

REVIEW ARTICLE

Assessing the potential impact of retaining native off-site tree species in woodland restoration

John L. Willis^{1,2}, Don C. Bragg^{3†}, Jeffery B. Cannon⁴, Kamal J. K. Gandhi⁵, Kathryn R. Kidd⁶, Adam D. Polinko⁷, Joshua J. Puhlick⁴, Daniel Saenz⁸, Mary Anne Sayer⁹, Christopher M. Schalk⁸, Andrew B. Self⁷, Courtney M. Siegert⁷, J. Morgan Varner¹⁰

Reestablishing appropriate tree species is an important step in converting off-site monocultures into woodlands. Species conversion is often necessary, as off-site exotic species rarely function like woodland species. However, when off-site tree species are native, and functionally redundant to woodland species, conversion may be unnecessary. To explore this possibility in the southeastern United States, we reviewed the literature on trait differences among the primary southern pines and qualitatively assessed the effect of their identity at the species and stand-levels. In this region, woodland restoration focuses on removing loblolly (*Pinus taeda*) and slash pine (*P. elliottii*) to reestablish longleaf (*P. palustris*) or shortleaf pine (*P. echinata*). Our review found minimal variation among species in understory flammability, fire resistance at maturity, and Red-cockaded Woodpecker (*Leuconotopicus borealis*) habitat at the stand-level. Longleaf and shortleaf pine were generally more resistant to abiotic and pest disturbance at the tree-level; however, stand-level differences in wind, drought, and boring insect resistance among southern pines growing in open forests were considered minimal. Retaining loblolly and slash pine will improve stand-level productivity in the short term, but creates regeneration problems due to low juvenile fire resistance and resilience. Ice resistance and long-term carbon sequestration will also likely be reduced by retaining loblolly and slash pine. Collectively, these results suggest that southern pine species are generally interchangeable at the stand-level in woodlands; although woodlands featuring loblolly and slash pine may be less stable in the face of disturbance than those dominated by shortleaf and longleaf pine.

Key words: flammability, forest structure, *Pinus* spp., Red-cockaded Woodpecker, resistance, restoration, southern pine

Implications for Practice

- When off-site tree species are native and functionally comparable to woodland species, retention becomes an increasingly viable restoration strategy, especially if woodland structure mitigates species-level trait differences.
- Underplanting within the retention strategy may not be necessary if a high-level of functional redundancy exists between off-site and woodland tree species.
- Woodlands featuring slash or loblolly pine may be less stable to disturbance than woodlands featuring shortleaf or longleaf pine.
- Periodic lengthening of the fire return interval to accommodate regeneration will be needed to increase the stability of loblolly and slash pine woodlands.

Introduction

Globally, temperate woodlands are among the most threatened ecosystems (Hoekstra et al. 2005), and one of the primary factors contributing to their decline has been the expansion of forest monocultures (Chazdon 2008; Veldman et al. 2015). Occupying 131 million hectares, monocultures often feature off-site tree species at high densities, low herbaceous diversity, decreased light availability, and degraded wildlife habitat (Kanowski

et al. 2005; Castaño-Villa et al. 2019; FAO 2020). Consequently, organizations tasked with restoring native ecosystems often convert monocultures back into woodlands (Gómez-Aparicio et al. 2009; Osem et al. 2015).

Foresters have traditionally addressed stand type conversions by clearcutting off-site species and planting once prevalent target species to match species composition of a reference

[†]Deceased.

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¹Southern Research Station, USDA Forest Service, Auburn, AL 36849, U.S.A.

²Address correspondence to J. L. Willis, email john.willis@usda.gov

³Southern Research Station, USDA Forest Service, Monticello, AR 71656, U.S.A.

⁴The Jones Center at Ichauway, Newton, GA 39870, U.S.A.

⁵D.B. Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602, U.S.A.

⁶Arthur Temple College of Forestry and Agriculture, Stephen F. Austin State University, Nacogdoches, TX 75962, U.S.A.

⁷Department of Forestry, Mississippi State University, Mississippi State, MS 39762, U.S.A.

⁸Southern Research Station, USDA Forest Service, Nacogdoches, TX 75965, U.S.A.

⁹Southern Research Station, USDA Forest Service, Pineville, LA 71360, U.S.A.

¹⁰Tall Timbers Research Station, Tallahassee, FL 32312, U.S.A.

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condition (hereafter “conversion strategy”) (Fig. 1) (Covington et al. 1997; Haddad et al. 2021). Adopting the conversion strategy can successfully reestablish target species, create open canopy conditions, and disrupt undesirable ecological feedbacks created by off-site species (Nowacki & Abrams 2008; Freeman & Jose 2009); yet conversion also removes large trees from the landscape, requires multiple decades to develop mature structure, and can be expensive.

An alternative approach to the conversion strategy emphasizes structural retention over immediate species conversion (hereafter “retention strategy”). First proposed by Kirkman et al. (2007), the retention strategy first creates forest structure by cutting off-site species to a woodland density (98–244 trees/ha, 35–70% stocking); species composition is then slowly accomplished through a combination of underplanting and periodic removals of off-site species (Fig. 2). Globally, variants of the retention strategy have been used to reestablish native vegetation beneath off-site monocultures (Ashton et al. 1997; Forbes et al. 2015). However, underplanting may be unnecessary if the off-site and target species are functionally similar (Londe 2021). In such situations, the similarity between species should negate the need to underplant reducing the time and cost of restoration.

One location where species redundancy could be incorporated into woodland restoration is the southeastern United States. Here, monocultures of loblolly (*Pinus taeda*) and slash (*P. elliotii*) pines were planted on tens of millions of

hectares of woodland sites once dominated by longleaf (*P. palustris*) and shortleaf (*P. echinata*) pines following agricultural abandonment (Guldin 2019; Oswalt et al. 2019). Attempts to restore woodlands in this region have historically applied the conversion strategy and have just recently considered retention. However, given the taxonomic similarities among southern pines, it is reasonable to expect that a retention strategy without underplanting could be a viable, cost-efficient alternative. Nevertheless, the biological trade-offs associated with perpetuating off-site southern pines as the overstory component of a mature woodland are not well understood.

To evaluate the potential importance of pine species identity in southeastern woodlands, we used Google-Scholar to conduct a literature review focused on trait differences among species and species effects on stand-attributes. Specifically, we targeted studies relevant to fire dynamics, forest health, resistance to abiotic disturbance, Red-cockaded Woodpecker (RCW; *Leuconotopicus borealis*) habitat, hydrology, and forest productivity. We then used this information to qualitatively assess the effect of southern pine species on understory flammability, fire response, resistance to forest threats (boring insects, wind, drought, and ice), RCW habitat, hydrology, productivity, and long-term carbon sequestration potential, at the tree and stand-levels. These tree and stand-level attributes were selected based on conversations with land managers and our collective experience of important considerations in woodland restoration. While



Figure 1. An example of the conversion strategy in southern pines involves: (A) mature loblolly pine monoculture that is clearcut (B) followed by (C) aerial site preparation to control competing vegetation, (D) hand planting the desired species (in this case, longleaf pine), and (E) seedling development. Source: Photo credit (C & D)—D. Clabo, Assistant Extension Professor, University of Georgia.

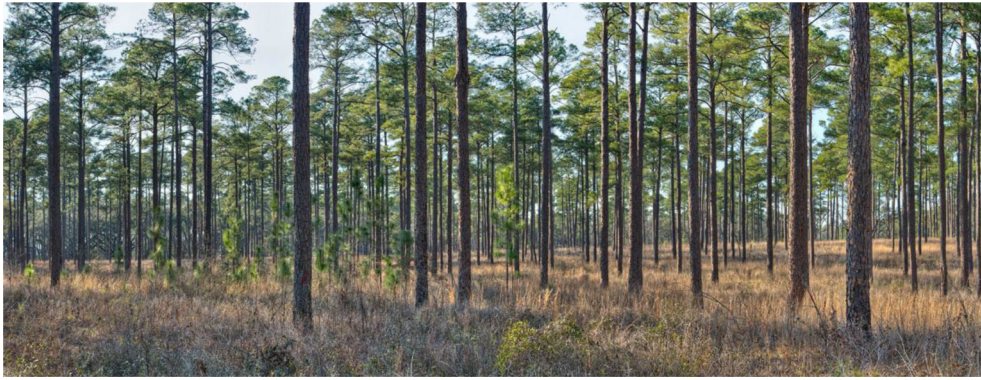


Figure 2. Example of a conversion strategy where longleaf pine has been underplanted beneath a slash pine overstory at the Jones Center at Ichauway, Georgia, United States. Source: Photo credit—R. T. Bryant.

our literature review focuses on the importance of pine species identity to woodland restoration in the southeastern United States, this evaluation process applies to any restoration effort where functional redundancy may exist (Martin 1999; Strauss 2001).

Fire Dynamics

Recurrent fire is essential for maintaining the vegetation structure and composition of pine woodlands. Southern pines are noted for their traits reflecting a long evolutionary history with fire (e.g. bark thickness, pruning rates, seed production and dispersal, seedling growth, and litter flammability) (Keeley & Zedler 1998; He et al. 2012; Varner et al. 2021; Varner et al. 2022). For example, both longleaf and shortleaf pine seedlings possess advantages over other pines in frequently burned environments. The “grass stage” of longleaf pine is an extremely rare trait worldwide in *Pinus* (He et al. 2012; Pile et al. 2017) (Fig. 3A). During the grass stage, longleaf pine have virtually no height growth for an extended period (1–20 years) followed by a “bolting” stage of rapid height growth (Pile et al. 2017) (Fig. 3B). Shortleaf pine lacks a grass stage but its seedlings and saplings vigorously resprout following topkill via dormant buds protected from fire by a basal crook (Fig. 3C & 3D); while loblolly and slash pines rarely resprout severely limiting their relative fire resilience (Mattoon 1915; Clabo & Clatterbuck 2019).

Once established, many southern pines quickly produce thick, fire-resistant bark, which enables vulnerable saplings to survive recurrent surface fires. Southern pines vary in their allocation to bark with longleaf allocating more early growth to bark than slash, loblolly, and (presumably) shortleaf pine (Jackson et al. 1999). However, all southern pines eventually develop sufficiently thick bark to withstand surface fires with minimal impacts; some southern pines can also reflush following fires that kill needles (Sayer et al. 2021). Another fire adaptation is the hastening of crown lifting to avoid foliage and bud damage from convective heating (McGuire et al. 2021). Although all southern pines raise their crowns following canopy closure, they differ in their rate of self-pruning (longleaf pine > shortleaf

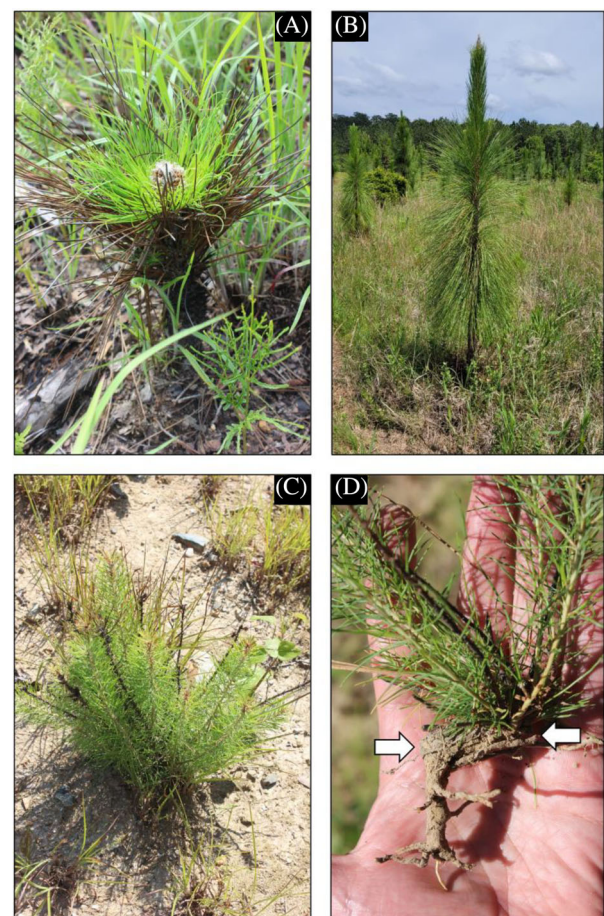


Figure 3. Traits that allow small longleaf and shortleaf pines to survive frequent surface fires: (A) the “grass stage” in longleaf pine produces a thick bundle of green needles that protect the fire-sensitive bud from high heat during a surface fire; during the grass stage, longleaf seedlings build large root systems, (B) allowing for them to rapidly “bolt” this bud up well above lethal heat from most surface fires. While small, shortleaf pine saplings are prolific sprouters (C) from buds located along a basal crook on the soil surface (D) and can resprout repeatedly until they grow large enough to escape topkilling by surface fires.

pine > slash pine > loblolly pine; Keeley & Zedler 1998) which corresponds with trends in fire tolerance.

Southern pines can also influence fire regimes and fuel characteristics. Fallen leaves, branches, and cones—litter—is a primary driver of fire behavior. Southern pine litter are quite flammable and rapidly burns with tall flames, brief smoldering, and nearly complete consumption (Varner et al. 2022). However, species-based differences arise in both needle dimensions and arrangement following senescence. The long needles of longleaf and slash pine often drape over shrubs and herbaceous fuels (Hendricks et al. 2002; Fill et al. 2016), while the shorter needles of loblolly and shortleaf pine tend to collect on the forest floor, lying horizontally and often beneath herbaceous fuels. These patterns in needle deposition produce different microenvironments that affect fuel moisture content (draped litter is drier) and decomposition (perched litter decomposes more slowly; Hendricks et al. 2002), both linked to flammability. Crown attributes also vary by species which influence light transmittance to the understory. Longleaf and shortleaf pine have open crowns that promote herbaceous growth and limit shading relative to the more closed crowns of loblolly and slash pine (Battaglia et al. 2003; Sharma et al. 2012). Thus, subtle differences in fire behavior manifest from the indirect effects of pine species on fuel structure and moisture at the forest floor.

Forest Health

Few empirical studies compare the susceptibility of southern pines to insects and diseases under similar environmental and structural conditions. Therefore, it is difficult to discern whether restoration strategies can affect forest health at the stand-level. The primary southern pines vary in their relative susceptibility to major pathogens and insect pests, providing some justification for adopting a conversion strategy. Loblolly pine stands tend to have the most forest health issues while longleaf pine stands have the least (Boyer 1990). Fusiform rust (caused by *Cronartium quercuum* f.sp. *fusiforme*) is primarily an issue in loblolly and slash pines, and its incidence is much higher in slash than longleaf pine, even when compared to rust-resistant slash pine genotypes (Barrows-Broadbent & Dwinell 1983; Barnard & Van Loan 2003; Moser et al. 2003). While loblolly and longleaf pines can be affected by littleleaf disease (caused by *Phytophthora cinnamomi*), the disease is best known for its impact on shortleaf pine, especially on poorly drained soils (Barnard et al. 1993; Schnake et al. 2021). Unless controlled by prescribed fire, brown spot needle blight (caused by *Lecanosticta acicola*) was once considered a major problem only for longleaf pine seedlings (Siggers 1934). However, this needle blight is now being considered an emerging threat to mid- and larger-sized loblolly pine (Boyer 1990; Pandit et al. 2020).

Compared to longleaf and slash pines, Nantucket pine tip moth (*Rhyacionia frustrana*) more frequently colonizes loblolly pine (Yates III 1966). Slash and loblolly pines have similar susceptibilities to this pest except during the first year after planting when loblolly pine exceeds slash pine in susceptibility (Asaro et al. 2004). Southern pine beetle (SPB; *Dendroctonus frontalis*) causes more damage to loblolly and shortleaf pines than longleaf

and slash pines (Blanche et al. 1983). While adult catches and infestations were similar, especially in mixed-pine stands, Friedenberg et al. (2007) reported that loblolly pine had 3–10 times more infestations and 3–116 times greater tree mortality than longleaf pine during SPB outbreaks. Since resin flow (as a defensive strategy) appears to be similar between longleaf and loblolly pines, the differential activity of SPB may be attributed to the open canopy structure that characterizes longleaf pine stands under frequent fire regimes (Martinson et al. 2007). In a recent study, Ritger (2023) reported that site conditions may contribute to defense, as resin flow of longleaf pine was higher on xeric sites compared to mesic sites; hence, there may be nuanced differences in defensive systems of southern pines based on edaphic conditions. Drought damage could also lead to infestations by secondary insects such as engraver beetles (*Ips* spp.), black turpentine beetle (*Dendroctonus terebrans*), and root-feeding beetles (e.g. *Hylastes* and *Hylobius*) that do not tend to show strong preferences among southern pine species when host defenses are compromised by injury (Connor & Wilkinson 1983; Vogt et al. 2020).

Resistance to Weather Disturbances

Resistance to weather-driven disturbances is an important trait in the southeastern United States, as severe events are regionally common. The ability of southern pines to withstand drought-related physiological disturbance is partially derived from interspecific trait differences. For example, longleaf pine is well-adapted to drought due to a greater investment in its root system, greater stomatal control under water stress, and lower investment in total leaf area compared to loblolly and slash pine (Samuelson et al. 2017, 2019; Garms & Dean 2019). Little is known about the mechanisms underlying shortleaf pine drought tolerance; yet it is often found dominating xeric sites and allocates more resources to coarse roots than loblolly pine following drought (Bradley & Will 2017).

Resistance to physical disturbances is less predictable than physiological events. While shortleaf pine is considered the most resistant southern pine to ice and snow damage because of its small needles, relatively pliable branches and bole, and compact crown, it can still experience extensive losses in severe events (Bragg et al. 2003). Longleaf pine along the coastlines does not grow as tall and has shorter needles compared to those growing in more sheltered locations; shorter trees with shorter needles likely improves wind resistance by reducing drag where hurricanes are most frequent (Patterson et al. 2016). However, some species traits thought to be most relevant to wind resistance are unreliable predictors. For instance, wood-specific gravity, a property linked to modulus of rupture and stem failure (Peltola et al. 2000; Via et al. 2003), is usually slightly higher in coastal taxa (slash and longleaf pines) and lower for the more interior species (loblolly and shortleaf pines) (Jenkins et al. 2004). Yet, higher wood-specific gravity was not a significant factor in the only static winching study comparing southern pine species under similar loads (Garms & Dean 2019).

Environmental context is important when evaluating species effects. Unfortunately, few studies provide sufficient controls

to separate the effects of species from those related to tree size, stand density, age, site conditions, and exposure. When controlling for tree size and age, loblolly pines were less likely to experience severe damage and mortality than longleaf pines following a severe ice storm (Bragg 2016). Compared to shortleaf pine, loblolly pine was twice as likely to be broken or damaged by ice in pure and mixed plantations (Boggess & McMillan 1954). Using several tree species impacted by Hurricane Michael, Rutledge et al. (2021) found that species, size, soil type, and their interactions influenced wind firmness. While their study confirmed that longleaf pine was the most wind-resistant southern pine across a wide range of soil types, Rutledge et al. (2021) also showed that slash pine could be as wind-resistant as longleaf pine on well-drained soils.

The ambiguity in disturbance resistance found among the southern pines arises in part from factors unrelated to species identity but more linked to stand structure. As an example, density-induced alterations of crown and root architecture have potentially important implications for disturbance resistance. High stand densities often produce carbon allocation shifts from root and foliage production to stem growth to increase access to light (Naidu et al. 1998). For instance, the development of an expansive root system (regardless of pine species) begins at an early age and responds to resource competition. Hence, inherent differences in drought tolerance can likely be offset by maintaining open stand conditions, which increase moisture availability and promote root system development (McDowell et al. 2006; Bottero et al. 2017). Because of lower competition for light and other resources, southern pines established in open forests have better developed root systems and are generally less vulnerable to drought and wind disturbance compared to those from high-density stands (Bottero et al. 2017; Bigelow et al. 2021).

RCW Habitat

Improving habitat for declining, threatened, and endangered species is an objective for woodland restoration worldwide (Lindenmayer et al. 2018). In the southeastern United States, many animal species require a conifer component in their habitat, although none require any specific southern pine (Masters 2007). However, southern pines differ in several measurable traits that directly and indirectly impact habitat for endangered species such as RCWs. For instance, bark rugosity (roughness) varies among southern pine species (shortleaf pine < loblolly pine < longleaf pine) and high bark rugosity has been linked to increased arthropod density (Collins et al. 2002; Horn & Hanula 2002). As arthropods are a primary food source for RCWs and other bark-foraging species (Collins et al. 2002; Horn & Hanula 2002), the degree of bark rugosity has potentially important implications for RCW habitat quality.

Pine species identity also affects important RCW tree characteristics. RCWs took significantly longer to excavate completed cavities in longleaf pine (6.3 years) compared to loblolly (2.4 years) and shortleaf pines (1.8 years), likely due to differences in resin flow (shortleaf pine < loblolly pine < longleaf pine) (Conner & Rudolph 1995). However, RCWs nested in

longleaf pine longer than loblolly or shortleaf pine. SPB-induced mortality has been shown to be more prevalent in the less resinous loblolly and shortleaf pine cavity trees compared to longleaf (Conner et al. 1991; Conner & Rudolph 1995). Life-span variation among southern pines may also contribute to habitat creation and sustainability, as tree species is an important predictor of snag availability. Longleaf and shortleaf pine have roughly twice the life expectancy of loblolly pine (Conner et al. 2001), which could affect snag and woody debris production and persistence. Although RCWs do not utilize snags directly, snags provide habitat for Pileated Woodpeckers (*Dryocopus pileatus*) which are known to damage RCW cavity trees (Saenz et al. 1998).

While interspecific trait differences suggest the potential for strong species effects on RCW habitat, a predictable pattern has not emerged. In eastern Texas, for example, longleaf pine snags stood significantly longer than those of loblolly, but not shortleaf pines (Conner & Saenz 2005). Excavation rate and the duration of cavity tree utilization were similar between loblolly and shortleaf pines. In stands with similar management histories, RCWs foraged more frequently in longleaf than slash pine stands (Porter & Labisky 1986); conflicting with earlier work indicating preferential selection of pond (*Pinus serotina*) and slash pine flatwoods and slash pine plantations over longleaf pine flatwoods (Nesbitt et al. 1978). Schaefer et al. (2004) reported that RCWs make more feeding trips, provision greater prey biomass to nestlings, and are in better body condition (mass) in mixed loblolly/shortleaf pine stands than in longleaf pine stands. Zwicker and Walters (1999) quantified RCW foraging behavior in the context of individual tree characteristics in stands containing longleaf, loblolly, pond, shortleaf, and slash pines. In this study, RCWs were only observed foraging on longleaf, loblolly, and pond pine, and there was no difference among pine species in the percentage of trees used for foraging. Rather, tree age and size were better predictors than pine species identity of RCW use, as they preferred to forage on older, larger trees (Zwicker & Walters 1999). Similarly, pine species identity was not important in the selection of trees for nest cavities in mixed-pine stands (Zwicker 1995).

Hydrology

As in many ecosystems, the largest source of variability within the hydrologic budget of southern pines relates to evapotranspiration, which varies as a function of tree structure and physiology. From a structural perspective, interception of incident rainfall on aboveground plant surfaces and subsequent evaporation of rainfall scale positively with increasing aboveground biomass. Open longleaf pine stands managed with frequent prescribed fire have reduced leaf area and therefore diminished rainfall interception and transpiration (Brantley et al. 2017; Qi et al. 2020). Consequently, net precipitation reaching the forest floor is greater in longleaf pine woodlands compared to closed canopy loblolly, slash, and shortleaf pine stands (Roth & Chang 1981). Indeed, restoring degraded longleaf pine woodlands has been shown to increase stream flow (Qi et al. 2022; Younger et al. 2023). However, no studies have examined the

effect of species identity on water dynamics while controlling for stand density. Both the quantity of transpiring leaf surface area and stomatal controls on transpiration during drought influence moisture loss. Longleaf pine has lower water use (Ford et al. 2008), transpiring 33% less than slash pine (Gonzalez-Benecke et al. 2011). This difference is likely due to lower leaf-to-sapwood area ratio and not inherent species-based physiological controls over water use (Samuelson et al. 2012). Additionally, the herbaceous understory associated with frequently burned longleaf pine woodlands has greater water use efficiency than the groundflora found in the absence of fire (Ford et al. 2008). Collectively, these factors suggest that water availability does not vary across southern pines because of innate species-level differences, but rather the structure imposed by management, especially prescribed fire and thinning to low density (Brantley et al. 2017). Furthermore, while no studies have examined the effects of southern pine species on water quality, it is known that forest management also influences this attribute. For example, immediately following prescribed fire, increases in inorganic nitrogen (nitrate NO_3^- , ammonium NH_4^+) is observed in soil solution (Klimas et al. 2020) which can be leached into surface waters. In most cases, nitrogen and other limiting nutrients are quickly taken up by plants returning soil pools to pre-fire levels within weeks to months, although site conditions may extend this timeline (Butnor et al. 2020). Thinning to a woodland density can also improve low flow rate in streams, which is important for regulating their nutrient and sediment contents (Patil et al. 2022; Qi et al. 2022). Thus, creating woodland structure alone is likely to improve water quality.

Productivity, Wood Quality, and Carbon Dynamics

Although productivity, wood quality, and carbon sequestration are not the primary objectives of most woodland restorations, they are important considerations when evaluating long-term outcomes of restoration treatments. Interspecific variation in height growth contributes to productivity differences among southern pines (Oliver & Larson 1996). These patterns evolve in response to competition in addition to disturbance type, frequency, and severity. For example, longleaf pine has less initial height increment compared to other southern pines while in the grass stage, but can grow at a comparable rate after height growth is initiated (Schmidtling 1987; Haywood et al. 2015). When comparing southern pine growth in planted monocultures, slash pine reached a larger volume on mesic sites relative to loblolly pine after 20 years, while slash pine and shortleaf pine performed comparably on xeric sites (Shoulders 1983). Longleaf and shortleaf pines yielded lower volumes compared to loblolly and slash pines (Shoulders 1983). However, Shoulders (1985) suggested that the poor stand-level volume growth of longleaf pine compared to other southern pines may be more associated with high mortality (and thus lower stand densities) rather than slower initial height growth. Nevertheless, it should be recognized that contemporary loblolly and slash pine monocultures have been planted with genetically improved trees that are likely to provide superior growth on all but the most xeric sites (Fox et al. 2007).

Southern pine growth patterns also have strong impacts on wood quality (defined as a set of properties for a particular end use; Schmulsky & Jones 2019). Across southern pine species, specific gravity increases from pith to bark (juvenile wood to mature wood transition), and interannually from low density earlywood to high-density latewood (Schimleck et al. 2022). Specific gravity and interannual variation in earlywood and latewood are similar among southern pines (Miles & Smith 2009). Regardless of species, the specific gravities of southern pines arising from the original forests are significantly greater than those produced in modern monocultures or managed natural-origin stands because juvenile wood proportion and stem growth are positively correlated.

Wood production and specific gravity are both directly related to carbon dynamics. Trees with greater specific gravities contain more carbon than those of lower wood density, assuming similar volumes. While loblolly and slash pine generally maximize volume production over a commercial rotation (25–40 years) (Jokela et al. 2010), longleaf pine sustains growth at ages exceeding 100 years and can surpass 400 years in age, thereby sequestering carbon longer than other southern pines (West et al. 1993; Meldahl et al. 1999). Inherent advantages in drought tolerance and longevity suggests that wood production and carbon sequestration may be better achieved with longleaf and shortleaf pine on xeric sites (Samuelson et al. 2012; Bradley & Will 2017). Longleaf pine may also accumulate more carbon belowground than other southern pines due to its greater allocation to roots and taproot depth (Samuelson et al. 2017). Yet, this capacity does not always translate into greater belowground carbon accumulation, as Butnor et al. (2012) found no significant difference in fine root fraction (<2 mm) soil C among planted loblolly, longleaf, or slash pine monocultures after 49 years.

Implications of Pine Species Identity

Regardless of ecosystem, species redundancy is critical to the success of the retention strategy (Kirkman et al. 2007). This appears to be the case in southern pines, as our review revealed a general pattern of redundancy across most investigated tree-level attributes (Fig. 4). Strong examples of redundancy were found in understory flammability, the primary ecological attribute for maintaining southeastern woodlands, as all investigated southern pines provided flammable litter capable of supporting a frequent fire regime (Fig. 5). Similarly, once maturity is reached, all southern pines possess sufficient bark thickness to survive low-intensity surface fire, which is important for maintaining continuous inputs of fuel and seed to the forest floor (Mitchell et al. 2009) (Figs. 4 & 5). Although interspecific differences in bark rugosity and resin production were found, southern pines proved broadly redundant in terms of providing habitat for RCWs (Figs. 4 & 5). Furthermore, tree-level litter flammability, fire resistance at maturity, and RCW habitat quality likely scale to the stand-level due to the general lack of overstory diversity in southeastern woodlands (Noel et al. 1998). Therefore, for these specific attributes, the retention strategy is likely to achieve a similar level of success regardless of whether underplanting occurs.

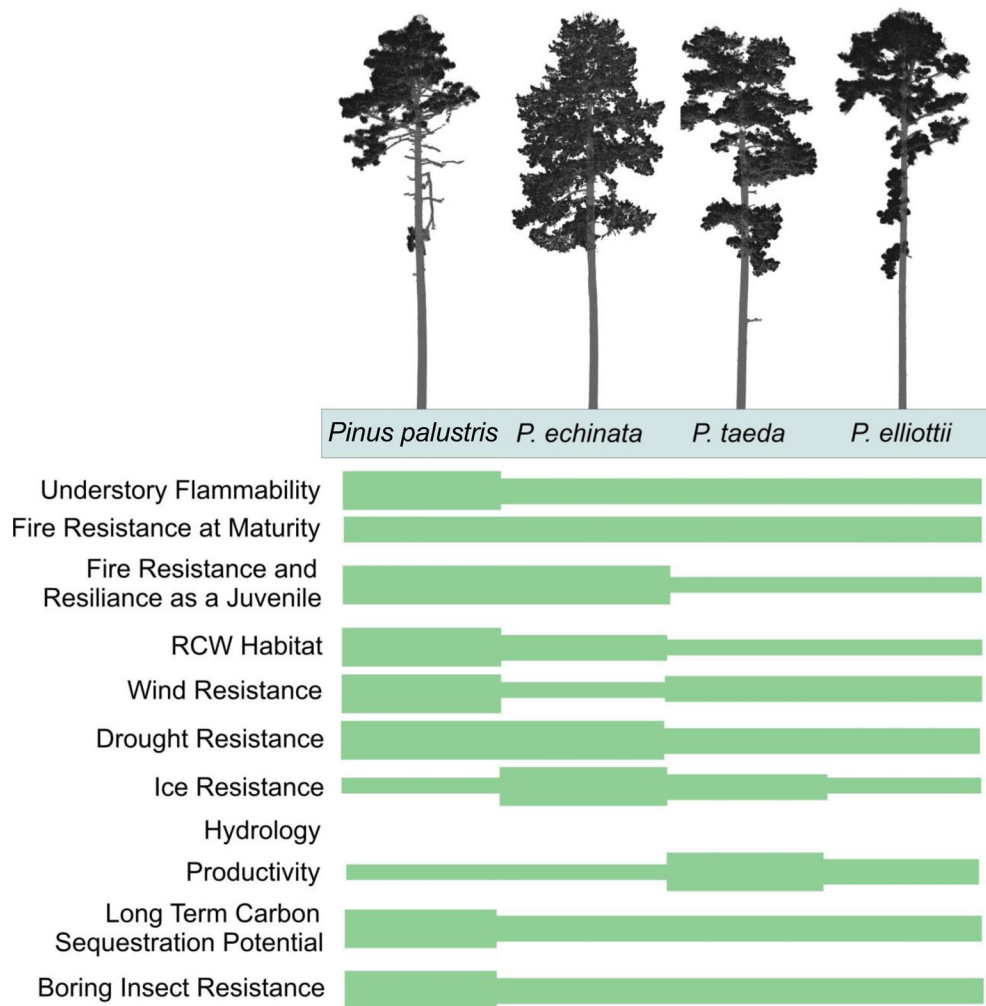


Figure 4. A qualitative assessment of interspecific variation among the four primary southern pines across a variety of tree-level attributes. A species-level functional advantage is depicted by an increased bar width. Functional redundancy is depicted by bars of equal width.

Pine species redundancy was less apparent across other tree-level attributes potentially complicating the use of retention without underplanting (Fig. 4). For example, loblolly and slash pine are less resistant to ice damage than shortleaf pine (Fig. 4). However, intensive cutting to transform monocultures into woodlands could temporarily exacerbate interspecific differences in ice damage resistance (Bragg et al. 2003) (Fig. 5). Ice-induced mortality has the potential to compromise RCW habitat, long-term carbon storage, and understory flammability through the addition of coarse woody fuels. Thus, in areas commonly affected by ice, it would be prudent to underplant shortleaf pine within the retention strategy.

The case for underplanting longleaf pine could also be made for increasing long-term carbon storage potential. No other southern pine possesses the same longevity or resistance to wind, drought, or boring insects (Fig. 4). However, the relative resistance advantage provided by underplanting longleaf pine may be offset by the creation of woodland structure. For example, longleaf pine wind

resistance has been shown to decrease with increases in stand openness (Polinko et al. 2022). Likewise, species-level differences in drought resistance among southern pines is likely to diminish in a woodland structure, as reducing stand basal area broadly increases drought resistance and resilience (Sohn et al. 2016) (Fig. 5). Reducing basal area also increases SPB resistance at the stand and landscape scales (Nowak et al. 2015) (Fig. 5). We suspect that woodland structure exerts a stronger influence on stand-level hydrology than southern pine species identity. However, existing studies comparing species effects on hydrological processes are confounded by stand density (Fig. 5).

One of the biggest concerns of applying the retention strategy without underplanting is the recruitment of new pine cohorts in a frequent fire regime. Indeed, loblolly and slash pine seedlings are often killed by recurrent fire potentially threatening the long-term sustainability of woodland structure (Stewart et al. 2005; Sharma et al. 2020; Robertson et al. 2021) (Figs. 4 & 5). Underplanting shortleaf or longleaf pine would increase the probability

	Inconclusive	Minimal	Moderate	Moderate to Strong	Strong
Understory Flammability					
Fire Resistance at Maturity					
Fire Resistance and Resilience as a Juvenile					
RCW Habitat					
Wind Resistance					
Drought Resistance					
Ice Resistance					
Hydrology					
Productivity					
Long Term Carbon Sequestration Potential					
Boring Insect Resistance					

Figure 5. The anticipated effect of pine species identity on stand-level attributes assuming the existence of woodland structure.

of sustained tree recruitment, but the odds of naturally regenerating loblolly or slash pine could be increased by periodically extending the burn rotation. Fire return interval could also be rotated among compartments within a stand to encourage patchiness, if desired. Loblolly and slash pine should quickly acquire fire resistance given their superior growth potential (Fig. 4). Once the new cohort becomes large enough to resist surface fire, burning could be resumed at 2-to-3-year intervals.

The retention strategy also has practical advantages for RCW habitat restoration and carbon sequestration. Retaining loblolly or slash pine at low density will accelerate the development of mature woodland structure by preserving the growth and carbon already accrued on residual trees, and by creating open-stand conditions that support rapid tree growth (Jokela et al. 2010) (Fig. 4). These combined effects of the retention strategy should reduce the time necessary to produce RCW host trees and increase the rate of carbon sequestration.

Conclusions

Off-site tree species planted in forestry monocultures often functionally differ from tree species historically found in woodlands. These differences often affect key stand-level attributes, which have negative consequences for woodland restoration. Hence, the conversion strategy is often the only feasible option for converting off-site monocultures into woodlands. However, when functional redundancy exists between species, the retention strategy becomes increasingly viable (Kirkman et al. 2007).

Based on our review of tree-level attributes, the differences among the four primary southern pines are generally minimal-to-moderate. Moreover, many of the species-level differences are likely to become less influential within a woodland structure. Thus, our review provides strong support for adopting the retention strategy to rapidly convert off-site southern pine

monocultures into woodlands. In many cases, our review also suggests the retention strategy may be successful without underplanting longleaf or shortleaf pine. However, if this approach is taken, alterations to the burning rotation will likely be needed to secure regeneration.

While retention without underplanting might be a viable alternative strategy for restoring southeastern woodlands, we are not suggesting that it should replace laudable efforts to restore longleaf and shortleaf pine within their historical range. Instead, we present this new variant of the retention strategy as another potential option for restoring woodlands where off-site species offer functional redundancy. We anticipate that incorporating functional redundancy into restoration prescriptions will not only benefit woodland restoration in the southeastern United States, but may also be broadly applicable to a variety of forest conservation efforts involving closely related species.

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This paper was written and prepared in part by U.S. Government employees on official time, and therefore it is in the public domain and not subject to copyright. The findings and conclusions in this publication are those of the authors and should not be construed to represent an official USDA, Forest Service, or United States Government determination or policy. Finally, the authors dedicate this work to the memory of D.C.B. His immense contributions to forestry will not be forgotten.

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