suitable for snag-using wildlife and for predicting snag availability.

Research at multiple spatial scales would help improve understanding of the effects of land use surrounding target management areas. Snag densities in many pine forests in the South are below levels considered optimum for supporting average populations of snag-dependent species (Harlow and Guynn 1983; McComb et al. 1986a), especially impacting species needing large diameter snags. Management recommendations for snag retention commonly include both stand- and landscape-level prescriptions such as: retaining snags within the stand (Land, Marion, and O'Meara 1989), interspersing hardwood reserves in retention blocks (McComb et al. 1986a; Taulman 1999) or streamside management zones (Mannan and Meslow 1984; Taulman 1999), and interspersing long-rotation stands among more intensively managed plantations (Cline, Berg, and White 1980). Distribution of snags across the landscape will affect wildlife species distribution by influencing availability of territories suitable for snag-dependent species. Disturbance-sensitive species of limited mobility must have some amount of available habitat near disturbed areas to act as refugia and as sources for recolonization, whereas more mobile species may make do with a more scattered or clumped distribution. Studies involving multiple spatial scales will provide land managers with information necessary to tailor management to meet the needs of a wide variety of species.

4.0 DEN TREES

4.1 Definition and Characteristics of Den Trees

For this review, we defined den trees as living trees that have ≥1 cavity accessible by an entrance hole of ≥2.5 cm diameter. Size and shape of the actual cavity are not a defining issue, as they are impossible to gauge from ground level, where most surveys take place, and because the diversity of potential users makes it possible that most cavities will be used by some species of wildlife for some purpose. Den trees are not always intermediate between living trees and snags; den trees may be toppled by windthrow and so do not become snags, while snags may be created from trees with no dens at all. Therefore, though both snags and den trees may provide cavities suitable for use by wildlife, we will consider den trees separately from snags.

Cavities result from fungal infection of dead or injured portions of trees and subsequent animal activity (Carey 1983). Initial wounds may be caused by fire, disease, insect attack, mechanical injury, limb loss, storm damage, or herbicide (DeGraaf and Shigo 1985). While such infections may eventually result in the death of the tree, the lag time between infection and death may be decades or centuries (Shigo 1984). Trees isolate areas of injured or infected wood through the process of compartmentalization; such compartments of weakened or decayed wood remain inside the tree throughout its lifetime (Shigo 1984). Living coniferous trees rarely contain cavities (Van Balen et al. 1982; McComb et al. 1986b; Melchiors and Cicero 1987), so den sites in living trees are confined mostly to hardwoods. Cavities created in living southern pines by red-cockaded woodpeckers are a notable exception to this generalization.

Once opened, cavities persist indefinitely, playing host to a progression of wildlife species as the cavity and entrance are modified (Baumgartner 1939; DeGraaf and Shigo 1985). Callus growth over the cavity opening may lead to loss of the cavity (Shigo 1984; Sedgwick and Knopf 1991), though such compartments may later be re-opened. Overall, cavities in living trees may provide up to 85% of available cavities in some forest types (Carey 1983; Fan, Shifley, et al. 2003).

Stand-level factors such as age, basal area, and site index are positively correlated with cavity abundance (Gysel 1961; Carey 1983; McComb et al. 1986b; Fan, Larsen, et al. 2003), though correlations may be weak due to the wide variety of causal agents (Carey 1983; Franklin, Shugart, and Harmon 1987; Allen and Corn 1990). Cavity abundance increased with stand age across all forest cover types in South Carolina and Florida, where stands ≥61 years of age had 3-17 times more dens than 0–30-year-old stands (McComb et al. 1986b). Jensen, Kabrick, and Jenner (2002) found larger diameter classes had higher proportions of cavity trees over all tree species surveyed in a Missouri second-growth oak-hickory-pine forest, and that the relationship between dbh and cavity occurrence was exponential. Because injuries are accumulated throughout the life of a tree (Shigo 1984), older trees are more likely to have cavity potential than younger ones. A greater number of compartmentalized injuries in older trees increases opportunities for excavators to find suitable areas for cavity creation.

Vulnerability to different injury and fungal agents varies among tree species (Franklin, Shugart, and Harmon 1987), influencing cavity occurrence (Carey 1983; McComb et al. 1986b; Melchiors and Cicero 1987; Allen and Corn 1990; Martin, Aitken, and Wiebe 2004; Kahler and Anderson 2006). Major cavity-producing species vary among regions and ecosystems, so results gleaned from one region are not necessarily applicable to others. For example, sweetgum, blackgum, and white oak were important cavity-producing trees in the Ouachita Mountains (Melchiors and Cicero 1987), while sugar maple, oaks, and black locust were more important in Monongahela National Forest (Kahler and Anderson 2006); quaking aspen was used for 95% of all cavity nests in mixed interior forests of British Columbia (Martin, Aitken, and Wiebe 2004).

Cavity abundance in Florida pine forests differed among ownerships, with industrial and non-industrial private lands having 31-38% as many cavities as public lands (McComb et al. 1986b). Stand origin was also a factor, with natural pine stands containing 4× as many den trees as plantations. However, plantations were also on average 30 years younger than natural stands, confounding the effect of regeneration method (McComb et al. 1986b). Among pine forest types, McComb et al. (1986b) found loblolly and pond pine forests somewhat more prone to cavity formation than slash and shortleaf pine forests.

Intensively managed stands may be especially low in abundance of den trees due to removal of suppressed/diseased trees during thinning or timber stand improvement (Hardin and Evans 1977; Newton 1994). Fan et al. (2004a) modeled cavity tree dynamics on a 3261-ha hardwood forest landscape in Missouri under 5 harvest regimes (no harvest, even-aged intensive, even-aged long rotation, uneven-aged, and mixed), and found that intensive even-aged management resulted in a 28-34% reduction of cavity trees compared to no harvest.

4.2 Wildlife Relationships with Den Trees

4.2.1 *General*

Den trees in the South are used by a wide variety of birds, mammals, and herpetofauna (Hardin and Evans 1977; Titus 1983), providing sites for food storage and protection from the elements and from predators. Dens provide greater thermal stability than exposed situations (Stains 1961; Johnson, Johnson, and Pelton 1978; Lentz, Marchinton, and Smith 1983) or nest boxes (McComb and Noble 1981b) due to the insulative properties of wood and protection from wind and precipitation. Hole-nesting species tend to choose dens with entrances just large enough for themselves to fit through, thus effectively excluding larger predators and potential competitors (Stulken and Kirkpatrick 1953; Robb et al. 1996). In general, cavity size is correlated with body mass (Martin, Aitken, and Wiebe 2004), which may give some thermal advantage (Robb et al. 1996); additional excavation may cause smaller species to abandon use of a cavity (Loeb 1993). Cavities in den trees may be more widely used by mammals than birds, with birds tending to use more cavities in snags (Carey 1983). Cavity use is often seasonal, and individual dens may benefit several species over the course of a year (McComb and Noble 1981a).

Dens are not likely to be used at their potential capacity due to selection for certain traits by users: size of cavity, entrance size and shape, aspect, height above ground, position of nearby limbs, covering vegetation, surrounding vegetation, proximity to other cavities, distance to water, and position in the landscape all potentially influence den usability and selection (Bellrose, Johnson, and Meyers 1964; McComb and Noble 1981a; Swallow, Gutierrez, and Howard 1986; Rendell and Robertson 1989, 1994; Belthoff and Ritchison 1990; Loeb 1993; Newton 1994; Robb et al. 1996; Henner et al. 2004; Martin, Aitken, and Wiebe 2004). When given the option, wildlife species may respond to a large number of criteria for choosing a cavity. Eastern screech owls in eastern Kentucky selected cavities based on cavity depth, cavity height, and entrance size (Belthoff and Ritchison 1990). Martin, Aitken, and Wiebe (2004) found measurements of cavity height, vertical depth, internal diameter, entrance area, and dbh useful in creating a nest web for avian and mammalian cavity-users. Henner et al. (2004) found that raccoons take landscape patterns surrounding the den into account, and that these preferences differ by gender.

Competition for suitable cavities may limit some species or cause them to accept cavities that are less than optimal. Southern flying squirrels occupied 10–21% of red-cockaded woodpecker (RCW) cavities in pine forests on Piedmont NWR in Georgia, and showed a preference for non-enlarged RCW cavities (Loeb 1993). In British Columbia Douglas fir forests, European starlings successfully out-competed less aggressive species to occupy a preferred cavity size (Martin, Aitken, and Wiebe 2004). Cavities may also be unavailable due to location within the territory of a conspecific (Newton 1994).

Species need suitable cavities for more than natal dens. Cavities are also used for roosting, loafing, escape, possible renesting attempts, and to avoid cavities with large parasite loads (Sanderson 1975; Short 1979; Nilsson 1984; Brown and Brown 1986). Based on Harlow and Guynn's (1983) determination of average population levels of secondary cavity nesters in southern forests, McComb et al. (1986b) calculated a need for 4.25 dens/ha in Southern pine forests, 5.7/ha in hardwoods, and 6.0/ha in mixed forests to support average populations in South Carolina and Florida. Some caution should be exercised when adding these numbers to McComb et al.'s (1986a) estimates for appropriate snag densities, as it is unclear how much overlap there may be between them. However, given that neither primary cavity-nesting birds nor mammals are accounted for in these estimates, they may be conservative.

Nest boxes are sometimes recommended as a management option to increase diversity in recently harvested (Sanderson 1975; DeGraaf and Shigo 1985) or intensively managed (McComb and Noble 1981a) forests. However, nest boxes do not always benefit cavity-nesters. Nest box use may be influenced by factors other than increased breeding density (Newton 1994; Carey 2002), and boxes may expose users to increased predation rates (Miller 2002).

4.2.2 *Southern Pines*

Possibly because den formation in pines is relatively uncommon, studies of dens in southern pine forests are extremely limited. Management for den trees using landscape-scale strategies, such as streamside management zones and green tree retention patches, has not been investigated for its impact on den-dependent wildlife in pine-dominated systems. While information on red-cockaded woodpecker (RCW) cavity use is widely available, that information is of limited application, since RCW distribution is comparatively restricted. Also, such papers are generally concerned with the impact of competition for cavities on RCWs rather than the utility of RCW-created cavities for other cavity users. We have included one RCW study to indicate the relationships between RCWs as cavity producers and other wildlife as secondary users.

Loeb (1993) investigated use of RCW-created cavities by other species in pine-dominated forests of central Georgia. Because the primary purpose of the study was to determine potential for negative impacts on RCW reproductive success, inspections of cavities were limited to the RCW breeding season. Southern flying squirrels were the most consistent users, averaging 17% occupancy. Other bird species, particularly Eastern screech owls, tufted titmice, and great crested flycatchers, occupied 7% of RCW cavities. Black rat snakes, raccoons, and gray squirrels were responsible for 1% occupancy. Evidence of use by unknown species (e.g., nesting material, seed hulls) was found in 65% of cavities, indicating that RCW cavities were providing services for other species outside of the RCW breeding season. Because the survey took place during a very limited portion of the year, and because surveys did not account for possible roosting by diurnal species, cavity use by species other than RCWs was almost certainly underestimated.

McComb and Noble (1981a) compared nest box and natural cavity use among mature bottomland, riverfront hardwood, and mixed hardwood-pine forests in Louisiana and Mississippi. Monthly inspections of cavity use in the mixed hardwood-pine forest found total vertebrate occupation of 12.5% of natural cavities and 16.6% of nest boxes. Cavity use was mostly seasonal; herpetofaunal use was highest in summer and early fall, mammal use peaked in winter, and birds exhibited peaks in winter and during spring nesting. The authors also measured 16 habitat variables and cavity characteristics and determined correlations with cavity use for five avian and four mammalian species. They hypothesized that a mixture of natural cavities and boxes of different size placed only in desirable locations would serve to maximize species diversity, reduce interspecific competition, and lower the costs of nest box use.

The potential needs of den-using wildlife species in pine forests are largely a matter of conjecture. McComb et al. (1986b) calculated a need for 4.25 dens/ha in Florida pine forests to support average populations of secondary avian cavity-nesters. Some caution should be exercised when adding these numbers to McComb et al.'s (1986a) estimates for appropriate snag densities, as it is unclear how much overlap there may be between them. However, given that neither primary cavity-nesting birds nor mammals are accounted for in these estimates, they may yet be conservative. Further work is needed to determine the densities of den trees that may meet biodiversity goals in managed pine forests.

4.3 Information Gaps and Research Directions

Retention of den trees and potential den trees is often recommended to ensure a continuous supply of dens (Sanderson 1975; McComb and Noble 1981a; Titus 1983; DeGraaf and Shigo 1985; McComb et al. 1986b; Newton 1994). Given that den trees are expected to last for decades and to provide multiple services (e.g., mast production, vertical structure), efforts should be made to determine which tree species within different regions and forest types provide the best combinations of cavity potential and other wildlife services.

Multivariate analysis of wildlife communities has proved helpful in identifying relationships between tree species, den excavators, and den users (Martin, Aitken, and Wiebe 2004). Analyses can extend beyond single species or even several species to encompass community-wide relationships (Martin and Eadie 1999). Analyzing such relationships in southern forest ecosystems is necessary to identify keystone den tree species for development of priorities for retention and promotion, and to develop predictive models for wildlife use and response to management.

The great variety of potential causative agents makes prediction of cavity-tree density (CTD) difficult at small scales (Carey 1983; Melchiors and Cicero 1987); however, predictability of CTD at larger scales may be reliable in some ecosystems. Regression models developed by Fan et al. (2004b) to predict CTD in the Missouri Ozarks performed increasingly well as landscape size increased, stabilizing quickly between landscape sizes of 100 and 1000 ha with $R^2 \geq 0.98$. This resulted in prediction errors of <10%. Furthermore, the models required knowledge only of the proportions of stands in 4 broad age classes (seedling/sapling, pole, sawtimber, and old-growth) (Fan et al. 2004b). Predictive models for southern forest communities should be developed and validated to enable managers to make reliable long-term predictions based on different management scenarios.

Careful research on the effectiveness of nest boxes would be helpful for determining when and where they might be most useful, especially in intensively managed forests. These studies should be multi-year projects focused on changes in breeding density, nest success relative to natural cavities, and predator ecology (Waters, Noon, and Verner 1990; Newton 1994; Carey 2002; Miller 2002). Also, because nest box size, number, and placement are easily manipulated, their use in stands with few natural cavities would allow a closer examination of competition (both inter- and intra-specific) and desirable densities of den trees for management of given species.

There are also significant research questions about landscape scale strategies for retaining den trees. Given the low incidence of den creation in pines, strategies for den tree management should include landscape features intermixed with pine stands. Future research should focus on den creation, maintenance, and use in streamside management zones and riparian buffers. The effects of these and of retention patches on distribution and population demographics of den-using species should be a high priority. Given the difficulty of predicting den abundance at the stand level, special attention should be given to development of predictive models at the landscape level.

5.0 ISOLATED WETLANDS

5.1 Definition and Characteristics of Isolated Wetlands

The term "isolated wetlands" refers to relatively small, non-permanent wetlands, natural or man-made, that are geographically disjunct from other wetlands. In the Southeast, they include Carolina bays, pocosins, Coastal Plains ponds, gum ponds, cypress domes, sinkhole wetlands, woodland vernal ponds, inter- and intra-dunal wetlands, seepage slope wetlands, inactive floodplain wetlands, natural ponds, and excavated ponds (see Tiner 2003 for descriptions). Perhaps because of controversy over federal legislation and regulations, much of the recent research has focused on isolated wetlands <4 ha in surface area (Semlitsch and Bodie 1998; Gibbs 2000; Snodgrass et al. 2000; Zedler 2003). Given the variety of isolated wetlands under this umbrella, generalizations will not be entirely applicable for all types of isolated wetlands.

The water source for isolated wetlands varies from rainwater to groundwater to spring-fed. They are often, but not necessarily, linked with other wetlands hydrologically via subsurface flow or intermittent overflow (Leibowitz 2003; Tiner 2003; Whigham and Jordan 2003). The hydrology of isolated wetlands is ephemeral. Most rely on precipitation events for filling, and are thus most likely to fill in late winter to early spring, followed by loss of water though evapotranspiration leading to complete drying by mid- to late summer, though occasional late-season precipitation may lead to refilling for a time (Semlitsch et al. 1996). Hydroperiod in isolated wetlands is closely correlated with rainfall levels (Semlitsch et al. 1996; Bonner, Diel, and Altig 1997). During drought cycles, ponds may remain dry throughout the year (Dodd 1992; Semlitsch et al. 1996). Because hydroperiod is affected not only by pool morphometry, but also by precipitation, evapotranspiration, and groundwater exchange, pool size is not an adequate indicator of hydroperiod (Brooks and Hayashi 2002).

Vegetation cover in isolated wetlands varies from none in open ponds to overstories of trees in cypress domes, tall pocosins, and gum ponds (Tiner 2003). Vegetation can affect the ecology of ponds through shading, providing organic inputs, and serving as a pathway for evapotranspiration. Adjacent vegetation can protect ponds from sedimentation and excess nutrient input, and may moderate temperatures (Castelle, Johnson, and Connolly 1994).

5.2 Wildlife Use of Isolated Wetlands and Adjacent Uplands

5.2.1 *General*

Herpetofauna are the vertebrate group most closely associated with isolated wetlands. Herpetofauna using isolated wetlands include amphibians with biphasic life cycles, and reptiles that utilize ponds for foraging and mating, but which may leave the pond for nesting and refugia. The lack of large predatory fish in seasonal ponds removes a significant source of predation on amphibian larvae (Wilbur 1980; Porej and Hetherington 2005), and many amphibian species (e.g., ambystomids) are adapted specifically to breed in temporary ponds (Wellborn, Skelly, and Werner 1996). At least 10 anuran and 5 salamander species in the Southeastern Coastal Plain are dependent on isolated wetlands for breeding sites (Moler and Franz 1987). Dodd (1992) monitored herpetofaunal use of a temporary pond in a north Florida longleaf pine sandhills community, capturing 42 species (16 amphibian, 26 reptile), representing 29% of salamander species, 74% of frogs, 40% of turtles, 78% of lizards, and 65% of snake species known from the 3750 ha Ordway Preserve. A 16-year continuous survey of herpetofauna entering and exiting a 1-ha Carolina bay in South Carolina netted 27 amphibian species (Semlitsch et al. 1996). A survey of 444 seasonally flooded ponds on private, industrial forest lands over 35 counties in south Georgia, south Alabama, and north Florida identified 16 salamander species, 24 anuran species, 34 reptile species, and 37 fish species associated with the ponds (Wigley, Sweeney, and Sweeney 1999).

Seasonal drying of isolated wetlands concentrates prey species important to wading birds (Ogden, Kushlan, and Tilment 1976; Kushlan 1979) and small ponds may support large wading bird rookeries (Moler and Franz 1987, Richardson and Gibbons 1993). Scheffers, Harris, and Haskell (2006) found habitat adjacent to ephemeral ponds in Tennessee hardwood forests exhibited greater bird abundance, species richness, and diversity than controls, with differences in species richness increasing as spring migration progressed. Egrets, coots, and migratory waterfowl use Carolina bays in the Sandhills region of the Carolinas (Richardson and Gibbons 1993). During periods of drought, isolated ponds may provide refuge to bird species dispersing from affected areas (Beissinger and Takekawa 1983).

Mammal use of isolated wetlands is not emphasized in the literature, although pocosins are mentioned as refuges for black bear and white-tailed deer (Richardson and Gibbons 1993), and smaller mammals such as bobcat, marsh rabbit, and gray squirrel (Monschein 1981). Clark, Lee, and Funderburg (1985) trapped or observed 40 mammalian species in pocosins, Carolina bays, and associated communities, and found that mammal communities associated with pocosins changed as seral stage advanced. Mitchell et al. (1995) captured 10 small mammal species in undisturbed pocosin forests in North Carolina, and did not detect differences in small communities between undisturbed pocosin forests and pine plantations possibly because pocosin-like habitat persisted in managed stands. Isolated wetlands provide important commuting and foraging areas for bats in southern forests (Menzel 1998; Wilhide 1998; Menzel et al. 2005a, 2005b).

Breeding success of amphibians in isolated wetlands is most strongly influenced by hydroperiod length and timing (Pechmann et al. 1989; Semlitsch et al. 1996). If hydroperiod is too short, entire cohorts may die before metamorphosis (Semlitsch et al. 1996; Bonner, Diel, and Altig 1997; Semlitsch 2000). Larvae may respond to reduced hydroperiods with early metamorphosis, but such metamorphs may be relatively small and may experience reduced or delayed reproduction. Extended hydroperiods may be detrimental for many anuran species as salamander larvae prey upon tadpoles. Because reproductive season is species-specific, the timing of inundation limits which species will use a pond. Narrow-mouthed toads bred successfully in a Carolina Bay only when the pond refilled for a period of several weeks in summer after previous drying killed potential tadpole predators (Semlitsch et al. 1996).

Pond size may not be an adequate predictor of its contribution to biodiversity. Russell, Guynn, and Hanlin (2002a) focused on habitat affiliations of herpetofauna associated with 5 isolated wetlands ranging from 0.38-1.06 ha in an industrial pine forest in the South Carolina Coastal Plain. Wetland size was not consistently related to richness, diversity, or evenness of herpetofauna, nor were herpetofaunal communities more similar at ponds of similar size. More amphibians than expected were captured at the three smallest ponds, fewer than expected at the largest; more reptiles than expected were captured at the smallest pond.

Wildlife species associated with isolated ponds are also dependent on upland habitat (Gibbons 2003). Amphibians which migrate to ponds for breeding may stay only a few days, and may use upland habitat long distances from the breeding pool. Regosin et al. (2005) found that a minimum of 13% of eastern newts, 40% of wood frogs, 52% of blue-spotted salamanders, and 60% of spotted salamanders captured at a breeding pond in Massachusetts wintered >100 m from the pond. Five of 8 turtle species found in a Carolina bay used upland refugia up to 165 m from the pond (Buhlmann and Gibbons 2001). Dodd (1996) captured 4 toad and 2 tree frog species 914 m away from the nearest water body in upland high pine forest and sand oak hammock in Florida. Based on a literature review, Semlitsch and Bodie (2003) estimated core habitat for amphibian populations ranging from 159-290 m from the wetland edge, and 127-289 m for reptiles.

Some herpetofaunal species travel away from and between wetlands as part of home range use or dispersal. Dodd and Cade (1998) observed a directional component in dispersal of narrow-mouthed toads and striped newts from isolated ponds in Florida, indicating that these species' movements were influenced by adjacent habitat. Florida cooters and yellow-bellied sliders tended to emigrate directly from a drying Carolina bay toward permanent water (Buhlmann and Gibbons 2001). Copper-bellied water snakes in Ohio and Michigan made use of several ponds as part of their home range, necessitating travel through adjacent uplands (Roe, Kingsbury, and Herbert 2004). This indicates that, when managing for these species, habitat conditions in adjacent uplands should be a consideration.

Metapopulation theory is proposed in the literature to explain herpetofaunal population dynamics in isolated wetlands (Gibbs 1993; Marsh and Trenham 2001). Widely separated isolated ponds are thought to be more vulnerable to extinction events from stochastic causes, primarily drought cycles. When pools affected by drought are in close proximity to non-affected pools, they are considered as more likely to benefit from rescue efforts, as animals emigrating from non-affected pools can reestablish populations in them (Semlitsch and Bodie 1998). Extinction and repopulation events at individual ponds are common. Among 14 species of amphibians distributed over 37 ponds in southeastern Michigan, 34 extinction and 40 colonization events were recorded over a 26-year period (Skelly, Warner, and Cortwright 1999), indicating that such events are normal. Extinction risk of metapopulations increases as ponds become more isolated. Gibbs (1993) modeled metapopulation extinction risk for wetland-associated organisms over a 50-year period following simulated removal of small wetlands from a hypothetical 1963-ha circular mosaic of large and small wetlands. Small pond removal increased inter-wetland distance by 67%. Extinction risk was estimated to increase for small mammals from 0 to 15%; for small birds and turtles, the number of simulations with population numbers falling below 50 individuals increased from 50 to 74% for birds, and from 4 to 36% for turtles. Modeled populations of frogs and salamanders never fell below 1500 and 11000, respectively, due to high rates of population increase.

Explanations other than wetland proximity have also been forwarded to explain turnover of species associated with isolated wetlands. Skelly, Warner, and Cortwright (1999) related differences in amphibian assemblages to successional stage of isolated ponds in Michigan and concluded that amphibian species turnover may be influenced more by deterministic rather than stochastic events. Life history and survival rate in upland habitat may determine species persistence during years of catastrophic reproductive failure, with long-lived species being less dependent on consistent reproduction than short-lived species (Taylor, Scott, and Gibbons 2006). Species with low reproductive potential and risky dispersal strategies may require more habitat for persistence than those with high reproductive rates and better survival during dispersal (Fahrig 2001).

5.2.2 *Southern Pines*

The impact of upland management surrounding isolated wetlands has been investigated for herpetofauna in several studies in southern pine forests (Table 5.1). It must be noted that most of these studies have limitations on their inferential power due to pseudo-replication, short duration, or lack of pre-treatment data. Chazal and Niewiarowski (1998) accepted pseudo-replication in order to make better use of available long-term data from a particular Carolina bay in their experimental design. Similarly, Hanlin et al. (2000) accepted pseudo-replication in order to compare their results with previous work at the same location. Means, Palis, and Baggett (1996), while extending over 23 years, was entirely observational; Russell et al. (2002), a true experiment with pre-treatment data, was of relatively short term (3 years total, 1.5 years post-treatment). Randomization of treatments was found only in two studies (Enge and Marion 1986, Russell et al. 2002), one of which was pseudo-replicated (Enge and Marion 1986).

Russell et al. (2004) pointed out that southeastern Coastal Plain forests, which have evolved with fire to create large areas of sub-climax pine forests, are likely to harbor herpetofaunal communities different from those in hardwood dominated landscapes such as the southern Appalachians, where many studies of forest management impacts on herpetofauna have taken place. The applicability of much of the work done in southern hardwood systems to these pine forests is questionable. For example, work on mole salamanders in South Carolina indicates that they may be able to maintain themselves in clearcut areas as long as there is sufficient cover in the form of CWD or leaf litter (Chazal and Niewierowski 1998). Russell et al. (2002) found only temporary declines in abundance of both snakes and turtles in clearcut and site-prepared stands adjacent to small ponds on industrial pine forests; other herpetofaunal groups were either unaffected, or, in the case of bronze frogs, may have benefited from treatment. Although these studies are encouraging, further research is warranted. Observations such as those by Means, Palis, and Baggett (1996) caution against blanket acceptance and widespread application of a few short-term studies from a single state.

Microclimate may be an important factor for determining amphibian abundance and distribution (deMaynadier and Hunter 1995; Harper and Guynn 1999). Microsite variables may explain the seeming resilience of some herpetofauna in disturbed pine uplands. Chazal and Niewierowski (1998) hypothesized that similarities between sites in soil moisture, organic content, and litter contributed to the lack of treatment effect on mole salamanders penned in a 4-month-old clearcut compared with salamanders penned in an adjacent, undisturbed 40-year-old pine forest. Mosely, Castleberry, and Ford (2004) suggested that either CWD or pine litter of sufficient depth contributed to adequate microclimate conditions for mole salamanders under mature pines. Conversely, Russell, Guynn, and Hanlin 2002; Russell et al. 2002) found no correlation between either litter or CWD in adjacent uplands and reptile or amphibian diversity at isolated wetlands before (Russell et al. 2002a) or after harvest and site preparation in the uplands (Russell et al. 2002), however, no comparisons were attempted at the species level, so microhabitat effects may have been obscured by opposing species preferences.

Table 5.1 Studies of Upland Management Impacts on Herpetofauna Associated with Isolated Wetlands in Southern Pines

Study and Context	Experimental Design	Key Results and Observations	Comments
Chazal and Niewiarowski (1998) Clearcut and 40-yr-old loblolly plantation, within 300m of a Carolina bay in South Carolina.	Monitored mole salamanders placed in 10×10-m enclosures for 5-6 months. Analyzed for both demographic and environmental parameters.	No differences found for any demographic parameter, including: recapture rate, body length and mass, nonpolar lipids for carcasses and eggs, clutch size, and time to emergence. Authors conjectured that similarities between sites in soil moisture, organic content, and litter may have contributed to the lack of treatment effect.	Salamanders in clearcuts were not exposed to the actual disturbance. Pseudo-replicated.
Russell et al. (2002) 18–25-yr-old industrial pine forests surrounding 5 small isolated wetlands in coastal South Carolina.	Divided area surrounding wetlands into clearcut, clearcut with site prep, and reference stands. Herpetofaunal communities sampled before treatment and 0.5 years and 1.5 years post-treatment.	Abundance of snakes and turtles was reduced in both site prepared and clearcut stands relative to controls 0.5 months post-treatment; abundance of both were similar to control stands 1.5 years following treatment. Bronze frogs increased in site prepared and clearcut areas 1.5 years post-treatment. No treatment effect was detected for overall reptile abundance or species richness, nor for richness or abundance of any amphibian grouping. Found no evidence to suggest amphibians emigrated from clearcuts into reference stands.	Post-treatment sampling period of only 18 months.
Enge and Marion (1986) 3 watersheds in 40-yr-old slash pine in Florida.	Watersheds assigned to reference, and to clearcut with either minimal or intensive mechanical site prep. Sampled 2-3 years post-treatment.	Species richness did not differ among treatments for amphibians; reptile species richness was lower in the intensively prepared site. Abundance of all herpetofauna was 3× greater in the reference than in either treatment plot, and was still significant after removal of the most abundant species, which was found almost exclusively in the control forest.	Pseudo-replicated. No pre-treatment comparison.

(Continued on next page)

Table 5.1 Continued

Study and Context	Experimental Design	Key Results and Observations	Comments
Means et al. (1996) Intensive slash pine silviculture across highway from National Forest in Florida	Observational study monitored cross-highway movement of flatwoods salamander for 3 periods over 23 years following conversion of one area to intensively managed plantations	Across road migration decreased from 7.9/hr to 0.1/hr. Authors discounted drought, road mortality, collecting, and acid rain as possible causes, and theorized that slash pine silviculture had degraded salamander habitat by altering hydrology, soil infrastructure, plant communities, and terrain.	No pre-treatment observations. No replication or randomization.
Hanlin et al. (2000) 3 forests types (40-yr-old slash pine, 41-yr-old loblolly pine, and >60-yr-old hardwood) surrounding a restored Carolina bay in South Carolina.	Surveyed amphibian populations daily in each forest type for 3 years following restoration of the bay. Compared results among years and to surveys performed 18 years earlier (Bennett et al. 1980).	The hardwood site had the greatest abundance for all years combined, but also had the lowest diversity. The slash pine site expressed the highest diversity for each year and overall. 83% reduction in overall abundance (regardless of forest type) between summer surveys in 1977-1978 and 1994-1996. The authors attributed this to pond restoration activities, which eliminated leaf litter and woody debris from the bay and its margins, as well as altering adjacent vegetation from mesic shrubs to an open herbaceous community.	No randomization. Pseudo-replicated.

5.3 Information Gaps and Research Directions

In spite of a plethora of studies documenting abundance, diversity, and richness of herpetofauna under different forest management regimes, very little has been done to document demographic responses of herpetofauna populations to management actions (e.g., Enge and Marion 1986; Raymond and Hardy 1991; Chazal and Niewiarowski 1998). Without such information, managers will not know whether their decisions contribute to habitats functioning as sources or sinks for herpetofauna. Because herpetofauna populations associated with isolated wetlands already exhibit radical population swings due to annual variance in hydroperiod, demographic studies are crucial to take knowledge beyond the potentially misleading results of abundance and density (Van Horne 1983). In addition, naturally occurring peaks and valleys in population necessitate studies of several years' duration to ensure that results are not clouded by non-treatment impacts.

Most studies of wildlife associated with isolated wetlands have been observational, often without replications or pretreatment data (deMaynadier and Hunter 1995, Russell et al. 2004). While limited in inferential power, they have been useful for producing hypotheses which should now be tested experimentally. For example, Means, Palis, and Baggett (1996) hypothesized that silvicultural actions were responsible for fewer observed movements of flatwoods salamander across a road. Also, they conjectured that salamander presence in cypress ponds within the plantation matrix was due to a 1-ha unmanaged buffer zone surrounding each pond. A long-term manipulative experiment to investigate buffer zones of various sizes or buffers managed with various silvicultural treatments would allow these hypotheses to be tested and would potentially elucidate strategies for integrating salamander management with plantation management.

The effects of forest management actions on microclimate features in uplands surrounding isolated wetlands should be investigated to determine their impacts on herpetofauna populations. Comparisons of microhabitat use between managed pine and natural pine or pine-hardwood systems coupled with studies of silvicultural impacts on microhabitat elements may indicate which silvicultural methods in uplands surrounding isolated wetlands maximize similarities of microhabitat elements important to herpetofauna. Candidate features for study include CWD, hardwood shrubs, soil pH, and leaf litter (deMaynadier and Hunter 1995).

Alteration of wildlife communities associated with isolated wetlands is natural and happens without any human interference (Semlitsch et al. 1996; Skelly, Warner, and Cortwright 1999), and changes in community composition should be interpreted carefully. Silvicultural treatment will lead to habitat conditions more favorable to some species than to others (Enge and Marion 1986; Cromer, Lanham, and Hanlin 2002; Russell, Guynn, and Hanlin 2002; Renken et al. 2004; Loehle et al. 2005b); similarly, wildlife in different regions of the South may be adapted to differing levels and types of disturbance (Russell et al. 2002, 2004). Research which tests for regional or community-based effects would enable forest managers to implement actions founded on conditions particular to their situation, tailoring anthropogenic disturbance to better mimic natural disturbances to which local communities are adapted.

Isolated wetlands are subject to wide variance in availability and productivity due to changing patterns of precipitation. Recolonization of an area by an extirpated species may depend on periodic emigration from other ponds within the species' dispersal distance. Some reptile species may travel long distances, using several wetland sites over the course of a year (Joyal, McCullough, and Hunter 2001; Roe, Kingsbury, and Herbert 2004), and thus are better thought of as a single population than as a metapopulation. Management of single isolated wetlands may therefore be less important (at least for herpetofauna) than management of clusters of ponds (Gibbs 2000; Joyal, McCullough, and Hunter 2001; Marsh and Trenham 2001) covering the entire hydroperiod gradient (Snodgrass et al. 2000).

Research should be undertaken to determine whether and at what level managing clusters of ponds may contribute more to species diversity and stability than managing single ponds.

The experiment by Russell et al. (2002) was well-designed and informative, and we recommend it as a pattern for future studies of impacts of silvicultural activities on pond-dependent wildlife. Further experimentation should include sampling of additional upland sites to determine microhabitat use, survivorship, and fecundity. We encourage studies of greater duration to explore potential long-term impacts. Replication at different locales using locally appropriate stand establishment techniques is needed to give insight into the effects of differing disturbance levels. Such studies should consider microhabitat features considered important to target species. In addition, we recommend analyses of community composition along with species-, age- and gender-specific niche use to determine how species react and interact under treatment-caused habitat changes.

6.0 STREAMSIDE MANAGEMENT ZONES

6.1 Definition and Characteristics of Streamside Management Zones

Streamside management zones (SMZs) are areas of riparian and upland vegetation retained along water channels. Though we are reviewing them primarily in the context of a stand-level habitat element, the variable length and inherent connectivity of SMZs places them just as legitimately at the level of a landscape element. Currently, recommendations for SMZ widths are primarily to preserve stream water quality by controlling excessive sedimentation and nutrient input (Lee, Smith, and Boutin 2004; Williams, Lipscomb, and Post 2004). However, SMZ widths established for water quality may not be sufficient to meet some objectives for wildlife communities.

SMZs along water channels provide high-quality wildlife habitat and multiple additional advantages. It is clear that riparian areas are beneficial for a wide spectrum of taxa, and at least contain a different species pool if not greater species richness relative to uplands (Sabo et al. 2005). Therefore, loss of riparian vegetation may impact wildlife diversity disproportionately compared to loss of other vegetation types. Furthermore, Meiklejohn and Hughes (1999) emphasized that while species richness, diversity, and density may remain similar among differing riparian study types, communities may vary widely among ecological designations, such as edge and interior species. This difference in species composition is well-illustrated by Dickson, Williamson, and Conner (1995), who detected early succession species in the vegetation of narrow SMZs and mature forest associates in the wide zones.

Streams form a natural connective network, and protected areas along streams may provide movement corridors, including bird migration pathways (Wilson and Twedt 2003; Lee, Smith, and Boutin 2004) and flight corridors for bats. SMZs can be a source of rare stand elements, such as mature trees and snags. They are logical locations within managed forest landscapes to provide stand structural features that may be less abundant in more intensively managed stands (Wigley and Melchiors 1994) without constraining forest management operations. SMZs may have greater levels of flying insects than surrounding land (Whitaker, Carroll, and Montevecchi 2000), and bat foraging activity may be concentrated over rivers and lakes (Menzel et al. 2005a). SMZs also contribute to stream habitat quality for aquatic taxa including herpetofauna (Semlitsch and Bodie 2003; Petranka and Smith 2005). Streamside vegetation traps sediments and chemicals, stabilizes stream banks, and reduces water temperature extremes with shade (Lee, Smith, and Boutin 2004). Instream CWD from adjacent forestland shapes water flow, ultimately developing pools and stream heterogeneity (Lindenmayer and Franklin 2002).

Managers typically determine appropriate and unique riparian buffer width for streams and isolated wetlands on the basis of location, wetland size, channel size, riparian slope, disturbance intensity, and management goals, as well as landscape context. Wenger (1999) recommended that, for optimum wildlife benefits, buffers should be at least 100 m to each side in some locations throughout a landscape. Wider buffers (150 to 400 m; Semlitsch and Bodie 2003) may be more appropriate for some management purposes, for example, connecting wetlands to high quality adjacent sites. On the other hand, narrower buffers (30 m wide; Wenger 1999; Lee, Smith, and Boutin 2004) may be all that is necessary to meet some biodiversity-related objectives and to preserve water quality. Wigley and Melchiors (1994) urged caution when recommending riparian buffer widths for meeting wildlife/biodiversity objectives, and concluded that variable-width riparian buffers may be more desirable in many cases to allow operational flexibility and incorporation of important habitat features, such as mature trees and snags, that may not fit within a fixed-width buffer.

6.2 Wildlife Use of Streamside Management Zones in Southern Pines

Despite awareness of the theoretical benefits of SMZs, as well as applications due to riparian management guidelines and regulations (Williams, Lipscomb, and Post 2004), there is little published research on the impacts of SMZs on wildlife in southern pine systems. This was the case in 1994 (Wigley and Melchiors 1994) and remains the case currently (Wenger 1999; Baker and Hunter 2002; Russell et al. 2004).

Few studies have directly examined herpetofauna use of SMZs bordering southern pines (Table 6.1). Rudolph and Dickson (1990) documented more herpetofauna in wider zones of 50 to 95 m than in narrow zones adjacent to young loblolly pine plantations (2-4 years) in Texas. Although Fogarty (2005) studied older mixed forest stands (>25 years) extending at least 120 m in width from a stream's edge rather than buffers, he recommended buffers of 25-50 m due to high amphibian concentration at these widths in Mississippi. In contrast, reptiles were distributed evenly throughout riparian zones.

Avian response to SMZ width in pine systems has been studied in several locations (Table 6.1). Avian species richness and abundance increased with width, at least up to 700 m, in buffers bordering pine plantations in Georgia (Hodges and Krementz 1996). Based on probability of occurrence, the authors suggested that 100-m buffers should be sufficient to maintain the 6 most common neotropical bird species. In east Texas, Dickson, Williamson, and Conner (1995) also recorded increased bird abundance with SMZ width (15-25 m, 30-40 m, 50-95 m) adjoining young loblolly plantations (2-5 years). Thurmond, Miller, and Harris (1995) found that breeding and wintering avian density was greatest in narrow buffers (15-18 m) bordering a pre-canopy closure pine plantation in Georgia. Nevertheless, all buffer zones had greater bird density than the pre-canopy closure pine plantation. The mature riparian control contained the greatest density of forest interior specialists and neotropical species (Thurmond, Miller, and Harris 1995). Kilgo et al. (1998) studied bottomland hardwood forest widths ranging from less than 50 m to greater than 1 km along either closed canopy pine or field-scrub. Species richness increased with buffer width and abundance tended to be greatest in the narrowest and widest widths. The authors proposed that the narrow zones contained greater abundance due to edge habitat and species, as well as packing into smaller areas. Additionally, to maintain a complete avian assemblage, they suggested that SMZs may need to exceed 500 m, based on probability of occurrence (Kilgo et al. 1998). Lastly, in modeling studies from South Carolina, Arkansas, and West Virginia managed forests of different types, species richness respectively remained the same, increased, and decreased with distance to water (Loehle et al. 2005a; Mitchell et al. 2006).

Table 6.1 Studies of Wildlife Response to Streamside Management Zone Widths in Southern Pine Forests

Study and Context	Species Group	Variable and Technique	SMZ Width (m)	Key Results and Observations	Comments
Fogarty (2005) 21 mature mixed forest sites extending from streams in Mississippi.	Amphibians and reptiles	Abundance; visual searches along transects	Transects sampled at 0, 25, 50, 75, 100 m distances away from streams	Amphibian abundance decreased with distance from streams. Reptile abundance was generally even throughout.	Observational study on dispersion from streams.
Rudolph and Dickson (1990) 6 young (2-4 years) pine plantations in eastern Texas.	Amphibians and reptiles	Abundance of taxonomic (4) and ecological (2) groups; drift fences with funnel traps or artificial shelters along transects plus visual searches	Narrow (0-25), medium (30-40), wide (50-95)	Greatest abundance of all groups in wide SMZs. In plantations, abundance of reptiles overall and of lizards was greatest next to wide SMZs.	Only 2 replications of each width. No accounting for differing vegetation and ground cover characteristics. Short-term study (2 years). Differing areal extent of SMZs.
Dickson et al. (1995) 9 young (2-5 years) pine plantations in eastern Texas.	Birds	Abundance; transects	Narrow (15-25), medium (30-40), wide (50-95)	Avian abundance increased with riparian buffer width.	No accounting for differing vegetation characteristics. 2-year study. Bird transects extended beyond SMZ widths. Differing areal extent of SMZs.

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Table 6.1 Continued

Study and Context	Species Group	Variable and Technique	SMZ Width (m)	Key Results and Observations	Comments
Hodges and Krementz (1996) Floodplain swamp adjacent to pine plantations in Georgia.	Birds	Species richness, abundance of 6 focal species; points along transects	Narrow (< 350), medium (400-700), wide (> 1000)	Avian species richness and abundance of 3 species increased with SMZ width.	Unequal subsampling (points per transect) and replication (transects per width class).
Kilgo et al. (1998) Bottomland hardwood forest bordering closed canopy pine forests or field-scrub in South Carolina.	Birds	Species richness and abundance; point counts	< 50, 50-150, 150-300, 300-1,000, >1,000	Species richness increased with buffer width; abundance was greatest in the narrowest and widest widths.	Possible comparison problems due to varying proportion of edge and areal extent among wide-ranging width classes.
Thurmond et al. (1995) Young pine plantation with chemical site preparation compared to mature forest control in Georgia.	Birds; spring and winter	Density of total number bird species and ecological groups (4); points along transects	Narrow (15-18), medium (28-30), wide (49-53 m)	Breeding and wintering avian density was greatest in the narrow SMZ. Density was lowest in the plantation; the greatest density of interior species was found in the mature forest control.	Pseudoreplicated. Small maximum width. Pines harvested from SMZs. No accounting for differing vegetation characteristics. 2 year study. Varying widths of bird survey transects.

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Table 6.1 Continued

Study and Context	Species Group	Variable and Technique	SMZ Width (m)	Key Results and Observations	Comments
Miller et al. (2004) 3 types of pine forests (young, closed canopy, and thinned) and natural riparian forests in Arkansas.	Small mammals	Relative abundance, species richness, evenness, diversity; removal trapping along transects	1-20, 21-40, 41-60, 61-100, >100	Narrow SMZs had greater small mammal abundance and species richness than wider SMZs. Species richness and abundance were greater in SMZs next to young and thinned plantations than in closed canopy plantations.	Richness and variance possibly affected by sampling intensity (different class width area and number of transect lines). Pines harvested from SMZs.
Dickson and Williamson (1988) 6 young pine plantations in eastern Texas.	Small mammals	Abundance; live trapping along transects	Narrow (<25), medium (30-40), wide (>50)	Greater abundance of small mammals in narrow SMZs.	Each width replicated only twice. No accounting for differing vegetation characteristics. 2 year study. Differing areal extent of SMZs.
Thurmond and Miller (1994) Young pine plantation with chemical site preparation compared to mature forest control in Georgia.	Small mammals	Abundance; removal traps along transects	Narrow (15-18), medium (28-30), wide (49-53 m)	Abundance and composition varied by treatment type.	Pseudoreplicated. Pines in SMZs harvested. No accounting for differing vegetation characteristics in SMZ classes. Unbalanced sampling. Differing areal extent of SMZs.

It may be important to note that two of the avian studies were performed in whole (Hodges and Krementz 1996) or in part (Kilgo et al. 1998) along large river bottoms, and thus may not reflect conditions typical of SMZs in most managed pine landscapes. Their value in this context lies in their treatment of area-sensitive species, specifically the neotropical migrants that were the focus of those studies. In neither case was adjacent pine plantation an adequate substitute for additional area of bottomland forest (Hodges and Krementz 1996; Kilgo et al. 1998). Taken together, these studies indicate that richness and abundance of neotropical migrants along stream bottoms is directly related to area of bottomland vegetation, and thus conversion of bottomland forests to pine plantations may result in decreased populations of these species.

Studies of small mammals associated with SMZs in southern pine landscapes generally suggest that narrow buffer widths are sufficient for the species studied (Table 6.1). In Arkansas, Miller et al. (2004) found that narrow (<20 m wide) SMZs in pine plantations had greater small mammal abundance and species richness than wider zones. Additionally, species richness and catch per unit effort were greater in SMZs adjacent to young (pre-canopy closure) and thinned plantations than closed canopy plantations. Thus, the structure of plantations adjacent to SMZs appeared to influence small mammal community structure within the buffers more than buffer width (Miller et al. 2004). In east Texas pine plantations before crown closure, Dickson and Williamson (1988) also found that small mammals were more abundant in narrow (<25 m) than medium (30–40 m) or wide (>50 m) buffers and attributed this difference to dense, brushy vegetation, abundant seeds, and logging slash in the narrow buffers. In contrast, Thurmond and Miller (1994) documented that total small mammal abundance during summer was greatest in mature riparian forests, whereas species composition varied by both season and habitat type (i. e., mature forest, buffer width, and young pine plantation).

6.3 Information Gaps and Research Directions

Methodology for future studies of SMZs should incorporate replication to insure greater inferential power, and provide for a time frame of at least three years. Studies should explore adjoining pine plantations in different stages of development, as the age of adjacent stands will impact both the vegetation and wildlife communities within them and within SMZs. Buffer widths should contain an equal area in each distance class, or at least analysis should account for areal differences in surveys. Maximum width should extend to at least 100 m to insure inclusion of varying species composition. Changes in vegetation associated with riparian zonation and transition to upland vegetation, need careful consideration and standardization in order to account for differences in vegetation characteristics from buffer zone width. Research objectives should include testing for differences among buffer width classes in species richness, composition (including area-sensitive species), abundance, and especially various metrics of reproductive success.

The potential for SMZs to provide habitat for substantially different communities than surrounding forest (Sabo et al. 2005) needs to be explored more fully. Landscape-level diversity may be significantly enhanced by management of habitat elements within SMZs that prove more difficult to accommodate in pine plantations. For example, large diameter hardwoods and snags in SMZs on plantation dominated landscapes in the South have been shown to be important to adult male red bats (Elmore, Miller, and Vilella 2004) and Southern flying squirrels (Taulman 1999), respectively. Because SMZ management may include some level of harvest (Blinn and Kilgore 2001), it is important to quantify the habitat contributions of large trees in SMZs as nesting sites, hunting perches, mast producers, den trees, and sources of snags and CWD. Comparisons of wildlife presence, abundance, and fitness among stands with differing levels of SMZ harvest would help identify levels of commercial use commensurate with various biodiversity goals.

To maximize their contribution to biodiversity, SMZs should act both as refuges from adjacent disturbed stands, and as sources of wildlife which use and repopulate those stands. Studies of wildlife movement in and out of SMZs in response to management actions both in the SMZs and surrounding forest are needed and should be coupled with measurements of wildlife use and fitness to determine the potential utility of SMZs for acting as species reservoirs and for promoting use of adjacent stands. This will involve studying SMZs of different widths, contents, and juxtapositions within the landscape.

There is minimal research on the value or use of SMZs as movement corridors. SMZs may provide connectivity between habitat patches that is not provided in surrounding forests. A significant question, however, is whether special provisions for connectivity are even necessary in managed pine landscapes. Under current management strategies, which species are able to move at sufficient rates to maintain functional connectivity? Research should explore the potential role of SMZs as movement and dispersal corridors for large mammals, herpetofauna, bats, and birds.

7.0 CONCLUSIONS

We reviewed biodiversity response to five stand-level habitat features: CWD, snags, den trees, isolated wetlands, and SMZs. Coarse woody debris is used by a large number of wildlife species, but it is unclear whether this use is obligatory or facultative and benefits supplied by pine litter may substantially overlap those supplied by CWD in other forest types. Snags increase wildlife species diversity and richness by providing nesting and roosting sites for cavity-nesting species and foraging sites for insectivores; however, the impact of snag distribution on fauna has not been adequately investigated. Den trees, which are mostly confined to hardwood species, provide multiple habitat values within managed pine landscapes such as mast and vertical structure. However, little is known about optimum density, juxtaposition, and distribution of den trees at the stand or landscape scales.

Isolated wetlands and SMZs occur within managed stands, but are landscape-scale features as well. Although there is good understanding of which species use isolated wetlands, the impacts of silvicultural practices in adjacent uplands on these species are not well known, and most extant research in pine systems has limitations. Streamside management zones contain a heterogeneous mix of habitat elements not always found in pine plantations, and have the potential to greatly increase biodiversity in pine-dominated landscapes, to provide refuges for disturbance sensitive species, and to serve as population sources for recolonization of disturbed sites. Studies of biodiversity response to SMZ width in pine-dominated landscapes have produced inconsistent and even conflicting results, and it seems unlikely that a single recommended width will suffice for all situations. Management of sites adjacent to SMZs may have as much or greater impact on biodiversity than SMZ width.

Because few manipulative studies have been conducted, long-term manipulative experiments, complete with pre-treatment data and adequate replication, would greatly enhance understanding of biodiversity response to dynamics and management of these habitat features. Based on this review, we identified the following research needs:

- demographic studies to determine where associations of individual species with selected habitat features lie along the gradient from facultative to obligatory;
- relationships between herbicide use and CWD and snag dynamics, and the usefulness of herbicide-created snags to wildlife species;
- long-term experimental studies in different regions of the South to investigate relationships between various levels of retained stand structural features and biodiversity response (how much is enough?);

- predictive models of wildlife response to dynamics of selected habitat features; and
- multiple scale analysis of the contributions of key structural features (SMZs, den trees, snags, and CWD) to biodiversity, including different strategies for retention (e.g., retaining den trees, snags, and CWD in patches versus distributed across the harvested stand).

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APPENDIX A

SCIENTIFIC NAMES OF SPECIES MENTIONED IN THE TEXT

Trees:

Common Name	Scientific Name
American elm	*Ulmus americana*
Basswood	*Tilia americana*
Blackgum	*Nyssa sylvatica*
Black locust	*Robinia pseudoacacia*
Chestnut oak	*Quercus prinus*
Douglas-fir	*Pseudostuga menziesii*
Eastern hophornbeam	*Ostrya virginiana*
Loblolly pine	*Pinus taeda*
Longleaf pine	*Pinus palustris*
Mockernut hickory	*Carya tomentosa*
Pitch pine	*Pinus rigida*
Pond pine	*Pinus serotina*
Ponderosa pine	*Pinus ponderosa*
Post oak	*Quercus stellata*
Quaking aspen	*Populus tremuloides*
Sand pine	*Pinus clausa*
Shagbark hickory	*Carya ovata*
Shortleaf pine	*Pinus echinata*
Slash pine	*Pinus elliottii*
Southern red oak	*Quercus falcata*
Sugar maple	*Acer saccharum*
Sweetgum	*Liquidambar styraciflua*
Tulip poplar	*Liriodendron tulipifera*
White oak	*Quercus alba*
Virginia pine	*Pinus virginianus*

Birds:

Common Name	Scientific Name
American coot	*Fulica americana*
Brown-headed nuthatch	*Sitta pusila*
Carolina chickadee	*Poecile carolinensis*
Carolina wren	*Thryothorus ludovicianus*
Eastern screech owl	*Otus asio*
Eastern towhee	*Pipilo erythrophthalmus*
Eastern wood-pewee	*Contopus virens*
European starling	*Sturnus vulgaris*
Great crested flycatcher	*Myiarchus crinitus*
Pileated woodpecker	*Dryocopus pileatus*
Red-bellied woodpecker	*Melanerpes carolinus*
Red-cockaded woodpecker	*Picoides borealis*
Tufted titmouse	*Parus bicolor*

Herpetofauna:

Common Name	Scientific Name
Black rat snake	*Elaphe obsolete obsoleta*
Blue-spotted salamander	*Ambystoma laterale*
Bronze frog	*Rana clamitans clamitans*
Copper-bellied water snake	*Nerodia erythrogaster neglecta*
Eastern newt	*Notophthalmus viridescens*
Flatwoods salamander	*Ambystoma cingulatum*
Florida cooter	*Pseudemys floridana*
Mole salamander	*Ambystoma talpoideum*
Narrow-mouthed toad	*Gastrophryne carolinensis*
Southern toad	*Bufo terrestris*
Spotted salamander	*Ambystoma maculatum*
Striped newt	*Notophthalmus perstriatus*
Wood frog	*Rana sylvatica*
Yellow-bellied sliders	*Trachemys scripta*

Mammals:

Common Name	Scientific Name
Black bear	*Ursus americanus*
Bobcat	*Felis rufus*
Cotton mouse	*Peromyscus gossypinus*
Cotton rat	*Sigmodon hispidus*
Golden mouse	*Ochrotomys nuttalli*
Gray squirrel	*Sciurus carolinensis*
Least shrew	*Cryptotis parva*
Marsh rabbit	*Sylvilagus palustris*
Raccoon	*Procyon lotor*
Red bat	*Lasiurus borealis*
Southern flying squirrel	*Glaucomys volans*
Southern short-tailed shrew	*Blarina carolinensis*
White-tailed deer	*Odocoileus virginianus*