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Identifying trade-offs and opportunities for forest carbon and wildlife using a climate change adaptation lens

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Abstract

On a warming planet, a key challenge natural resource managers face is protecting wildlife while mitigating climate change—as through forest carbon storage—to the greatest extent possible. But in some ecosystems, habitat restoration for imperiled species may be incompatible with maximizing carbon storage. For example, promoting early successional forest conditions does not maximize stand-level carbon storage, whereas uniformly promoting high stocking or mature forest conditions in the name of carbon storage excludes species that require open or young stands. Here, we briefly review the literature regarding carbon and wildlife trade-offs and then explore four case studies from the Northern Forest region of the United States. In each case, human activities have largely dampened the influence of natural disturbances; restoring or emulating these disturbances is typically required for habitat restoration even when doing so equates to less carbon storage at the stand level. We propose that applying a climate adaptation lens can help managers and planners navigate these trade-offs and steer away from maladaptive practices that may ultimately reduce adaptive capacity. Instead, critically evaluating the consequences of stand-level management actions on both carbon and wildlife can then facilitate landscape-scale climate adaptation planning that supports a diversity of habitats alongside opportunities to invest in maximizing forest carbon.

KEYWORDS
carbon storage, climate change mitigation, disturbance, early successional habitat, restoration, woodlands

1 | ONGOING CHANGES CHALLENGE SINGLE-OBJECTIVE MANAGEMENT

The Northeast and Great Lakes region of the United States excels at growing trees and supports a diversity of forest and woodland types. These forests and woodlands generate innumerable ecosystem services—including carbon storage and sequestration—while affording diverse habitats for a host of resident and migratory wildlife species. Moreover, they are expected to provide important conduits and refugia for species tracking suitable climatic conditions (Lawler et al., 2013; Morelli et al., 2020). In the face of climate change, a central challenge is how to

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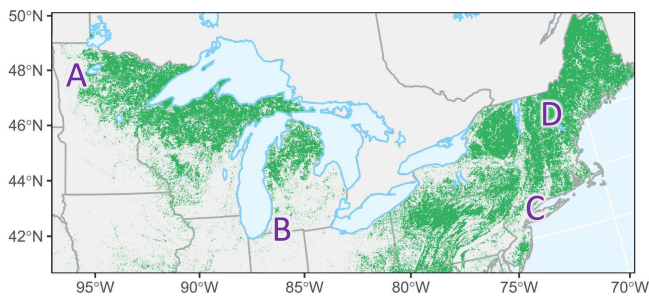
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FIGURE 1 Forest cover, indicated in green, in the Northeast and Great Lakes region of the United States. Letters indicate the approximate locations of the case studies explored herein: (a) Minnesota's tallgrass aspen parklands; (b) Michigan's oak savanna; (c) coastal pitch pine-scrub oak barrens; (d) New England's northern hardwoods. Although these case studies fall within the United States, these forest and woodland systems—as well as the trade-offs discussed—extend into Canada

protect this rich biodiversity while mitigating climate change—as through forest carbon—to the greatest extent possible.

The region's breadth of habitats reflects its position at a crossroads in time and space. Spatially, the region transitions from temperate broadleaf systems to the boreal biome to the north and temperate grasslands to the west (Figure 1) and supports some of the greatest community species richness in the temperate zone (Scheiner & Rey-Benayas, 1994). Past glaciation and glacial refugia resulted in a complex mosaic of soils that underpins much of this biological diversity (Ciolkosz et al., 1989). Following ice sheet retreat, multiple natural disturbance agents—beaver (*Castor canadensis*), flooding, wind, hurricanes, ice, and fire—maintained meadows, shrublands, and early successional conditions scattered to varying degrees throughout the otherwise forested landscape (Lorimer & White, 2003).

The region's forests also bear the indelible imprint of centuries—even millennia—of human activities. In some contexts, Indigenous peoples promoted mast and fruit trees and maintained woodland conditions through burning (Munoz et al., 2014). After extensive land clearing by European settlers, especially in southern New England, forests have largely rebounded, though are now declining in area and contiguity due to development (Thompson et al., 2017). In northern New England and to the west, large areas of closed-canopy forests remain, especially on Tribal lands (Waller & Reo, 2018), although much has been converted to agriculture in the Great Lakes states. Where the forest biomes give way to grasslands, open woodlands and savannas have undergone dramatic densification and mesophication—a self-reinforcing transition to shade-tolerant, mesic species—due in part to fire exclusion (Nowacki & Abrams, 2008).

These historical changes have shaped not only the structure, composition, and configuration of forests and woodlands, but also the wildlife—and our *expectations* of wildlife—therein.[1] For example, recent declines of migratory bird species that rely on early successional habitat may be attributed, in part, to the maturation of forests across much of the Northeast (Hunter et al., 2001; King & Schlossberg, 2014). Fire exclusion, beaver trapping, flood-control dams, and defoliator suppression are primary examples of how humans have diminished the influence of small- to moderate-scale natural disturbances and contributed to the homogenization of forest conditions across the region (Nowacki & Abrams, 2008; Schulte et al., 2007), to the detriment of some wildlife species. To protect and recover such species—and to abide by regulatory mandates (e.g., Endangered Species Act)—we must strategically evaluate how and where to reintroduce or emulate disturbances that promote habitat for disturbance-dependent species (DeGraaf & Yamasaki, 2003; King & Schlossberg, 2014). And yet, this long-standing tenant of ecology and wildlife management—the importance of heterogenous habitat conditions across the landscape—may be increasingly ignored, especially by the public, as forest carbon storage and sequestration take center stage, which we discuss below.

2 | A COMMITMENT TO CARBON

The erosion of important habitat for many wildlife species is compounded by the risks of climate change—both impending and underway (Swanston et al., 2018). Across taxa, many species are projected to face population declines, range contractions, and even extinction due to climatic changes per se (e.g., increasing drought and weather extremes) and/or stressors (e.g., nonnative insects and pathogens) that are amplified by climatic changes (Ceballos et al., 2017; Rosenberg et al., 2019). These and other climate-related risks compel us to swiftly curtail greenhouse gas emissions and keep as much carbon out of the atmosphere as possible, which includes leveraging the tremendous capacity of our forests to sequester and store carbon. Indeed, the forests of the northeast and Great Lakes region remain an important carbon sink (Ma et al., 2020; Pugh et al., 2019).

Accordingly, interest in increasing forest carbon storage and sequestration has grown dramatically in recent years. Ambitious global, regional, and local efforts and initiatives have focused on avoided forest conversion, reforestation, replanting, and improved forest management in the name of carbon. For example, global leaders recently committed to halting deforestation by 2030 at the United Nations Framework Convention on Climate

Change (UNFCC) 26th Conference of the Parties (https://ukcop26.org/glasgow-leaders-declaration-on-forests-and-land-use/). A year prior, in 2020, the World Economic Forum launched a global initiative to support the planting and protection of one trillion trees (https://www.1t.org). Within the United States, the Biden Administration made the ambitious commitment to protect 30% of lands by 2030 in *Tackling the Climate Crisis at Home and Abroad* (Exec. Order No. 14008, 2021), and individual states have committed (e.g., within state climate action plans) to counteracting carbon emission through reforestation and forest conservation. Other formal programs such as the United Nations' REDD+ (https://redd.unfccc.int) and both international and domestic forest carbon markets are transacting more carbon credits (and more money) each year (Ecosystem Marketplace, 2021). Less formally, there is a flurry of interest among forest landowners, including many family forest owners, in managing their land for carbon, with both nonprofit organizations and for-profit entities launching programs to support this interest (e.g., the Family Forest Carbon Program, a partnership between The Nature Conservancy and the American Forest Foundation; https://www.familyforestcarbon.org/).

Accompanying these programs and initiatives is mounting public pressure to cease all forest management (e.g., harvests) that may seemingly compromise carbon storage, especially on public lands. For example, advocates of "proforestation," a nascent movement emerging in New England, call for "growing forests intact to their ecological potential" (Moomaw et al., 2019), which largely equates with a hands-off approach to forest management. Relatedly, in Massachusetts, two bills were recently introduced in the state legislature—one would prevent harvesting on state lands (H.912, MA 2021b) and another would prevent renewable energy subsidies from going toward wood fuels (H.954, MA 2021a)—based on the notion that harvesting wood and using wood fuels have negative carbon outcomes.

3 | THE RELATIONSHIP BETWEEN CARBON AND WILDLIFE HABITAT

This growing recognition of the critical role that intact forests play as a natural climate solution is heartening, and fortunately, many of the restoration and forest management strategies that seek to enhance carbon storage and sequestration may benefit many wildlife species for which more in situ carbon directly corresponds with more and improved habitat conditions. For example, old, structurally complex northern hardwood stands with abundant snags and downed wood store large quantities of carbon (Ford &

Keeton, 2017) while affording important habitat for species like pine marten (*Martes americana*), black-throated blue warbler (*Setophaga caerulescens*), and the early hairstreak (*Erora laeta*). However, many other and often imperiled wildlife species rely on habitat conditions that are typically maintained by disturbance and that inherently store less carbon—for example, early successional forests or open woodlands.

What happens when strategies to maximize carbon on the ground do not tidily align with disturbance-oriented strategies to promote important habitat for imperiled wildlife species? As we (the authors) have repeatedly heard during targeted conversations with natural resource managers across the region as well as via more formal listening sessions (Janowiak et al. 2020) and surveys (Schattman et al., 2021), many managers are acutely aware of this question as public pressures mount to avoid any forest management that seemingly compromises carbon storage. Even within the growing body of literature that examines the relationship between carbon storage and wildlife habitat or biodiversity, the importance of maintaining heterogeneous habitat conditions is frequently obscured. Here, we briefly review this literature before suggesting that the lens of climate change adaptation may help us to navigate these potential trade-offs between carbon and wildlife. The literature on this relationship is not (yet) extensive in our focal region of the Northern Forest; we therefore consider studies elsewhere in the United States.

3.1 | A review of the research addressing carbon and wildlife

This trade-off between carbon storage and wildlife habitat for some species may be clearest at the stand scale, typically on the order of a hectare to 100 hectares, where specific carbon pools (e.g., live trees, downed wood) can tip the carbon equation one way or the other while also serving as habitat elements to which individual species respond (Crosby et al., 2020; Hunter, 2005). However, with some important exceptions, much of the research to date that examines the relationship between carbon and wildlife—or biodiversity more generally—does so at broad scales or does not precisely resolve individual species' responses to those "mesofilter" habitat elements (Hunter, 2005). The relationship between carbon storage and wildlife outcomes is therefore often inferred and generalized as positive without nuanced empirical substantiation. That said, some studies are careful to point out that the spatial scale of analysis can strongly influence this apparent relationship (e.g., Blumstein & Thompson, 2015).

Many of these studies examine if and how metrics associated with carbon storage and wildlife (e.g., habitat suitability indices) co-vary following forest management. For example, in one study, harvesting scenarios with varying degrees of tree retention were applied across Vermont in a forest growth-and-yield model and evaluated against occupancy models for over 50 bird species. Given the diversity of habitat requirements, more intensive prescriptions were found to enhance biodiversity outcomes but reduce in situ carbon storage (Schwenk et al., 2012). A simulation study in Missouri similarly reported mixed relationships between changes in avian abundance and management-induced carbon storage (carbon stores were inferred, not quantified; LeBrun et al., 2017). In most cases, these studies do not resolve, mechanistically, how the marginal change in carbon storage affects marginal changes in habitat, though some studies point to structural components (e.g., snags) as key modulating factors (e.g., Kline et al., 2016). Notably absent from these forest management studies are the carbon dynamics associated with leakage—that is, the shifting of harvesting activities elsewhere when harvesting in one location is reduced. Although management prescriptions alone cannot address this market issue, the carbon conclusions of forest management studies ought not ignore the broader carbon dynamics that are ultimately, if indirectly, induced by management decisions.

Others have examined the co-occurrence of high levels of habitat quality or species richness and carbon storage—or "hotspots"—at broad spatial scales. Perhaps unsurprisingly, the most intact natural landscapes or areas that are formally protected are where these hotspots tend to occur (Blumstein & Thompson, 2015; Hanna et al., 2020; Lecina-Diaz et al., 2018), though benefits to wildlife vary by taxa and species guild (Polasky et al., 2011). These results can inform conservation prioritizations at broad spatial scales but may be less relevant to stand-level management.

In some cases, a sharper lens on individual species reveals more nuanced patterns of the relationships between carbon and wildlife. For example, Ojibwe and Menominee Tribal forests support higher carbon stores than non-Tribal land, a pattern in part attributable to lower white-tailed deer (*Odocoileus virginianus*) densities (Waller & Reo, 2018). In the southeast United States, red-cockaded woodpeckers (*Picoides borealis*) rely on low-density longleaf pine (*Pinus palustris*) maintained by frequent fire; a simulation of thinning and prescribed burning showed that, at the stand level, continued carbon sequestration was incompatible with restoring woodpecker habitat (Martin et al., 2015). We found only one study that *directly* quantifies management effects on both tree carbon and wildlife populations: three decades after

riparian forest restoration in central California, bird density and diversity declined while above- and belowground tree biomass (carbon) increased. With the exception of this study (Dybala et al., 2019), most studies infer wildlife benefits from habitat elements, intactness, or suitability indices. Although these are reasonable proxies for many species, the simple equating of, for example, greater aboveground tree biomass to greater wildlife benefits belies the fact that, while some species may benefit, others may not.

Others have broadly examined the potential impact of forest carbon programs on wildlife habitat. Linking an econometric model and species distribution models for 35 forest-dependent vertebrates across the Pacific Northwest, researchers concluded that access to carbon markets may amplify the habitat loss predicted under climate change largely due to shifts in landowner planting behavior (Hashida et al., 2020). Others have shown that income associated with forest carbon offsets may reduce the cost of acquiring land for habitat protection, thus yielding positive biodiversity outcomes (Schuster et al., 2014). Importantly, many have examined the ecological and social implications of carbon programs on the international stage (e.g., REDD+), including how wildlife benefits may be limited or unevenly distributed at best (Beaudrot et al., 2016; Phelps et al., 2012; Seddon et al., 2020). Here, we focus on carbon and wildlife considerations in the Northeast and Great Lakes region, but tradeoffs and potential synergies are clearly not constrained to the United States.

Above all, what this brief review of the literature reveals is that the story of carbon and wildlife is complicated and that the nuances of species-specific habitat requirements must not be obscured. We need direct trade-off characterizations that are empirical (not inferred), species-specific, and that span multiple scales. This is particularly true with the continued emergence of programs that uniformly promote higher stocking and mature conditions across forest and woodland types in the name of carbon. Instead, the carbon calculus must consider the stand-level implications where management actions are implemented, as well as the broader landscape in which those stands are embedded and at which conservation and climate adaptation planning must occur.

4 | NAVIGATING TRADE-OFFS WITH THE LENS OF CLIMATE ADAPTATION

Why is it important to characterize and account for these potential trade-offs between carbon and wildlife? As more

attention is focused on maximizing forest carbon, we risk unintentionally compromising the long-term sustainability of other objectives (e.g., habitat restoration) across the landscape (Bradford & D'Amato, 2012). Characterizing trade-offs and critically evaluating the consequences of alternative management options can help avoid maladaptive practices that may ultimately reduce ecological complexity and the adaptive capacity of forested systems (Elmqvist et al. 2003; Messier et al. 2015). This sort of critical evaluation of stand-level management actions can then facilitate landscape-scale planning that supports a diversity of habitats while also suggesting where we ought to invest in maximizing forest carbon. Finally, characterizing trade-offs can steer us toward beneficial, win-win scenarios that may otherwise be obscured (Howe et al., 2014). To be clear, we are not impugning efforts to maximize forest carbon storage. Rather, we are underscoring the need to explicitly acknowledge and balance potential trade-offs associated with pursuing one management objective above all others across the forested landscape.

Here, we suggest that the lens of climate adaptation may help us to navigate these potential trade-offs, and we illustrate this proposition below by examining four specific forest and woodland habitat types historically maintained by disturbance. Climate change adaptation has, in the past, been deemphasized or even dismissed, out of concern that it may divert attention from tackling the underlying causes of climate change (Pielke et al., 2007; Stein et al. 2013). But the need to address the growing impacts of climate change on both human and natural communities is increasingly clear, as an essential complement to climate change mitigation.

In the conservation and forest management contexts, climate change adaptation seeks to identify vulnerabilities and climate impacts and then to strategically respond by avoiding, moderating, or accommodating those anticipated changes (Peterson et al., 2011; Stein et al. 2013). It is inherently an on-going, adaptive process with no finish line to cross; after all, it is fundamentally about managing and making challenging decisions in the face of inexorable change (Stein et al. 2013). As such, climate adaptation compels us to consider the broader spatial and temporal contexts in which management actions are embedded (Bradford et al., 2018; Peterson et al., 2011) as, for example, range shifts unfold and suitable climatic conditions expand or contract. It thereby prioritizes landscape diversity, complexity, and connectivity, among other key principles that already underpin conservation and ecological forest management, but that are particularly critical in the face of climate change (Stein et al. 2013; D'Amato & Palik 2021). This holistic climate adaptation lens frees us from broad-scale adherence to single

objectives (e.g., maximizing in situ carbon storage) and reminds us that, in the context of forest management, "simplification is rarely beneficial" (Franklin et al. 1986). Although these guiding principles are not novel, what is relatively new is the urgent need to manage forests for carbon benefits while not compromising wildlife habitat, and these principles of climate adaptation can help us to navigate that need. Additionally, there is growing recognition that proactive climate adaptation actions may simply be required to maintain forest productivity and carbon stocks (Hof et al., 2017; Ontl et al., 2020).

As the case studies we examine below illustrate, applying the lens of climate adaptation uncovers apparent trade-offs between carbon and wildlife habitat and illuminates landscape-scale management paths that accommodate both goals, while achieving other co-benefits. In each, promoting habitat for imperiled species is incompatible with maximizing in situ tree carbon storage at the stand scale. But by pursuing a mosaic of habitat conditions at the landscape scale, we protect ecosystem adaptive capacity—and therefore carbon—in the face of change while accommodating a range of species' needs, well beyond the species examined herein (Figure 2; Messier et al. 2019; Aquilué et al. 2020). For example, in the Northeast's spruce-fir forests, the imperiled Canada lynx (*Lynx canadensis*) and marten (*Martes americana*) rely on young and old stand conditions, respectively. Many birds and bats differentiate daily behaviors between different stand structures and so require adjacent patches of both mature and early successional forests (Ethier & Fahrig 2011). In addition, supporting biodiversity through habitat diversity in turn safeguards important ecosystem processes

Habitat to be restored and maintained	Habitat quality for focal species	Stand-level carbon storage in trees	Habitat and wildlife species diversity	Risk of carbon release from severe disturbance	Enhanced resilience and adaptive capacity
Early successional n. hardwoods	↗	↘	↗	↘	↗
Tallgrass aspen parklands	↗	↘ *	↗	↘	↗
Oak savanna	↗	↘ *	↗	↘	↗
Pitch pine-scrub oak barrens	↗	↘	↗	↘	↗

Stand-level effects   Landscape-level effects

FIGURE 2 Likely stand-level and landscape-level effects of restoring or maintaining habitat conditions for focal species in the four case studies. Purple arrows indicate likely positive effects, while orange arrows indicate likely negative effects. Asterisks indicate cases in which soil carbon may increase over the long-term as native grasses and other herbaceous vegetation reestablish, despite a decrease in stand-level carbon storage in trees

and services. For example, wild bees, which are critical pollinators, increase in abundance and diversity with the interspersion of different forest age classes (Roberts et al., 2017). Plus, such heterogeneity can afford wiggle-room for community re-shuffling and stepping stones for species on the move (Crone et al. 2019; Morelli et al., 2020).

In restoring disturbance to enhance ecological complexity and habitat diversity—even if that means relinquishing some aboveground carbon storage in certain contexts—we can also enhance resilience for both natural and human communities in the face of increasingly severe disturbances (Lavorel et al. 2015; Messier et al. 2019). In the examples below, restoring low severity fire and reducing fuels in fire-prone systems reduces the risk of catastrophic wildfire and associated carbon loss (Liang et al. 2018). In other settings, restoring healthy floodplain forests may require favoring native, late successional tree species (e.g., silver maples [*A. saccharinum*], American elm [*Ulmus Americana*]) that can withstand inundation and mitigate flood risk (e.g., via removals of invasive species as well as tree planting). Restoring beavers, especially in upland forested areas, leads to localized tree mortality but can increase water retention and hydrologic stability in the face of more extreme precipitation events (Dittbrenner et al. 2018; Westbrook et al. 2020).

4.1 | Trade-off case studies

Here, we explore four forest and woodland contexts in which maximizing carbon—specifically, aboveground tree biomass—can run counter to supporting key habitat for focal wildlife species that are current conservation priorities (Figure 3). Of course, there are many other contexts in which the converse is true, such that lessons from these case studies are not transferrable to all ecosystems across the entire region. But in each of these four cases, restoring or emulating natural disturbance, as through ecological silviculture (Palik et al. 2021), is typically required for maintaining key habitat. Those disturbances can also generate the sort of ecological complexity and heterogeneity that inherently enhances adaptive capacity (e.g., via functional diversity) in the face of ongoing change (Aquilué et al. 2020; Brice et al., 2020).

Though these case studies are drawn from the Northeast and Great Lakes region of the United States (following our targeted conversations with public lands managers in the region), maintaining open or early successional conditions for imperiled species that depend upon it is a common concern for wildlife managers elsewhere such that the lessons herein may be broadly applicable—for example, in sagebrush-steppe systems and subalpine meadows facing conifer encroachment (Miller et al. 2017; Lubetkin et al. 2017) and in regions
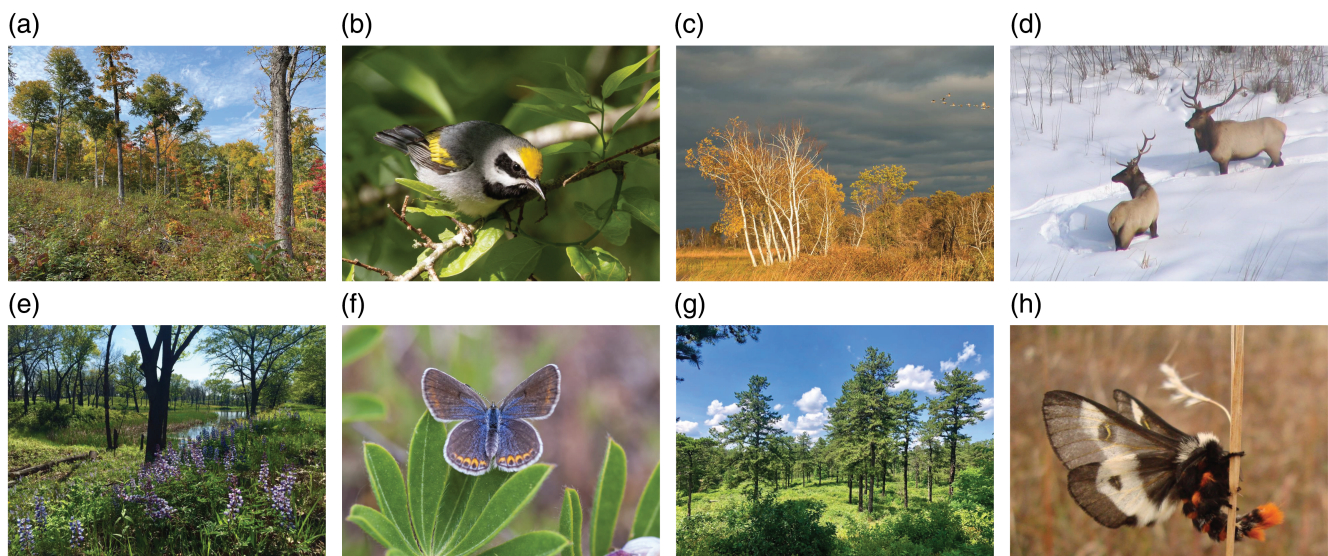
FIGURE 3 Examples of forest and woodland ecosystems (left column) in which restoring or maintaining habitat for imperiled species (right column) may be incompatible with maximizing carbon storage in trees at the stand scale. (a) Early successional conditions in a northern hardwood stand (photo credit: C. Littlefield); (b) Golden-winged Warbler, which has experienced one of the steepest declines of any North American songbird (photo credit: B. Arrigoni); (c) Minnesota's tallgrass aspen parklands (photo credit: J. Pennoyer); (d) elk populations have made a comeback in northern Minnesota after extirpation in the early 20th century (photo credit: M. Deters); (e) Midwest oak savanna with abundant wild blue lupine (photo credit: C. Martin); (f) the federally endangered Karner blue butterfly lays eggs almost exclusively on lupine (photo credit: M. Hitchiner); (g) pitch pine-scrub oak barren stand (photo credit: E. Jamison); (h) like other invertebrates, the barrens buckmoth is in decline due to loss of habitat (photo credit: I. Clearwater)

where dense tree planting may be used to accelerate recovery from logging or stand-replacement disturbance (Swanson et al. 2011).

4.2 | Early successional habitat in New England's northern hardwoods

There is currently less early successional forest (and certainly less old forest) across parts of New England's northern hardwoods than ever before, as forests have rebounded from European settler clearing (King & Schlossberg, 2014; Lorimer & White, 2003). Moreover, we have dampened disturbances that once maintained early successional habitat. For example, the extensive influence of beavers has been greatly diminished given their past extirpation and continued discouragement of their activities in settled areas (Rosell et al., 2005). Even exogenous disturbances like hurricanes have a diminished influence, as younger forests can be relatively resistant to damage (Foster & Boose, 1992).

Species that rely on early successional habitat have declined, too, perhaps most notably breeding songbirds (Hunter et al., 2001). Many of these species strongly respond to the structure within early successional patches as well as patch size. The golden-winged warbler (*Vermivora chrysoptera*; Figure 3b), for example, has experienced one of the steepest declines of any North American songbird. The species nests near the ground in early successional patches no smaller than 1 ha, and often relies on surrounding mature forest for foraging (Roth et al., 2019). Other songbirds require larger openings (e.g., 10 ha), such as those created by silvicultural clear-cuts, and are absent from smaller harvest openings in part because edge-related nest predation decreases and soft mast availability increases with patch size (King et al., 1998). Many of these early successional obligates depart as stand development proceeds (DeGraaf & Yamasaki, 2003). This holds true for game species as well, like American woodcock and ruffed grouse, which often motivate management for early successional conditions.

This turn-over with stand succession highlights the importance of relatively frequent, patchy disturbances in maintaining a "shifting patch mosaic" of habitat conditions (Pickett & White, 1985). With the declining influence of natural disturbances, restoration and active forest management have become important levers for maintaining such a mosaic, as has expressly managing for habitat elements and intolerant and intermediate tree and shrub species. For example, patch cuts with retention can mimic the wind- and ice-storms characteristic of the northern hardwoods and reintroduce varying-sized patches of early successional

habitat, which may not otherwise be accomplished with silviculture systems (e.g., single-tree selection) that create small canopy gaps (Figure 3a; Seymour et al. 2002; DeGraaf et al. 2006). Of course, relative to mature forests, early successional forests store less carbon overall, although they sequester carbon at relatively high rates. From a climate adaptation lens, trading-off that maximal carbon storage for habitat heterogeneity spanning young to old forests across the landscape is perhaps more than compensated for. Such heterogeneity may afford microclimatic buffering that ameliorates warming on a local scale (Frey et al. 2016) as well as "stepping stones" as species track suitable climatic conditions (Morelli et al., 2020). Landscape heterogeneity may also accommodate more community reshuffling, particularly for long-lived species like trees that may otherwise lag climatic changes (Brice et al., 2020).

Finally, in New England, there is a "surplus" of middle-aged forests that were largely initiated within the same window of farm abandonment (late 1800s to mid-1900s), with plenty to accelerate toward old forest conditions, as well as restore to early successional conditions (Lorimer & White, 2003). However, management plans to enhance the representation of early successional conditions through silviculture—particularly on public lands like the Green Mountain National Forest (e.g., the Early Successional Habitat Creation Project, https://www.fs.usda.gov/project/?project=53629) and state lands in Vermont—have met substantial opposition (e.g., by groups like Standing Trees, https://www.standingtreesvermont.org/). Those opposed frequently invoke the climate crisis as a compelling reason for not harvesting any trees from local forests. However, the current homogeneity of forest conditions across large swaths of the landscape—which neither supports a diversity of habitats for imperiled species nor confers the adaptive capacity that heterogeneity would (Aquilué et al. 2020; Brice et al., 2020)—goes largely unmentioned.

4.3 | Tallgrass Aspen parklands of northern Minnesota

Along the margin of the Great Plains and boreal forests in Northern Minnesota are the tallgrass aspen parklands—a quilt of grasslands, groves of aspen (*Populus tremuloides*), shrub thickets, peatlands, and wetlands (Figure 3c). This landscape reflects the enduring legacy of massive glacial lakes that receded 10,000 years ago, leaving behind poorly drained sediments that have interacted with continental precipitation gradients to largely preclude tree establishment. However, widespread draining and drying from agricultural ditching, peatland

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mining, road network development, and fire exclusion has enabled the encroachment of woody vegetation. The transformation of such systems to relatively closed-canopy forests can occur rapidly and has reduced herbaceous species richness across North America's grasslands and savannas (Ratajczak et al. 2012).

Most wildlife species in the tallgrass aspen parklands, however, benefit from the natural mosaic of vegetation types that historically characterized these systems. Some species avoid expansive tree cover, due to perceived increase in predation risk (Lautenbach et al., 2017) while "islands" of trees and shrubs provide important movement corridors for others. Elk (*Cervus canadensis*; Figure 3d), for example, having rebounded from regional extirpation thanks to restoration efforts, rely on tree cover for movement and protection, but venture into open expanses for foraging (Hinton et al. 2020). The sharp-tailed grouse (*Tympanuchus phasianellus*) and sandhill crane (*Antigone canadensis*) have also largely recovered from dramatic declines. Sharp-tailed grouse nest in shrubby areas and consume tree buds during the winter, but otherwise rely on open areas for feeding and for performing courtship displays in their dancing grounds, or "leks" (Niemuth & Boyce 2004). The species is quick to abandon areas when trees become too dense. The sandhill crane strongly depends on open grasslands and shallow wetlands. Loss of these landscape conditions to tree encroachment and channelization compromises not only breeding success rates, but also removes important roosting "stopovers" during multiple populations' migration through the upper Midwest en route to wintering grounds along the Gulf or Mexico and elsewhere (Saunders et al. 2019).

These focal wildlife species, among others, rely on the sort of mosaic that restoration efforts aim to achieve, although restoration is hindered in part by reduced access to markets that process lower-grade wood (e.g., due to ongoing mill closures). Shearing and mowing, harvest openings, prescribed burns, and hydrologic reconnection efforts essentially keep parts of the landscape in "arrested development" by limiting tree encroachment into open areas and maintaining parkland habitat conditions. Of course, limiting tree cover means inherently foregoing carbon storage in trees. However, intact grasslands and peatlands store an exceptional amount of carbon belowground, and restoration accelerates carbon sequestration rates (Alexandrov et al. 2020). Plus, the "rewetting" of peatlands can reduce carbon emitted from burns and smoldering belowground (Turetsky et al. 2015) while supporting localized groundwater recharge. This risk reduction is all the more important as climate change amplifies fire and drought risk. Thus, restoring and maintaining the natural mosaic of

the tallgrass aspen parklands not only promotes climate adaptation and mitigation, but also serves multiple wildlife species, in a way that continued tree encroachment and homogenization of habitat conditions would not.

4.4 | Southern Michigan's savannas

The oak savannas of southern Michigan and elsewhere in the Midwest now occupy a fraction of their pre-European settlement area due to conversion to agriculture, preferential removal of certain tree species, and ongoing land-use change. The pockets of savanna that remain are increasingly dense and have less herbaceous species diversity, as wildfire and Indigenous burning have been excluded from the landscape (Hanberry & Abrams, 2018). The dominance of scattered, fire-tolerant oaks—including white oak (*Quercus alba*), black oak (*Q. velutina*), and bur oak (*Q. macrocarpa*), among many other species—has given way to more mesic species such as red maple (*Acer rubrum*). This pattern of "mesophication" is self-reinforcing: fire exclusion enables denser conditions of less fire-adapted species and shifts the microclimate toward shaded, wetter conditions with less flammable fuel beds (Nowacki & Abrams, 2008). Deep oak tap roots and sprouting ability are no longer particularly advantageous traits in these fire-excluded conditions.

However, multiple imperiled wildlife species depend on these unique traits, on native herbaceous species more generally, and on the patchiness that frequent fire affords. For example, the eastern box turtle (*Terrapene carolina carolina*) burrows along oak tap roots or into stump holes to hibernate (Claussen et al., 1991). Greater tree densities, accompanied by shallow root systems, stymie these behaviors. The eastern massasauga (*Sistrurus catenatus*) is one of many reptiles that have specific microhabitat needs for thermoregulation that sparse canopy cover and small-scale patchiness historically afforded by fire (Cross et al., 2015). Finally, the federally endangered Karner blue butterfly (*Lycaeides melissa samuelis*) tends to lay eggs in recent burn patches where wild lupine (*Lupinus perennis*) is abundant and flush with nutrients released by fire (Figures 2e-f). Extensive canopy cover does not serve this lepidopteran—nor the reptilian species above—whereas large open areas with heterogeneous shade do (Grundel et al., 1998).

This is another context in which the thinning and burning or mastication of woody plants required to maintain open savanna conditions with scattered trees reduces tree carbon. But again, there is tremendous belowground carbon storage capacity in native grasses. Plus, promoting herbaceous diversity and vegetative patchiness can afford climatic microrefugia (e.g., via a matrix of shaded and

open conditions) that not only serve these ectothermic species now, but will also support them in adapting to increasingly hot, dry conditions (Walsh 2017; Bassett et al. 2020). Furthermore, mechanical treatments to remove woody growth can benefit small mammals and birds that in turn predate on nonnative pests such as gypsy moths that may well expand under climate change (Larsen et al. 2018). Restoration efforts by conservation organizations, public agencies (e.g., the Michigan Department of Natural Resources' Working for Wildlife Program, www.mi.gov/workingforwildlife) as well as assistance for private landowners (e.g., via the Natural Resources Conservation Service) have maintained momentum for restoring Midwestern savannas. However, reticence toward prescribed burns (e.g., related to the health impacts and potential damage) and concerns for reductions in timber supply by managing for low-density conditions, among other issues, have complicated widespread restoration (Dey & Kabrick, 2015).

4.5 | Coastal pitch pine and scrub oak barrens

Along the northeast coast and in sandy inland pockets are pitch pine barrens, a globally imperiled ecosystem characterized by the fire-adapted pitch pine (*Pinus rigida*) with thickets of scrub oak (*Q. ilicifolia*) and understories of blueberries (*Vaccinium* spp.; Figure 3g). Here, too, fire exclusion has resulted in canopy closure while enabling the establishment of competitors and invasive species. Development, recreational overuse, plantations of higher-market value species (e.g., red pine, *P. resinosa*), and the ongoing expansion of the southern pine beetle (*Dendroctonus frontalis*) further imperil these unique systems (Aoki et al., 2018).

Rare and dwindling animal species, especially invertebrates, rely on the barrens. The barrens buckmoth (*Hemileuca maia*; Figure 3h) and pine barrens bluet (*Enallagma recurvatum*), for instance, largely depend on specific host plants. In turn, insectivorous birds like the whip-poor-will (*Antrostomus vociferous*) that forage at night and primarily consume moths have been declining in recent decades (Spiller & Dettmers 2019). Mammals like the New England cottontail (*Sylvilagus transitionalis*) have also traditionally occupied the pine barrens, but tree densification has increasingly diminished habitat suitability, leaving this species all the more vulnerable to extirpation.

In addition to reducing important habitat conditions for these imperiled species, densification and the ascendance of woody species other than pitch pine may amplify drought stress, render stands more susceptible to

disease and pests, and increase fire severity, which can release a large pulse of carbon. Climate change will only exacerbate these stressors. Mastication, thinning, and prescribed fire may help alleviate drought stress (Gleason et al., 2017) and reduce invasion vulnerabilities (Aoki et al., 2018). These activities, of course, reduce in situ carbon storage, which the public has been quick to point out in multiple contexts—for example, where MassWildlife has restored pitch pine barrens on state lands (https://www.mass.gov/service-details/pine-barrens-restoration-timber-harvest). However, mitigating higher severity fire risk may ultimately keep more carbon out of the atmosphere (Scheller et al. 2011; Liang et al. 2018). Plus, if biomass removals (e.g., of unhealthy red pine plantations) are allocated to mass timber that displaces more carbon-intensive building materials or to bioenergy that displaces fossil fuels, the carbon equation may be further improved (though bioenergy carbon dynamics and impacts to wildlife habitat are subject to much debate [e.g., McKechnie et al., 2011; Jones et al., 2021]).

5 | REASONS FOR OPTIMISM

Given development pressures and other threats to forests and woodlands, is restoration and maintenance of these habitat conditions feasible? Yes: these challenges are not intractable, and strategically tackling them is critical in the face of climate change. Luckily, there are a growing number of spatial prioritization tools and cost-share or incentive programs to support these efforts—for example, Vermont Conservation Design (https://vtfishandwildlife.com/conserve/vermont-conservation-design), Maine's Beginning with Habitat (https://www.maine.gov/ifw/fish-wildlife/wildlife/beginning-with-habitat/index.html), Illinois' Acres for Wildlife (https://www2.illinois.gov/dnr/conservation/wildlife/Pages/AcresWildlife.aspx), and the Natural Resources Conservation Service's Working Lands for Wildlife (https://www.nrcs.usda.gov/wildlife), to name a few. Tools and programs like these strive to support and link on-the-ground management at the stand scale with broader landscape-scale or state-wide targets of, for example, young or old forest area. Of course, achieving a diversity of conditions across the landscape is complicated by increasingly small ownerships (Butler et al. 2020), which underscores the important role of individual landowners (Loeb & D'Amato 2020) and that we must carefully convey to the public the trade-offs of adhering to a single management objective (e.g., maximizing carbon storage) across a given region.

Managers and researchers are increasingly resolving what practices may be maladaptive, which enables us to home in on no-regrets approaches to management. Still,

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there are well-intentioned policies and programs afoot that may undermine climate change adaptation, mitigation, and wildlife protection. For example, the most common protocols currently used in domestic forest carbon markets (e.g., those of the American Carbon Registry, the Climate Action Reserve, among others) evaluate only carbon outcomes. Accordingly, there is little incentive for landowners or forest carbon project developers to pursue a diversity of forest habitat conditions within individual projects (though some international standards strive to, e.g., Verra's Climate, Community, and Biodiversity Standards, https://verra.org/project/ccb-program/). In these protocols, a stronger consideration of biodiversity outcomes could ensure that a diversity of habitats is not inadvertently sacrificed in the pursuit of maximizing carbon. Similarly, ambitious tree planting and reforestation initiatives ought to prioritize creating healthy, functional forest ecosystems, pursuing biodiverse, resilient plantings, and relying on natural regeneration whenever possible (Castro et al., 2021; di Sacco et al., 2021).

In the policy domain, legislation aimed at increasing carbon by halting harvests on public lands or promoting renewable energy may have unintended consequences. For example, not removing tree biomass in some contexts is incompatible with habitat restoration. And while society simply must pursue renewable energy, developers should not target forestland for energy development. By one estimate, one quarter of natural land conversion in Massachusetts over 5 years was due to solar development (Ricci et al., 2020); solar arrays ought to be situated over parking lots or landfills instead of cleared forest. These are the sort of maladaptive practices that we must address with a careful reconciliation of carbon and habitat trade-offs at multiple spatial scales. For example, as policymakers establish roadmaps and enact laws to mitigate climate change (e.g., the Global Warming Solutions Acts of multiple states), plans to leverage the natural climate solution of forest carbon storage ought to be crafted with habitat diversity targets in mind (Seddon et al. 2019).

All told, restoring and maintaining the composition, structure, and functions of forest and woodland habitats across the Northeast and Great Lakes region—and beyond—can jointly support climate change adaptation, mitigation, and innumerable wildlife species. It is imperative to recognize that climate change itself is one of the most serious threats facing wildlife in this region and globally, and we do not have the luxury of unlimited time to devise the "perfect" balance of maximizing carbon storage and wildlife habitat across the landscape. Pursuing strategies that critically assess vulnerabilities and risks, explicitly acknowledge trade-offs, and prioritize ecological complexity and landscape heterogeneity may well be the best way to keep carbon out of the atmosphere while protecting wildlife and, in general, hedging our bets in an uncertain future.

CONFLICT OF INTEREST
The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS
Caitlin E. Littlefield and Anthony W. D'Amato conceived of this paper; Caitlin E. Littlefield conducted research and targeted conversations with managers; Caitlin E. Littlefield wrote the first draft; Anthony W. D'Amato provided critical review.

DATA AVAILABILITY STATEMENT
There are no data associated with this paper.

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This paper reflects the authors' own original research in a truthful and complete manner.

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ENDNOTE
[1] Throughout, we consider the term "wildlife" to encompass all vertebrate and invertebrate animal species that public agencies (e.g., the U.S. Fish and Wildlife Service and state-level equivalents) manage and may establish conservation targets for. Current wildlife conservation targets and desires or expectations for wildlife populations may depart substantially from historical levels and baselines, particularly levels before the arrival of Europeans and associated decimation of Native American populations (Alagona et al., 2012; Mann, 2005). Indeed, some wildlife populations may have been released following European settlement; early successional obligates, for example, likely benefited from settler land clearing (Foster et al., 2002). Thus, we acknowledge that current conservation targets may well be artifacts of the population dynamics observed within the past century or two rather than reflective of (illusive) historical baselines prior to European arrival. Nevertheless, these targets are what underpin

today's conservation objectives and management and so we focus on them here and do not elaborate extensively on the historical trends of each species we address in the case studies below.

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