The Environmental Consequences of FOREST FRAGMENTATION in the Western Maine Mountains

Janet McMahon, M.S.



Occasional Paper #2

Maine Mountain Collaborative

P.O. Box A, Phillips, ME 04966

© 2018 Janet McMahon.

Permission to publish and distribute has been granted by the author to the Maine Mountain Collaborative.

This paper is published by the Maine Mountain Collaborative as part of an ongoing series of informational papers. The information and views expressed in this paper are those of the author and do not necessarily reflect the views of the Maine Mountain Collaborative or its members.

I thank Dr. Malcolm Hunter, Jr., Dr. Ray "Bucky" Owen and Barbara Vickery for their peer review of this paper. I also thank the many ecologists, biologists, foresters and others who provided information, analysis and, in some cases, early review of all or parts of this paper, including: Mark Anderson, George Appell, Maisie Campbell, Andrew Cutko, Thomas R. Duffus, Phillip deMaynadier, Merry Gallagher, R. Alec Giffen, Sarah Haggerty, Daniel Harrison, Peter McKinley, Michael Pounch, David Publicover, Jeffrey Reardon, Sally Stockwell, Karin Tilberg and Andrew Whitman. Finally, I give special thanks to Daniel Coker, senior spatial scientist at The Nature Conservancy, Maine for his analysis of state road and habitat block data and map preparation and to Ann Gosline, for her tireless logistical support and encouragement.

Cover photos:

Western Maine Mountain vista by Charlie Reinertsen Photography. Photo-illustration of development by Waterview Consulting.

Photo on page 1: Western Maine Mountains by Charlie Reinertsen Photography.

Photos on page 5: Moose by Maine Department of Inland Fisheries and Wildlife. Black bear by Terry Spivey—Image Number: 1374239, CC BY-SA 3.0. Canada lynx by Eric Kilby, https://www.flickr.com/photos/ekilby/8154273321 River otter and brook trout by U.S. Fish and Wildlife Service. American marten by U.S. Department of Agriculture. Spruce grouse by Dick Daniels (http://carolinabirds.org/)—Own work, CC BY-SA 3.0, https://commons.wikimedia. org/w/index.php?curid=10767940



The Environmental Consequences of Forest Fragmentation in the Western Maine Mountains

ABSTRACT

The extraordinary ecological values of the Western Maine Mountains region are under threat from a process called "habitat fragmentation." Habitat fragmentation occurs when habitats are broken apart into smaller and more isolated fragments by permanent roads, utility corridors, buildings, clearings or changes in habitat conditions that create discontinuities in the landscape. Research in Maine, the Northeast and around the world demonstrates unequivocally that fragmentation—whether permanent or temporary—degrades native terrestrial and aquatic ecosystems and reduces biodiversity and regional connectivity over time and in a number of ways. Negative effects include:

- increased mortality and habitat loss from construction of roads and other fragmenting features
- increased mortality and other direct impacts associated with infrastructure after construction
- changes in species composition and reduced habitat quality from edge effects
- changes in species composition and behavior as habitat patch size declines
- changes in hydrology and reduced aquatic connectivity
- introduction and spread of exotic species
- changes in the chemical environment
- pressures on species resulting from increased fishing, hunting, and foraging access
- loss of scenic qualities and remote recreation opportunities

Fragmentation has already significantly degraded ecosystems in much of the eastern United States and in temperate forests throughout the world. By contrast, in large part because historical forest management maintained vast connected forest blocks in the region, the Western Maine Mountains' biodiversity, resilience and connectivity are unparalleled in the eastern United States. The region is a haven for populations of many of Maine's iconic species, including moose, lynx, marten, brook trout, and rare forest birds, and provides an essential corridor for species to move to other northeastern states, the North Woods and Canada in a time of climate change. To maintain the region's unique values, it is essential to avoid introduction of new fragmenting features, especially those that would permanently intrude into intact blocks of forest habitat, such as new utility corridors and new high volume roads. It is also critically important to find ways to support landowners who seek to maintain large intact forest blocks and to support them in managing forests for connectivity and structural complexity. If proactive steps are taken now, there is a tremendous opportunity to avoid habitat fragmentation and maintain the region's many ecological values—values that have defined Maine for generations and are of critical importance in North America.

INTRODUCTION

The Western Maine Mountains lie at the heart of the most intact and least fragmented landscape remaining in the eastern United States. This vast region lies near the northern terminus of the Appalachian Mountain range in the United States and includes some of its highest peaks. It extends from the Katahdin region 160 miles southwest to Boundary Bald Mountain and the Mahoosucs Range on Maine's western border, encompassing an area of more than five million acres. It is a region of extraordinary ecological importance, both because it is the key ecological linkage between the forests of the northern Appalachians and those to the north, south and west, and because of the biodiversity it harbors.1

The southern edge of the Western Maine Mountains region marks the divide between the most resilient² and connected landscapes of the Northern Appalachian-Acadian Forest Ecoregion³ and more fragmented and less resilient landscapes to the south and west. This paper summarizes the potential deleteri-



Figure 1. The Western Maine Mountains region.

ous impacts of forest fragmentation on the flora, fauna and ecosystems of the region. Fragmentation is generally defined as the breaking apart of a continuous landscape into smaller and more isolated fragments (Forman 1995). In the Western Maine Mountains, fragmentation occurs when permanent features such as roads, utility corridors, buildings or clearings create breaks in the forested landscape (Charry 1996). Recent work by Di Marco et al. (2018) shows that there is a direct correlation between the risk of species extinction and human footprint. Impacts such as direct habitat loss, habitat degradation through increased isolation of plant and animal populations, greater exposure to edge effects, and invasion by disturbance-adapted species are cumulative, leading to degraded ecosystems over time and, eventually, loss of regional connectivity and biodiversity (Watson et al. 2018; Lindenmayer and Fischer 2006; Haddad et al. 2015). This is the situation in much of the eastern United States and in temperate forests throughout the world.

¹ For a detailed description of the ecological values of the Western Maine Mountains, see McMahon (2016).

² Resiliency refers to the ability of a region to maintain species diversity and ecological function as the climate changes.
³ Ecoregions are large units of land with similar environmental conditions–especially landforms, geology and soils, which share a distinct assemblage of natural communities and species. The Northern Appalachian-Acadian Forest Ecoregion includes the mountainous regions and boreal hills and lowlands in northern New England and Maritime Canada. The ecoregion includes the Adirondack Mountains, Tug Hill, the northern Green Mountains, the White Mountains, the Aroostook Hills, New Brunswick Hills, the Fundy coastal section, the Gaspé peninsula and all of New Brunswick, Nova Scotia and Prince Edward Island (Anderson 2006).

In the classic definition of fragmentation, habitat patches are surrounded by a "matrix"⁴ of lands dominated by human activities, such as farmland or urban centers (Hunter and Gibbs 2007). By contrast, the Western Maine Mountains region is a forested landscape, largely unfragmented by major roads and other permanent features. This matrix of managed forestland provides valuable habitat for most of Maine's forest species and generally serves to connect patches of mature or undisturbed habitat. However, changes in the forest landscape from harvesting can also have fragmenting effects, especially for species that require mature forest or forest interior habitat. The degree of impact depends on factors such as the species in question, harvest intensity, and the size of harvest blocks. Although these impacts are generally temporary, they are of concern—particularly in combination with impacts of permanent fragmentation—and are in need of further study.

This paper begins with an overview of the ecological significance and condition of the Western Maine Mountains' landscape and a brief review of how the region has changed over time due to forest fragmentation associated with land use change and forest management. This is followed by a summary of the potential impacts of current and future fragmentation on the region's biodiversity, resilience in the face of climate change, and ability to serve as the critical link between the forests of the northern Appalachians and those to the north, south and west. To paraphrase Aldo Leopold (1966), the region needs to be viewed as an integrated whole rather than a collection of conservation lands and private commercial land holdings. Private and public landowners, through their land use decisions and management, will play a key role in maintaining the region's ecological values into the future.

Habitat fragmentation and why it matters

Hunter and Gibbs (2007) wrote that a modern traveler looking down from a plane generally does not see vast expanses of unbroken landscape but instead will likely see a landscape like a patchwork quilt—a mosaic of different land uses. Hunter and Gibbs define "habitat fragmentation" as the gradual breaking apart of a natural landscape into smaller habitat blocks. They wrote that fragmentation typically begins when people build roads into a natural landscape and then "perforate" the landscape further with associated development. This typically leads to additional roads, energy infrastructure and land conversion and, over time, results in "patches" of natural habitat that are smaller and farther apart (Fig. 2). Larger habitat patches in a landscape mosaic are better able to support stable populations of more species than small ones. Hunter and Gibbs attribute this to three things: First, larger patches have a greater variety of environments-different elevations, soils, geology, streams and wetlands, which in turn support a greater variety of species. Second, larger patches will support more species that require larger home ranges. Finally, animals and plants from other patches can more easily migrate in to replenish struggling or declining species if similar habitat patches are close by and if the areas in between (matrix habitat) are connected and allow for movement. Fragmenting landscapes into smaller habitat patches over time is a leading cause of degradation of ecosystems and loss of biodiversity.

⁴ Matrix forest can be defined as the largest background patch in a landscape and is characterized by extensive cover, high connectivity, and/or exerts a dominant role on ecological processes (Forman 1995). In the Western Maine Mountains, most of the region is considered matrix forest.



Figure 2. The left column shows a hypothetical progression from: (1) initial fragmentation by a new road or other linear feature, (2) a landscape fragmented by the road and associated development "perforating" the landscape and (3) a landscape with additional sprawling fragmenting features, resulting in progressive fragmentation of the landscape into smaller natural areas. The right column shows an actual example of change between 1956 to 1995 from a partially fragmented landscape to a highly fragmented landscape in a southern Maine community. Photo-illustrations in left column by Waterview Consulting. Photos in right column courtesy of the Greater Portland Council of Governments.

Figure 3. (following page) The Western Maine Mountains provide critically important core habitat for species that are iconic to Maine and a host of rare animals and plants. Photos are of moose, black bear, Canada lynx, river otter, American marten, spruce grouse, and brook trout. Photo credits, see inside front cover.

THE REGION TODAY

A diverse, resilient and connected landscape⁵

From the standpoint of biodiversity, the Western Maine Mountains region is exceptional. It includes all of Maine's high peaks and a rich diversity of ecosystems, from alpine tundra and boreal forests to ribbed fens and floodplain hardwood forests. It is home to more than 139 rare plants and animals, including 21 globally rare species and many others that are found only in the northern Appalachians. It includes more than half of the United States' largest globally important bird area,⁶ which provides crucial nesting habitat for 34 northern woodland songbird species and critical habitat for high-elevation and coniferous-forest specialist birds such as Bicknell's thrush-a state endangered species-bay-breasted warbler and black-backed woodpecker. Maine is the last stronghold for wild brook trout in the eastern United States, supporting 97% of its intact lake and pond wild trout populations. Seventy-three percent of these wild brook trout lakes are in the Western Maine Mountains (Whitman et al. 2013; DeGraaf 2014). The region provides core habitat for umbrella species⁷ such as American marten and Canada lynx-habitat that supports more than 85% of all of Maine's terrestrial vertebrate wildlife species, including iconic species of the north, such as the common loon, black bear, bobcat and moose (Hepinstall and Harrison in prep.; DeGraaf and Yamasaki 2001).

In addition to its remarkable biodiversity, the region is exceptional because it remains a largely unfragmented, lightly settled and connected landscape. It lies at the heart of the Northern Appalachian-Acadian Forest Ecoregion, which is the largest and most continuous area of temperate forest in North America, and perhaps the world (Haselton et al. 2014; Riitters et al. 2000). This high degree of connectivity, combined with large elevation gradients and a diversity of physical landscapes, makes the Western Maine Mountains a highly resilient landscape in the face of climate change and a critical ecological link between undeveloped lands to the north, south, east and west. Resilient sites are those that are projected to continue to support biological diversity, productivity and ecological function even as they change in response to climate change. In The Nature Conservancy's Conservation Gateway climate resilience map of the eastern United States, the Western Maine Mountains stand out in terms of biodiversity, climate flow⁸ and

⁸ Climate flow is defined by The Nature Conservancy as the movement of species populations over time in response to the climate. Intact forested areas typically allow high levels of plant and animal movement.



⁵ This summary of the region's ecological significance is adapted from McMahon (2016).

⁶ The National Audubon Society gave this global designation to the region because of its high bird richness and abundance as well as the extent and intactness of its forests, which lie within the Eastern Atlantic Flyway—the major migratory route for hundreds of neotropical bird species.

⁷ Hunter and Gibbs (2007) define umbrella species as those with large home ranges and broad habitat requirements. Protecting habitat for their populations protects habitat for many other species across a broad set of ecosystems.

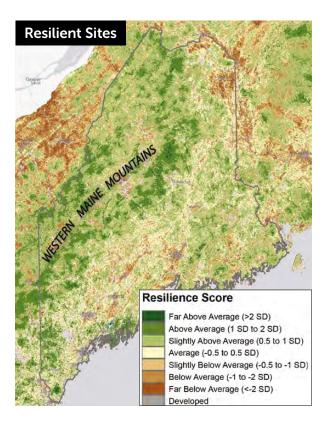


Figure 4. This map shows that the Western Maine Mountains provide sites of above and far-above-average resiliency throughout the region. Resilient sites are expected to buffer their resident species from climate change and continue to support biodiversity, productivity, and ecosystem function even as they change in response to climate change. Analysis and graphic courtesy of The Nature Conservancy, Maine.

Sources and Sinks

Hunter and Gibbs (2007) define "sources" as subpopulations that produce a substantial number of emigrants that disperse to other patches and "sinks" as subpopulations that cannot maintain themselves without a net immigration of individuals from other subpopulations. The Western Maine Mountains region harbors significant source populations of many species and already serves as a north-south and east-west link between peripheral sink populations in New Hampshire and Vermont and source populations in northeastern Maine and the Gaspé (Carroll 2007). climate-resilient sites.⁹ Eighty percent of the region is of above-average resilience, based on geophysical setting and local connectedness (Fig. 4).¹⁰ This compares to 60% for the state as a whole and an average of 39% in southern Maine. A review of The Nature Conservancy's Conservation Gateway maps for the rest of New England and the eastern United States indicates that resiliency is even lower outside of Maine, making the Western Maine Mountains one of the most resilient and connected landscapes east of the Mississippi. In addition, it is the critical link between the other highly resilient areas in the Northern Appalachian-Acadian Forest Ecoregion—the Adirondacks, the St. John and Allagash valleys and the Gaspé.

Climate-resilient sites are more likely to sustain native plants, animals and natural processes into the future. The region is expected to retain more species as the climate changes than other parts of the state because its varied topography offers ample microclimates and thus more options for rearrangement (Anderson et al. 2012; Anderson et al. 2013). Northern Maine already has the highest species richness of mammalian carnivores in the eastern United States,¹¹ and the Western Maine Mountains support the largest moose, lynx, and marten populations in the lower 48 states. Furthermore, the region is a stronghold for brook trout, land-locked salmon, spruce grouse and a host of other species. In addition to providing a refuge for northern and coldwater species, the region serves as a source of individuals that can recolonize new habitats as they become avail-

⁹ Resilient sites buffer their resident species from the direct effects of climate change by providing temperature and moisture options in the form of connected microclimates that can differ by as much as 10–15°C. Sites with high microclimate diversity allow plants and animals to persist locally even as the regional climate appears unsuitable, thus slowing down the rate of change.

¹⁰ Geophysical setting is a landscape classification that considers topography, elevation range, wetland density and soil variety. Local connectedness is the absence of barriers or fragmenting roads, dams, development, etc. that prevent plant and animal populations from taking advantage of local microclimates.

¹¹ The region supports breeding populations of 7 species of mustelids (fisher, marten, mink, ermine, long-tailed weasel, river otter, striped skunk), 3 species of canids (grey fox, red fox, coyote), and 2 cats (bobcat, lynx).

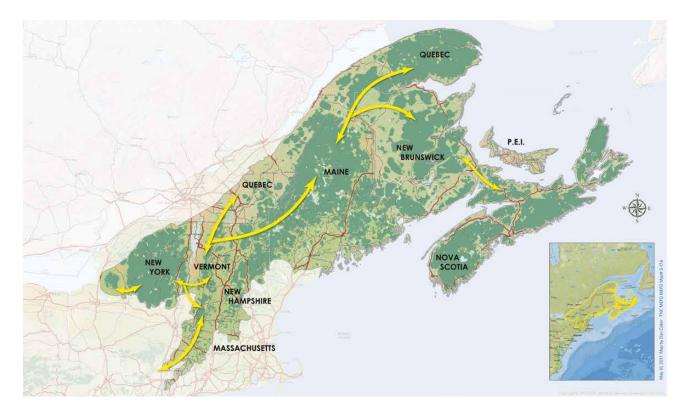


Figure 5. Northern Appalachian Region Forest Cover and Critical Linkages. Map courtesy of The Nature Conservancy, Maine.

able. For example, the region links moose populations at the southern edge of their range in New Hampshire and Vermont that are increasingly impacted by climate change and parasitic infections by ticks with larger, healthier populations in northern Maine and Quebec.

At a continental scale, northern Maine will become an increasingly important dispersal corridor as species move north into Canada (Trombulak and Baldwin 2010) (Fig. 5). Species survival may depend not only on the presence of refugia but also on how quickly the climate changes. Loarie and others (2009) modeled projected rates of temperature change in different ecosystems under different emissions scenarios during the 21st century. They found that the rate of change is expected to be lowest in mountainous biomes and temperate coniferous forests, suggesting that the landscapes of the Western Maine Mountains are more likely to effectively shelter many species into the next century than areas with low relief (Loarie et al. 2009; Loarie et al. 2008; Thuiller et al. 2005). Whitman et al. (2013) emphasize the importance of conserving cool refuges such as cold stream networks, mountains, and closed canopy forests to help species survive and transition as Maine's climate changes.

A forested landscape

The Western Maine Mountains region is ~97% forested (excluding water), which is about 8% higher than the average forest cover in Maine, the most forested state in the nation (Fig. 6, following page, for a regional comparison) (New England Forestry Foundation, NEFF, in press).¹² The North Woods of Maine, of which the

¹² Percentages of land in conservation ownership and forest management for the Western Maine Mountains are derived from other studies that focused on slightly different geographic boundaries. Schlawin and Cutko percentages were calculated for the Central-Western-White Mountains section of the USFS Bailey Ecoregion map of Maine (Bailey 1995). The 2018 NEFF analysis is of an area they refer to as the Mountains of the Dawn region.

region is a part, is the only place in the eastern United States where such a large area of contiguous land has remained continuously forested since European settlement. This is due to a variety of factors, including limited suitability for agriculture, soils that are productive for tree growth, remoteness from more heavily settled areas, and the timber and nontimber values of its vast forest—most of which has been in private and corporate own-ership and actively managed for forest products for more than two centuries.

State/Region	% Forestland		% Change from	Approximate
	2007	2017	2007–2017	Change in Acres
Western Maine Mountains	96.8%	96.5%	-0.3%	-12,000
Maine	89.8%	89.2%	-0.6%13	-116,000
Connecticut	55.3%	58.4%	3.1%	95,000
Massachusetts	61.2%	60.6%	-0.5%	-26,000
New Hampshire	83.8%	82.8%	-1.0%	-57,000
Rhode Island	54.0%	54.4%	0.4%	3,000
Vermont	77.3%	76.0%	-1.3%	-80,000
New England (incl. ME)	80.3%	79.8%	-0.5%	-184,000
New England (excl. ME)	71.1%	70.8%	-0.3%	-67,000

Figure 6. Forested Area as a Percent of Total Area (excluding water) in the New England states. Percent change is change in percent of forestland from 2007–2017.¹⁴ Adapted from NEFF (in press).

Managed forestland in the Western Maine Mountains is composed primarily of naturally regenerated forests. According to most recent FIA data,¹⁵ only 2% is planted, and most of this is with native species (Ten Broek and Giffen 2018). Under natural conditions, forest types generally occur in predictable patterns associated with climatic gradients and soil conditions determined by glacial deposition (NEFF in press; Legaard et al. 2015). Northern hardwood species predominate across lower hilltops and mid-slopes, with higher site quality. Spruce-fir species predominate on ridge tops, high elevation slopes and poorly drained lowlands. Mixed wood stands commonly occur along ecotones or as a result of successional dynamics following disturbance.

¹³ Considering just land area, Maine is 89% forested (FIA 2017 data).

¹⁴ Data are from the Forest Inventory and Analysis (FIA) Program of the U.S. Department of Agriculture (USDA) Forest Service. Percentages are for forestland, as a percentage of sampled land area, as opposed to total area, which would include area in water. Percent change is measured from the first complete inventory cycle (generally 2002/3 to 2007) to the latest complete inventory cycle (2017 estimates) (NEFF, in press).

¹⁵ The FIA Program of the USDA Forest Service annually surveys the country's forests to determine trends in forest area and location; tree species composition, size and health; total tree growth, mortality and removals by harvest; wood production and utilization rates by various products; and forest land ownership. The inventory has recently expanded to collect data on soils, understory vegetation (including invasives), tree crown conditions, coarse woody debris and lichen community composition on a subsample of plots.

Shade-intolerant hardwood species commonly follow intense disturbance. Periodic defoliation by spruce budworm is the most prominent large-scale natural disturbance. Small scale disturbances that result in small canopy gaps such as windthrow and senescence are also common (Legaard et al. 2015; Lorimer and White 2003; Seymour et al. 2002). Managed carefully, in time, these naturally regenerating forests should allow natural structural and successional processes to take place and provide habitat for a full suite of native wildlife species (NEFF in press).

A brief summary of current land use

Virtually all of the forestland in the Western Maine Mountains not specifically set aside for reserves or other conservation purposes is commercially managed for a variety of forest products. About 88% of these managed lands are privately held (NEFF in press). Since the 1990s, the North Maine Woods, including the Western Maine Mountains region, has undergone a dramatic transition in ownership. Large swaths of the region have passed from industrial landowners—who had long-term management goals because their timberland supplied their own mills-to timber investment management organizations, real estate investment trusts and other financial investors, whose investment strategies usually involve holding land for a much shorter period (Irland 2005; Lilieholm et al. 2010; Trombulak and Baldwin 2010). Between 1994 and 2005, forest products industry ownership of forestland declined from 59% to 16%, and the percentage held by investors such as publicly traded real estate investment trusts rose from 3% to 40% (Barton et al. 2012). Today, the majority of the Western Maine Mountains is owned by investors.¹⁶ Some landowners, such as Weyerhaeuser (formerly Plum Creek), have secured rezoning of forestland to allow for resorts and residential subdivisions in remote, lightly settled landscapes (Lilieholm et al. 2010; Hagan et al. 2005). In addition to a shift in ownership, the number of landowners has increased and size of land holdings has decreased significantly in the past two decades (Hagan et al. 2005). For example, the 2.3 million-acre Great Northern Paper ownership of 1989 had been transferred to at least 15 different landowners as of 2005. The impacts of the increased parcelization and turnover of landholdings on biodiversity and connectivity are unclear, but likely to be negative.

Legally conserved lands¹⁷ make up about 29% of the region's area. Forest management is allowed on 20 of this 29%. The remaining 9% is forever-wild or in reserves. Most conserved land that allows timber harvesting is privately held and under conservation easement. It is worth noting that most of Maine's forever-wild acreage is in the Western Maine Mountains, primarily in Baxter State Park, the White Mountain National Forest, The Nature Conservancy's Debsconeag Lakes Wilderness Area, Bureau of Parks and Land's Nahmakanta Ecological Reserve, Mahoosuc Unit and Bigelow Reserve, and additional lands within the 100-Mile Wilderness and the National Park Service's Appalachian Trail Corridor (Schlawin and Cutko 2014). Most of these reserves are centered around mountainous areas. They constitute some of the largest roadless areas in the state and New England (Publicover and Poppenwimer 2002) and contribute to the exceptional resilience of the region.

¹⁶ As of 2017, predominant landowners in the Western Maine Mountains included Weyerhaeuser, Wagner Forest Management, MacDonald Investment, BBC Land LLC, Katahdin Timberlands and E.J. Carrier (James W. Sewall Company 2017 map of Forest Land Owners of the State of Maine).

¹⁷ Conservation lands include those where forest management can take place (Type 1) and those where extractive uses are not allowed (Type 2). The latter are sometimes termed "forever wild" or "reserve" lands. These lands include places such as Acadia National Park, the National Park Service's Appalachian Trail, federal Wilderness Areas in the White Mountain National Forest and Moosehorn Wildlife Refuge, State Ecological Reserves, many land trust ownerships and much of Baxter State Park (Schlawin and Cutko 2014).

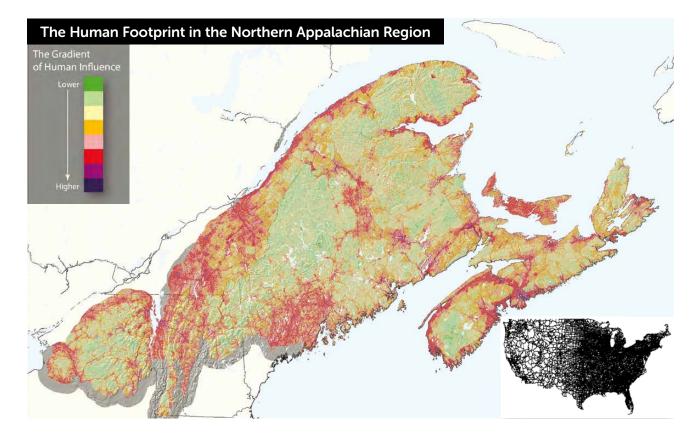


Figure 7. The Human Footprint map of the ecoregion and the map of the U.S. highway system (inset), viewed together, show that the Western Maine Mountains and Maine's North Woods are much less fragmented than any other area in the eastern half of the country. Human Footprint data from Two Countries One Forest, map courtesy of The Nature Conservancy, Maine.

Currently, the Western Maine Mountains region has a far lower density of major permanent roads than more developed areas of Maine, and New England as a whole.¹⁸ The Land Use Planning Commission (2010) estimate of public road density in the unorganized towns was 0.1 miles per square mile compared to an average of 1 to 3 miles per square mile in the organized towns. In settled portions of the northern Appalachians, public road building remains an ongoing process. Baldwin and others (2007) found that approximately 1,200 miles of roads were built in settled landscapes in Maine between 1986–2003, impacting more than 92,000 acres of adjacent habitats. Furthermore, they estimated that regular, public roads in the Northern Appalachian-Acadian Forest Ecoregion as a whole—especially those that provide access to subdivisions, would double by 2013 (Baldwin et al. 2007). The majority (93.5%) of these new roads perform local functions and are short (<1,000 feet in length) residential roads typical of sprawl. Increased permanent road and energy infrastructure development within and along the boundaries of the Western Maine Mountains has the potential to impact tens of thousands of acres through direct habitat loss and edge effects, which will have a significant impact on regional connectivity.

Prior to the 1970s, there were few logging roads in the region. Those that existed were largely primitive and narrow and used for supplying remote logging and sporting camps. This changed when the river drives

¹⁸ Good data on private roads in the unorganized towns are lacking. 2010 estimates from the Land Use Planning Commission indicate that there are on the order of 1,500 miles of public roads and over 20,000 miles of private roads in the unorganized towns.

ended and salvage operations during the spruce budworm outbreak of the 1970s and 1980s began. In 1997, the Maine Department of Conservation estimated that there were ~20,000 miles of private roads on the approximately 10 million acres of unincorporated land in Maine, with an anticipated 500 miles of new road being added each year (Publicover and Poppenwimer 2002; Maine Department of Conservation 1997). If this trend is accurate, based on a simple proportion and not accounting for roads that are reclaimed or abandoned, there would be between 10,000 and 15,000 miles of private logging roads within the five million-acre Western Maine Mountains region today. Aside from major haul roads, most logging roads in the region are low-volume, unimproved, single-lane, dirt or gravel roads without significant, cleared verges. Compared to public roads, these roads receive episodic use from forestry machinery and relatively light use by the public for fishing, hunting and other recreation where these activities are permitted (Alec Giffen, personal communication). Major haul roads such as the Golden Road, Telos Road, and Ragmuff Road receive more use and have a larger footprint and hence a greater fragmenting effect.

The Western Maine Mountains region, along with the Adirondacks, contains the most extensive roadless areas in Maine and the eastern United States (The Nature Conservancy Conservation Gateway). Publicover and Poppenwimer (2002) conducted a detailed inventory of "roadless areas" in the Northeast, which they defined as areas greater than 5,000 acres with no public roads, discernable active private logging roads or areas that have been heavily harvested in the past two to three decades. They estimated that, in 1996–1997, 43 roadless areas in the Western Maine Mountains fit this definition, encompassing about 870,000 acres, 15% of the region. The largest areas were Baxter State Park, the Debsconeag Lakes area and White Mountains National Forest. An additional 55 areas (mostly smaller tracts on private land) were scattered throughout other parts of the state to the north and east. By 2000, the number of roadless areas in the Western Maine Mountains for of coadless areas in the Western Maine at the state to the north and east. By 2000, acres (Publicover and Poppenwimer 2006). Currently, the region is estimated to contain 46 such areas encompassing about 603,000 acres,¹⁹ and most areas outside of the Western Maine Mountains have been eliminated due to road building and harvesting over the past two decades (Publicover and Poppenwimer, unpublished data).

Today, although there is an extensive system of logging roads in place, approximately 48% of the region's forest is more than one kilometer (3,300 feet) from the edge of a permanent public or major logging road,²⁰ which is beyond the distance where the most degrading road "edge" effects occur²¹ (Laurance et al. 2002; Laurance et al. 2017).²² This compares to only 5% of forestland beyond this threshold in southern Maine and a global average of 30% (Haddad et al. 2015) (Fig. 8a and 8b, following pages).

Rural development in the Western Maine Mountains is limited, occurring primarily along the region's southern and eastern edges, on some lake shores, and along permanently paved roads. This development consists primarily of single-family camps and homes, sporting camps, small subdivisions and small businesses, such

²¹ See page 17 for a fuller discussion of edge effects.

¹⁹ In a classic example of fragmentation, the increase in the number of roadless areas is due to several formerly large contiguous areas being separated into multiple much smaller areas.

²⁰ The E911 roads dataset used here is the most comprehensive statewide dataset for permanent roads. It includes all public and major private roads in organized towns and should be a reasonable indicator of major/permanent roads in the North Maine Woods (Daniel Coker, senior spatial scientist, The Nature Conservancy, personal communication). It was not possible to determine which smaller roads were included or excluded.

²² The area included in the Western Maine Mountains region for purposes of this analysis include nearly all of the Central-Western–White Mountains biophysical section and approximately one third of the St. John Upland biophysical section, as defined in Bailey (1995).

as general stores. The only major highways in the region are Route 201, Route 6/15 and Route 16/27. There are no major transmission lines crossing the undeveloped portions of the Western Maine Mountains north of Indian Pond. Six wind farms have been constructed in the southwestern portion of the region (U.S. Energy Information Administration 2017).²³ Between 2007 and 2017, approximately 116,000 acres (0.6%) of Maine's forest were converted to nonforest land uses. The Western Maine Mountains lost an estimated 12,000 acres during this period (NEFF in press).

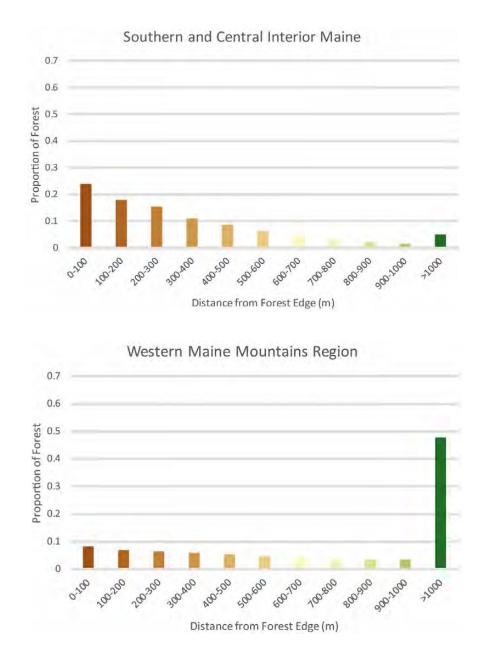


Figure 8a. Comparative percentage of distance to edge in southern and central interior Maine and in the Western Maine Mountains region based on data reflected in Figure 8b, following page. Analysis courtesy of The Nature Conservancy, Maine.

²³ As of 2017, wind farms in the region include Kibby and Chain of Ponds, Bingham Wind, Record Hill, Saddleback Ridge, Spruce Mountain Wind and Canton Mountain (U.S. Energy Information Administration 2017).

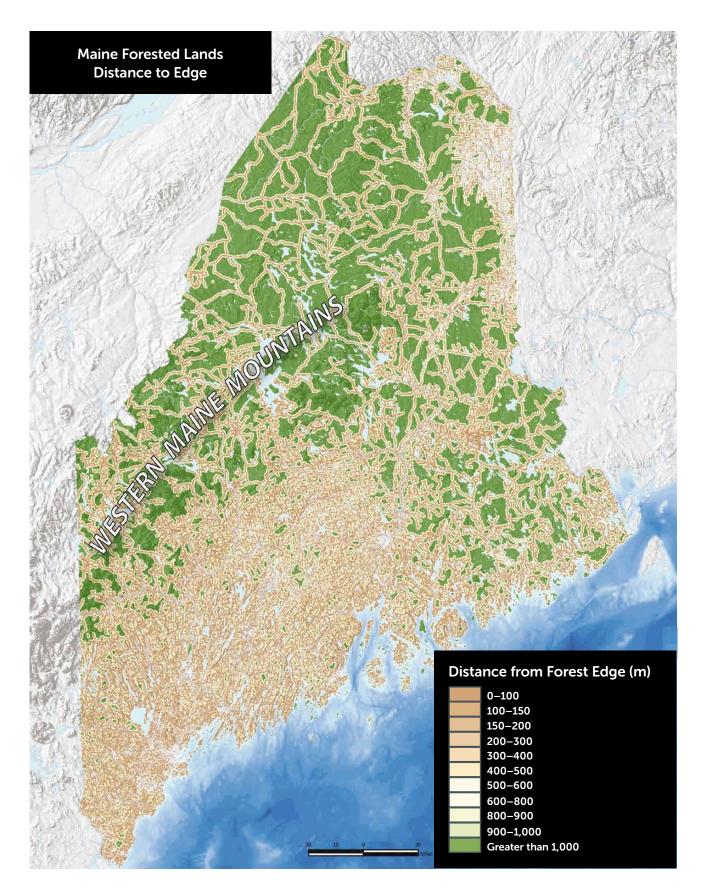


Figure 8b. Habitat blocks (green) and major roads are shown. Forest distance from an edge varies dramatically from northern Maine to southern Maine. Analysis and graphic courtesy of The Nature Conservancy, Maine.

A SUMMARY OF FOREST FRAGMENTATION IMPACTS

Forest fragmentation defined

Forest fragmentation is often defined as the breaking apart of forested landscapes into smaller and more isolated pieces. Implicit in this definition are changes in habitat patch size and distance between patches, as well as changes in the condition of the surrounding forest. These changes typically occur simultaneously and continuously, resulting in a large cumulative impact over time. However, it is a much more complicated process than this. In the Western Maine Mountains, fragmentation is largely caused by permanent features such as public roads, subdivisions and energy infrastructure. These features not only reduce the total amount of forest in a landscape, but they alter the environment in adjacent habitat because of edge effects. Fragmenting feature, which, in turn, greatly increases the amount of forest edge next to a road, clearing or other fragmenting feature, which, in turn, greatly increases the total amount of land impacted. In addition, connectivity is impacted by the quality of habitat that remains in the surrounding forest. The extent that this forestland retains habitat value and is "permeable" to the movement of plants and animals depends on how it is managed and the species in question.

Forest fragmentation has the potential to compromise the Western Maine Mountains' biodiversity and connectivity and to drive ecological processes beyond the range of natural variability (Rowland et al. 2005). Different species are affected by fragmentation in different ways, depending on biological attributes such as habitat specialization, niche specialization, home range size, dispersal ability, mobility and a host of other factors (Lindenmayer and Fischer 2006). Some effects are immediate and local in extent while others occur at a landscape scale and are cumulative, playing out over decades or more. Other effects may be temporary, such as clearings created by timber harvests, or relatively minor, such as impacts associated with narrow, lightly used woods roads.

Research in Maine, the Northeast, and around the world demonstrates unequivocally that forest fragmentation—whether permanent or temporary—reduces native biodiversity and regional connectivity over time. A review of the literature indicates that fragmentation negatively affects terrestrial and aquatic ecosystems in a number of ways. The most severe effects, which are caused by roads, energy infrastructure, subdivisions and other permanent forms of fragmentation include:

- increased mortality and habitat loss from construction of roads and other fragmenting features
- increased mortality and other direct impacts associated with infrastructure after construction
- changes in species composition and reduced habitat quality from edge effects
- changes in species composition and behavior as habitat patch size delines²⁴
- changes in hydrology and reduced aquatic connectivity
- introduction and spread of exotic species
- changes in the chemical environment
- pressures on species resulting from increased fishing, hunting, and foraging access
- loss of scenic qualities and remote recreation opportunities

In addition, forest management can have transitory fragmenting effects, such as acting as a barrier for species that need large connected areas of mature forest to thrive. New research suggests that this may compromise the ability of managed forestland to function as habitat or an ecological linkage for some species (see for example, Simons-Legaard et al. 2013).

²⁴ The terms "habitat patch," "patch," and "fragment" are used interchangeably in this paper.

Although each of these impacts are described separately on the following pages, they are interrelated and occur to varying degrees depending on the type of fragmenting feature, whether the feature results in permanent loss of habitat, the time elapsed since fragmentation began, and the habitat requirements of the species involved. It is essential to keep in mind that fragmentation is a continuous and cumulative process where the impacts of many smaller fragmenting features combine to create a large and often unpredictable regional impact, resulting in ongoing environmental degradation and species loss over time.

Mortality and habitat loss from construction of roads and other human infrastructure

Construction of roads, utility corridors and other human infrastructure kills any sessile or slow-moving animal and all vegetation in the path of the feature (Trombulak and Frissell 2000). Direct habitat loss from the footprint of these features can be significant. New projects have the potential to significantly increase the rate of fragmentation in the region. For example, the proposed New England Clean Energy Connect Project would destroy nearly 1,000 acres of wetland and forest habitat in the Western Maine Mountains, and edge effects from the permanently cleared utility corridor and access roads would increase the impacted area by an additional 13,000 acres, assuming a 1,000-foot edge effect on either side). In addition, during the 1–2 year construction period, an estimated 500 acres would be needed for roads and staging areas and additional wetlands would be filled. Other documented impacts of roads and utility corridor construction include elevated mortality of trees and other species in the adjacent forest, mortality of soil biota from physical changes in the soil under and adjacent to the roads, mortality of aquatic species from direct transfer of sediment into nearby streams and wetlands, and avoidance and other changes in behavior due to vehicle noise and light (Trombulak and Frissell 2000; Laurance et al. 2002; Laurance et al. 2017; Charry 2007).

Mortality and other impacts of infrastructure after construction is complete

Mortality of animals from road collisions is well documented (Van der Ree et al. 2015; Charry 2007; Trombulak and Frissell 2000). Roads and other linear infrastructure negatively impact wildlife through increased mortality, decreased habitat amount and quality, changing species movement patterns, and fragmentation of populations into smaller subpopulations, which are more vulnerable to local extinction. Roads are considered a driving factor in the decline of many species globally, from moose and grey wolves to insects and other invertebrates (Van der Ree et al. 2015; Benitez-Lopez et al. 2010; Andrews et al. 2008; Glista et al. 2007; Muñoz et al. 2015). They can also impede restoration efforts. For example, a 1989–1992 effort to reintroduce Canada lynx to New York state failed because the released lynx were largely transient and suffered high road mortality throughout the region (Daniel Harrison, professor of wildlife ecology, University of Maine, personal communication).



Figure 9. Canada lynx crossing road. Road collisions can be a major cause of lynx mortality. Photo by Jeremiah John McBride, CC BY-ND 2.0, https://www.flickr.com/photos/bullfrogphoto/3411471411.

In Maine and elsewhere, research indicates that amphibians and reptiles are particularly susceptible to roadkill because many species, such as wood frogs and spotted salamanders, migrate between wetlands where they breed and uplands where they live during the nonbreeding season. In addition, individuals are generally inconspicuous and sometimes slow-moving, and in the case of turtles, it takes a long time for individuals to become sexually mature—which increases the likelihood that animals will be killed by collision before they are able to reproduce, and young are vulnerable after hatching (Baldwin et al. 2007; Gibbs and Shriver 2002; Rosen and Lowe 1994; Fahrig et al. 1995). Road size, density and traffic volume and distance from wetlands, streams and pools affect the magnitude of these impacts. For example, dense networks of wide roads with high traffic volume can have significant impacts on breeding



Figure 10. Wood turtle crossing road. Declining turtle populations in many parts of Maine are attributed to road collisions. Photo by John Mays.

populations of turtles. Roads are the major cause of decline of spotted and Blandings turtles in southern Maine (Beaudry et al. 2008) and are contributing to the decline of wood turtles in the state, since these species move from streams to uplands to nest (Compton 1999). According to Gibbs (2002), "as little as 2–3% additive annual mortality is likely more than most turtle species can absorb and still maintain positive population growth rates."

In addition to direct mortality, roads and utility corridors may serve as conduits for the movement of organisms across the landscape that are detrimental to native forest species—fostering the spread of alien plants and predators, or as a barrier or filter that prevents or impedes the movement of some sensitive species (Forman and Alexander 1998). For example, white-footed mice and some other rodent species are reluctant to cross roads (Merriam et al. 1989; Oxley et al. 1974). Others, such as black bears, have been documented to shift their home ranges away from areas with high road densities, and some predator and prey species may preferentially travel along road corridors, increasing the risk of collision and altering predator-prey interactions (Brody and Pelton 1989; Trombulak and Frissell 2000). Highly fragmented landscapes that result in unsuitable habitat around ponds at distances greater than 3,300 feet (1 kilometer) can preclude the recolonization of pools by amphibians and result in local extinctions of other wetland-dependent taxa, including small mammals, nonbreeding amphibians, and reptiles (Laan and Verboom 1990; Gibbs 1993). DeMaynadier and Hunter (2000) found that salamander populations avoid crossing wide (~40 feet) heavily used logging roads, while the impacts of narrow (<16 feet) woods roads were insignificant. Hung culverts and other drainage infrastructure associated with roads can also act as barriers, preventing upstream fish passage and access to breeding and feeding habitat for aquatic species. This is discussed further under aquatic connectivity.

As energy infrastructure expands in the Northeast and elsewhere, additional impacts are becoming apparent, such as avian and bat collisions with transmission lines and wind turbines; altered reproductive success and physiology of insects, mammals, birds, trout, and other species groups associated with electromagnetic radiation; loss of roosting sites; and altered movement patterns (Rytwinski and Fahrig 2015, Smallwood 2013; Jochimsen et al. 2004; Fensome and Matthews 2016; Van der Ree et al. 2015). In addition to direct collisions, there is growing evidence that electromagnetic radiation from transmission lines can have significant impacts on wildlife. For example, Fernie and Reynolds (2005) conclude that exposure of birds to electromagnetic radiation "altered the behavior, physiology, endocrine system, and the immune function of birds, which generally resulted in negative repercussions on their reproduction or development. Such effects were observed in multiple species, including passerines, birds of prey, and chickens in laboratory and field situations, and in North America and Europe." Long-term and before-and-after studies are needed on other species groups.

Changes in species composition and reduced habitat quality from edge effects

When a forest is fragmented by a road, clearing or other disturbance, there will be a zone of impact along the forest edge.²⁵ Edge habitat is typically windier, warmer, and drier than the forest interior (Hunter and Gibbs 2007). The extent of this "edge effect" is greater along high contrast edges—such as between a utility corridor and a forest, than along low contrast edges—such as between a regenerating clearcut and adjacent uncut forest. The relative amount of edge increases as patches become smaller and more complex in shape (Fig. 11a and Fig. 11b). The amount of edge is also greater for long narrow clearings, such as roads and utility corridors, than for more compact clearings of the same size, such as clearcuts.

The habitat lost or altered by edge effects can be many times greater than the footprint of the fragmenting feature itself (Laurance et al. 2017; Harper et al. 2005; McGarigal et al. 2001; Tinker et al. 1997). The longestrunning forest fragmentation study from the Amazon indicates that the impact zone of fragmenting features such as permanent roads can extend from 30 feet to more than 1,300 feet into adjacent forestland (Laurance et al. 2002; Laurance et al. 2017). Increased insolation, changes in air temperature and humidity, altered plant, animal and microbial species composition, species invasions, and a host of other edge effects were observed. South of the Western Maine Mountains, most forests are well within the range where human activities, altered microclimate, and nonforest species may influence and degrade forest ecosystems. Here, habitat fragmentation often leads to the establishment of early successional habitat along forest edges because plants adapted to interior mature forest conditions typically have low dispersal capacities compared to disturbance-adapted "weedy" plants (Harper et al. 2005). This favors generalist species at the expense of forest interior species. In the United States, there is a great body of research that documents the impacts of development and edge habitat on birds (see reviews by Forman and Alexander 1998, Lindenmayer and Fischer 2006, and Van der Ree et al. 2015). For exam-

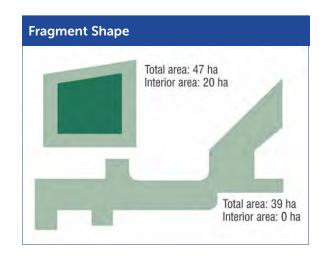


Figure 11a. Shape affects the percent of area affected by edge effects, as is shown by a comparison of the interior area available in two different shaped blocks of land. Adapted by Barbara Charry for Maine Audubon, from Verner et al. Wildlife 2000 1986, reprinted by permission of Wisconsin Press.

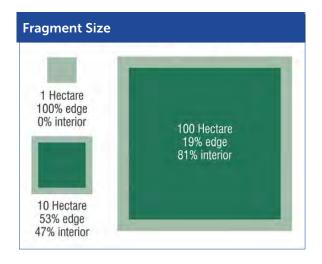


Figure 11b. Size affects the percent of interior area affected by edge effects, as shown in this comparison of the interior area of three different sized blocks. As fragment (block) size increases, the relative proportion of edge habitat decreases and interior habitat increases. Adapted by Barbara Charry for Maine Audubon, from Landscape and Urban Planning (36) Collinge, pg. 64, reprinted with permission from Elsevier Science.

²⁵ The edge of a habitat patch can be broadly defined as a marginal zone where the microclimatic and other ecological conditions differ from the those in the patch's interior (Lindenmayer and Fischer 2006; Matlack 1993).

ple, the decline of many ground-nesting, forest-interior species in the Northeast, such as the ovenbird and wood thrush, have been attributed to increased predation pressure from raccoons, cats and other generalist species that thrive along forest edges (Ortega and Capen 1999; De Camargo et al. 2018). Increased nest predation and reduced reproductive success can extend more than 2,000 feet into the adjacent forest. Other forest species, such as interior-forest–feeding bats, are affected by changes in insect prey, roosting habitat and other habitat features in forest edges (Grindal and Brigham 1998). The relationship between edge effects and patch size is complicated. Rosenberg et al. (1999) found that tanager species respond differently in different parts of their range and that landscape features interact to create population sources and sinks. The more continuity of forest cover and presence of many forest age classes on the landscape may reduce some species' sensitivity to edge effects.

The following table (Fig. 12) provides a summary of penetration distances of different edge effects associated with permanent fragmenting features documented from a 22-year experiment on forest fragmentation in the Amazon (Laurance et al. 2002; Laurance et al. 2017). Although analogous studies have yet to been done in the Northeast, there is abundant evidence that many of these edge effects are contributing to species declines and extinctions in the region (see reviews by Pfiefer et al. 2017 and Harper et al. 2005). One type of edge effect—invasion by exotic species—is discussed in more detail on page 22.

Disturbances that penetrate > 100 m	Disturbances that penetrate 50–100 m	Disturbances that penetrate 20–50 m	
Increased wind disturbance	Reduced soil moisture	Higher understory foliage density	
Elevated tree mortality/damage	Lower canopy-foliage density	Increased seedling growth	
Invasion of disturbance- adapted butterflies	Increased air temperature	Invasion of disturbance-adapted plants	
Altered species composition of leaf-litter ants	Increased temperature and vapor pressure deficit	Lower leaf relative-water con- tents	
Invasion of disturbance- adapted beetles	Reduced understory bird abun- dance	Lower soil moisture content	
Altered species composition of leaf-litter invertebrates	Elevated litter fall	Higher vapor pressure deficit	
Altered abundance and diver- sity of leaf-litter invertebrates	Increased photosynthetically active radiation in understory	Higher leaf conductance	
Altered height of greatest foli- age density	Lower relative humidity	Increased phosphorus content of falling leaves	
Lower relative humidity	Increased number of treefall gaps	Reduced density of fungal fruit- ing bodies	
Faster recruitment of distur- bance-adapted trees	Figure 12. Documented Edge Effects Associated with Permanent Fragmenting Features from the Biological Dynamics of Forest Fragments Project. (Adapted from Laurance et al. 2002; Laurance et al. 2017.)		
Reduced canopy height			

Although the Western Maine Mountains region has an estimated 10,000 miles of logging roads, the edge effects along most of these are less than that of typical roads in developed parts of the state because of lower traffic volumes, narrower road widths, unpaved surfaces, limited verge clearing and because some roads are gated when not in use. Nevertheless, studies in other areas suggest the cumulative impact of logging road networks can be significant (McGarigal et al. 2001; Forman and Alexander 1998). While the pace of private road construction has likely slowed as landowners have their modern transportation network mostly built out and some older roads have been abandoned, others are being replaced with newer, better and likely larger surfaces. The only place where road density is decreasing is in designated reserves where public agencies and conservation organizations have worked to close roads. More information is needed to evaluate the overall impacts of the logging road system on forest fragmentation in the region.

Changes in species composition and behavior as habitat patch size declines

A habitat patch is a relatively homogeneous habitat area that differs from its surroundings. Hunter and Gibbs (2007) give three main reasons why large habitat patches have more species than small ones. First, a large patch will almost always have a greater variety of environments than a small fragment, and each will provide niches for different species. Second, a large patch is likely to have both common and uncommon species, but small fragments are likely to have only common species. For instance, species with larger home ranges, such as black bear or bobcat, are unlikely to survive in smaller fragments. Finally, small fragments will, on average, have smaller populations that are more susceptible to being extirpated than a large population.²⁶

Habitat requirements are species-specific. In Maine, patch size appears to be particularly critical for species associated with mature forest conditions, larger patch sizes and forest interiors. Many Maine birds, such as red-shouldered hawk, black-throated blue warbler, Canada warbler, ovenbird and wood thrush, require hundreds of acres of continuous, relatively closed-canopy forest to reproduce successfully, as do mammals with large home ranges, such as moose, bobcat, black bear and American marten (Charry 1996; Askins 2002). For example, Chapin et al. (1998) found that resident American martens established home ranges in areas where median intact forest patch size ranged from 375 to 518 acres, for males and females respectively. These area-sensitive and habitat specialist species will start disappearing when the size of habitat blocks falls below a certain threshold (Askins 2002; Blake and Karr 1984; Whitcomb et al. 1981). Roads, clearings, residential development and other features can act as barriers, preventing animals from using habitat that is nearby for breeding or feeding. Populations can become subdivided, and eventually animal species are lost from an area as it gets too small to support an isolated population, or is too far from a source population for recolonization to occur (Lindenmayer and Fischer 2006; Charry 1996; Forman and Alexander 1998; Laurance et al. 2017; and others). Conversely, species sensitivity to fragmentation may be lower in regions with greater overall forest cover (Rosenberg et al. 1999).

Hanski (1998) hypothesizes that when the total amount of suitable habitat in the landscape falls below 20–30%, the viability of local populations is reduced. Other studies suggest that population declines accelerate when available habitat falls below even higher thresholds (Andrén 1994). For example, Homan et al. (2004) found that wood frogs were less likely to occupy breeding pools where the amount of suitable forest habitat

²⁶ In 1967, MacArthur and Wilson put forward the groundbreaking theory that island size and degree of isolation are highly correlated with biodiversity. Hunter and Gibbs observed that while island biogeography theory does not always directly apply to terrestrial landscapes, it provided insights fundamental to understanding the effects of reducing patch size and connectivity in terrestrial landscapes.

within approximately ~3,300 feet (1 kilometer) was less than 45% and spotted salamanders were less likely where forest habitat within ~1,150 feet of a pool was less than 40%.

Forest fragmentation also influences plant populations. In their *State of the Plants* report, the New England Wildflower Society (2015) documented a mean 67% loss of previously recorded range for 71 rare plant species. One of the main contributing factors was fragmentation of habitat across species' ranges, which isolated populations and reduced their ability to disperse.

Small size combined with increased isolation of habitat patches can also affect behavior, biology and interactions of species. Impacts include reduced breeding success, changes in predator-prey relationships, changes in ability to disperse and increased competition for resources (Lindenmayer and Fischer 2006). For example, before their demise as a result of chestnut blight, it was believed that stands of American chestnut needed to be above a certain size to produce enough seed to overcome pressure from seed predators (Rosen-zweig 1995; Lindenmayer and Fischer 2006).

Changes in hydrology and reduced aquatic connectivity

Fragmentation of terrestrial habitats often leads to fragmentation of river and stream networks. The division and isolation of watersheds and stream networks by dams, roads and culverts is one of the primary threats to aquatic species in Maine and the United States (Martin and Apse 2011). Intact forested blocks are essential to protecting stream networks. Forested stream corridors intercept sunlight, moderating water temperature (Moore et al. 2005). Riparian trees also contribute the majority of coarse organic material, in the form of leaves and downed wood, and fallen leaves frequently form the base of the food webs of small streams (Vannote et al. 1980). Large woody material generated from large fallen trees adjacent to streams has a major influence on stream ecosystem structure and function (Dolloff and Warren 2003).

The impact of aquatic fragmentation on aquatic species generally involves loss of access to quality habitat for one or more life stages of a species. For example, dams and impassable culverts prevent brook trout

populations from reaching upstream thermal refuges, which are critically important as the climate warms. In addition, roads can have significant effects on the physical environment. Roads can interrupt subsurface flows and patterns in aquatic systems when water flows are rerouted into road ditches and culverts (Lindenmayer and Fischer 2006; Forman and Alexander 1998). The impervious nature of roads increases runoff, erosion, sedimentation and water-level fluctuations, and can flood adjacent wetlands (Andrews et al. 2008; Al-Chokhachy et al. 2016). Temporary pools in ditches and ruts can be population sinks for amphibians that breed there instead of higher quality vernal pools (Andrews et al. 2008).



Figure 13. Cool mountain streams, like this one in the High Peaks region of the Western Maine Mountains, provide critical habitat for brook trout and other coldwater species. Photo by Charlie Reinertsen Photography.

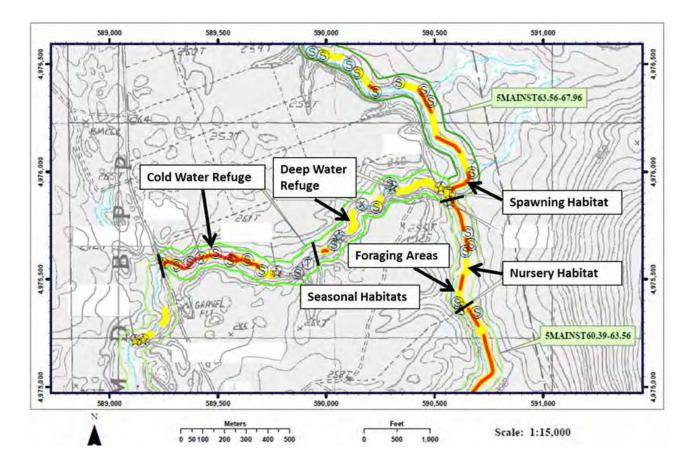


Figure 14. Fish need to move: brook trout use a variety of in-stream habitats to meet their daily and annual needs for feeding, resting and breeding. They often move up and down streams and into tributaries to find food and refuge. Graphic modified from the Maine Atlantic Salmon Atlas (2006) by Alex Abbot and the U.S. Fish and Wildlife Service's Gulf of Maine Coastal Program.

A bellwether species in the Western Maine Mountains is brook trout, which requires cool, clean, connected networks of streams and lakes (Fig. 14). A 2006 range-wide study of this species found that Maine is the only state in the eastern United States with extensive intact populations of wild, self-reproducing brook trout in lakes and ponds. Furthermore, Maine is the last true stronghold for stream-dwelling populations of wild brook trout, supporting more than twice the number of intact subwatersheds than the other sixteen states in their eastern range combined (Trout Unlimited 2006). Although wild brook trout waters are found elsewhere in northern Maine, they are most prevalent in the Western Maine Mountains (Trout Unlimited 2006; DeGraaf 2014). The high habitat integrity of the region is due to a combination of cool temperatures and an abundance of large, connected stream networks. The cooler region provides optimal conditions, with fewer competing, nonnative fish species than the southern or coastal parts of the state. Large patch size of intact brook trout habitat allows fish to migrate to cooler water when portions of their habitat grow too warm.

The Nature Conservancy's Conservation Gateway maps show a region with few dams and high stream connectivity. This is not the case for much of southern Maine, where many public- and private-road stream crossings in the region do not meet recommended standards.²⁷ Maintaining aquatic connectivity is critical to

<sup>These include: (1) spanning the entire width of the natural stream; (2) setting the elevation to match the natural stream;
(3) matching the slope to the natural stream; and (4) ensuring that the stream bed is made up of natural materials (see Maine Department of Transportation and www.maineaudubon.org/projects/stream-smart).</sup>

maintaining brook trout populations in northern Maine (Trout Unlimited 2006; Fesenmyer et al. 2017; Coombs and Nislow 2014). Conserving habitat for this umbrella species, in turn, will ensure the survival of other plants and animals that require pristine aquatic habitats.

Introduction and spread of exotic species

Invasion by exotic plant species is a common and widespread impact of fragmentation that can result in displacement of native species. In general, non-native invasive plant species thrive in disturbed and early successional habitats. Invasive plants can become established in roadside ditches, along utility corridors, on soils disturbed by residential or commercial development and on soils disturbed by timber harvests that border developed areas. In addition, seeds can be introduced in road fill and through planting of exotic ornamental species. Common traits of invasives include rapid growth, light and drought tolerance, bird-disseminated seeds, and the ability to outcompete native plants (Webster et al. 2006).

Invasive non-native woody plant species have the potential to profoundly alter the structure and function of forest ecosystems. Invasive woody and herbaceous plants rapidly colonize forest edges and may penetrate more than 330 feet into the forest interior, altering or eliminating habitat for native plants (Charry 1996). Wetland and aquatic invasives pose a similar threat in wetland and aquatic ecosystems. Because many invasive plant species have the ability to form dense monocultures, they have a competitive advantage in forest understories, particularly in edge habitat. In addition, most species have relatively few—if any—natural predators in their introduced ranges (Webster et al. 2006; Woods 1993). Other impacts include changes in soil chemistry and biota—which may suppress native tree regeneration—and reduced or eliminated foods used by pollinators, fruit and seed eaters and herbivores (Silander and Klepeis 1999; Charry 1996; Webster et al. 2006; Burnham and Lee 2010; Ehrenfield et al. 2001; Heneghan et al. 2006; Hunter and Mattice 2002).

Large forest blocks appear to resist woody plant invasions better than land that has a history of agricultural or residential use (Mosher et al. 2009). The resistance of large intact forest blocks to invasion probably stems from two main factors: the deep shade created by mature trees and the buffering effect of large block size, which serves to isolate interior portions of the forest from invasive seeds. If present land use trends continue, increased fragmentation of forest parcels may allow edgeadapted invasive plants such as glossy buckthorn, oriental bittersweet, Japanese barberry, and bush honeysuckles to get a deeper foothold into forest blocks. Eventually, this could allow woody invaders to take advantage of disturbances such as logging within the major forest blocks of the region, displacing native species as a result (Mosher et al. 2009; Webster et al. 2006; Silveri et al. 2001).



Figure 15. Oriental bittersweet infestation in Cape Elizabeth, Maine. Photo from Maine Natural Areas Program, Maine.gov.

Many terrestrial invasive plant species and wetland invasives, such as purple loosestrife and phragmites, are already well established in southern Maine and have expanded to the edges of the Western Maine Mountains (*iMapInvasives Database*). These species thrive in utility corridors and roadside ditches (Fig. 16). With roughly one third of Maine's flora comprised of nonnative plant species (and most of these already established in the southern part of the state), the cause-and-effect relationship between fragmentation and the establishment of non-native plant species poses a significant threat to native species and habitats in northern Maine (Mosher et al. 2009; Charry 1996).

Woody invasive plants are part of a much larger invasion of alien species of plants, insects, and disease that has the potential to fundamentally alter the composition and structure of eastern forests (Webster et al. 2006). Invasions by insects such as emerald ash borer, Asian longhorn beetle, and browntail moth are tied to both inadvertent transport by people and climate change. The relationship between the spread of these species and forest fragmentation is unclear, although new roads will increase the likelihood of transport by people and vehicles into the region.



Figure 16. Phragmites, an invasive exotic grass, established along a southern Maine highway. Photo by Janet McMahon.

There is currently a low incidence of terrestrial invasives in the Western Maine Mountains, although invasive plant species are established along the southern border of the region. No aquatic invasive plant species, invasive insect pests or invasive tree species, such as Norway maple and black locust, are currently documented in the Western Maine Mountains. Three invasive herbs have been confirmed in the interior of the Western Maine Mountains and sixteen invasive herbs and shrubs have been confirmed at the region's margin, primarily in developed areas²⁸ (*iMapInvasives Database*) (Fig. 17, following page). Fragmentation from major utility corridors, roads and new residential and commercial development has the potential to open the region to these and other invasives.

²⁸ MNAP lists 68 species of invasive plant species that are currently documented in Maine or are probable. I reviewed MNAP's *iMapInvasives Database* to determine presence/absence of all documented species in the region. The three species confirmed in the Western Maine Mountains' interior include reed canary grass, common reed and coltsfoot. Because field effort in the region is low compared to other parts of the state, invasive species occurrences may be under-reported. I have not surveyed the Western Maine Mountains systematically, however, my observations in areas visited suggest that most terrestrial invasive plant species are absent or rare, especially in the region's interior.

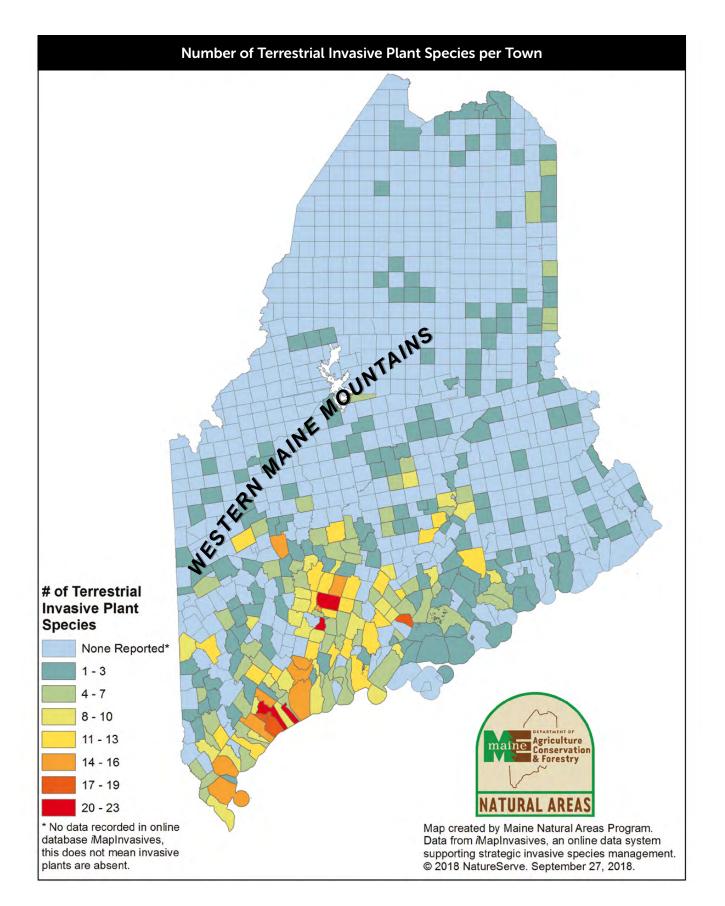


Figure 17. Documented terrestrial invasive plant species in Maine. The Western Maine Mountains are relatively free of terrestrial plant species. Fragmentation from major utility corridors, roads and new residential and commercial development has the potential to open the region to these invasives. Map courtesy of the Maine Natural Areas Program in the Maine Department of Agriculture, Conservation and Forestry.

Changes in the chemical environment

Use and maintenance of roads, utility corridors and windfarms contribute at least five different general classes of chemicals to the environment: heavy metals, salt, organic molecules, ozone and nutrients (Trombulak and Frissell 2000). These are mostly derived from fuel additives, deicing salts and herbicides. Contamination of soils, plants and animals can extend tens to hundreds of meters from a road or power line right of way depending on the contaminant, wind, and if the chemicals reach flowing water. Trombulak and Frissell summarize a number of impacts on plants and animals, such as the poisoning of habitats so they no longer have adequate carrying capacity, mortality or reduced health and growth from exposure, bioaccumulation of chemicals that makes species toxic to predators and increased concentrations of salts that can attract large mammals to roadsides, increasing vehicle collision risk. The high skin permeability of amphibians make them particularly susceptible to toxins from road salts and other chemicals (Andrews et al. 2008).

Pressures on species resulting from increased fishing, hunting and foraging access

Increased road density and access into remote areas can lead to increased hunting, trapping, fishing, poaching, disturbance to wildlife, trampling and other direct human impacts on biodiversity in forest and aquatic ecosystems (Laurance et al. 2002 and 2017; Haddad et al. 2015; Brocke et al. 1988). A study of the relationship between density of publicly accessible roads and moose populations in Nova Scotia found that natural populations declined when road density exceeded a threshold of 0.6 km/km² (~1.4 mi/mi²). This was attributed to the fact that most moose hunting occurred along roads (Beazley et al. 2004). They concluded that road density may be among the key factors influencing habitat productivity, and thus critical habitat area and population viability, for moose in mainland Nova Scotia, as well as for other species sensitive to the effects of roads, such as Canada lynx, American marten and black bear.

The USDA Forest Service has found that illegal introduction and harvest of fish species are more likely to occur in areas with ready access (Gucinski et al. 2000). Increased road density and improved access into remote ponds have been linked to regional declines of lake trout and introduction of invasive fish species such as smallmouth bass in northern Ontario (Kaufman et al. 2009). In Maine, unauthorized introductions of invasive fish species, such as small and largemouth bass, are threatening native fish species populations—especially brook trout—and can ultimately impact entire aquatic systems. In the past, the majority of introductions occurred in populated portions of the state, but in the past decade, introductions are occurring at a higher rate in western and northern Maine where most of the state's wild brook trout populations are located. Improved road access and development are likely contributing factors (Merry Gallagher, research fisheries biologist, Maine Department of Inland Fisheries and Wildlfe, personal communication). Increased access is also likely to lead to overharvesting of species such as chaga, ginseng and ramps that are collected for food, medicine and other purposes.

Loss of scenic qualities and remote recreation opportunities

Maine has a long tradition of hunting, fishing, guiding and remote camping that is closely bound to the undeveloped and scenic character of its northern forests, lakes and mountains. These uses are a major and growing economic driver in northern Maine (David Publicover, senior staff scientist, Appalachian Mountain Club, personal communication). Degradation of the skyline caused by utility corridors, major road right of ways, sprawl from development, wind farms and associated light pollution are general aesthetic impacts of for-



Figure 18. Fishing at Lake Mooselookmeguntic. Photo by Sarah Haggerty.

est fragmentation. These affect remote recreation and other human values associated with large undeveloped areas. Most vistas from mountains and water bodies in the Western Maine Mountains provide long scenic and unbroken views. Roads are generally screened by the forest canopy, but wind towers and transmission lines with wide, cleared right of ways are conspicuous features on the landscape. Other than Routes 201, 16/27 and 6/15, there are currently no major highways or transmission corridors impacting the high scenic value of the region. The proposed New England Clean Energy Connect Project transmission corridor would be one of the largest fragmenting features in the Western Maine Mountains region, dividing it in two and crossing 53.5 miles of forest.

Potential fragmenting effects associated with forest management

Many species that need intact forest patches for their core habitat are also affected by the condition of the matrix forest surrounding these patches. It is well recognized that the condition of the matrix forest that surrounds intact mature habitat patches can affect regional biodiversity and landscape connectivity. In general, connectivity and biodiversity are reduced when the matrix forest becomes simplified in terms of species and structural diversity. Prevedello and Vieira (2010) found that a matrix that is more similar in structure to intact habitat patches will increase functional habitat and decrease isolation of patches. Timber harvesting can have a significant fragmenting effect, although the degree of impact depends on the extent, intensity and frequency of harvesting. As the extent and intensity of harvesting increases, the extent of interior forest habitat—especially large contiguous blocks—decreases. And while the impact of any individual harvest is temporary, cumulative harvesting patterns typically create a shifting mosaic of early successional stands, edge habitat and interior forest habitat across the landscape.²⁹

Managed forest makes up about 90% of the Western Maine Mountains. While this forest remains largely unfragmented by permanent features such as public roads and residential development, it has been greatly

²⁹ It is important to note that forest management and timber harvesting can be practiced in a manner that maintains or enhances wildlife habitat over time (DeGraaf et al. 2007).

modified by forest practices in the past half century. In the presettlement forest, where large-scale standreplacing disturbances were rare events, the majority of the landscape would have been composed of older stands that were allowed to develop uninhibited into a late-successional condition (Lorimer 1977; NEFF in press). Today, although a full suite of native tree species remains, there has been a broad ecological shift away from late successional taxa, such as red spruce and hemlock, in favor of early- and mid-successional taxa, such as red maple and aspens (Thompson et al. 2013). In the past half century, large areas of spruce-fir forest

have been converted to deciduous and mixed types due to regeneration of hardwoods after high-intensity sprucefir harvests. In addition, the total amount of mature forest on the landscape has decreased along with the patch sizes in which these mature forests occur, and there is a correspondingly larger amount of edge between intact mature forest and harvested forest (NEFF in press; Legaard et al. 2015). Today only 1.4% of Western Maine Mountains forests are in a late-successional condition³⁰ and only 3% are classified as large saw timber³¹ by the Maine Forest Service (NEFF in press). This compares to a presettlement forest where 59% or more of the forest was older than 150 years (Thompson et al. 2013; Lorimer and White 2003; Barton et al. 2012). An initial assessment of Ecological Reserve Monitoring data quantifies differences in forest structure between older stands in reserves and Maine's managed forests. Ecological reserves have greater average live-tree basal area, more large and very large trees, more standing dead trees, and more downed woody material (Kuehne et al. 2018). In short, the combination of spruce budworm era salvage cuts in the 1970s and 1980s and widespread partial harvesting³² since the 1990s has created a modern forest that is younger, more homogeneous, and less coupled to local climatic controls (Thompson et al. 2013).³³

The result of these structural changes is a change in both plant and animal species composition at all forest stages (Legaard et al. 2015).³⁴ Species that require larger connected patches of older forest are particularly susceptible. For ex-

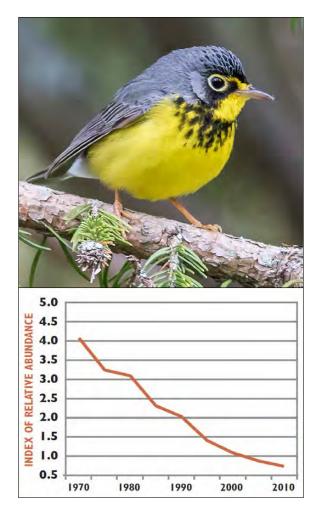


Figure 19. Species requiring mature coniferous or mixed forest habitat, such as the Canada warbler, are decreasing due in part to loss of summer breeding habitat. Graphic courtesy of Maine Audubon.

³⁰ Late-successional stands are greater than 120 years old, have a multi-storied canopy, and have at least 15 trees per acre (either alive or standing dead) > 16" DBH (diameter at breast height). Unmanaged late-successional stands tend to have cohorts of trees of different ages, large living and dead trees, large-diameter logs on the forest floor, vertical structural complexity and different-sized canopy gaps (Franklin et al. 2002).

³¹ Stands with > 100 ft² basal area in trees > 5.0" DBH in which trees > 15" comprise at least 50% of the basal area.

³² Partial harvests are areas that have been subject to a commercial partial harvest, including shelterwood and any other harvest method involving partial overstory removal (McGarigal et al. 2001; Legaard et al. 2015). The result is typically a dispersed low-density canopy.

 ³³ See Legaard et al. (2015), Simons-Legaard et al. (2018) and NEFF (in press) for detailed analyses of current forest condition.
 ³⁴ Legaard et al. (2015) used a time series of Landsat satellite imagery (1973–2010) to evaluate cumulative landscape changes in an area of western and northern Maine that included about half of the Western Maine Mountains.

ample, Payer and Harrison (2003) found that forests with large patches of large trees in a mature condition, either deciduous or coniferous, generally provide the structural stand attributes required by a wide variety of species such as American marten, northern flicker, wood thrush and northern long-eared myotis (a bat) (NEFF in press). Although not researched in Maine, a similar pattern is evident for forest birds in boreal habitats to the north. For example, Schmiegelow et al. (1997) found that, as the acreage of older forest declined, neotropical migrant bird species that require mature forest conditions declined in both connected and isolated fragments of such habitat, and resident species declined in isolated fragments.

Changes in forest structure also impact pool-breeding amphibians, which in the Northeast are sensitive to harvesting practices that reduce overstory canopy levels to less than 50%. Canopy closure, along with natural litter composition and coarse woody material within 100 to 400 feet of vernal pools, are important habitat elements required by salamanders and other amphibians (deMaynadier and Houlahan 2008; Popescu and Hunter 2011; Ross et al. 2000).

Changes in the composition and structure of the matrix forest as a result of harvesting, although temporary, can also impact generalist species such as white-tailed deer. Near the northern edge of their geographic range, where snow can restrict mobility and access to forage, white-tailed deer depend on mature conifer forests for wintering habitat. In a 1975–2007 time-series Landsat imagery analysis, Simons-Legaard et al. (2018) documented that fragmentation and reduction of mature conifer forest habitat significantly reduced the amount of deer wintering areas³⁵ in the Western Maine Mountains. The extent of currently zoned deer wintering habitat and habitat under cooperative agreement in the region is currently estimated to be only 34% of what is recommended (Nathan Bieber, personal communication). Simons-Legaard et al. conclude that continued forest-type conversion is expected to extend the effects of habitat fragmentation on northern deer populations and other species that require mature conifer forest into the future (Simons-Legaard et al. 2018).

Other than research on forest trees, there has been little research on the impacts of patch size and condition on vascular and nonvascular plants. Some lichen, liverwort and bryophyte species are dependent on the woody debris and dead and dying trees associated with older stages of spruce-fir forest development. These structural features can require several decades to recover, unless the woody material is intentionally left (Selva 1994; Gawler et al. 1996; Rowland et al. 2005). Small isolated populations can become too far apart to recolonize the areas in between and exchange genetic information.

We are just beginning to understand the scope of these changes in the forest matrix and their long-term effects on species dispersal, richness, abundance and persistence, community composition and ecosystem function. While connectivity within the matrix forest of the Western Maine Mountains is currently high, there is growing evidence that American marten, forest birds and other species that require larger patches of mature forest are declining in the region as the stepping stones of suitable habitat become fewer and farther between. This topic is in urgent need of study by the scientific community.

³⁵ The Maine Department of Inland Fisheries and Wildlife defines deer wintering areas as forested areas used by deer when (a) snow gets to be more than 12 inches deep in the open and in hardwood stands, (b) the depth that deer sink into the snow exceeds 8 inches in the open and in hardwood stands, and (c) when mean daily temperature is below 32 degrees Fahrenheit. Ideal wintering areas (primary winter shelter) are dominated by mixed or monospecific stands of cedar, hemlock, spruce and fir, with a stand height of 35 feet.

LONG-TERM CONSEQUENCES OF FOREST FRAGMENTATION

Fragmentation is a continuous and cumulative process that leads to degraded habitats and loss of species over time. There is a growing body of research that suggests that the ecological dynamics in fragmented landscapes are a stark contrast to the dynamics in intact landscapes (Haddad et al. 2015). Although there are currently few long-term studies of the impacts of permanent forms of forest fragmentation on biodiversity and connectivity in the Northern Appalachian-Acadian Forest Ecoregion, research from elsewhere shows strong and consistent responses of organisms and ecosystem processes to fragmentation arising from decreased habitat patch size, decreased connectivity and the creation of habitat edges (Haddad et al. 2015; Lindenmayer and Fischer 2006). In general, the greater the difference between forested patches and their surrounding environment and the smaller and more isolated patches become, the greater the impact on biodiversity and ecosystem function. Haddad et al. (2015) identify three processes that drive long-term and progressive impacts of fragmentation: (1) temporal lags in extinction, (2) immigration lags and (3) ecosystem function debt.

Extinction debt

Temporal lags in extinction, or "extinction debt" is simply the delayed loss of species due to fragmentation. Hagan and Whitman (2004) suggest that we may be accruing "extinction debt" in Maine forests, describing the process as follows:

Once old forest elements such as large trees or logs are lost from a stand (e.g., as a result of a clearcut, or even a selection cut), it can take centuries for the species [dependent on such features] to return to that location. A species first has to wait for these structural features to redevelop, and then the species has to find them. Scientists are beginning to understand that forest continuity is key to many forest species. [This temporal] continuity refers to the persistence of big trees and big logs in a forest stand over a very long period of time (centuries), even though the stand might be subjected to many different disturbances, such as fire, wind, disease, or even selection logging. Species that move or disperse slowly through the landscape, and prefer large old trees or logs, are the species most at risk to the loss of older forests.

In addition to the inability of organisms to disperse, extinction debt from fragmentation may be tied to genetic traits of populations, rarity, reproductive mode, life span and a host of other factors (Haddad et al. 2015). Extinction debt is often overlooked because many of the species lost tend to be small and uncharismatic, such as insects, fungi and mosses—and yet these species may be critical for ecosystem function. In the Western Maine Mountains, changing land use patterns from permanent and temporary forms of fragmentation have already caused changes in species composition and will likely cause changes in plant and animal abundance over time. Two of these changes include the increased proportion of early successional species and the largescale reduction in the structural complexity of forest stands on which other forest organisms and ecological processes may depend (Rowland et al. 2005; Hagan and Whitman 2004). To fully understand the implications of extinction debt in the forests of the Western Maine Mountains, more long-term studies are needed.

Immigration lag

In general, smaller and isolated fragments are slower to accumulate species after disturbance than large or connected habitat blocks. In other words, because it takes longer for species to recolonize small patches, the successional transition from cleared land to mature forest conditions may take longer to occur (Haddad et al. 2015; Cook et al. 2005). This phenomenon is called "immigration lag" (Haddad et al. 2015).

tation studies have been done in agricultural or suburban landscapes, long after the onset of fragmentation. Research on industrial forest land suggests that the process of immigration lag is a complex one. For example, Hagan et al. (1996) found that densities of several forest-dwelling bird species can increase within a forest stand soon after the onset of fragmentation as a result of displaced individuals packing into remaining habitat. However, because forest songbirds are highly territorial during the breeding season they cannot simply shift elsewhere unless there is unoccupied habitat. Furthermore, it is widely thought that these species establish territories in the best habitat available. If displaced, they could be forced into poorer quality habitat resulting in reduced pairing success and productivity over time. This was the case for ovenbirds in the Hagan et al. (2015) study. Their models and data suggest that large tracts of forest are important because they are relatively free from the variety of plant and animal population dynamics that might take place near new edges, including the encroachment of individuals displaced by habitat loss. Immigration lag may also mask the risk of invasion by exotic species since there may be a long lag between introduction, colonization, and rapid range expansion of some invasive species (Webster et al. 2006).

Ecosystem function debt

Ecosystem functions, such as nutrient cycling and decomposition rates, can also be reduced or lost over time—a process called ecosystem function debt. Evidence suggests that during forest succession, this delayed loss of function is greater in smaller, more isolated fragments (Cook et al. 2005; Billings and Gaydess 2008). The mechanisms for this are complex. Functional debt can result when fragmentation causes food webs to be simplified as species are lost, or when altered forest succession patterns resulting from permanent fragmentation or forest practices that cause changes in tree density, light and moisture, which impair ecosystem function (Haddad et al. 2015).

While there is abundant evidence that the forests of the Western Maine Mountains continue to change as silvicultural practices interact with natural successional processes and a changing climate, Legaard et al. (2015) and Simons-Legaard et al. (2018) are the first two studies to document spatial changes in the forest over time in Maine. Their research suggests that the long-term processes described above are beginning to play out in the Western Maine Mountains. The American marten provides an example of how a species responds to long-term habitat changes associated with fragmentation. While the forests of the region currently support marten, recent research suggests that forest harvest practices on two-thirds of Maine's commercial forestland are creating habitat that no longer serves the needs of this umbrella species, and by implication the many other terrestrial forest vertebrate species that use similar habitat (Hepinstall and Harrison in prep.); Simons-Legaard et al. 2013; Fuller and Harrison 2005; Homyack et al. 2010; McMahon 2016).

A changing climate

If left unchecked, increased fragmentation from permanent and temporary features is expected to exacerbate the impacts of climate change on biodiversity and connectivity in the region. Whitman et al. (2013) summarize how Maine's biodiversity and ecosystems are likely to change in the coming decades.

The region can anticipate shifting species distributions, with an increasing number of novel species moving in from the south and many species with northern distributions moving north. Changes in seasonal rainfall patterns may exacerbate late summer dryness and increase levels and frequency of drought stress for plant communities and aquatic systems. Increasing temperatures may allow wildlife parasites such as winter moose tick (*Dermacentor albipictus*) and forest pests such as hemlock woolly adelgid (*Adelges*





tsugae) to become more prevalent, stressing native wildlife populations and degrading their habitats. Because each species will respond individually to these threats, the composition of natural communities and wildlife habitats that we take for granted will change. While populations of some species and their habitats will increase, climate change could lead to extirpation of other species and significant changes to natural communities and wildlife habitats (Cahill et al. 2012).

Forest fragmentation increases the vulnerability of Maine's native flora and fauna to climate change (Fernandez et al. 2015; Rustad et al. 2012). For example, declines in the diversity of native flora in New England's mixed northern hardwood forests are attributed to a high degree of habitat specialization, a highly fragmented range, depauperate understories due to repeated clearing and barriers to dispersal (New England Wildflower Society 2015). Three of the top four stressors are caused or aggravated by forest fragmentation, including habitat conversion, invasives and succession. All of these stressors are expected to become more pronounced as the climate changes.

The resiliency of the Western Maine Mountains in the face of climate change is largely due to the extent and connectivity of the region's forests. These forests provide far greater benefits to climate stabilization than the alternative of land development (Fahey et al. 2010). Because heavily forested areas sequester more carbon than they emit and the wood they produce can be used to substitute for more energy- and emissions-intensive building materials, keeping forested lands intact will help mitigate climate change regionally. Conversely, developed lands are net sources of carbon dioxide to the atmosphere (Fahey et al. 2010).



Figure 21. Fall in the Western Maine Mountains. Photo by Charlie Reinertsen Photography.

CONCLUSIONS

The Western Maine Mountains region is an ecological treasure that faces unprecedented threats from forest fragmentation. New land uses and policies that fragment the region's forests—such as the proposed New England Clean Energy Connect transmission corridor, the Land Use Planning Commission's proposed changes to the adjacency rule, which would allow new commercial and residential development to stretch for miles along currently undeveloped public roads, and large scale developments, such as Weyerhaeuser's Moosehead Lake concept plan—have the potential to profoundly change the ecology of the region by bringing extensive new human infrastructure into remote areas and creating new nodes of development (Lilieholm et al. 2010). In addition, forest practices have created a younger more homogeneous forest, conditions that threaten species that require large patches of older forest, such as American marten and many songbirds. However, when the land remains forested, even if harvesting temporarily modifies forest composition and structure, the potential for connectivity is retained because forest patches can regrow and expand. By contrast, once a utility corridor, road or development is in place, it effectively forever disrupts the connectivity of the landscape.

Fragmentation increases the risk of species extinctions and exotic invasions and decreases the ability of species to respond to a warming climate. The capacity of the Western Maine Mountains to sustain biological diversity and ecosystem integrity into the future will hinge upon the total amount and quality of its forests, wetlands and streams and their degree of connectivity. Unless proactive steps are taken, these changes have the potential to forever alter and degrade one of the most intact forested landscapes in the eastern United States and compromise its ability to serve as a critical ecological link between forests of the Northeast and Canada.

To maintain the region's unique values, it is essential to avoid introduction of new fragmenting features, especially those that would permanently intrude into intact forest blocks, such as new utility corridors, new

centers of development, and new high volume roads. It is also critically important to find ways to support landowners who seek to maintain large intact forest blocks and to find ways to support them in managing forests for greater spatial and temporal connectivity and structural complexity. Maintaining an unfragmented and intact forest is not only critical to the region's biodiversity and ecological health, but it is crucial to Maine's economy and a defining part of the Maine way of life.

The biodiversity, resilience and connectivity of the Western Maine Mountains are unparalleled in the eastern United States. The region offers one of the last opportunities for large landscape-scale conservation with protected areas connected through linkages and stepping stones embedded within an intact forest matrix (Keeley et al. 2018). As one of the few temperate forests in the world managed through natural regeneration, the Western Maine Mountains region continues to support a full complement of native forest wildlife and is the last regional stronghold for brook trout, moose, lynx, marten and a host of other species. It remains a highly connected forested landscape—one that is far less fragmented than increasingly developed lands to the south. The actions of landowners, conservation organizations, government officials and agencies, and local communities and citizens together will determine whether these species and the region's many unique values persist into the future.



Figure 22. Canoeing on Flagstaff Lake. Photo by Sally Stockwell.



Figure 23. Unbroken view in the High Peaks region of the Western Maine Mountains. Photo by Charlie Reinertsen Photography.

LITERATURE CITED

- Al-Chokhachy, R., T.A. Black, C. Thomas, C.H. Luce, B. Rieman, R. Cissel, A. Carlson, S. Hendrickson, E.K. Archer, and J.L. Kershner. 2016. Linkages between unpaved forest roads and streambed sediment: Why context matters in directing road restoration. *Restoration Ecology* 24(5), 589–598.
- Anderson, M.G. 2006. The Northern Appalachian/Acadian Ecoregion: Conservation assessment, status and trends. The Nature Conservancy.
- Anderson, M.G., M. Clark, and A. Olivero Sheldon. 2012. *Resilient sites for terrestrial conservation in the Northeast and Mid-Atlantic Region*. The Nature Conservancy, Eastern Conservation Science. 122 pp.
- Anderson, M.G., M. Clark, C.E. Ferree, A. Jospe, and A. Olivero Sheldon. 2013. *Condition of the northeast terrestrial and aquatic habitats: A geospatial analysis and tool set*. The Nature Conservancy, Eastern Conservation Science. Boston, Massachusetts. 171 pp.
- Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: A review. *Oikos*, *71*(3): 355–366.
- Andrews, K.M, J.W. Gibbons, and D.M. Jochimsen. 2008. Ecological effects of roads on amphibians and reptiles: A literature review. *Herpetological Conservation*, *3*: 121–143.
- Askins, R.A. 2002. *Restoring North America's birds: lessons from landscape ecology*. Yale University Press, New Haven, Connecticut.
- Bailey, R. 1995. *Description of the ecoregions of the United States* (2nd ed; revised and expanded 1st ed., 1980). Misc. Publ. No. 1391, USDA Forest Service, Washington DC. 108 pp. with map.
- Baldwin, R.F., S.C. Trombulak, M.G. Anderson, and G. Woolmer. 2007. Projecting transition probabilities for regular public roads at the ecoregion scale: A Northern Appalachian/Acadian case study. *Landscape and Urban Planning*, 80: 404–411.
- Barton, A.M., A.S. White, and C.V. Cogbill. 2012. *The changing nature of the Maine woods*. University of New Hampshire Press, Durham, New Hampshire.
- Beaudry, F., P.G. deMaynadier, and M.L. Hunter, Jr. 2008. Identifying road mortality threat at multiple scales for semi-aquatic turtles. *Biological Conservation*, 141: 2550–2563.
- Beazley, K.F., T.V. Snaith, F. MacKinnon, and D. Colville. 2004. Road density and potential impacts on wildlife species such as American moose in mainland Nova Scotia. *Proceedings of the Nova Scotia Institute of Science, Vol. 42, Pt. 2*: 339–357.
- Benitez-Lopez, A., R. Alkemade, and P.A. Verweij. 2010. The impacts of roads and other infrastructure on mammal and bird populations: A meta-analysis. *Biological Conservation*, 143: 1307–1316.

- Billings, S.A., and E.A. Gaydess. 2008. Soil nitrogen and carbon dynamics in a fragmented landscape experiencing forest succession. *Landscape Ecology*, 23(5): 581–593.
- Blake, J.G., and J.R. Karr. 1984. Species composition of bird communities and the conservation benefit of large versus small forests. *Biological Conservation*, *30*(2): 173–187.
- Brocke, R.H., J.P. O'Pezio, and K.A. Gustafson. 1988. A forest management scheme mitigating impact of road networks on sensitive wildlife species. In Degraaf, R.M., and W.M. Healy (eds.), *Is forest fragmentation a management issue in the northeast?* GTR-NE-140, USDA Forest Service, Northeastern Forest Experimental Station, Radnor, Pennsylvania: 13–17.
- Brodey, A.J., and M.R. Pelton. 1989. Effects of roads on black bear movements in North Carolina. *Wildlife Society Bulletin*, *17*: 5–10.
- Burnham, K.M., and T.D. Lee. 2010. Canopy gaps facilitate establishment, growth, and reproduction of invasive *Frangula alnus* in a *Tsuga canadensis* dominated forest. *Biological Invasions, 12*: 1509–1520.
- Cahill, A., M. Aiello-Lammens, M. Fisher-Reid, X.Hua, C. Karanewsky, H. Ryu, G. Sbeglia, F. Spagnolo, J. Waldron, O. Warsi, and J. Wiens. 2012. How does climate change cause extinction? Proceeding of the Royal Society B doi:10.1098/rspb.2012.1890.
- Carroll, C. 2007. Interacting effects of climate change, landscape conversion, and harvest on carnivore populations at the range margin: Marten and lynx in the Northern Appalachians. *Conservation Biology, 21*: 1092–1104.
- Chapin, T.G., D.J. Harrison, and D.D. Katnik, 1998. Influence of landscape pattern on habitat use by American marten in an industrial forest. *Conservation Biology*, *12*(6): 1327–1337.
- Charry, B. 2007. *Conserving wildlife on and around Maine's roads*. Beginning with Habitat, Maine Audubon Society, and the Maine Department of Transportation. Maine Audubon Society, Falmouth, Maine.
- Charry, B. 1996. Conserving wildlife in Maine's developing landscape. Maine Audubon Society, Falmouth, Maine.
- Compton, B.W. 1999. *Ecology and conservation of the wood turtle* (Clemmys insculpta) *in Maine* (thesis). University of Maine, Orono, Maine, USA.
- Coombs, J.A., and K.H. Nislow. 2014. *Riparian prioritization and status assessment for climate change resilience of coldwater stream habitats within the Appalachian and Northeastern regions*. University of Massachusetts Department of Environmental Conservation and USDA Forest Service Northern Research Station. Amherst, Massachusetts.
- Cook, W.M., J. Yao, B.L. Foster, R.D. Holt, and L.B. Patrick. 2005. Secondary succession in an experimental fragmented landscape. Community patterns across space and time. *Ecology*, *86*(5): 1267–1279.
- De Camargo, R.X., V. Boucher-Lalonde, and D.J. Currey. 2018. At the landscape level, birds respond strongly to habitat amount but weakly to fragmentation. *Diversity and Distributions, 24*: 629–639. https://doi. org/10.1111/ddi.12706
- DeGraaf, D. 2014. Report back to the legislature on public law 2013, Chapter 358, Section 8: Proposed plan for managing state heritage fish waters. Maine Department of Inland Fisheries and Wildlife. Augusta, Maine.
- DeGraaf, R.M., and M. Yamasaki. 2001. *New England wildlife: Habitat, natural history, and distribution*. University Press of New England. Hanover, New Hampshire and London.
- DeGraaf, R.M., M. Yamasaki, W.B. Leak and A. Lester. 2007. Technical guide to forest wildlife habitat management in New England. University of Vermont Press, Lebanon, New Hampshire.
- deMaynadier, P.G., and J.E. Houlahan. 2008. Conserving vernal pool amphibians in managed forests. In Calhoun, A.L., and P.G. deMaynadier (eds.), *Science and Conservation of Vernal Pools in Northeastern North America* (pp. 253–289). CRC Press, Boca Raton, Florida.
- deMaynadier, P.G., and M.L.J. Hunter. 2000. Road effects on amphibian movements in a forested landscape. *Natural Areas Journal, 20*(1): 56–65.
- Di Marco, M., O. Venter, H.P. Possingham, and J.E.M. Watson. 2018. Changes in human footprint drive changes in species extinction risk. *Nature Communications*, *9*(1): 4621 (2018) doi: 10.1038/s41467-18-07049-5
- Dolloff, C.A., and M.L. Warren. 2003. Fish relationship with large wood in small streams. In S. Gregory, K. Boyer, A. Gurnell (eds.), *The ecology and management of wood in world rivers* (pp. 179–194). American Fisheries Society, Bethesda, Maryland.

- Ehrenfield, J.G., P. Kourtev, and W. Huang. 2001. Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecological Applications*, *11*(5): 1287–1300.
- Fahey, T.J., P.B. Woodbury, J.J. Battles, C.L. Goodale, S.P. Hamburg, S.V. Ollinger, and C.W. Woodall. 2010. Forest carbon storage: Ecology, management, and policy. *Frontiers in Ecology and the Environment*, 8: 245–252.
- Fahrig, L., J.H. Pedlar, S.E. Pope, P.D. Taylor, and J.F. Wegner. 1995. Effect of road traffic on amphibian density. *Biological Conservation*, 73: 177–182.
- Fensome, A.G., and F. Mathews. 2016. Roads and bats: A meta-analysis and review of the evidence on vehicle collisions and barrier effects. *Mammal Review*, 46(4): 311–323.
- Fernandez, I.J., C.V. Schmitt, S.D. Birkel, E. Stancioff, A.J. Pershing, J.T. Kelley, J.A. Runge, G.L. Jacobson, and P.A. Mayewski. 2015. *Maine's climate future: 2015 update*. University of Maine, Orono, Maine. 24 pp.
- Fernie, K.J., and J. Reynolds. 2005. The effects of electromagnetic fields from power lines on avian reproductive biology and physiology: A review. *Journal of Toxicology and Environmental Health, Part B, 8*: 127–140.
- Fesenmyer, K.A., A.L. Haak, S.M. Rummel, M. Mayfield, S.L. McFall, and J.E. Williams. 2017. *Eastern brook trout conservation portfolio, range-wide habitat integrity and future security assessment, and focal area risk and opportunity analysis.* Final report to National Fish and Wildlife Foundation. Trout Unlimited, Arlington, Virginia.
- Ford, S.E., and W.S. Keeton. 2017. Enhanced carbon storage through management for old-growth characteristics in northern hardwood-conifer forests. *Ecosphere*, *8*(4): e01721. 10.1002/ecs2.1721
- Forman, R.T.T. 1995. Land mosaics: The ecology of landscapes and regions. Cambridge University Press, New York.
- Forman, R.T.T., and L.E. Alexander. 1998. Roads and their major ecological effects. *Annual Review of Ecological Systematics*, 29: 207–231.
- Forman, R.T.T., and R.D. Deblinger. 2000. The ecological road-effect zone of a Massachusetts (USA) suburban highway. *Conservation Biology*, 14: 36–46.
- Franklin, J.F., T.A. Spies, R. van Pelt, A. Carey, D. Thornburgh, D.R. Berg, D.B. Lindenmayer, M. Harmon, W. Keeton, and D.C. Shaw. 2002. Disturbances and the structural development of natural forest ecosystems with some implications for silviculture. *Forest Ecology and Management*, 155: 399–423.
- Frelich, L.E., C.M. Hale, S., Scheu, A.R. Holdsworth, L. Heneghan, P.J. Bohlen, and P.B. Reic. 2006. Invasion into previously earthworm-free temperate and boreal forests. *Biological Invasions*, *8*: 1235–1245.
- Fuller, A.K., and D.J. Harrison. 2005. Influence of partial timber harvesting on American martens in North-Central Maine. *Journal of Wildlife Management*, 69: 710–722.
- Gawler, S.C., J.J. Albright, P.D. Vickery, and F.C. Smith. 1996. *Biological diversity in Maine: An assessment of status and trends in the terrestrial and freshwater landscape*. Report prepared for the Maine Forest Biodiversity Project. Maine Natural Areas Program, Augusta. 80 pp. + appendices.
- Gibbs, J. P. 1998. Distribution of woodland amphibians along a forest fragmentation gradient. *Landscape Ecology*, *13*: 263–268.
- Gibbs, J.P. 1993. Importance of small wetlands for the persistence of local populations of wetland-associated animals. *Wetlands*, *13*: 25–31.
- Gibbs, J.P., and W.G. Shriver. 2002. Estimating the effect of road mortality on turtle populations. *Conservation Biology*, *16*(6): 1647–1652.
- Glista, D.J., T.L. DeVault, and J.A. DeWoody. 2007. Vertebrate road mortality predominantly impacts amphibians. *Herpetological Conservation and Biology*, *3*(1): 77–87.
- Grindal, S.D., and R.M. Brigham. 1999. Short-term effects of small-scale habitat disturbance on activity by insectivorous bats. *Journal of Wildlife Management*, 62(3): 996–1003.
- Gucinski, H., M.J. Furniss, R.R. Ziemer, and M.H. Brookes (eds.). 2000. Forest roads: A synthesis of scientific information. USDA Forest Service.
- Haddad, N.M., L.A. Brudvig, J. Clobert, K.F. Davies, A. Gonzalez, R.D. Holt, T.E. Lovejoy, J.O. Sexton, M.P. Austin, C.D. Collins, W.M. Cook, E.I. Damschen, R.M. Ewers, B.L. Foster, C.N. Jenkins, A.J. King, W.F. Laurance, D.J. Levey, C.R. Margules, B.A. Melbourne, A.O. Nicholls, J.L. Orrock, D. Song, and J.R. Townshend. 2015. Habitat fragmentation and its lasting impacts on Earth's ecosystems. American Association for the Advancement of Science. Science Advances, 1(2), 9 pp.

- Hagan, J.M., L.C. Irland, and A.A. Whitman. 2005. Changing timberland ownership in the Northern Forest and implications for biodiversity. Manomet Center for Conservation Sciences. Report # MCCS-FCP- 2005-1.
 25 pp. Brunswick, Maine.
- Hagan, J.M., and A.A. Whitman. 2004. Late successional forest: A disappearing age class and implications for biodiversity. *Forest Mosaic Science Notes, 2*: Manomet, Brunswick, Maine.
- Hagan, J.M., W.M. Vander Haegen, and P.S. McKinley. 1996. The early development of forest fragmentation effects on birds. *Conservation Biology*, *10*(1): 188–202.
- Hanski, I. 2000. Extinction debt and species credit in boreal forests: Modeling the consequences of different approaches to biodiversity conservation. *Annals of Zoology, 37*: 271–280.
- Harper, K.A., S.E. Macdonald, P.J. Burton, J. Chen, K.D. Brosofske, S.C. Saunders, E.S. Euskirchen, D. Roberts, M. Jaiteh, and P.A. Esseen. 2005. Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology*, 19: 768–782.
- Haselton, B., D. Bryant, M. Brown, and C. Cheeseman. (2014 draft analysis). Assessing relatively intact large forest blocks in temperate broadleaf and mixed forests major habitat type. Tierra Environmental and The Nature Conservancy.
- Heneghan, L., F. Fatemi, L. Umek, K. Grady, K. Fagen, M. Workman. 2006. The invasive shrub European buckthorn (*Rhamnus cathartica, L.*) alters soil properties in Midwestern U.S. woodlands. *Applied Soil Ecology, 32*:142–148.
- Hepinstall, J.A., and D.J. Harrison (in preparation). Department of Wildlife Ecology, University of Maine.
- Homan, R.N., B.S. Windmiller, and J.M. Reed. 2004. Critical thresholds associated with habitat loss for two vernal pool-breeding amphibians. *Ecological Applications*, 14: 1547–1553.
- Homyack, J.A., D.J. Harrison, and W.B. Krohn. 2010. Effects of precommercial thinning on snowshoe hares in Maine. *Journal of Wildlife Management*, *71*(1): 4–13.
- Hunter, J.C., and J.A. Mattice. 2002. The spread of woody exotics into the forests of a northeastern landscape, 1938–1999. *Journal of the Torrey Botanical Society, 129*(3): 220–227.
- Hunter, M.L., Jr., and J. Gibbs. 2007. Fundamentals of conservation biology (3rd ed.). Blackwell Publishing. 482 pp.
- *iMapInvasives Database*. NatureServe. www.imapinvasives.org
- Irland, L.C. 2005. U.S. forest ownership: Historic and global perspective. *Maine Policy Review*, 14(1): 16–22.
- Jochimsen, D.M., C.R. Peterson, K.M. Andrews, and J.W. Gibbons. 2004. Literature review of the effects of roads on amphibians and reptiles and the measures used to minimize those effects. Idaho Fish and Game Department, USDA Forest Service.
- Kaufman, S.D., E. Snucins, J.M. Gunn, and W. Selinger. 2009. Impacts of road access on lake trout (*Salvelinus namaycush*) populations: Regional scale effects of overexploitation and the introduction of smallmouth bass (*Micropterus dolomieu*). *Canadian Journal of Fisheries and Aquatic Sciences*, 66: 212–223.
- Keeley, A.T.H., D.D. Ackerly, D.R. Cameron, N.E. Heller, P.R. Huber, C.A. Schloss, J.H. Thorne, and A.M. Merenlender. 2018 (in press). New concepts, models and assessments of climate-wise connectivity. *Environmental Research Letters*, 13(7). https://doi.org/10.1088/1748-9326/aacb85
- Kuehne, C., Puhlick. J.J., and A.R. Weiskittel. 2018. *Ecological reserves in Maine: Initial results of long-term monitoring*. General Technical Report. 62 pp.
- Laan, R., and B. Verboom. 1990. Effect of pool size and isolation on amphibian communities. *Biological Conservation*, 54(3): 251–262.
- Laurance, W.F., J.L.C. Camargo, P.M. Fearnside, T.E. Lovejoy, G.B. Williamson, R.C.G. Mesquita, C.F.J. Meyer, P.E.D. Brobrowiec, and S.G.W. Laurance. 2017. An Amazonian rainforest and its fragments as a laboratory of global change. *Biological Reviews*, 93(1). 25 pp. doi: 10.1111/brv.12343
- Laurance, W.F., T.E. Lovejoy, H.L. Vasconcelow, et al. 2002. Ecosystem decay of Amazonian forest fragments: A 22 year investigation. *Conservation Biology*, *16*: 605–618.
- Legaard, K.R., S.A. Sader, and E.M. Simons-Legaard. 2015. Evaluating the impact of abrupt changes in forest policy and management practices on landscape dynamics: Analysis of a Landsat image time series in the Atlantic Northern Forest. *PLoS ONE*, *10*(6): e0130428. doi: 10.1371/journal. pone.0130428
- Leopold, Aldo. 1966. A Sand County almanac: With essays on conservation from Round River. Oxford University Press.

- Lilieholm, R.J., L.C. Irland, and J.M. Hagan. 2010. Changing socio-economic conditions for private woodland protection. In Trombulak, S.C., and R.F. Baldwin (eds.), *Landscape-scale conservation planning* (pp. 67–98). Springer, New York.
- Lindenmayer, D.B., and J. Fischer. 2006. *Habitat fragmentation and landscape change: An ecological and conservation synthesis*. Island Press, Washington, DC.
- Loarie, S.R., P.B. Duffy, H. Hamilton, G.P. Asner, C.B. Field, and D.D. Ackerly. 2009. The velocity of climate change. *Nature*, *462*(24): 1052–1055.
- Loarie, S.R., B.E. Carter, K. Hayhoe, S. McMahon, R. Moe, C.A. Knight, and D.D. Ackerly. 2008. Climate change and the future of California's endemic flora. *PLoS One*, *3*: e2502.
- Lorimer, C.G. 1977. The presettlement forest and natural disturbance cycle of Northeastern Maine. *Ecology* (58): 139-148.
- Lorimer, C.G., and A.S. White. 2003. Scale and frequency of natural disturbances in the northeastern US: Implications for early successional forest habitats and regional age distributions. Forest Ecology and Management 185: 41–64.
- LUPC. 2010. Comprehensive Land Use Plan. Maine Department of Agriculture, Conservation and Forestry. https://digitalmaine.com/lupc_docs/6
- MacArthur, R.H., and E.O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey. 203 pp.
- Maine Department of Conservation. 1997. Comprehensive land use plan for areas within the jurisdiction of the Maine Land Use Regulation Commission. MDOC Land Use Regulation Commission, Augusta, Maine.
- Maine Department of Inland Fisheries and Wildlife (no date). *Guidelines for wildlife: Managing deer wintering areas in northern, western and eastern Maine*. Maine Department of Inland Fisheries and Wildlife, Augusta, Maine.
- Maine Department of Transportation (no date). Stream Smart road crossing pocket guide. State of Maine Aquatic Resources Management Strategy Forum.
- Martin, E.H., and C.D. Apse. 2011. Northeast aquatic connectivity: An assessment of dams on northeastern rivers. The Nature Conservancy, Eastern Freshwater Program.
- Matlack, G.R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. *Biological Conservation, 66*: 185–194.
- McGarigal, K., W.H. Romme, M. Crist, and E. Roworth. 2001. Cumulative effects of roads and logging on landscape structure in the San Juan Mountains, Colorado (USA). *Landscape Ecology*, *16*: 327–349.
- McMahon, J. 2016. *Diversity, continuity and resilience: The ecological values of the Western Maine Mountains*. Occasional Paper No. 1. Maine Mountains Collaborative, Phillips, Maine. 20 pp.
- Merriam, G.M., M. Kozakiewiez, E. Tsuchya, and K. Hawley. 1989. Barriers as boundaries for metapopulations and demes of *Peromyscus leucopus* in farm landscapes. *Landscape Ecology*, *2*: 227–236.
- Mosher, E.S., J.A. Silander, Jr., and A.M. Latimer. 2009. The role of land-use history in major invasions by woody plant species in the northeastern North American landscape. *Biological Invasions*, *11*: 2317. doi: 10.1007/s10530-008-9418-8
- Muñoz, P.T., F.P Torres, and A.G. Megias. 2015. Effects of roads on insects: a review. *Biodiversity Conservation*, 24: 659–682.
- New England Forestry Foundation (NEFF) (in press). Landscape scale resource inventory and wildlife habitat assessment for the Mountains of the Dawn. New England Forestry Foundation, Littleton, Massachussetts.
- New England Wild Flower Society. 2015. State of the plants: Challenges and opportunities for conserving New England's native flora. Framingham, Massachusetts.
- Ortega, Y.K., and D.E. Capen. 1999. Effects of forest roads on habitat quality for ovenbirds in a forested landscape. *The Auk*, *116*(4): 937–946.
- Oxley, D.J., M.B. Fenton, and G.R. Carmody. 1974. The effects of roads on populations of small mammals. *Journal of Applied Ecology*, *11*: 51–59.
- Payer, D.C., and D.J. Harrison. 2003. Influence of forest structure on habitat use by American marten in an industrial forest. *Forest Ecology and Management*, *179*(1–3): 145–156.

- Pfiefer, M., V. Lefebvre, C.A. Peres, C. Banks-Leite, O.R. Wearn, C.J. Marsh, S.H.M. Butchart, V. Arroyo-Rodriquez, J. Barlow, A. Cerezo, L. Cisneros, N. D'Cruze, D. Faria, A. Hadley, S. Harris, B.T. Klingbeil, U. Kormann, L. Lens, G.F. Medina-Rangel, J.C. Morante-Filho, P. Oliveir, S.L. Peters, A. Pidgeon, D.B. Ribeiro, C. Scherber, L. Schneider-Maunory, M. Struebig, N. Urbina-Cardona, J.I. Watling, M.R. Willig, E.M. Wood, and R.M. Ewers. 2017. Creation of forest edges has a global impact on forest vertebrates. *Nature*, 551: 187–191.
- Popescu, V.D., and M.L. Hunter, Jr. 2011. Clear-cutting affects habitat connectivity for a forest amphibian by decreasing permeability to juvenile movements. *Ecological Applications*, *2*1(4): 1283–1295.
- Prevedello, J.A. and M.V. Vieira. 2010. Does the type of matrix matter? A quantitative review of the evidence. Biodiversity Conservation 19: 1205–1223.
- Publicover, D.A., and C.J. Poppenwimer. 2006. *Roadless areas in the northern forest of New England: An updated inventory*. AMC Technical Report 06-1. Appalachian Mountain Club Research Department, Gorham, New Hampshire.
- Publicover, D.A., and C. Poppenwimer. 2002. *Delineation of roadless areas in the Northern Forest of New England using satellite imagery*. AMC Technical Report 02-1. Appalachian Mountain Club Research Department, Gorham, New Hampshire.
- Riitters, K., J. Wickham, R. O'Neill, B. Jones, and E. Smith. 2000. Global-scale patterns of forest fragmentation. *Conservation Ecology*, 4(2): 3.
- Rolek, B.W., D.J. Harrison, C.S. Loftin, and P.B. Wood. 2018. Regenerating clear cuts combined with postharvest forestry treatments promote habitat for breeding and post-breeding spruce-fir avian assemblages in the Atlantic Northern Forest. *Forest Ecology and Management, 427*: 392–413.
- Rosen, P., and C. Lowe. 1994. Highway mortality of snakes in the Sonoran Desert of southern Arizona. Biological Conservation, 68: 143–148.
- Rosenberg, K.V., J.D. Lowe, and A.A. Dhondt. 1999. Effects of forest fragmentation on breeding tanagers: A continental perspective. *Conservation Biology*, *13*(3): 568–583.
- Rosenzweig, M.L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge.
- Ross, B., T. Fredericksen, E. Ross, W. Hoffman, M.L. Morrison, J. Beyea, M.B. Lester, B.N. Johnson, and N.J. Fredericksen. 2000. Relative abundance and species richness of herpetofauna in forest stands in Pennsylvania. *Forest Science*, *46*: 139–146.
- Rowland, E.L., A.S. White, and W.H. Livingston. 2005. A literature review of the effects of intensive forestry on forest structure and plant community composition and the stand and landscape levels. Maine Agricultural and Forest Experiment Station. Miscellaneous Publication 754.
- Rustad, L., J. Campbell, J.S. Dukes, T. Huntington, K.F. Lambert, J. Mohan, and N. Rodenhouse, 2012. *Changing climate, changing forests: The impacts of climate change on forests of the northeastern United States and eastern Canada*. Gen. Tech. Rep. NRS-99. USDA Forest Service, Northern Research Station. Newtown Square, Pennsylvania. 48 pp.
- Rytwinski, T., and L. Fahrig. 2015. The impacts of roads and traffic on terrestrial wildlife populations. In Van der Ree, R., D.J. Smith, and C. Grilo (eds), *Handbook of road ecology* (Chapter 28). John Wiley & Sons.
- Schlawin, J., and A. Cutko. 2014. A conservation vision for Maine using ecological systems. Maine Natural Areas Program, Maine Department of Agriculture, Conservation and Forestry, Augusta, Maine. http://www.maine.gov/dacf/mnap/about/publications/ra.htm
- Schmiegelow, F.K.A., C.S. Machtans, and S.J. Hannon. 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. *Ecology*, 78(6): 1914–1932.
- Selva, S.B. 1994. Lichen diversity and stand continuity in the northern hardwoods and spruce-fir forests of northern New England and western New Brunswick. *The Bryologist*, *97*: 424–429.
- Seiler, A. 2001. *Ecological effects of roads: A review*. Department of Conservation Biology, Uppsala University, Uppsala, Uppland, Sweden. 40 pp.
- Seymour, R.S., A.S. White and P.G. deMaynadier. 2002. Natural disturbance regimes in northeastern North America—evaluating silvicultural systems using natural scales and frequencies. *Forest Ecology and Management*, *155*(1-3): 357–367.
- Silander, J.A,. Jr., and D.M. Klepeis. 1999. The invasion ecology of Japanese barberry (*Berberis thunbergii*) in the New England landscape. *Biological Invasions, 1*: 189–201.

- Silveri, A., P.W. Dunwiddie, and H.J. Michaels. 2001. Logging and edaphic factors in the invasion of an Asian woody vine in a mesic North American forest. *Biological Invasions*, *3*: 379–389.
- Simons-Legaard, E.M., D.J. Harrison, and K.R. Legaard. 2018. Ineffectiveness of local zoning to reduce regional loss and fragmentation of deer wintering habitat for white-tailed deer. *Forest Ecology and Management*, *427*: 78–85.
- Simons-Legaard, E.M., D.J. Harrison, W.B. Krohn, and J.H. Vashon. 2013. Canada Lynx occurrence and forest management in the Acadian Forest. *The Journal of Wildlife Management*, 77(3): 567–578.
- Smallwood, K.S., 2013. Comparing bird and bat fatality-rate estimates among North American wind energy projects. *Wildlife Society Bulletin*, *37*(1): 19–33.
- Talluto, M.V., I. Boulangeat, S. Vissault, W. Thuiller, and D. Grave. 2017. Extinction debt and colonization credit delay range shifts of eastern North American trees. *Nature Ecology and Evolution*, 1(0182): 1–9.
- Ten Broeck, C., and R.A. Giffen. 2018. The potential role of intensive forest management in meeting needs for forest products, restoring forest types to lands they historically occupied, and relieving harvest pressures on natural forests. New England Forestry Foundation, Littleton, Massachusetts.
- The Nature Conservancy. 2013. Staying connected in the northern Appalachians: Mitigating fragmentation and climate change impacts on wildlife through functional habitat linkages. Final Performance Report-Summary. New Hampshire Fish and Game Department and the U.S. Fish and Wildlife Service.
- Thompson, J.R., D.N. Carpenter, C.V. Cogbill, and D.R. Foster. 2013. Four centuries of change in Northeastern United States forests. *PLoS ONE*, *8*(9): e72540. doi: 10.1371/journal.pone.0072540
- Thuiller, W., S. Lavorel, M.B. Araujo, M.T. Sykes, and I.C. Prentice. 2005. *Climate change threats to plant diversity in Europe*. Proceedings of the National Academy of Sciences. USA 102: 8245–8250.
- Tinker, D. B., C.A.C. Resor, G.P. Beauvai, K.F. Kipfmueller, C.I. Fernandes, and W.L. Baker, W. L. 1997. Watershed analysis of forest fragmentation by clearcuts and roads in a Wyoming forest. *Landscape Ecology*, *12*: 1–17.
- Trombulak, S.C., and C.A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology*, 14: 18–30.
- Trombulak, S.C., and R.F. Baldwin (eds.). 2010. Landscape-scale conservation planning. Springer, New York.
- Trout Unlimited. 2006. *Eastern brook trout: Status and trends*. Produced by Trout Unlimited for the Eastern Brook Trout Joint Venture. Trout Unlimited, Arlington, Virginia.
- U.S. Energy Information Administration. 2017. Maine State Energy Profile. https://www.eia.gov/state/?sid=ME
- Van der Ree, R., D.J. Smith, and C. Grilo (eds). 2015. Handbook of road ecology. John Wiley & Sons.
- Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*(1): 130–137.
- Villard, M.A., M.K. Trzcinski, and G. Merriam. 1999. Fragmentation effects on forest birds: Relative influence of woodland cover and configuration on landscape occupancy. *Conservation Biology*, *13*: 774–783.
- Watson, J.E., T. Evans, O. Venter, B. Williams, A. Tullock, C. Stewart, I. Thompson, J.C. Ray, K. Murray, A. Salazar, C. McAlpine, P. Potapov, J. Walston, J.G. Robinson, M. Painter, D. Wilkie, C. Filardi, W.F. Laurance, R.A. Houghton, S. Maxwell, H. Grantham, C. Samper, S. Wang, L. Laestadius, R.K. Runting, G. A. Silva-Chavez, J. Ervin, and D. Lindenmayer. 2018. The exceptional value of intact forest ecosystems. *Nature Ecology and Evolution*, *2*: 599–610. https://doi.org/10.1038/s41559-018-0490-x.
- Webster, C.R, M.A. Jenkins, and S. Jose. 2006. Woody invaders and the challenges they pose to forest ecosystems in the eastern United States. *Journal of Forestry*, *104*: 366–374.
- Whitcomb, R.F., C.S. Robbins, J.F. Lynch, B.L. Whitcomb, M.K. Klimkiewicz, and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. In R.L. Burgess and D.M. Sharpe (eds.), *Forest island dynamics in man-dominated landscapes* (pp. 125–205). Springer-Verlag, New York.
- Whiteley, A.R., J.A. Coombs, M. Hudy, Z. Robinson, A.R. Colton, K.H. Nislow, and B.H. Letcher, 2013. Fragmentation and patch size shape genetic structure of brook trout populations. *Canadian Journal of Fisheries and Aquatic Sciences*, 70(5): 678–688.
- Whitman, A., A. Cutko, P. deMaynadier, S. Walker, B. Vickery, S. Stockwell, and R. Houston. 2013. Climate change and biodiversity in Maine: Vulnerability of habitats and priority species. Manomet Center for Conservation Sciences (in collaboration with Maine Beginning with Habitat Climate Change Working Group). Report SEI-2013-03. 96 pp. Brunswick, Maine.