Maintaining Forest Diversity in a Changing Climate: A Geophysical Approach

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Abstract: *Forest conservationists need a method to conserve the maximum amount of biological diversity while allowing species and communities to rearrange in response to a continually changing climate. Here, we develop such an approach for northeastern North America. First we characterize and categorize forest blocks based on their geology, landforms, and elevation zones. Next, for each distinct geophysical combination we locate the forest blocks with the highest amount of internally connected natural cover, and that have complex topography and large elevation ranges increasing their micro-climatic buffering. We hypothesized that these blocks have the greatest resilience to climate change, and will maintain a diversity of species and processes into the future. Finally we identify a network of high scoring blocks representing all geophysical settings and we examine the potential connections among and between them to prioritize linkages where maintaining natural covers would likely facilitate important regional movements. By focusing on the representation of physical diversity instead of on the current species composition, we identify a network of sites that will represent the full spectrum of forest diversity both now and into the future. We advocate that this geophysical approach to identifying a network of core forest areas and key connectors be used to inform and augment the traditional conservation focus on large forest reserves nested within a matrix of well-managed forest.*

INTRODUCTION

Climate change in recent decades has already begun to affect the composition of forest ecosystems in the northeastern United States. Average annual temperatures have increased by nearly 1.8 degrees F since 1970 (Huntington and others 2009). Tree species migration appears indicated by much higher seedling densities for northeastern tree species in the northern parts of their ranges compared to central and southern parts (Woodall and others 2009). Climate-induced range shifts for other biota may also be underway. Bird species winter ranges in the eastern United States, for example, have shifted steadily north, although not as rapidly as temperature shifts (La Sorte and others 2012). Projections of geographic ranges under various global climate model scenarios suggest most tree species will experience large range shifts in response to rising temperatures and more erratic precipitation regimes during the next century (Iverson and others 2012). Differential migration rates and varied abilities to cope with environmental gradients and human land uses are likely to dramatically re-sort the species composition of forest communities (Rustad and others 2012). Our ability to predict future species composition at any given location is extremely limited, calling into question the ability of current conservation networks to maintain biodiversity in the future.

We believe the strong correlation of geophysical factors with geographic patterns of biodiversity allows a new approach to designing conservation networks that will be effective even as species and communities continuously rearrange in response to climate change (Anderson and Ferree 2010). Here, we summarize such an approach for northeastern North America. We first review geophysical underpinnings of species diversity. The strong correlation of geophysical factors—number of geological classes, landform diversity, and elevation—with species diversity suggests that conserving geophysical settings is the key to conserving current and future forest biodiversity. We next review internal connectivity, which increases the ability of forest blocks to maintain species diversity and ecological processes, and regional connectivity, which facilitates regional movement in response to changing climatic conditions. By focusing on the representation of physical diversity instead of current species composition, plus accounting for internal and regional connectivity, we identify a resilient network of sites that have the potential to represent the full spectrum of forest diversity now and into the future. It should be noted that forests in less resilient areas, such as flat lands and coastal areas, are still important for a wide variety of benefits from watershed protection, carbon storage, wildlife habitat, and timber production. Actively maintaining diversity at the site level within a resilient conservation network brings in additional factors, such as structural diversity, soil replenishment, and space to accommodate disturbance regimes, which are important for local management. We conclude with summarizing strategies to manage for diverse forests at the landscape scale within a regional forest conservation network.

ELEMENTS OF RESILIENCY

Site resiliency—that is the ability for ecosystems to retain species diversity and basic relationships among ecological features even as environmental conditions change—is driven by geophysical settings and landscape permeability in northeastern North America. Geophysical settings are important because they are the best predictors of species diversity at a regional scale, such as temperate northeastern North America (Anderson and Ferree 2010). While climate may be a better predictor of species diversity at a continental scale, most conservation decisions are made at regional, landscape, and site scales. In addition, landscape permeability and regional connectivity are critical elements of site resiliency since species and ecological processes will need to shift to new locations as temperatures and precipitation regimes affect their viability in any given location. Projections of tree species migration indicate many of today's natural forest communities will be substantially altered by the end of this century (Prasad and others 2007), though forests will continue to be the region's dominant ecosystem type. Assessing forest areas across the region based on their geophysical setting (e.g., geology, landform and elevation), internal patch permeability, and regional connectivity yields a potential network of natural strongholds for future diverse forest areas. This network can be compared against the current network of secured forest lands and help focus future land protection and forest restoration efforts.

"Site resilience" is distinguished from species or ecosystem resilience because it refers to the capacity of a geophysical site (40 ha to 4000 ha [90 acre to 9885 acre]) to maintain species diversity and ecological function as the climate changes (definition modified from Gunderson 2000). This is important since neither species composition nor the ranges of variation of its processes are static in the context of climate change. Our working definition of a resilient site is a structurally intact geophysical setting that sustains a diversity of species and natural communities, maintains basic relationships among ecological features, and allows for adaptive change in composition and structure. Thus, if adequately conserved, resilient sites are expected to support species and communities appropriate to the geophysical setting for a longer time than will less resilient sites.

Geophysical Settings

Several factors—including *geologic classes*, *elevation range, latitude,* and *area of calcareous substrate*—are highly correlated with the distribution of terrestrial species diversity in the northeastern United States and adjacent Canadian Maritime Provinces (Anderson and Ferree 2010). Regressing the total number of species against these factors yields a strongly predictive relationship for terrestrial biodiversity across the northeastern United States and adjacent Canada (Figure 1). These factors work equally well for predicting species diversity across the region even though, for example, Virginia shares only 30 percent of its biota with Prince Edward Island and the region spans 1,400 km of latitude. Moreover, the region has been in flux during the past century with many range expansions and contractions, extinctions, and species introductions. These changes appear not to affect the basic relationship between species diversity and geophysical factors. As a result, conserving the full spectrum of geological classes stratified across elevation zones and latitude offers an effective approach to conserving forest diversity under current and future climates.

To capture the spectrum of geophysical settings in the northeastern United States, Anderson and others (2012) used 405 hectare (1,000 acre) hexagons to classify geology, elevation, and landform types. The region's highly diverse geologic history is manifested in over 200 bedrock types which were grouped into nine geology classes based on shared genesis, weathering properties, chemistry, and soil textures (Robinson 1997). Likewise, elevation for the region, which ranges from sea level to 6,288 feet atop Mount Washington, NH, was divided into low, mid and high elevation classes. Finally, landform types have a major influence on species distribution and they were grouped into seventeen categories (see Figure 2).

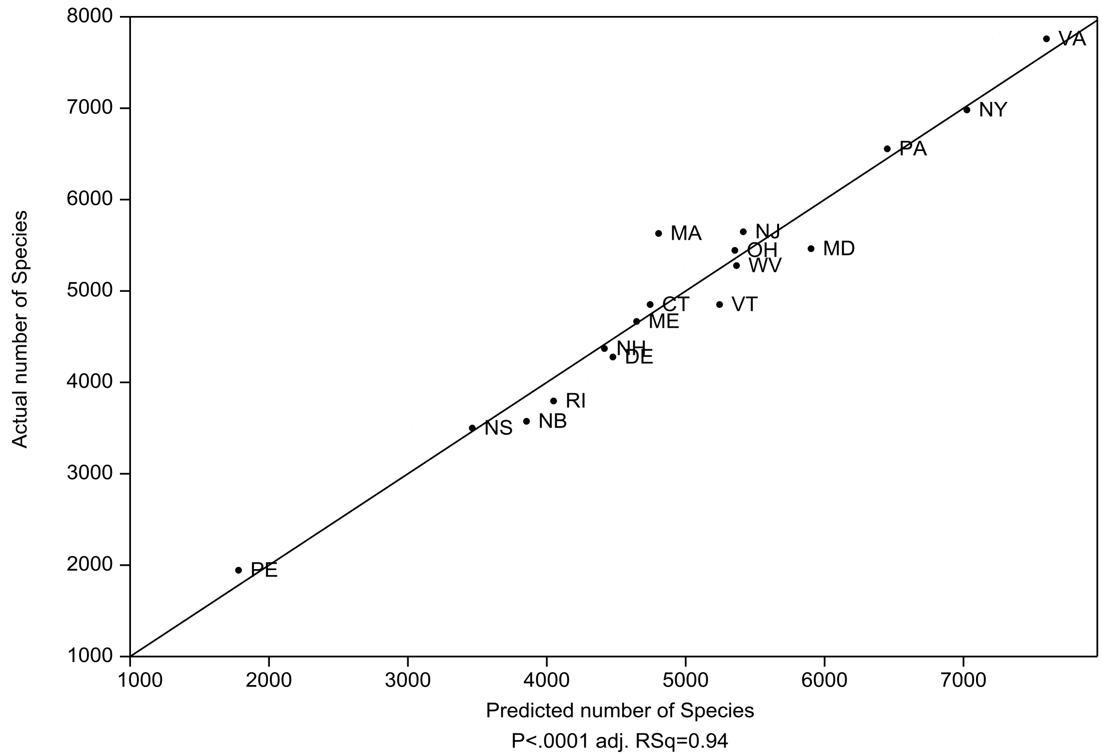


Figure 1. Actual state/province total species diversity plotted against predicted diversity based on number of geology classes, hectares of calcareous bedrock, latitude, and elevation range for northeastern North America.

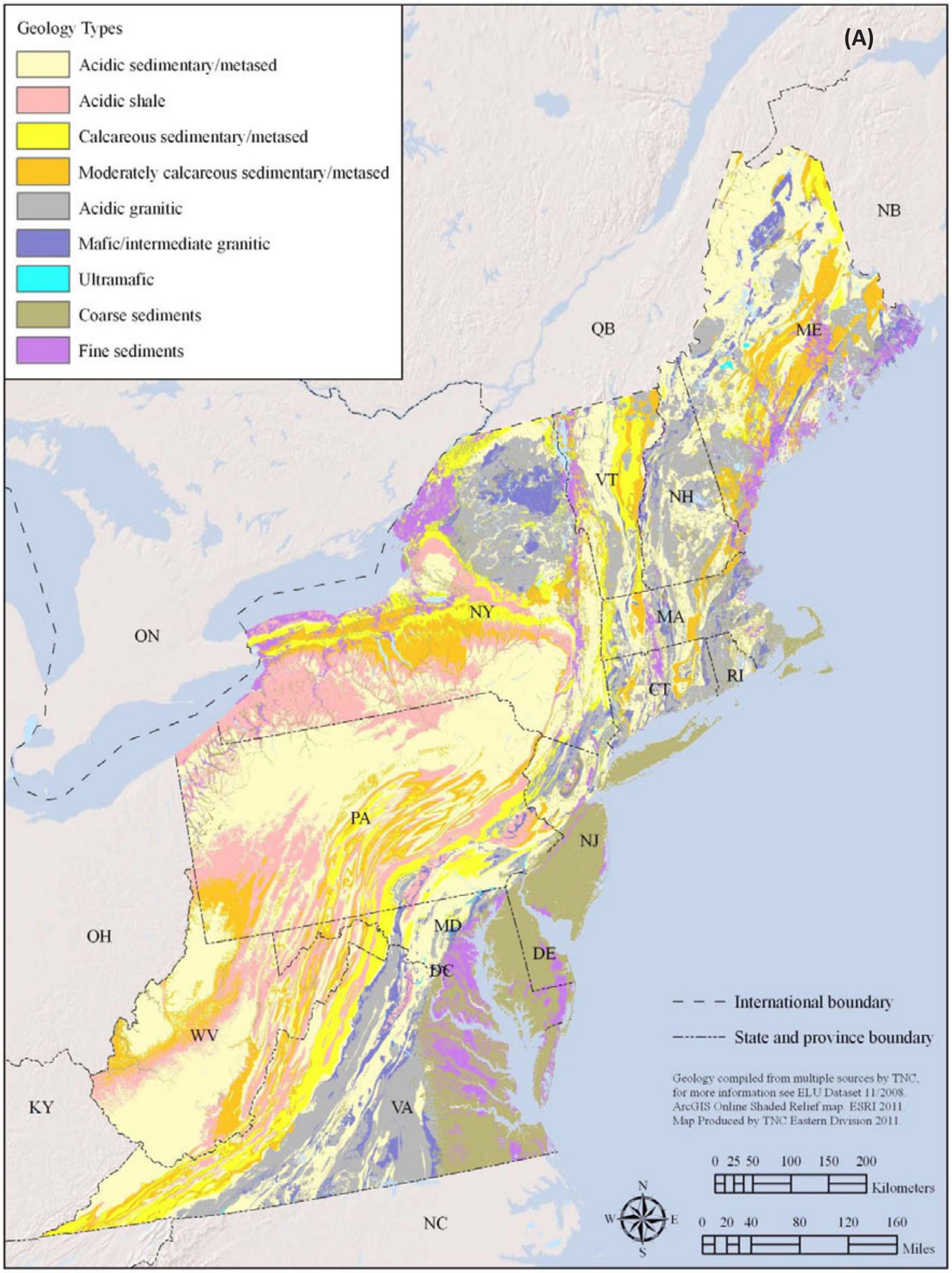


Figure 2. a) Geology classes; b) elevation zones, and; c) landform types that form the basis for classifying geophysical settings in the northeastern United States.

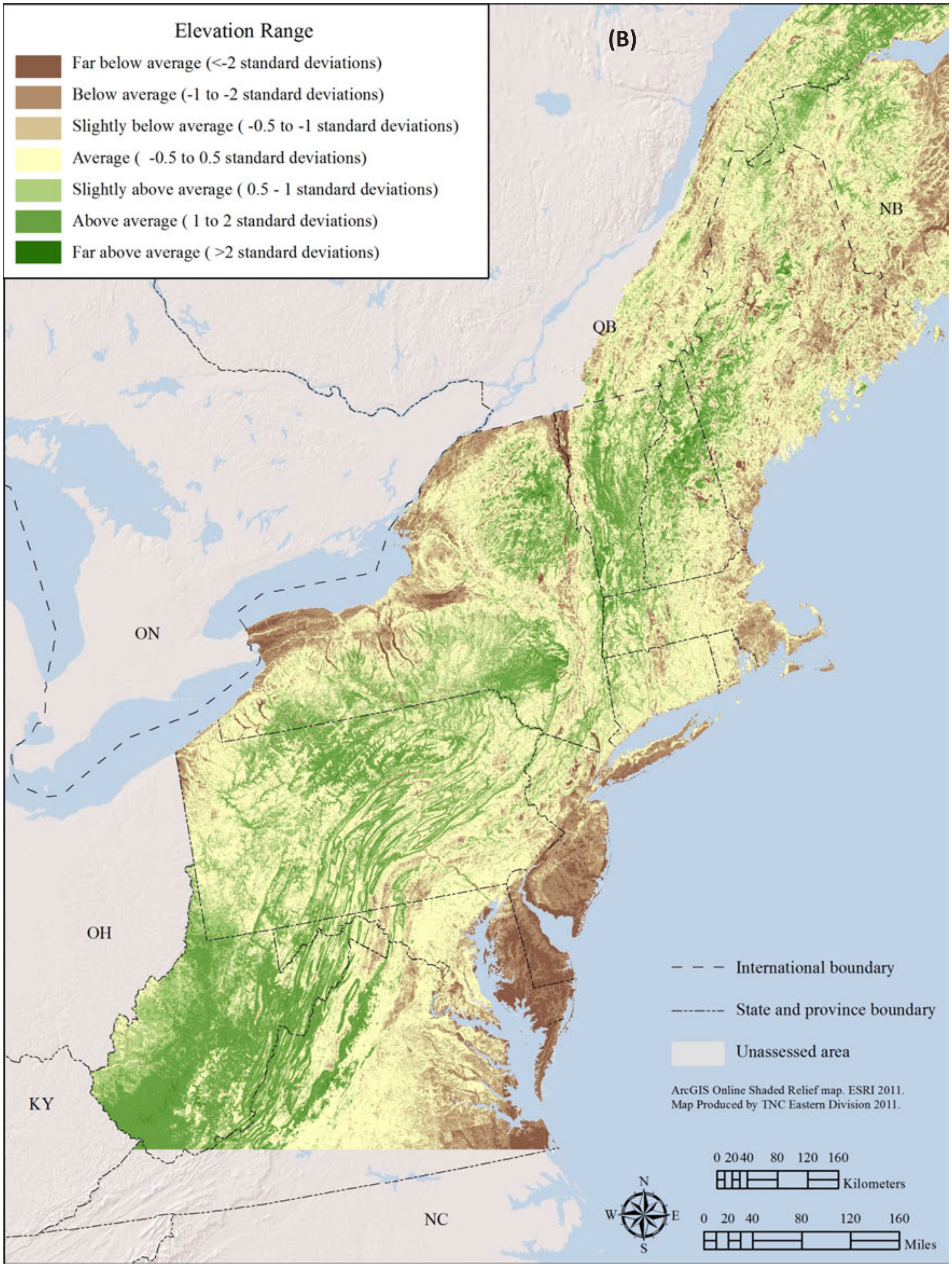


Figure 2. *Continued.*

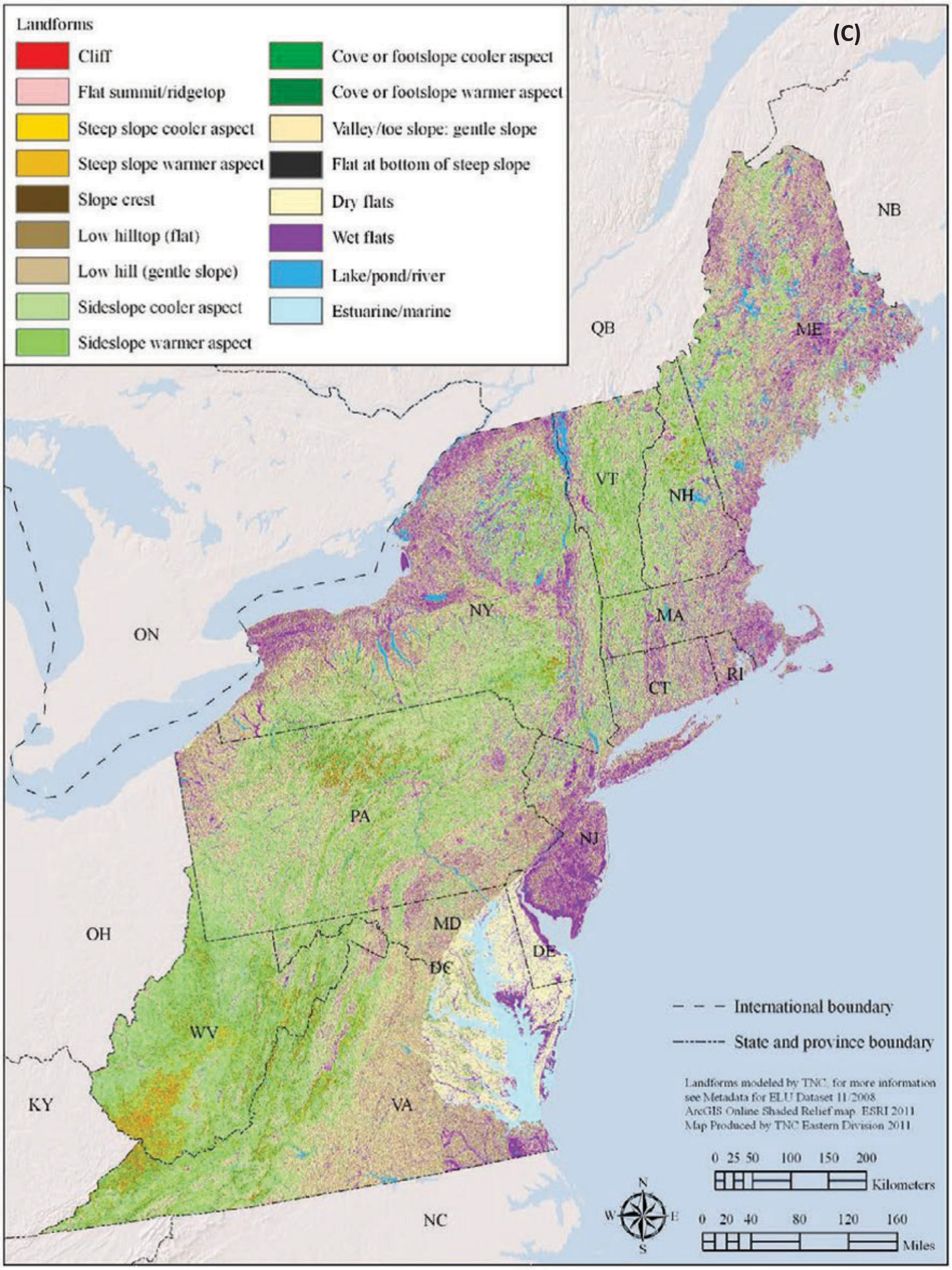


Figure 2. *Continued.*

Anderson and others (2012) then assigned each of the region's 156,581 hexagons—on the basis of hierarchical cluster analysis (McCune and Grace 2002) for similarity in terms of geology, elevation and landform—to one of 30 geophysical settings. These include 15 low elevation settings, 8 mid elevation settings, 6 high elevation settings and one miscellaneous high slope setting (see Figure 3). Examples of geophysical settings include "coastal coarse sand," "low elevation fine sediment," "mid elevation shale," and "high elevation granitic." Data from state natural heritage programs were used to identify natural community types associated with each geophysical setting. While the species at any given site are likely to change in response to a warming climate, the ecosystem types are likely to persist. Community types that have commonly been named after predominant plant species can now be referred to by their geophysical settings. For example, a Cattail (*Typha latifolia*)—Marsh Marigold (*Caltha palustris*)—marsh becomes a freshwater marsh ecosystem on shale at low elevation.

To assess the relative resiliency of sites associated with each geophysical setting, Anderson and others (2012) developed scores based on landscape complexity and local permeability (or connectivity), which are summarized below.

Landscape Complexity

Landscape complexity is driven by an area's topography and associated landforms and the length of its elevation gradients. Landscape complexity creates micro-topographic thermal climate options that resident species can move to, buffering them from changes in the regional climate (Willis and Bhagwat 2009) and slowing the velocity of change (Loarie and others 2009). Under variable climatic conditions, areas of high landscape diversity are important for the long-term population persistence of plants (Randin and others 2008), invertebrates (Weiss and others 1988), and presumably for the more mobile species that depend on them. For example, Weiss et al (1988) measured micro-topographic thermal climates in relation to butterfly species and their host plants. They concluded that areas of high local landscape complexity—even at the scale of tens of meters—are important for long-term population persistence under variable climatic conditions. Because species locations shift to take advantage of micro-climate variation and stay within their preferred temperature and moisture regimes, extinction rates predicted from coarse-scale climate models may fail to account for topographic and elevation diversity (Luato and Heikkinen 2008; Wiens and Bachelet 2010).

A landscape complexity index was developed by tabulating the number of landforms and elevation ranges within a 40 hectare circular area around every 30 meter cell. It was assumed that sites with a larger variety of landforms would provide more microclimate options within their local neighborhoods. The number of landforms ranged from 1-11 (there are 17 landform types across the region). Elevation gradients for the cells ranged from 1 to 795 meters, which were log transformed for analysis since the gradients were heavily skewed toward narrow ranges. The landform and elevation information were combined using a weighted sum with landform variety given twice the weight of elevation (Anderson and others 2012). The final index was:

$$\text{Landscape Diversity} = (2*LV = 1*ER)/3$$
$$\text{Where } LV = \text{landform variety, } ER = \text{elevation range}$$

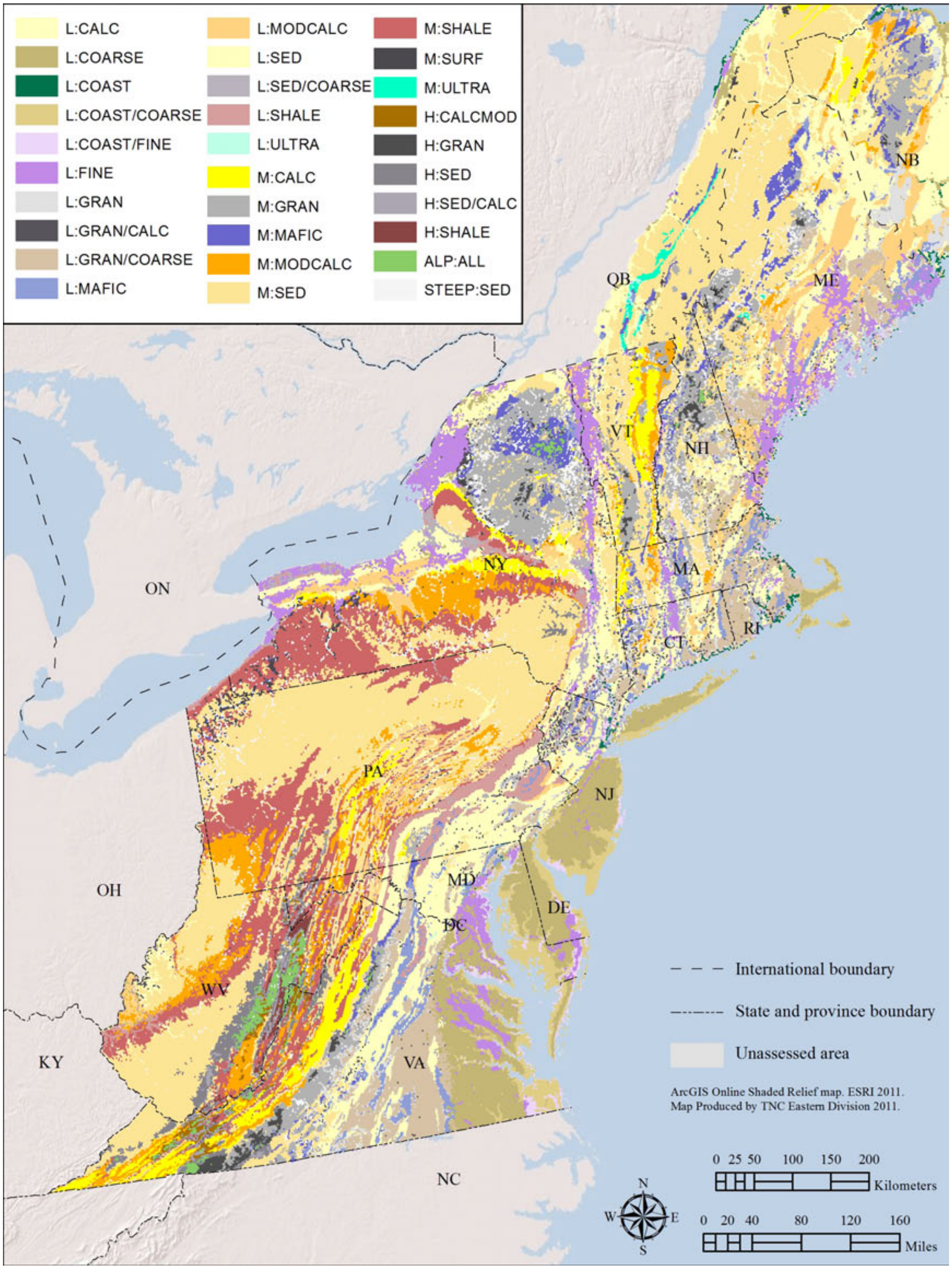


Figure 3. Thirty geophysical settings in the northeastern United States were classified on the basis of geology class, elevation zone and landform type.

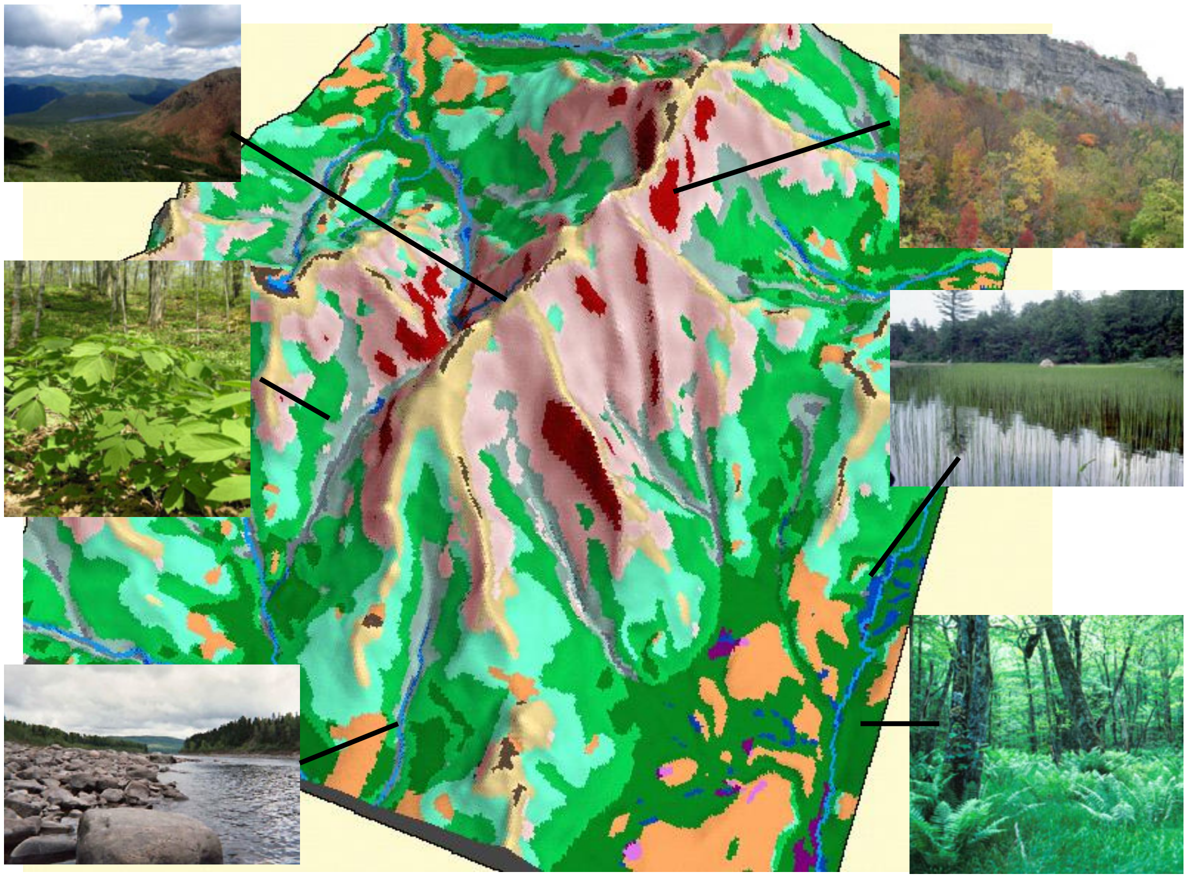


Figure 4. Landscapes with greater heterogeneity provide more options for species to move and rearrange at a given site.

Landscape Permeability

Landscape complexity is likely to offer less resilience if the site is geographically constricted since species populations and ecological processes could be overly confined as regional climate changes. Permeability is the degree to which a given landscape supports the movement of organisms and the natural flow of ecological processes such as water or fire (definition modified from Meiklejohn and others 2010). A highly permeable or locally connected landscape promotes resilience by facilitating local species movements and range shifts, and the reorganization of communities (Krosby and others 2010). Maintaining a connected landscape is a widely cited strategy for building climate change resilience (Heller and Zavaleta 2009). Botkin and others (2007) have suggested large landscape connectivity as an explanation for why there were few extinctions during the last period of comparably rapid climate change. Accordingly, our measure of permeability "local connectedness" is based on measures of landscape structure: the hardness of barriers, the connectedness of natural cover, and the arrangement of land uses.

To assess landscape permeability, Anderson and others (2012) used the resistant kernel analysis that assumes that the connectedness of two adjacent cells increases with their ecological similarity and decreases with their contrast (Compton and others 2007). The theoretical spread for a species or process out from a focal cell is a function of the resistance values of neighboring cells and their distance from the focal cell out to a distance of up to three kilometers. A focal cell score for local connectedness is equal to the amount of spread accounting for resistance divided by the theoretical amount spread if there was no resistance. Cell scores are then multiplied by 100 to create a range from 1 to 100 and converted to standard normal distributions for the region. The resistance surface was based on a classified land use map with roads and railroads embedded in the grid (NLCD 2001; Tele Atlas North America 2012). Land cover was simplified into six types including *natural land* (evergreen, deciduous, and mixed forest, shub/scrub, grassland, woody and herbaceous wetland), *water*, *artificial barrens, agriculture,* (pasture and cultivated), *low intensity developed* (developed open space, low intensity developed), and *high intensity developed* (medium density, high density and major roads). Natural land was given the lowest resistance score (10) and high intensity developed land was given the highest weight (100). Scores for the other land classes included artificial barrens (50), agricultural lands (80), and low intensity development (90).

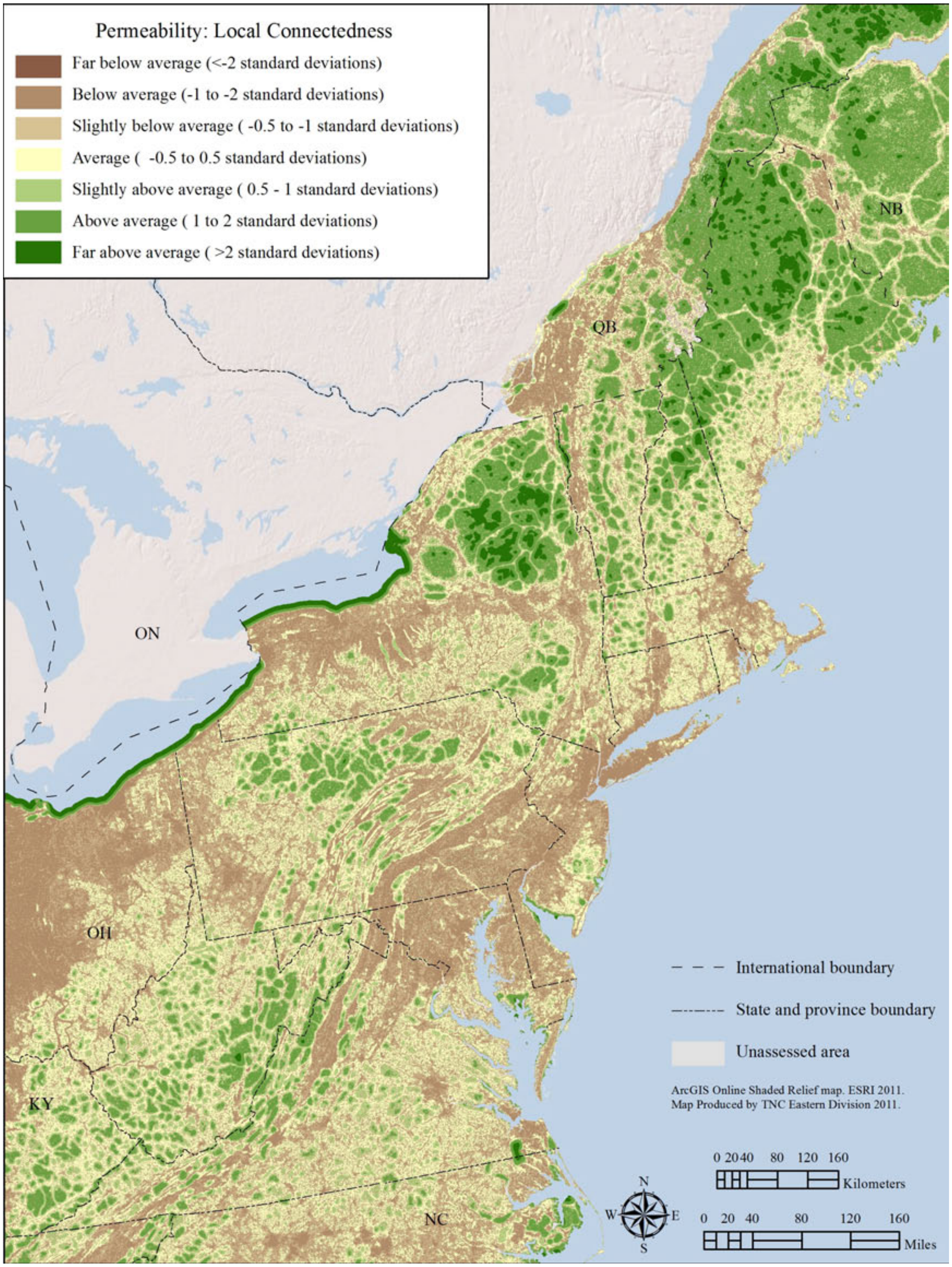


Figure 5. Landscape permeability for forest blocks in the northeastern United States.

RESILIENT FOREST CONSERVATION NETWORK

The landscape complexity and landscape permeability scores were combined to develop a single resiliency score for each 30 meter cell. The complexity and permeability scores were transformed into standardized normalized (Z-scores) in order to combine and compare resilience factors. Each factor was given the same weight in the integrated score:

Estimated Resilience = (LC1 = LC2)/2
Where LC1 = local connectedness and LC2 = landscape complexity

The results show a wide range of estimated resiliency for terrestrial ecosystems across the northeastern United States and Canadian Maritime Provinces (Figure 6a). The vast majority of areas with high terrestrial resiliency scores are forest ecosystems, although wetland and smaller patch communities are embedded within large blocks of resilient landscapes. A simplified map showing a regional network of resilient forest landscapes is shown in Figure 6b.

The last step in identifying a resilient conservation network is to locate regional linkages between large forest landscapes. Anderson and others (2012) used the Circuitscape software tool (McRae and Shah 2009), based on electric circuit theory, to identify potential larger-scale directional movements and pinpoint the areas where they are likely to become concentrated, diffused, or rerouted, due to the structure of the landscape. As with the local connectedness analysis, underlying data for this analysis includes land-cover and road data converted to a resistance grid by assigning weights to the cell types based on their similarity to cells of natural cover. However, instead of quantifying local neighborhoods, the Circuitscape program calculates a surface of effective resistance to current moving across the whole landscape. The output of the program, an effective resistance surface, shows the behavior of directional flows. Analogous to electric current or flowing water, the physical landscape structure creates areas of high and low concentrations similar to the diffuse flow, braided channels, and concentrated channels one associates with a river system. Three basic patterns can be seen in the output, as the current flow will: 1) *avoid* areas of low permeability, 2) *diffuse* in highly intact/highly permeable areas, or 3) *concentrate* in key linkages where flow accumulates or is channeled through a pinch point. Concentration areas are recognized by their high *current density*, and the program's ability to highlight concentration areas and pinch-points made it particularly useful for identifying the linkage areas that may be important to maintaining a base level of permeability across the whole region (Figure 7a). The Nature Conservancy's Central Appalachians Program has combined the regional resiliency and connectivity results into a network of "essential forests" and "key connectors" (Figure 7b).

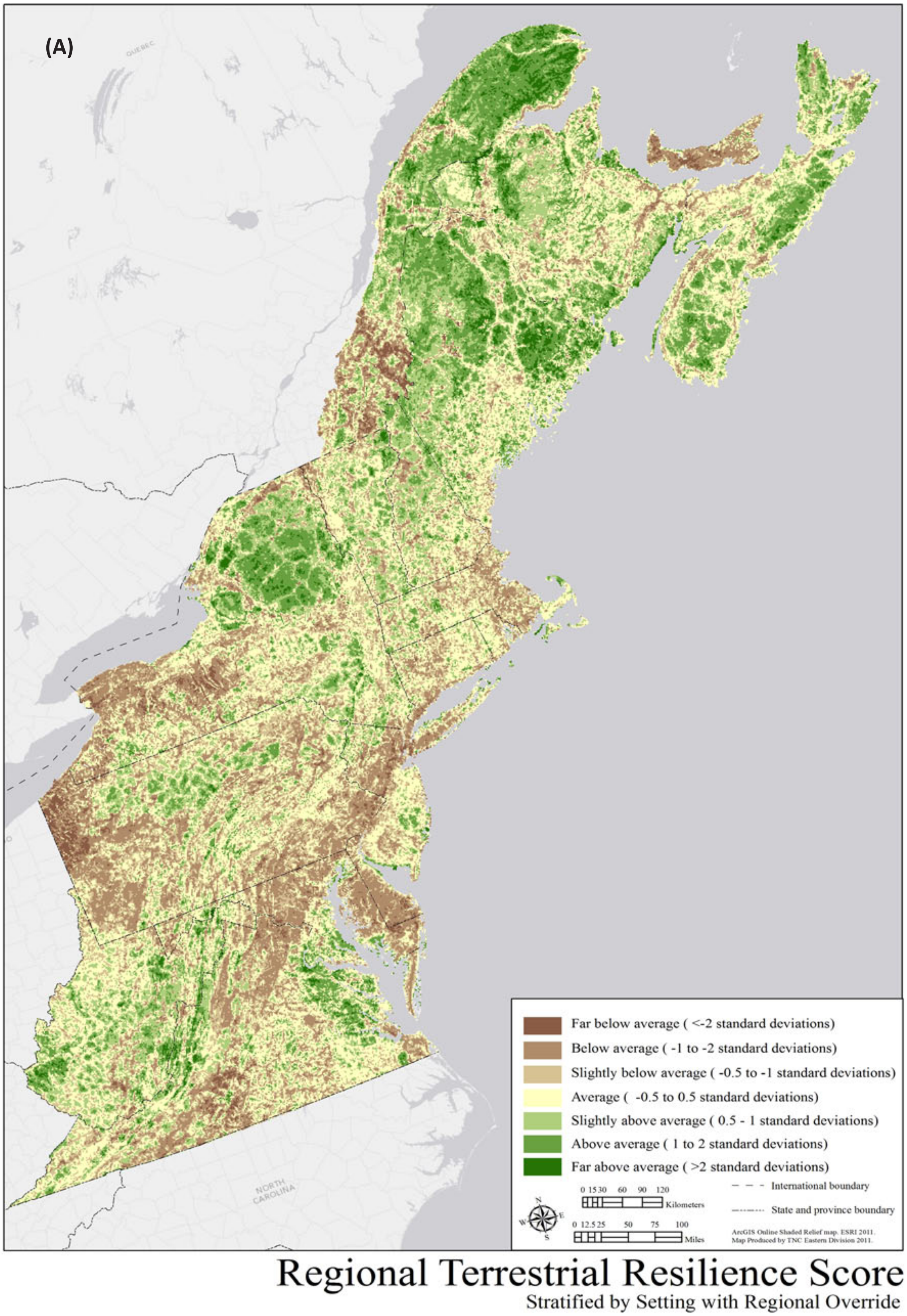
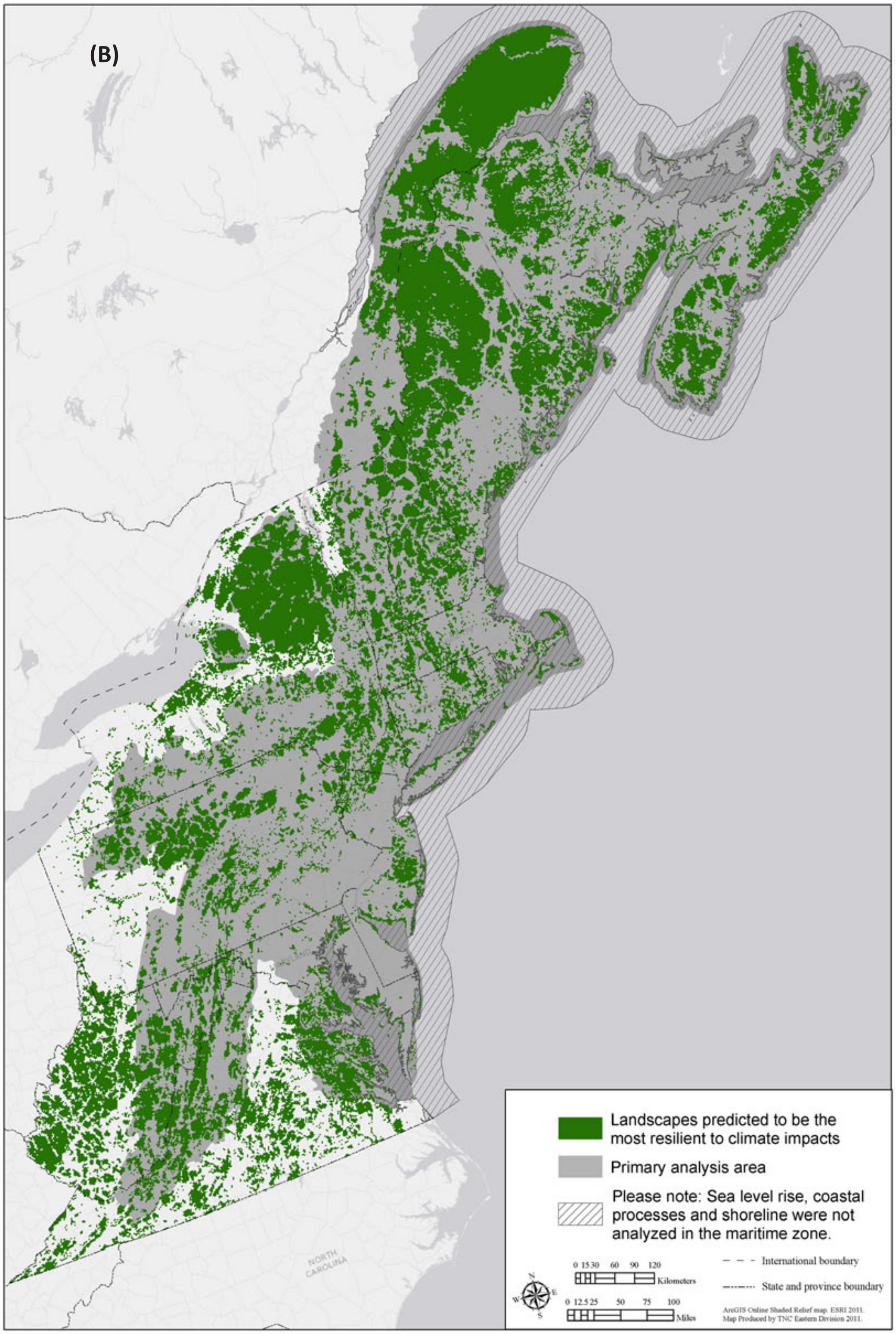


Figure 6a). Regional map showing ecological resiliency scores; b) Simplified map showing a network of resilient forest landscapes across the northeastern United States.



Regional Terrestrial Resilience: Above Average Areas
Stratified by Setting and Ecoregion with Regional Override

Figure 6. *Continued.*

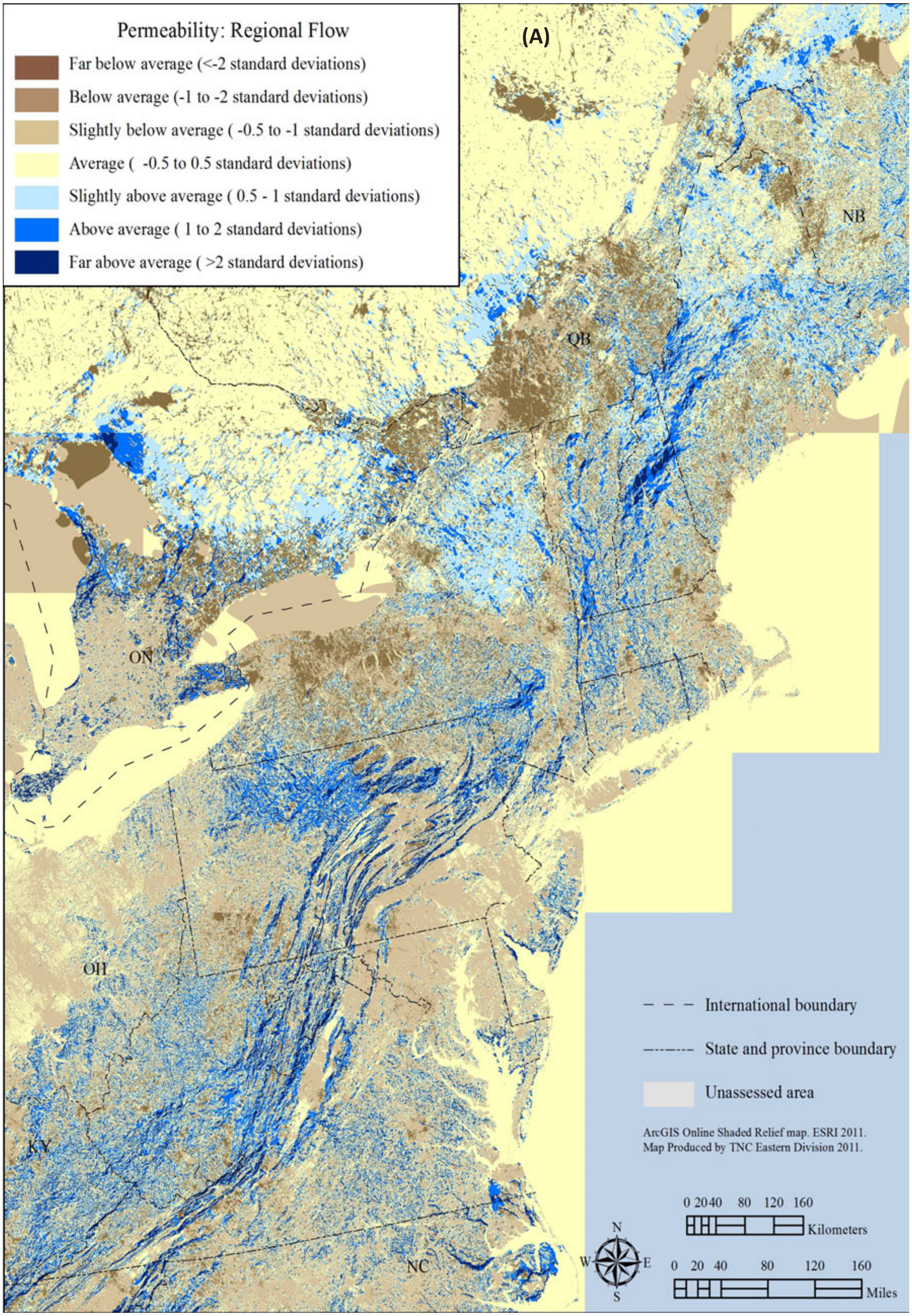


Figure 7a). Regional pinch points based on circuit theory (McRae and Shah 2009); b) Central Appalachians "essential forests" and "key connectors" network based on regional resiliency and connectively analyses (Anderson and others 2012).

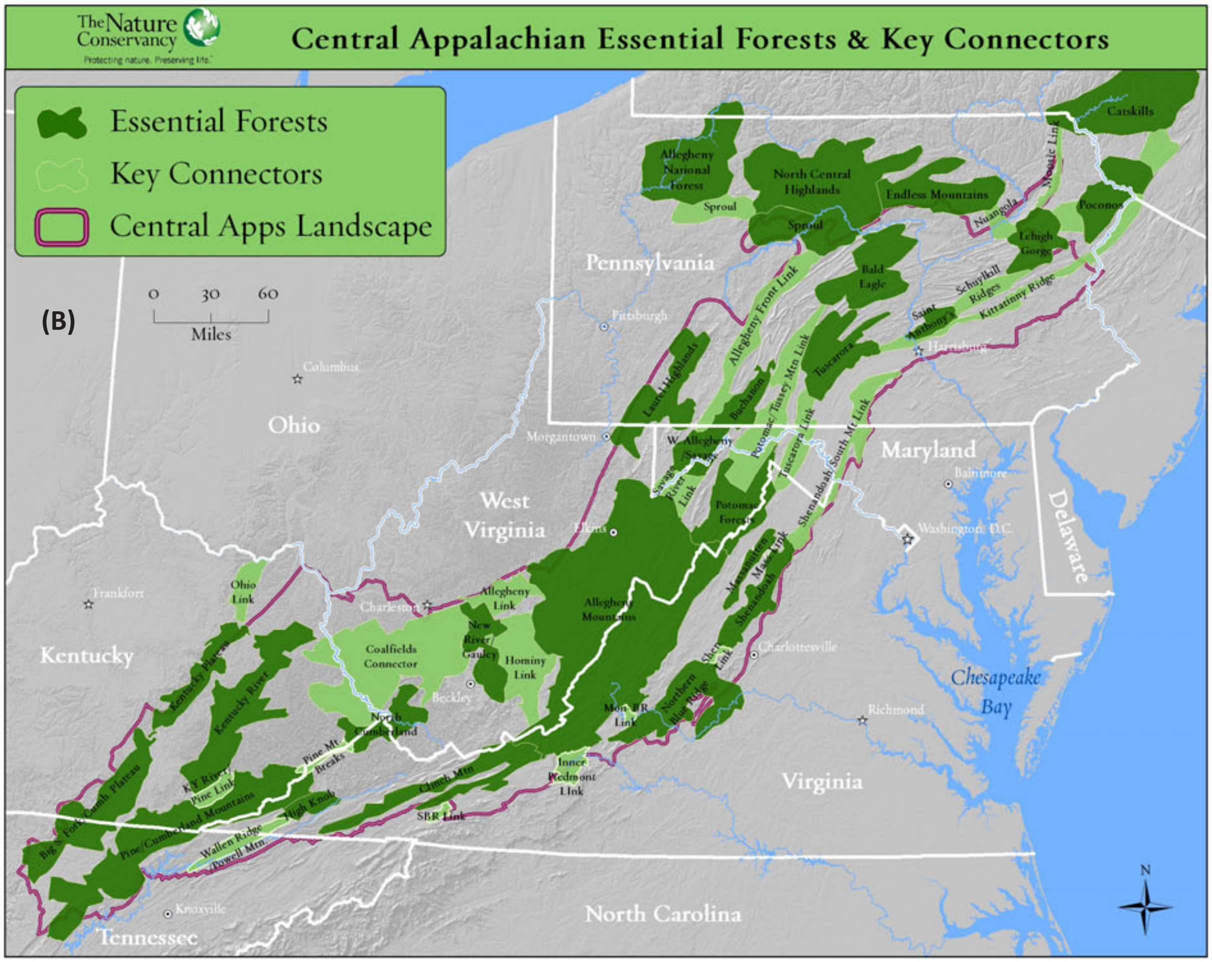


Figure 7. *Continued.*

MANAGING FOR RESILIENT FORESTS AT THE LANDSCAPE SCALE

While geophysical factors are important for maximizing the potential for conserving forest diversity other factors—especially biological—are important for actively maintaining or restoring biodiversity at a given site. Some factors, such as reducing stress from forest pests and pathogens, have been traditional tools in landscape forest management. Others, such as selecting species on the basis of their tolerance for anticipated temperature regimes, introduce new approaches to managing today's forests so they remain diverse and productive decades from now.

A wide variety of recommendations have been made to help managers prepare for future conditions, including the considerable uncertainty that accompanies climate projections at the landscape scale (Millar and others 2007; Heller and Zavaleta 2009; Puettmann 2011; Cornett and White 2013). We've grouped strategies for maintaining and improving ecological resilience at the landscape scale into three categories, which are briefly summarized below:

- Promote Diversity
- Reduce Existing Stresses
- Anticipate Future Conditions

Promote Diversity

Three dimensions of diversity can help forests be more productive and resilient at a landscape scale. *Species diversity* has been linked to ecosystem productivity and functioning by a variety of researchers (e.g., Tilman and others 1997; Chapin and others 2000, Flombaum and Sala 2008; Thompson and others 2009; MacDougal and others 2013). Because many forest species have very specific environmental requirements and functions (niche partitioning), their loss may lead to a reduction in productivity and/or function until the niche space is occupied by another similar species. Species diversity at the stand and landscape level is also associated with resistance to ecologically destructive disturbances such as severe fire and pest and pathogen outbreaks (Thompson and others 2009). Emphasis should be placed on increasing the native diversity of forest specialist and late-seral species associated with topographic and structural microclimates as opposed to generalist and non-native species associated with forest fragmentation. Management should increasingly consider model results (USFS Tree Atlas; LANDIS) and emerging data that provide information on which species may benefit from a changing climate (e.g., oaks, hickories) and which may suffer (e.g., beech, some maples, spruce). *Successional diversity* is another feature that can promote ecological productivity in the face of environmental change. A range of successional or age classes at the landscape scale promotes species and structural diversity by creating a mosaic of environmental gradients with respect to light, humidity, ambient temperature, and coarse woody debris. These gradients can help perpetuate a wider variety of disturbances, species and ecological functions that contribute to overall forest health than a landscape dominated by a single successional cohort (Franklin and others 2007). Likewise, *structural diversity* in forest ecosystems of any age class or mix of classes can promote forest ecological health as well as provide a wide range of habitats for a variety of species. Nurse logs, for example, facilitate the regeneration of moisture-sensitive species in northern hardwood forests. The acceleration of natural successional processes, such as the use of small patch cuts to simulate gap-phase dynamics, the creation of snags or the introduction of coarse woody can improve the ability of forest ecosystems to adapt to changing conditions (Cornett and White 2013).

Reduce Existing Stresses

Most effects from a changing climate on northeastern forests will be expressed through stresses that already exist in the region. The dominant existing regional stressor—habitat fragmentation—makes forests more vulnerable to the spread of invasive species, wind damage along exposed forest edges and altered species movement. Invasive plant species, insect pests and disease pathogens have been a growing threat to forest diversity and health for the past century. Warmer and wetter conditions are likely to expand the range of many pests and pathogens, such as hemlock wooly adelgid, while more frequent droughts will exacerbate others, such as gypsy moth outbreaks in oak forests (Boitcourt and Johnson 2010). Increased droughts may also increase the potential for catastrophic wildfire in certain forest types that have had excessive fuel accumulation for decades. Deer populations have had severe impacts on forest regeneration in many areas of the northeastern United States. While there is little evidence that white-tail deer populations will increase as a result of climate change, the combined effects of excessive browse and other stressors (i.e., atmospheric deposition) could compound the regeneration challenge for many tree and understory species under a changing climate regime (Galatowitsch and Frelich 2009).

Many forest management programs at the stand and landscape scales already address existing stresses but climate change could change the relative threat each poses to forests. In order to respond to these potential threats, management should attempt to improve the forests' ability to resist pests and pathogens, work to prevent the introduction and establishment of non-native and/or invasive pest and plant species (and remove existing populations), and manage herbivory that impacts regeneration (e.g., establishing deer fencing). Management can also reduce the risk of catastrophic fire by establishing fuel breaks, altering forest structure to minimize risk and severity of fires, or conducting prescribed burns to reduce fuel loadings. Chapin and others (2009) suggest that management targets for existing stressors should be updated to incorporate trajectories of expected change rather than relying on historic ranges of variability. Given uncertainties about exactly how these threats will change increases the importance of establishing monitoring networks to detect unexpected changes in stress impacts and management responses to them (Joyce and others 2009). Conn and others (2010) provide several recommendations to reduce the total amount of stress on forest ecosystems. These include: 1) strengthening state and local programs to slow forest loss and fragmentation; 2) revising forestry best management practices (BMPs) to account for expected impacts from climate change to existing and new stressors; 3) working with sustainable certification programs such as the Forest Stewardship Council (FSC) and Sustainable Forestry Initiative (SFI) to promote integration of climate adaptation measures into their performance measures, and 4) expanding state and local capacity to monitor and respond to pests, pathogens, storm damage and fire risk.

Anticipate Future Conditions

Forest management actions taken today can anticipate future conditions and reduce the ecosystem's vulnerability to expected disturbance (Bolte and others 2009). Actions that can be taken to anticipate future impacts include selecting or promoting tree species with a wide environmental tolerance, maintaining and restoring habitat connectivity to facilitate species movement, and stand/site design to minimize edges that are vulnerable to wind storms and invasive species. Current species that have a broad natural range with regard to temperature and moisture (i.e., oaks, *Tilia, Sorbus*, white pine) can be expected to do well (Iverson and others 1999). Species with a narrow range of ecological tolerance are likely to persist only in topographic micro-climates, and attention to the recruitment dynamics within these microsites may be important to long-term persistence of these species in the forest. This may be preferable to selecting species not currently in the area that may or may not be adapted well to future conditions. Prioritizing and protecting refugia of unique habitats or populations of sensitive or rare communities should therefore be a goal of management. Ultimately, any management activities should attempt to protect the fundamental ecological functions of that system, including the protection of soil quality and nutrient cycling, and maintaining and restoring hydrological flows.

The U.S. Forest Service has developed an adaptive management framework based on an alternative set of strategy categories including those that help forests better resist impacts, or be able to recover more quickly from impacts, or respond to changing impacts (see text Box 1).

Box 1. U.S. Forest Service Climate Change Response Framework

The Climate Change Response Framework was established by the U.S. Forest Service's Northern Institute of Applied Climate Science (climateframework.org) to help managers better understand the effects of stress on their forests and identify management options (Swanston and Janowiak, 2012). Their approach establishes an effective continuum of adaptation strategies, from developing fundamental management options, to developing strategies, approaches and tactics (Figure 8). In their continuum, adaptation strategies fall under three broad categories: resistance, resilience and response. Resistance actions—such as reducing invasive species impacts—improve the forests' defenses against anticipated changes or directly defend against disturbance to maintain relatively unchanged conditions. Resilience actions—such as promoting species and structural diversity—allow for some degree of change, but encourage a return to prior conditions after a disturbance, either naturally or through management. Response actions—such as moving species to new areas where they can remain within their climatic tolerances—intentionally accommodate change and enable ecosystems to adaptively respond to changing and new conditions (Swanston and Janowiak 2012).

Figure 8. A diagram of the process of the Climate Change Response Framework Adapted from Swanston and Janowiak 2012).

CONCLUSION

Forest conservationists need methods to conserve the maximum amount of biological diversity while allowing species and communities to rearrange in response to a continually changing climate. By focusing on the representation of physical diversity instead of on the current species composition, we identify a regional network of sites that will represent the full spectrum of forest diversity both now and into the future. We advocate that this geophysical approach to identifying a network of core forest areas and key connectors be used to inform and augment the traditional conservation focus on large forest reserves nested within a matrix of well-managed forest. At specific sites within a resilient forest conservation network, forest managers should continue to do many of the things we have long known are important for maintaining healthy forest ecosystems. These strategies include: 1) managing for species, structural, and successional diversity; 2) reducing existing stress from invasive species, habitat fragmentation, altered fire regimes, and other factors, and; 3) making forest management decisions—such as selecting species with broad tolerances—that anticipate future climatic conditions. Since there is considerable uncertainty about the rate and degree of future change, managers will need to remain flexible, experimental and innovative. Adaptive management frameworks will be increasingly essential for sustainable forest management within a resilient regional forest conservation network.

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