## Goals and objectives

Understanding how species coexist is important to developing management practices that sustain biodiversity and crop tree production in agroecosystems. Conventional forest management strategies homogenize growing conditions and focus productivity on one or few crop species (Puettmann et al., 2009; Messier and Puettmann, 2011). Such practices are often detrimental to the existence of non-crop species and system functionality. In North America, managed forest lands are no different, where ecosystem function and diversity of ecologically important indicator organisms like vascular plants and herpetofauna have declined significantly over the past century (Ellison et al., 2005; Butchart et al., 2010; USDA, 2011).

Maintaining species diversity, a measure of biodiversity, is important in managed systems because species have different ecologies or traits that, together, support ecosystem goods, services, and functions and provide resilience and adaptation to stress or perturbation. Previous studies have shown that canopy gaps created by natural disturbance can be mechanisms for diversity in unmanaged forests because gaps create variation in microclimatic conditions and associated resources allowing plant and animal species with different traits to coexist within gaps and across the forest matrix (Beckage and Clark, 2003; Hanson and Lorimer, 2007; Gavel et al., 2010). Theoretically, forest management practices that emulate natural canopy gap patterns, processes, and theory are expected to maintain or restore biodiversity (Seymour and Hunter, 1999).

We seek to determine if gap-based forest management, designed, in part, on natural disturbance patterns and processes, can maintain crop tree productivity along with diversity and functional traits of vascular plant community, herpetofauna, and arthropods across a broad geographic gradient. Our study ecosystems, the oak-hickory (*Quercus-Carya*) forests of the Appalachian Mountains and Cumberland Plateau and maple-beech-birch forests (*Acer-Fagus-Betula*) of the upper Great Lakes Region represent systems in which forest management activities focused on the restoration or maintenance of diversity is of ecological and economic importance. We hypothesize that harvest-created gaps of varying sizes, and the resultant heterogeneity in resource availability, creates an environment conducive to continued production of extractive and non-extractive ecosystem goods and services associated with diverse forests. Specific objectives are to (1) Quantify spatial and temporal heterogeneity in microclimatic conditions and soil resources within and among harvest-created gaps, (2) Evaluate the influence of resource availability, gap characteristics, and vegetation structure on species diversity, tree regeneration dynamics, and functional traits associated with tree seedlings, understory vascular plants, arthropods, and herpetofauna, and (3) Assess the influence of harvest-created gaps and resource availability on crop-tree productivity, and compare long-term potential of gap-based and conventional forest management approaches to sustain productivity and biodiversity.

## Background and Recent Activities

Concepts regarding the sustainability of forest ecosystems have changed dramatically over the past few decades. Previously, sustainability was largely determined by the ability of a system to produce a continuous supply of timber and timber-related products. As a consequence of this limited view of sustainability, the focus of forest management on many lands was to homogenize growing conditions and focus productivity in one or few crop species (Puettmann et al., 2009; Messier and Puettmann, 2011) at the expense of non-crop species and system functionality. Societal views on forests and the role of forest management, in particular, continue to evolve, with a less utilitarian view of forests and sustainability emerging (Bengston et al., 1999; Shindler and Carmer, 1999; Bengston et al., 2004). Today, the concept of sustainability is focused on balancing the ecological, social, and economic considerations associated with forests and forest management. The switch from managing for a sustained yield of timber to managing for the full range of services and values provided by forest ecosystems (e.g., biodiversity, wildlife habitat, watershed protection, resistance and resilience to disturbance), forest certification efforts and the management restrictions imposed by certifying organizations, and management of habitat associated with threatened and for endangered animal species (e.g., Indiana bat (*Myotis sodalis*), northern long-eared bat (*Myotis spetentrionalis*) has caused land and resource managers to re-examine the efficacy of using traditional silvicultural practices to meet current goals and objectives associated with forest management.

Within this more comprehensive and holistic view of sustainability is a growing recognition of the role biological diversity has in maintaining productive and resilient agroecosystems, including managed forests (Mace et al., 2012). Ecosystem services linked to the maintenance of biodiversity within and among trophic levels in managed forests include numerous tangible, or provisioning services, such as the production of wood and fiber (Zhang et al., 2012), forage production (Sanderson et al., 2004), and fresh water (Brantley et al., 2013), as well as services less easily quantified, including supporting and regulating services, including erosion control (Hales et al., 2009), carbon sequestration and storage (Bunker et al., 2005), and nutrient cycling (Tilman et al., 1996). Maintaining, restoring, or increasing biodiversity increases the ability of a system to respond to change or disturbance (Mori et al., 2012), and further acts as insurance allowing the system to function even if species are lost (Yachi and Loreau, 1999). Furthermore, maintaining high levels of biodiversity can act as a barrier to alien (e.g., non-native plants, insects, and pathogens) invasions (Kennedy et al., 2002); a disturbance that will continue to threaten the health and sustainability of eastern US forests (Miller et al., 2013; Keyser et al., 2014).

Widespread acknowledgement exists regarding the role of disturbance in controlling or shaping patterns of biological diversity (e.g., composition, species diversity, functional diversity) (White and Pickett, 1985). Anthropogenic disturbances, such as timber harvesting, tend to homogenize forest structure and composition at both stand- and landscape-levels (Mladenoff and Pastor 1993; Lorimer, 2001). In contrast, natural disturbances often create heterogeneity in the spatial and temporal availability of plant essential resources (e.g., light, nutrient, soil moisture) conducive to the establishment, growth, and recruitment of a variety of species and functional traits both within and among trophic levels (Pickett and White, 1985; Elliott et al., 2002; Ritter et al., 2005). In eastern hardwood forests, natural disturbance regimes are dominated by small to intermediate-sized, partial disturbance events that result from single-tree to small group tree mortality (i.e., gap-phase dynamics) and exogenous disturbances, such as wind and ice storm events and insect and disease outbreaks (White et al., 2011). Large, landscape-level disturbances are rare, occurring at very long timescales (Seymour et al., 2002; White et al., 2011).

Designing and implementing strategies and management activities based on natural disturbance regimes, consequently, has been proposed as a means to actively manage forest ecosystems for both extractive, provisioning ecosystem services, including wood and fiber, and non-extractive forest products, including the conservation of biodiversity within and among trophic levels at both the stand- and landscape levels (Seymour et al., 2002; Perera et al., 2004; Long, 2009). For instance, selection silvicultural systems, where trees are harvested singly (Lorimer, 1980; Runkle, 1982; Dahir and Lorimer, 1996) or in groups (Elliott et al., 2011), are example management approaches that closely emulate natural canopy gaps created in small to intermediate disturbances. Harvest-created gaps are mechanisms to influence species or functional group diversity of managed forests, because they generate variability in limited resources, including light (Canham et al., 1990), soil moisture (Gálhidy et al., 2006), and nutrients (Prescott, 2002) from gap center into the adjacent forest matrix. Harvests in these systems support ecological theory and the notion that canopy gaps have functional a role in biodiversity. Specifically, the resource heterogeneity resulting from the formation of canopy gaps, both natural and harvest-created, and the resultant species or functional group response (e.g., establishment, growth, and survival) to those resource gradients forms the basis for the Gap Partitioning Hypothesis (GPH) (Ricklefs, 1977; Denslow, 1980) (**Fig. 1**). Many short-term studies have failed to support, or have found only limited support, for the GPH as a mechanism for tree diversity (e.g., Gray and Spies, 1996; Busing and White, 1997; Beckage and Clark, 2003), although partitioning could occur over longer time spans as differential patterns of survival among species occur (e.g., Raymond et al., 2006). In general, there is greater support for niche partitioning in larger rather than smaller canopy gaps (Whitmore, 1989). As an alternative, Hubbell et al., (1999) proposed that stochastic events/processes rather than species-specific niches, in part, control diversity. Although there is only moderate support for the GPH among tree species, a plant community of limited species richness, recent studies have documented gap partitioning in the larger forest non-tree plant community (e.g., Fahey and Puettmann, 2007; Kern et al., 2013), suggesting that harvest-created canopy gaps can be a mechanism to conserve or increase within-stand biological and structural heterogeneity of species rich communities.

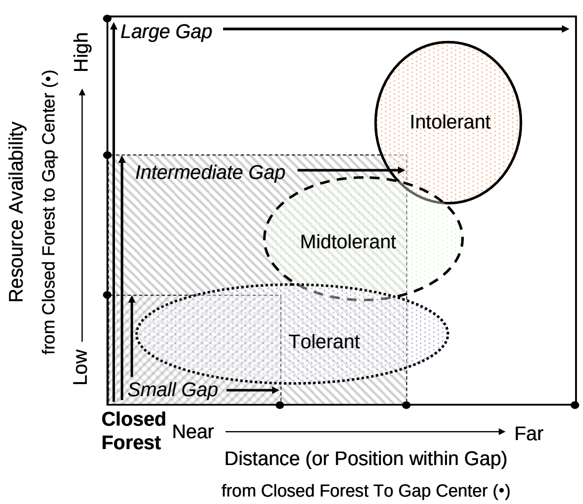


**Fig. 1.** The gap partitioning hypothesis predicts that composition is partitioned across gap sizes or within gap positions. Graph is a hypothetical relationship for shade tolerance strategies. Shade tolerance groups spatially partition resources within gaps (y-axis). Stress and competition constrain tolerance groups within the gap (x-axis). Tolerant species dominate in gap edge positions. Intolerant species dominate in large gap center positions. Midtolerant species are intermediate in gap position to tolerant and intolerant species, and, as a result, composition is partitioned by gap position. Gap size is also partitioned with intolerant species unique to large gaps, midtolerant species dominating in intermediate gaps, and shade tolerant species dominating small gaps.

Our proposed study will build upon current research conducted by PDs and others. The goal is to quantify and describe the effects of disturbance-based silvicultural system on the diversity of key ecosystem components in two ecologically and economically important broadleaf forest types in the eastern US. Recent work by PDs has demonstrated strikingly different outcomes of gap-based, or disturbance-based, forest management both within and across forest ecosystems.

**Project Rational and Significance**

In the eastern United States, the majority of forestland (87%) is privately owned (USDA, 2011). With a relatively minor amount of this forestland under formal protection, these public and privately owned “matrix forests” (Lindenmayer and Franklin, 2002) will play an essential role in providing the attributes necessary to sustain ecosystem function and contribute to the conservation of biodiversity at multiple spatial and temporal scales. Our study sites are located in the oak-hickory forests of the CHR (Cumberland Plateau of Kentucky and the southern Appalachian Mountains in western North Carolina) and the maple-birch-beech forests of the Northern Hardwood Region (NHR) (northern Wisconsin and the Upper Peninsula of Michigan). Together, these two forest types (oak-hickory and maple-birch-beech) comprise two-thirds of all broadleaf forests in the eastern U.S. Forest management efforts in these two regions have been focused primarily on timber production and extraction of economically valuable tree species. These matrix forests present an opportunity to restore and maintain primary ecosystem services, including the conservation of biodiversity, while continuing to provide the economic benefits from the production of timber and non-timber related forest products.

The economic benefits of forestry-related industries in these regions are substantial; exemplifying the socioeconomic importance of developing sustainable forestry practices that will maintain the flow of ecosystem services now, and into the future. In 2005, 75% of the total export value of forest products from the US was produced by the southern and northern regions of the US (USDA, 2011). At a more local level, the forest and wood products industry contributes an estimated $12.8 billion to the economy of Kentucky, with 2.5% of all employment linked to forestry-related industry (Kentucky Forestry Agriculture Economic Summary 2013-2014). In North Carolina, during 2011, 19% of all manufacturing jobs were directly or indirectly connected to the forest products industry, with an estimated $4.1 billion of North Carolina's Gross Domestic Product tied to the sustainable forestry practices and the production of forest products (North Carolina Forestry Association). In the Upper Peninsula of Michigan, 6% of all employment in the region is associated with the forest products industry (Leefers, 2007).

In addition, the ecological benefits of these diverse forests are substantial. In the CHR, mixed oak-hickory forests occupy over 50% of the forested land base (Johnson et al., 2002). These mixed-hardwood/oak-hickory forests are some of the most diverse temperate forests in North America, and harbor a high level of endemic and threatened and endangered plant and animal species (Trani-Griep and Collins, 2013). Over the past half-century, a decline in the diversity of oak-hickory forests has been observed. In many areas, lack of disturbance has permitted shade-tolerant red maple (*Acer rubrum*) to increase in abundance (Fei et al., 2011), while conventional silvicultural methods have reduced diversity by promoting the regeneration of shade-intolerant species, such as yellow-poplar and sweet birch (*Betula lenta*) (Loftis, 1983; Beck and Hooper, 1986; Beck, 1988). The potential loss of the ageing oak cohort (Keyser et al., 2014) due to insect and disease outbreaks, senescence, and regeneration failure resulting from ineffective forest management practices is particularly important in the CHR. Leaf physiognomy, leaf decomposition rates, and bark texture specific to oaks enhances arthropod abundance, which is a primary food source for many bird species (Rodewald, 2003), and contributes to higher bird diversity in oak forests than in forest types dominated by a single species. Furthermore, acorns, a 'keystone' forest resource for over 90 wildlife species (Martin et al., 1951) in the CHR, influence reproduction and survival of vertebrate species (Clark, 2004), including small mammals that are an important prey base for raptors and carnivores and predators of songbird nests (McShea, 2000). The distribution, abundance, and behavior of wildlife ranging from migratory birds to black bear (*Ursus americanus*) are associated with these diverse forests (McShea and Healy, 2002; Rodewald, 2003; Clark, 2004; McShea et al., 2007). Consequently, the failure to effectively manage for the diverse suite of species common throughout the CHR, including oaks, has the potential to impact a variety of ecosystem components within and across various trophic levels.

Similarly, in the northern hardwood forests, past management strategies have homogenized the regional forest composition and structure (Schulte; Mladenoff et al., 2007) and increased abundance of the crop species, sugar maple (*Acer saccharum*) (Schwartz et al., 2005). At the same time, ecologically and economically important species, such as yellow birch, have declined in abundance (Crow et al., 2002). Loss of yellow birch may have cascading effects on ecosystem functionality, because it provides forage and unique physiognomy qualities important to avian and insect communities (Holmes and Robinson, 1981). Thus, creative management approaches that emulate natural disturbance, such as gap-based management, are needed to increase compositional and structural heterogeneity and support a range of biota and ecosystem functions in the NHR as well.

Relative to the complex mosaic of stand structures and species assemblages that would have existed 'naturally', past land-use (e.g., exploitive logging, agriculture and subsequent land abandonment) and exogenous disturbance events (e.g., introduction of non-native insects and pathogens) coupled with conventional forest management activities focused on sustained timber production of a select few crop tree species have simplified forest structure and composition across multiple spatial scales (Roberts and Gilliam, 1995; Mladenoff and Pastor 1993; White et al., 2011; Schifley and Thompson, 2011) in the Northern and Central Hardwood Regions. The development of novel silvicultural systems designed and patterned after natural disturbances, or ones that incorporate key elements of a system's natural disturbance regime, into the management of eastern broadleaf forests has lagged behind that in other areas and forest types in the US (e.g., Pacific Northwest, ponderosa pine forests in the southwestern US, longleaf pine systems in the eastern US). Our proposed study seeks to reveal the effects of gap-based forest management on aspects of biodiversity, including species and functional trait diversity, of key ecosystem components and biota within and among forest types in the Northern and Central Hardwood Regions.

## *TREE REGENERATION*

Alternatives to 'business-as-usual' forestry practices are needed to meet the changing goals and objectives associated with forests and forest management. Business-as-usual models in the NHR and CHR include widespread application of single-tree selection and even- or two-aged regeneration methods, respectively, that emulate minimal aspects of natural disturbance (Seymour et al. 2002). The development and testing of gap- or disturbance-based silvicultural methods that utilize expanding gaps, gaps with seed-trees, and/or a range of gap sizes as an alternative are in need examination for their potential to restore and/or conserve biodiversity while continuing to produce a sustainable supply of timber and non-timber forest products. The efficacy of these approaches on tree regeneration is foundational to forest sustainability, biodiversity and economic revenue.

## *HERBACEOUS VEGETATION*

The understory plant community contributes to the production and sustainability of a wide variety of ecosystem goods and services. Although forest management practices are often designed and implemented to regenerate and recruit a specific suite of tree species, usually of commercial value, it is the ground layer flora that contributes the most to plant diversity in eastern broadleaf forests (Gilliam and Roberts, 2003). From the studies conducted in eastern broadleaf forests and listed in Gilliam (2007), for every tree species in a forest stand, there are, on average, four species in the herbaceous layer (Gilliam et al., 1995; Roberts and Zhu, 2002; Elliott et al., 1997; Elliott and Knoepp, 2005; Pittillo and Lee, 1984). Relative to its contribution to aboveground biomass, the forest understory plant layer contributes significantly to net primary productivity (Welch et al., 2007), influences and regulates nutrient cycling (Muller, 2003), and provides forage and habitat for game and non-game wildlife species (Cary and Johnson, 1995; Greenberg et al., 2007). In addition, the herbaceous layer can significantly influence tree seedling dynamics through competition, thereby influencing the structure and composition, and hence, diversity, of the forest overstory in managed forest ecosystems (Beckage et al., 2000; George and Bazzaz, 2003)

Quantitative information regarding the effects of gap-based management on species and functional diversity of the ground layer flora are limited. Ideally, harvest-created gaps emulate the heterogeneity in substrate and resource availability of naturally-created gaps from windthrow. The variable conditions of natural gaps increase species diversity as well as increase functional trait diversity in the ground layer (Elliott et al., 2011). Consequently, management activities patterned on natural gap formation in eastern broadleaf forests (Roberts and Gilliam, 1995) may be a mechanism by which to increase heterogeneity and biodiversity in forest understories (Fahey and Puettmann, 2007; Kern et al., 2014).

*ARTHROPODS*

Arthropods have been widely used as bio-indicators of ecosystem change (e.g., Longcore 2003; Rainio and Niemelä 2003; Latty et al. 2006; Ulyshen et al. 2006). Canopy disturbance in forested ecosystems can influence arthropod abundance and composition as a result of higher irradiance (Shure and Philips 1991; Greenberg and Forrest 2003; Latty et al. 2006), fluctuations in leaf litter depth (Duguay et al. 2000; Latty et al. 2006), and/or coarse woody debris dynamics (Ulyshen et al., 2004; Latty et al., 2006). For example, across 22 forest sites in northern Wisconsin and the Upper Peninsula of Michigan, Latty et al. (2006) found that opening area, coarse woody debris volume, percent cover of ground-layer vegetation, and forest floor depth were all important variables in structuring carabid beetle communities (Carabidae). Similarly, clear patterns in family level abundance were observed by Shields et al. (2008) between gaps of different sizes and the forest matrix in a study in the Upper Penninsula of Michigan. Carabids were consistently more abundant in the forest matrix than openings, but the differences were not statistically significant. Likewise, in North Carolina, Greenberg and Forrest (2003) found that ground-dwelling arthropods were less abundant in canopy openings than surrounding forests; likely, as a result of differences in microclimate and litter layer depths.

As reviewed above initial responses of forest arthropods to canopy openings have been investigated in some detail; however, much less is known about changes in arthropod abundance and composition as gaps mature, and few studies have paired arthropod sampling with as detailed data on microclimate, vegetation, and predation (herpetofauna) as proposed herein. This information is needed to better understand the long-term consequences of forest management in time and space on biological diversity. Given their predominantly predatory nature, the sensitivity of forest-specialist carabids to changes in forest canopy cover, and their wide distribution, carabids have been suggested as useful bio-indicators in forest ecosystems (Lövei and Sunderland 1996; Oates et al. 2005; Latty et al. 2006; Ulyshen et al. 2006). Consequently, we propose to study this family in detail.

*HERPTOFAUNA*

Both reptiles and amphibians (herpetofauna) are important components of forested ecosystems in North America. For example, salamander densities range from 3,000 to 18,000 individuals/ha in eastern North American forests and some snake species may exceed 1,000 individuals/ha

(Burton and Likens, 1975; Fitch 1975; Hairston, 1987; Petranka, 1993; Petranka and Murray, 2001). Exceptional densities suggest the importance of herpetofauna in forest trophic dynamics as they convert large quantities of invertebrate prey to vertebrate biomass and provide a food resource to mammals, birds, and other forest-dwelling animals (Davic, 1983; Petranka, 1998; Davic and Welsh, 2004). Through predation of invertebrates, reptiles and amphibians also influence nutrient cycling and energy flow within forests (i.e., Davic and Welsh, 2004). For example, predation by salamanders on arthropods results in higher rates of leaf litter retention (Wyman, 1998; Best and Welsh, 2014, but see Homyack et al., 2010; Hocking and Babbitt, 2014). These findings suggest that herpetofauna may play a significant role in forest ecosystem processes such as soil building, plant nutrient cycling and carbon capture (Welsh and Hodgson, 2013).

Recently, herpetofauna have been touted as outstanding indicators of forest ecosystem health (Welsh and Droege, 2001; Welsh and Hodgson, 2008; but see Kroll et al., 2009). Reptiles and amphibians are often easily and cost-effectively monitored, individuals occupy small home ranges (1-4 $m^2$) and population sizes, of some species, exhibit considerable interannual stability in undisturbed forests relative to other animal groups (Hairston, 1987).Yet, reptile and amphibian populations respond quite differently to forest management. Canopy removal, loss of leaf litter, loss of downed woody debris, that lead to changes in environmental conditions often negatively impact amphibian populations (Welsh and Droege, 2001; Tilghman et al., 2012). In a recent review by Tilghman et al., (2012) that incorporated 24 studies examining the effects of canopy removal on salamanders, salamander populations almost always declined following timber removal; mean harvest-related declines ranged from 29% for long-term response to partial canopy removal to 62% for short-term responses to clearcutting. Conversely, timber harvest often creates thermal environments that lead to increases in abundance of some reptile species (Perison et al., 1997; Cantrell et al. 2013). Todd and Andrews (2008) found that thinning of pine stands lead to higher abundances of small woodland snakes, although clear cutting greatly reduced snake populations.

Knowledge on the response of herpetofauna to gap-based forest management is quite limited (but see Messere and Ducey, 1998). Gap-based management may provide thermal and habitat heterogeneity that can increase herpetofauanal biodiversity. Yet, gaps, due to their small size and similarity to natural disturbance, may reduce the long-term, negative responses seen in clear-cut stands. Furthermore, previous studies have not paired herpetofauna abundance and richness with detailed information on prey abundances (i.e., invertebrates) and microhabitat structure (i.e., herbaceous vegetation) and have not examined how herpetofauna populations change as gaps age.

**Project Relation to Program Area Priorities**

This project addresses Program Area Priority – Agroecosystem Management (A1451) under the Renewable Energy, Natural Resources, and Environment Program Area. This program area priority seeks to develop and evaluate innovative agroecosystem management practices and systems for their potential to enhance ecosystem services. Within the eastern broadleaf forest biome, current forest management practices homogenize forest structure and simplify species compositional diversity at both stand- and landscape-level, often at the expense ecologically important biota and ecosystem functions. Our proposed study seeks to compare and contrast the short- and longer-term effects of disturbance-based forest management practices that creatively emulate canopy gap functions on the diversity of four key ecosystem components – (1) tree regeneration, (2) ground-layer flora (3) arthropod community, and (4) herpetofauna – as well as the ability of disturbance-based management strategies to maintain crop tree productivity for sustained timber production within and among ecologically and economically important forests of the Central and Northern Hardwood Regions of the eastern US.

**Project's Potential for Improving Sustainability of Agroecosystems**

Healthy agroecosystems, including managed forests, provide a multitude of ecosystem goods and services, including timber and fiber and associated economic revenue, watershed protection, clean water, forage production for game and non-game wildlife species, erosion control, carbon sequestration and storage, and nutrient cycling. The switch from managing for primarily timber production and extraction to managing for the full range of services and values provided by forest ecosystems (e.g., timber and non-timber forest products, biodiversity, wildlife habitat, watershed protection, resistance and resilience to disturbance), public attitudes towards forest management (e.g., Saunders and Swihart, 2013), sustainable forest certification efforts, and management of habitat associated with threatened and endangered plant and animal species has caused land and resource managers on both public and private lands to re-examine the efficacy of business-as-usual management approaches.

This research project is designed to test the efficacy of disturbance-based silviculture to manage species diversity and crop-tree production in second-growth, mixed broadleaf forests in the eastern US. Based on ecological theory and natural disturbance studies, we hypothesize the spatial and temporal heterogeneity in resource availability and microclimatic conditions produced by gap-based management will facilitate plant and animal species with functionally different traits to coexist within and among gaps and the forest matrix. As forest management on public lands becomes focused on resilience and resistance to disturbance, the need to find alternative or novel silvicultural practices that conserve or restore biodiversity will be required to meet management goals and objectives (UDSA, Forest Service, National Forest System Land Management Planning, 2012). For private landowners interested in managing lands for a variety of benefits (e.g., wildlife habitat, periodic revenue), the increasingly negative views towards traditional, even-aged silvicultural methods (Saunders and Swihart, 2013; Pakkala et al., 2011) further emphasizes the need for research to develop effective alternative methods to manage matrix forest land. If our hypothesis is supported, implementing gap-based silviculture as an alternative, or complement to traditional silvicultural practices, will provide for a sustainable supply of timber and fiber while conserving biodiversity in forests where the restoration or maintenance of diversity is of critical ecological and economic importance.