Conservation Biology

Contributed Paper

Estimating Climate Resilience for Conservation across Geophysical Settings

MARK G. ANDERSON, MELISSA CLARK, AND ARLENE OLIVERO SHELDON

The Nature Conservancy, Eastern Conservation Science, Eastern North America Division, Boston, MA 02111, U.S.A., email manderson@tnc.org

Abstract: *Conservationists need methods to conserve biological diversity while allowing species and communities to rearrange in response to a changing climate. We developed and tested such a method for northeastern North America that we based on physical features associated with ecological diversity and site resilience to climate change. We comprehensively mapped 30 distinct geophysical settings based on geology and elevation. Within each geophysical setting, we identified sites that were both connected by natural cover and that had relatively more microclimates indicated by diverse topography and elevation gradients. We did this by scoring every 405 ha hexagon in the region for these two characteristics and selecting those that scored >SD 0.5 above the mean combined score for each setting. We hypothesized that these high-scoring sites had the greatest resilience to climate change, and we compared them with sites selected by The Nature Conservancy for their high-quality rare species populations and natural community occurrences. High-scoring sites captured significantly more of the biodiversity sites than expected by chance ($p < 0.0001$): 75% of the 414 target species, 49% of the 4592 target species locations, and 53% of the 2170 target community locations. Calcareous bedrock, coarse sand, and fine silt settings scored markedly lower for estimated resilience and had low levels of permanent land protection (average 7%). Because our method identifies—for every geophysical setting—sites that are the most likely to retain species and functions longer under a changing climate, it reveals natural strongholds for future conservation that would also capture substantial existing biodiversity and correct the bias in current secured lands.*

Keywords: biodiversity, climate change, connectivity, conservation planning, fragmentation, geology, North America, protected areas

Identificación de Sitios Duraderos para la Conservación Usando la Diversidad del Paisaje y las Conexiones Locales para Estimar la Capacidad de Recuperación al Cambio Climático

Resumen: *Los conservacionistas necesitan un método mediante el cual poder conservar la diversidad biológica mientras permiten que las especies y las comunidades se reorganicen con respecto al clima cambiante. Desarrollamos y probamos tal método, el cual basamos en características físicas asociadas con la diversidad ecológica y la capacidad de recuperación del sitio con respecto al cambio climático, en el noreste de Norteamérica. Mapeamos comprensivamente 30 escenarios geofísicos distintos basados en la geología y la elevación. Dentro de cada escenario geofísico identificamos sitios que estaban conectados por una cubierta natural y que tenían relativamente más microclimas indicados por la topografía diversa y los gradientes de elevación. Hicimos esto al puntuar cada hexágono de 450 ha en la región con estas dos características y al seleccionar aquellos que tuvieron una puntuación >SD 0.5 por encima del puntaje combinado promedio para cada escenario. Nuestra hipótesis fue que estos sitios con altas puntuaciones tuvieron la mayor capacidad de recuperación. Los comparamos con los sitios seleccionados por The Nature Conservancy por sus poblaciones de alta calidad de especies raras y sus ocurrencias de comunidades naturales. Los sitios con altos puntajes capturaron significativamente más de los sitios de biodiversidad de lo que se esperaba por casualidad ($p < 0.0001$): 75% de las 414 especies objetivo, 49% de las 4592 localidades de especies objetivo y 53%*

Paper submitted February 13, 2013; revised manuscript accepted December 1, 2013.

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

Conservation Biology, Volume 28, No. 4, 959–970
© 2014 The Authors. *Conservation Biology* published by Wiley Periodicals, Inc., on behalf of the Society for Conservation Biology.
DOI: 10.1111/cobi.12272

de las 2710 localidades de comunidades objetivo. Los escenarios de lecho rocoso calcáreo, arena gruesa y limo fino tuvieron puntos marcadamente más bajos para la capacidad de recuperación estimada y tuvieron niveles bajos de protección permanente de suelo (en promedio 7%). Ya que nuestro método identifica – para cada escenario geofísico – sitios que tienen mayor probabilidad de retener especies y funciones más tiempo bajo un clima cambiante, revela baluartes naturales para la conservación futura que también capturaría biodiversidad existente sustancial y corregiría el sesgo en tierras que actualmente están aseguradas.

Palabras Clave: Áreas protegidas, biodiversidad, cambio climático, conectividad, fragmentación, geología, Norteamérica, planeación de la conservación

Introduction

Climate change is expected to alter species distributions, modify ecological processes, and exacerbate environmental degradation (Pachauri & Reisinger 2007). To offset these effects, the need is greater than ever for strategic land conservation. Conservationists have long prioritized land acquisitions based on rare species or natural community locations (Groves 2003). Now they need a way to set priorities that will conserve biological diversity and maintain ecological functions, despite climate-driven changes in community composition and species locations (Pressey et al. 2007). We devised such an approach to identify potential conservation areas based on geophysical characteristics that influence a site's resilience to climate change.

Geology defines the available environments and determines the location of specialist species. In eastern North America, for example, limestone valleys support fen plants, mussels, and cave fauna, whereas inland sand plains support species adapted to dry acidic soils and fire. Geophysical variables (geology, latitude, and elevation) explain 92% of the variation in the species diversity of the eastern states and provinces, far more than climate variables do (Anderson & Ferree 2010). Because biodiversity is so strongly correlated with the variety of geophysical settings, conserving the full spectrum of geophysical settings offers a way to maintain both current and future biodiversity, providing an ecological stage for a different set of species, which turnover through time (Beier & Brost 2010).

Geophysical diversity as a surrogate for species diversity has a long history in conservation planning (e.g., Hunter et al. 1988; Faith & Walker 1996; review in Rodrigues & Brooks 2007), and recently it has been recognized for its potential role in conservation planning under climate change (Schloss et al. 2011). We used different aspects of geophysical diversity for different purposes: geological representation to capture species diversity and topographic and elevation diversity to identify places that have the maximum resilience to climate change.

Our use of the term *site resilience* is distinguished from *ecosystem* or *species resilience* because it refers to the capacity of a geophysical site (40–4000 ha) to maintain species diversity and ecological function as the climate changes (definition modified from Gunderson 2000). Because neither the site's species composition nor the range of variation of its processes are static under climate change, our working definition of a resilient site was 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.

We developed a method to estimate site resilience as the sum of two quantitative metrics: landscape diversity (i.e., diversity of topography and range of elevation in a site and its surrounding neighborhood) and local connectedness (i.e., permeability of a site's surrounding land cover). Using a geographic information system (GIS), we calculated these metrics for every 405 ha hexagon cell in the Northeast United States and Atlantic Canada and used the results to estimate the site resilience of specific places.

Landscape diversity, the variety of landforms created by an area's topography, together with the range of its elevation gradients, increases a site's resilience by offering micro-topographic thermal climate options to resident species, buffering them from changes in the regional climate (Willis & Bhagwat 2009; Ackerly et al. 2010; Dobrowski 2010) and slowing down the velocity of change (Loarie et al. 2009). Under variable climatic conditions, areas of high landscape diversity are important for the long-term population persistence of plants, invertebrates, and other species (Weiss et al. 1988; Randin et al. 2008). Because species shift locations to take advantage of micro-climate variation, extinction rates predicted from coarse-scale climate models that fail to account for topographic and elevation diversity have been disputed (Luoto & Heikkinen 2008; Wiens & Bachelet 2010).

Landscape permeability is the degree to which a given landscape is conducive to the movement of organisms and the natural flow of ecological processes such as wildfire (definition modified from Meiklejohn et al. 2010). A highly permeable landscape promotes resilience by facilitating local movements, range shifts, and the reorganization of communities (Krosby et al. 2010). Maintaining

a connected landscape is the most widely cited strategy in the scientific literature for building climate change resilience (Heller & Zavaleta 2009). Accordingly, measures of permeability such as local connectedness are based on landscape structure: the hardness of barriers, the connectedness of natural cover, and the arrangement of land uses.

A climate-resilient conservation portfolio includes sites representative of all geophysical settings selected for their landscape diversity and local connectedness. We developed a method to identify such a portfolio. First, we mapped geophysical settings across the entire study area. Second, within each geophysical setting we located sites with diverse topography that were highly connected by natural cover. Third, we compared the identified sites with the current network of secured lands (i.e., land with permanent protection from conversion) and with The Nature Conservancy's (TNC) assessment of important biodiversity sites identified based on rare species and natural community locations. Using this information, we identified biases in current conservation and identified places that could serve as strongholds for diversity both now and into the future.

Methods

Study Area

The area studied included 14 states of the New England and Mid-Atlantic regions of the United States and three provinces of Atlantic Canada (here after the region): Maine, New Hampshire, Vermont, New York, Massachusetts, Rhode Island, Connecticut, Pennsylvania, Delaware, New Jersey, Maryland, Ohio, West Virginia, Virginia, New Brunswick, Nova Scotia, Prince Edward Island, and portions of Quebec. The area covers 870,247 km^2, supports over 13,500 species of plants, vertebrates, and macro-invertebrates, and has a wide diversity of lithologies and topography.

The boundaries of TNC's terrestrial ecoregions (TNC 2012) were used as a stratifying framework. The ecoregions were developed in conjunction with the USDA Forest Service and are a modification of Keys et al.'s ecoregions (1995). Six ecoregions were fully contained within the area of interest: Central Appalachian, Chesapeake Bay, High Allegheny Plateau, Lower New England, North Atlantic Coast, and Northern Appalachian/Acadian. Six other ecoregions had a portion of their full extent included in the region.

Mapping Geophysical Settings

To map the region's geophysical settings, we compiled bedrock and surficial geology data sets for each state and province at the scale of 1:125,000. We grouped the >200 bedrock types into nine lithogeochemical classes based on genesis, chemistry, and weathering properties (Table 1). Elevation data were taken directly from a 30-m digital elevation model (DEM) (Gesch 2007) and classified into six elevation zones corresponding to major changes in dominant vegetation (Table 1). Geology classes and elevation zones matched those described in Anderson and Ferree (2010).

In the GIS, all information was summarized on a grid of 156,581 hexagons on which each hexagon was 405 hectares. This hexagon size allowed us to maintain relatively fine-scale detail while accounting for spatial error in the location of features such as rare species or bedrock outcrops. The hexagon grid fully tessellated the entire region and the individual hexagons (referred to as sites) can readily aggregate to delimit larger areas.

We used a cluster analysis to assess the geophysical similarity between hexagons and group them into geophysical setting types. For each hexagon, we tabulated the type and abundance of each geology class, elevation zone, and landform type (described below). Then we performed a hierarchical cluster analysis in PC-ORD (McCune & Mefford 1999) with the Sorensen similarity index and a flexible beta linkage technique with beta set at 25 to group similar hexagons. We defined the geophysical setting groups by studying the dissimilarity scores and identifying the relatively homogenous clusters.

Estimating Site Resilience

We developed separate estimates of landscape diversity and connectedness for every 30-m cell and then combined these to estimate resilience for each 30-m cell. Subsequently, for each hexagon we calculated the mean and standard deviation of each individual and combined factor based on the 30-m grid cells contained within the hexagon.

Landscape diversity summarized the variety of landforms, elevation range, and density of wetlands in a given search area. The landform variety component was based on a spatially comprehensive landform model that delineated 11 surface features: cliff and steep slope, summit and ridge-top, northeast facing side slope, southwest facing side slope, cove and slope bottom, low hill, low hilltop flat, valley and toe slope, dry flat, wet flat, and water (Fig. 1). The model, an expansion of Conacher and Darymple's (1977) nine-unit land surface model, delimits recognizable landforms as combinations of slope, land position, aspect, and moisture accumulation that correspond to local topographic environments with distinct combinations of moisture, radiant energy, and deposition. Technical methods for mapping landforms were based on Fels and Matson (1996) and are described in detail in Anderson et al. (2012). The model was derived from a 30-m DEM.

Table 1. The 30 geophysical settings used as a framework for assessing site resilience to climate change relative to geology classes and elevation zones.

	Elevation range[b]				
Lithology[a]	*Coastal 0–6 m*	*Low 6–244 m*	*Mid 244–762 m*	*High 762–1097 m*	*Alpine >1097 m*
Acidic sedimentary Mudstone, claystone, siltstone, nonfissile shale, sandstone, breccia, conglomerate, greywake, Arenites, slate, phyllite, pelite, schist, pelitic schist, granofel, quartzite	L:COAST/BEDROCK	L:SED	M:SED	H:SED	ALPINE
Acidic shale Fissile shale	L:COAST/BEDROCK	L:SHALE	M:SHALE	H:SHALE	ALPINE
Calcareous Limestone, dolomite, dolostone, other carbonate-rich clastic rocks, marble	L:COAST/BEDROCK	L:CALC	M:CALC	H:CALC/MOD[a]	ALPINE
Moderately calcareous Calcareous shale and sandstone, calc-silicate granofel, calcareous schist and phyllite	L:COAST/BEDROCK	L:MODCALC	M:MODCALC	H:CALC/MOD[a]	ALPINE
Acidic granitic Granite, granodiorite, rhyolite, felsite, pegmatite,(granitic gneiss, charnocktites, migmatites	L:COAST/BEDROCK	L:GRAN	M:GRAN	H:GRAN/MAFIC[a]	ALPINE
Mafic Anorthosite, gabbro, diabase, basalt, diorite, andesite, syenite, trachyte, greenstone, amphibolites, epidiorite, granulite, bostonite, essexite	L:COAST/BEDROCK	L:MAFIC	M:MAFIC	H:GRAN/MAFIC[a]	ALPINE
Ultramafic Serpentine, soapstone, pyroxenite, dunite, peridotite, talc schist	L:COAST/BEDROCK	L:ULTRA	M:ULTRA	N/A	N/A
Coarse sediment Unconsolidated sand, gravel, pebble, till	L:COAST/COARSE	L:COARSE	M:SURFICAL	N/A	N/A
Fine sediment Unconsolidated mud, clay, drift, ancient lake deposits	L:COAST/FINE	L:FINE	M:SURFICIAL	N/A	N/A
Mixed Roughly equal mixtures of two geology classes	N/A	L:SED/COARSE L:GRAN/CALC L:GRAN/COARSE	N/A	H:SED/CALC	N/A
Very steep slopes at any elevation	N/A	STEEP	STEEP	STEEP	STEEP

[a]*At high elevations, we combined calcareous with moderately calcareous and granite with mafic.*
[b]*Abbreviations: L, low; M, mid elevation; H, high elevation; Calc, calcareous; ModCalc, moderately calcareous; Sed, sedimentary; Gran, granitic; Ultra, ultramafic.*

We used a focal variety analysis to tabulate the number of landforms within a 40-ha circular area around every 30-m cell. The size of the search area was derived by systematically testing many possible sizes (4–400 ha) to find the one with the highest between-cell variance and thus the maximum discrimination between sites (i.e., too large and all sites had all landforms, too small and all sites had only one landform). For consistency, we used a 40-ha area for all the landscape diversity metrics. Because sites with a larger variety of landforms provide more microclimate options, cells were scored by their landform number from 1 to 11 (Fig. 1). Our assumption was that most plant and vertebrate populations could access this relatively small neighborhood to locate suitable microclimates.

To assess the local elevation range, we used a focal range analysis on the DEM to tabulate the range in elevation within a 40-ha circular search area around each 30 m cell. Cells were scored by their elevation range (1–795 m) and log transformed to approximate a normal distribution.

We combined the results into a single metric and weighted landform variety twice as much as elevation range because the landform model delineates contrasting micro-climates more precisely than elevation. Before

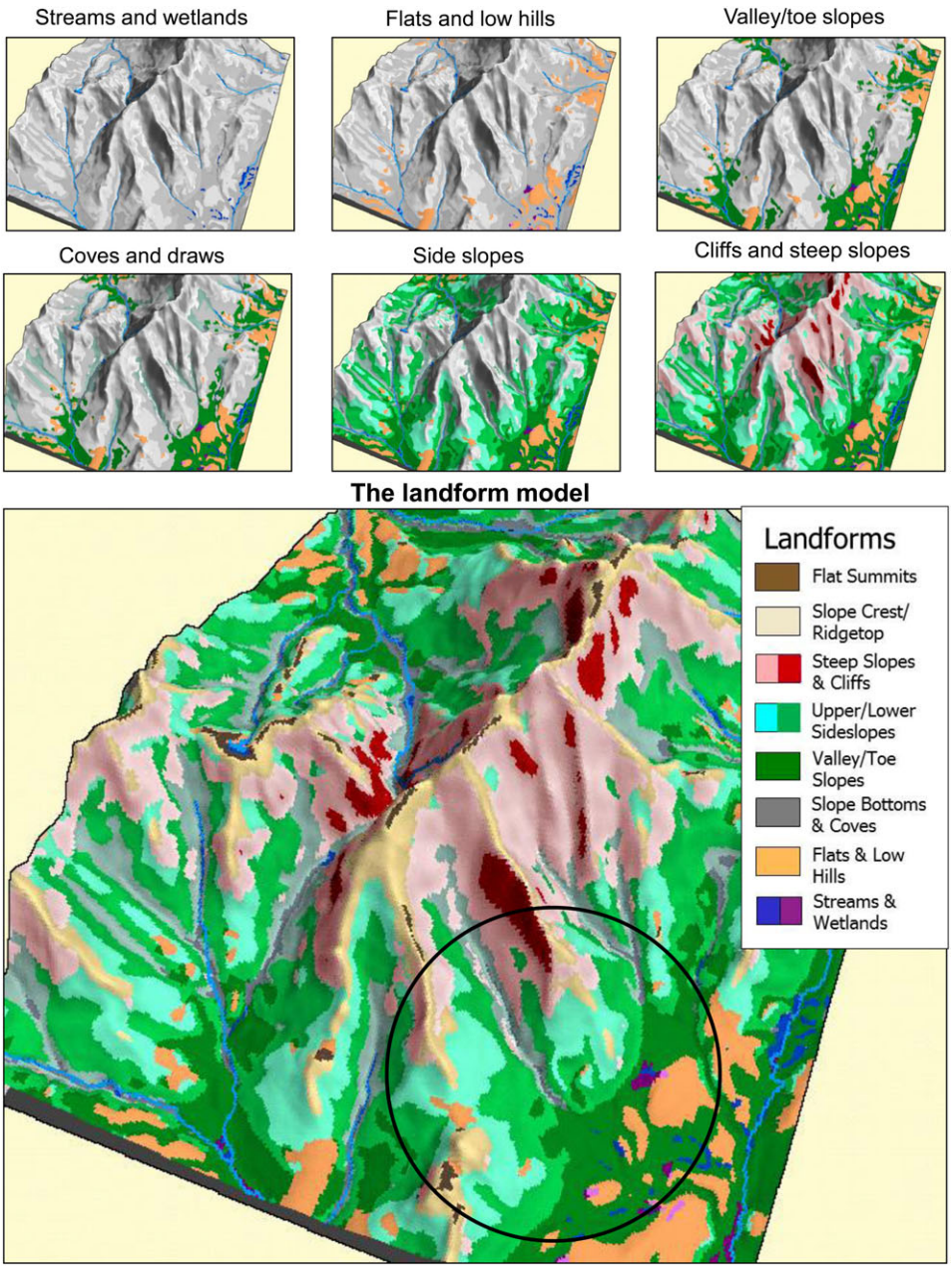


Figure 1. The full landform model mapped for Mount Mansfield, Vermont (U.S.A.), showing the estimated number of microclimates (8 within the black circle); the progression from flats to slopes (small maps); and how the full landform model lies across the landscape (large map). The relative size of the 40-ha focal area is shown in the black circle (adapted from Anderson et al. 2012).

combining, we transformed both metrics to standardized normal distributions. The final index was landscape diversity = (2*landform variety + 1*elevation range)/3.

In extremely flat areas, the landscape diversity index could not provide useful discrimination between many equivalent cells. For these areas (<0.5% slope), we added wetland density as a finer-scale indicator of subtle microtopographic features not captured by the wet flat element in the landform model. We combined the National Wetland Inventory (USFW 2012), National Land Cover Database wetlands (NLCD 2001), and the Northern Appalachian/Acadian wetlands (TNC 2012) into a single data set and used a focal function to calculate the density of surrounding wetlands for every 30-m cell in the region. To account for the flat topography, we used two circular search areas (a 40-ha area and a 400-ha area) and combined the results into a weighted index that gave twice the weight to the 40-ha search area. Wetland density was defined as total area of wetlands divided by the size of the search area, and the index was wetland density = (2*density of 40 ha + 1*density of 400 ha)/2.

We converted the scores to a standard normal distribution. In cells with <5% slope, we added the wetland density scores to the two other landscape diversity metrics as follows: landscape diversity in flats = (2*landform variety +1*elevation range + 1*wetland density)/4.

Local connectedness was designed to estimate the degree of permeability, or conversely the degree of resistance, surrounding each cell in the region. We used a resistant kernel analysis and software created by the

UMASS CAPs program to measure connectedness (Compton et al. 2007). The algorithm measures the connectivity of a focal cell to its ecological neighborhood when the cell is viewed as a source of movement radiating out in all directions.

The metric is built on the assumption that the permeability of two adjacent cells increases as their ecological similarity increases and decreases as their similarity decreases. Contrasting elements are scored with resistance weights to reflect differences in structure, composition, degree of development, or use. The theoretical spread of a species or process outward from a focal cell is a function of the resistance values of the neighboring cells and their distance from the focal cell out to a maximum distance of 3 km. The local connectedness score for a cell was equal to the area of spread accounting for resistance divided by the theoretical area of spread if there were no resistance.

Our resistance surface was based on a classified land use map with roads and railroads embedded in the grid (NLCD 2001; Tele Atlas North America, ESRI 2012). We simplified the land cover into six basic elements and assigned resistance weights to each category based on a simplified version of Compton's similarity index, where natural land was given the lowest resistance weight (10) and high intensity developed land was given the highest weight (100). Minor roads were overlaid on the grid and added 10 points of resistance to the cell containing them. We tested the sensitivity of the outcomes to the resistance weights by running the analysis for three test areas and systematically changing the weights. We finalized the weights by reviewing the test results with a team of state-based conservation scientists until we reached agreement. The final weights were as follows (NLCD classes in parenthesis): 10, natural lands and water (evergreen, deciduous, and mixed forest, shrub or scrub, grassland, woody and herbaceous wetland, water); 50, unnatural barrens (barren); 80, agricultural or modified lands (pasture, cultivated); 90, low intensity development (developed open space, low intensity developed); 100, high intensity development (medium intensity developed, high intensity developed, major roads). We aggregated the 30 m resistance surface to a grid of 90-m cells to reduce the considerable processing time before running the resistant kernel algorithm and computing the score for each cell. Cell scores ranged from 0 to 1 and were converted to a standard normal distribution for the region.

We estimated a site resilience score by summing the landscape diversity and local connectedness grids into a single metric. We used standard normalized values and gave equal weight to each factor: estimate of resilience score = (landscape diversity + local connectedness)/2. Our assumption was that the two factors are complementary and mutually reinforcing (e.g., micro-climatic diversity has more value if the area is connected and visa versa). The final output was a 30-m grid of estimated site resilience.

For each hexagon, we calculated the mean and standard deviation of landscape diversity, local connectedness, and site resilience based on the 30-m grid cells contained within the hexagon. We transformed the hexagon scores to standard normal distributions, normalizing the values to three extents: region, through the mean and standard deviation of all hexagons in the region; geophysical settings through the mean and standard deviation of all hexagons of each geophysical setting type; and setting within ecoregions the mean and standard deviation of all geophysical setting types within each ecoregion. For analysis purposes, we considered the mean the range of values from SD –0.5 to 0.5 and high-scoring hexagons those hexagons with mean resilience scores >SD 0.5.

Biodiversity and Secured Lands

Sites with high-quality biodiversity features were compiled from nine ecoregional assessments completed by TNC (2012). For each hexagon, we summarized the type and amount of high-quality biodiversity features (species and communities) within it and the amount of land permanently secured for conservation. We converted biodiversity data sets (points and polygons) to points based on the polygon's centroid and used only occurrences with precise locations. The TNC portfolio of sites contains a selective subset of all features in the region including the locations of 4592 viable populations of rare species and 2170 high-quality examples of representative natural communities. The data have a high degree of consistency because they were reviewed by experts within each ecoregion and assessed with a standard set of criteria. Viability criteria were based on the size, condition, and landscape context of the occurrence. The assessments were performed by teams of scientists, including experts on various taxa, and the final selection of sites was based solely on the quality of the biodiversity feature and a set of distribution and numeric goals. No optimization software was used to select sites. The portfolios represent a set of sites that, if conserved, would collectively protect the full biological diversity of an ecoregion.

To compare the portfolio sites with the resilience scores, we categorized the hexagons into standard deviation groups (SD +2.5, +1.5, +0.5, –0.5, –1.5, and –2.5) based on the mean resilience score of the hexagon. For this step, hexagons were scored with respect to their setting and ecoregion and with respect to all sites in the region and were assigned whichever score was higher. This adjustment, affecting 9% of hexagons, corrected for the fact that some of the highest scoring places in the region were only average for their setting because some settings had such inherently high resilience scores.

Information on land securement was compiled from state, federal, local, and private sources and was standardized across states (details in Anderson and Olivero Sheldon 2011). The data set included only land permanently secured against conversion to development and contained over 9.8 million ha of public and private lands permanently protected by fee or easement. Only land intended for nature conservation (GAP status 1 or 2) or multiple uses (GAP status 3) was included. Data for the TNC portfolio and secured lands were for the U.S. portion of the study only.

Results

Geophysical Settings

The cluster analysis of hexagons by their geophysical attributes resulted in the identification of 30 distinct settings. Of these, 20 were dominated by a single geology-elevation combination. Ten settings were less homogenous; they had two geology types but similar landforms (Table 1). Elevation, followed by geology, had a dominant influence on the results. Only one cluster was defined by landforms (extreme slopes). Of the rest, 15 were low-elevation, 8 were mid-elevation, and 6 were high-elevation sites. We noted data problems in the narrow coastal zone (1–6 m elevation) due to inconsistent shoreline and ocean mapping; thus, our confidence in the results for the coastal zone is low.

Estimated Resilience Scores

Estimates of site resilience scores (hereafter resilience scores) for each geophysical setting revealed large differences among the settings when normalized to the mean of the region. Acidic and resistant bedrock settings (granite, mafic, acidic sedimentary) had the highest estimated resilience, averaging >SD 0.18 above the mean. In contrast, alkaline and more erodible settings (calcareous, coarse sand, fine silt) had the lowest estimated resilience, averaging <SD –0.23 below the mean (Fig. 2a). These patterns were reflected in the separate landscape diversity and local connectedness scores and in the combined index, indicating that landscapes in the latter geologies were both flatter and more fragmented.

Estimated resilience scores decreased consistently as elevation decreased. Alpine areas averaged SD 0.54 above the mean, but coastal areas averaged SD –0.52 below the mean (Fig. 2a). The lowest scoring settings were all low elevation settings coarse sand, fine silt, and calcareous bedrock; all scored <SD –0.20 below the mean.

Patterns of Land Securement

Conservation status differed markedly by geophysical setting, and the differences paralleled the patterns seen for

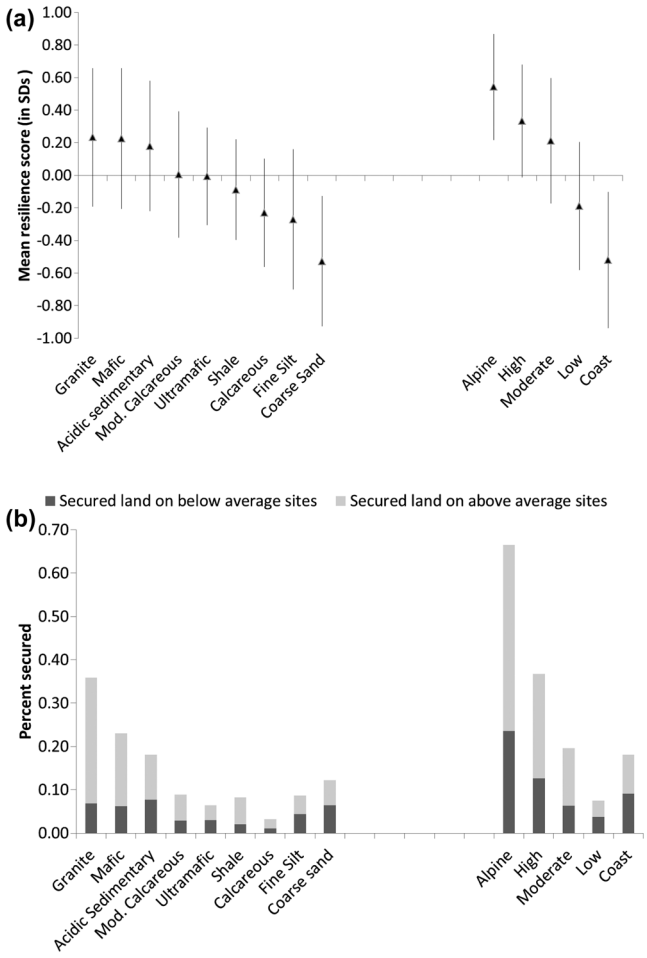


Figure 2. (a) Mean climate-change resilience scores (SD 1) and (b) degree of securement (land permanently protected from conversion) on sites with above-average and below-average mean resilience scores by geology class (left) and elevation zone (right). The units are standardized to the average score for the region.

the resilience scores. High-elevation areas and resistant acidic substrates had the highest level of securement, and low-elevation calcareous or surficial substrates had the lowest (Fig. 2b). When examined across all elevations, the estimated resilience score was positively correlated with the percent securement ($r = 0.66$). However, when the low elevation zone was examined alone, the reverse was true ($r = -0.27$), suggesting that land securement was not driving the resilience score.

Comparison with Places Selected for Their Current Biodiversity

TNC's biodiversity sites were contained in 3271 hexagons of which 78% (species) and 81% (communities) had average or better resilience scores (Tables 2 & 3). Chi-square

Table 2. Distribution of The Nature Conservancy sites with viable species populations and high-quality communities relative to the sites' score for resilience to climate change.

		Resilience score (%)						
Group	*Total*	*>SD 2.5*	*>SD 1.5*	*>SD 0.5*	*SD -0.5 to 0.5*	*<SD -0.05*	*<-1.5 SD*	*<SD -2.5*
Species taxonomic group[a]								
Vertebrate total	41	0.20	0.56	0.93	1.00	1.00	1.00	1.00
Amphibian	5	0.00	0.40	0.80	1.00	1.00	1.00	1.00
Bird	12	0.25	0.67	1.00	1.00	1.00	1.00	1.00
Mammal	16	0.13	0.50	0.94	1.00	1.00	1.00	1.00
Reptile	8	0.38	0.63	0.88	1.00	1.00	1.00	1.00
Invertebrate total	166	0.08	0.33	0.69	0.91	0.96	0.99	1.00
Plant total	207	0.11	0.46	0.77	0.91	0.99	1.00	1.00
All taxa	414	0.11	0.42	0.75	0.92	0.98	1.00	1.00
Species occurrences[b]								
Vertebrate total	977	0.01	0.11	0.52	0.77	0.96	0.99	1.00
Amphibian	91	0.00	0.18	0.71	0.79	0.98	1.00	1.00
Bird	334	0.01	0.07	0.44	0.77	0.96	0.99	1.00
Mammal	362	0.01	0.08	0.52	0.75	0.96	1.00	1.00
Reptile	190	0.03	0.22	0.60	0.82	0.95	0.97	1.00
Invertebrate total	1359	0.03	0.11	0.44	0.79	0.94	0.99	1.00
Plant total	2256	0.02	0.13	0.50	0.78	0.96	0.99	1.00
All species	4592	0.02	0.12	0.49	0.78	0.95	0.99	1.00
Community occurrences[b]								
Barren	225	0.04	0.27	0.57	0.85	0.98	1.00	1.00
Woodland	169	0.08	0.22	0.60	0.82	0.99	1.00	1.00
Forest	482	0.04	0.21	0.66	0.87	0.99	1.00	1.00
Cliff and talus	167	0.04	0.18	0.63	0.84	0.96	0.99	1.00
Bog	298	0.02	0.19	0.61	0.82	0.98	1.00	1.00
Alpine	36	0.00	0.00	0.83	0.83	0.83	0.97	1.00
Floodplain	102	0.01	0.11	0.36	0.80	0.96	1.00	1.00
Dune	103	0.02	0.06	0.31	0.86	0.98	1.00	1.00
Swamp	461	0.02	0.10	0.39	0.75	0.96	0.99	1.00
Grassland	38	0.00	0.11	0.39	0.74	0.95	1.00	1.00
Marsh	89	0.02	0.07	0.34	0.64	0.99	0.99	1.00
All communities	2170	0.03	0.16	0.53	0.81	0.98	1.00	1.00
Actual versus expected number								
Species actual ($n = 4592$)		92	466	1681	1348	796	176	33
Species expected ($n = 4592$)		28	280	1111	1754	1111	280	28
Communities actual ($n = 2170$)		63	295	801	608	350	44	9
Communities expected ($n = 2170$)		13	132	525	829	525	132	13

[a]*Scores from left to right show the accumulating number of TNC-selected rare species.*
[b]*Scores from left to right show the accumulating number of TNC-selected species and community locations.*

tests confirmed that the distribution of these sites was skewed toward the high-scoring sites (SD > 0.5); 49% of the species occurrences (802 more than expected by chance, $p < 0.0001$) were in high-scoring sites. Similarly, 53% of the community occurrences (489 more than expected by chance, $p < 0.0001$) were in high-scoring sites.

Correspondence between the biodiversity portfolio sites and the high-scoring geophysical sites varied with taxa group. For example, the portfolio targeted 5 amphibian species in 91 locations; the high-scoring sites captured 4 of the 5 taxa and 71% of the locations (Table 2). The portfolio targeted 12 bird species in 334 locations; the high-scoring sites captured all 12 species and 44% of the locations. On average, the high-scoring sites captured 75% of the 414 target species and 49% of the 4592 portfolio locations. For communities, high-scoring sites captured 63–83% of alpine, cliff, and forest portfolio sites and 31–39% of the wetland and low elevation sites (i.e., floodplain, dune, swamp, marsh), suggesting that our addition of wetland density in flat areas did not overcorrect for the inherent lack of landform variety in those areas.

The influence of landscape diversity and local connectedness on the integrated resilience scores was close to equal for most taxa groups and community types (Table 3). By transforming the data to standard normal distributions before combining them, we ensured that the factors had equal mathematical weight, but in specific locations one factor could have more influence on the score. Across all species occurrences, landscape diversity scores had a slightly larger influence on the resilience score than connectedness (51%:49%), but the reverse was true for vertebrates alone (48%:52%, Table 3). In all, there

Table 3. Average scores for The Nature Conservancy's species and community sites with respect to landscape diversity, local connectedness, and site resilience.[a]

Group	*Number of occurrences*	*Resilience score*	*Landscape diversity*	*Local connectedness*	*Landscape diversity (avg.% contribution)*	*Local connectedness (avg.% contribution)*
Species						
Vertebrate total	977	0.35	0.03	0.21	48	52
Amphibian	91	0.52	0.03	0.38	46	54
Bird	334	0.23	−0.10	0.15	47	53
Mammal	362	0.28	0.03	0.15	49	51
Reptile	190	0.60	0.28	0.32	51	49
Invertebrate total	1359	0.29	0.23	0.05	53	47
Plant total	2256	0.39	0.20	0.15	51	49
All species	4592	0.35	0.17	0.13	51	49
Community						
Barren	225	0.73	0.41	0.33	51	49
Woodland	169	0.73	0.31	0.38	49	51
Forest	482	0.60	0.27	0.36	49	51
Cliff and talus	167	0.59	0.26	0.23	50	50
Bog	298	0.54	0.18	0.30	49	51
Alpine	36	0.45	−0.58	0.42	39	61
Floodplain	102	0.27	0.31	−0.02	55	45
Dune	103	0.25	0.16	0.15	51	50
Swamp	461	0.18	0.13	0.04	52	48
Grassland	38	0.18	0.14	0.04	51	49
Marsh	89	0.07	0.05	0.02	50	50
All communities	2170	0.46	0.22	0.23	50	50

[a]*Scores for site resilience, landscape diversity, and local connectedness are the mean of the z scores in units of SD.*

was a robust correspondence between areas that scored high for their geophysical setting based on their physical properties and those that were identified based on their biodiversity values.

Resilience Scores within Ecoregion and Settings

The map and data set we created identified high-scoring areas for estimated site resilience with respect to their ecoregion and geophysical setting (Fig. 3). This map of high-scoring areas included underprotected settings with unique diversity but little land securement. Additionally, the map identified sites that scored high for both estimated resilience and for high-quality current biodiversity.

Discussion

We found strong correspondence between sites identified for climate resilience based on their geophysical characteristics and those selected for the high quality of their biodiversity features; the latter set had 78% (species) and 81% (communities) of their locations in sites that scored average or better for site resilience (Tables 2 & 3). Settings composed of calcareous bedrock or surficial substrates scored markedly lower for estimated resilience and had much lower levels of securement (Fig. 2), despite harboring high levels of diversity (Anderson & Olivero Sheldon 2011). Because our method identified sites for every geophysical setting that are likely to retain species and functions longer under a changing climate, it reveals places for future conservation that could correct the bias in current secured lands.

Our analysis was based on those attributes that appear to be predictive of site resilience and that could be mapped at a regional scale. Although our analysis was as transparent, comparable, and consistent as possible, we approached resilience to climate change as a relative concept because there are no clear absolute thresholds. Scientists have limited understanding of how climate-induced changes will interact with each other, how those interactions will play out on the landscape, and how systems will transform. By conserving all types of geophysical settings and using site resilience criteria to select places for conservation action, one could expand the variety of diversity conserved and increase the probability of its persistence over time. An advantage of this approach is that it is robust to uncertainty in predictions of climate change impacts. This approach, however, is not intended to replace basic conservation principles such as the importance of reserve size, threat reduction, and appropriate land management; rather, it is a coarse-filter strategy (sensu Hunter et al. 1988) for making informed decisions when facing large uncertainties.

We found inherent differences in site resilience among the geophysical settings, and those differences were paralleled by a lack of securement. The underprotected and low-scoring geophysical settings corresponded to

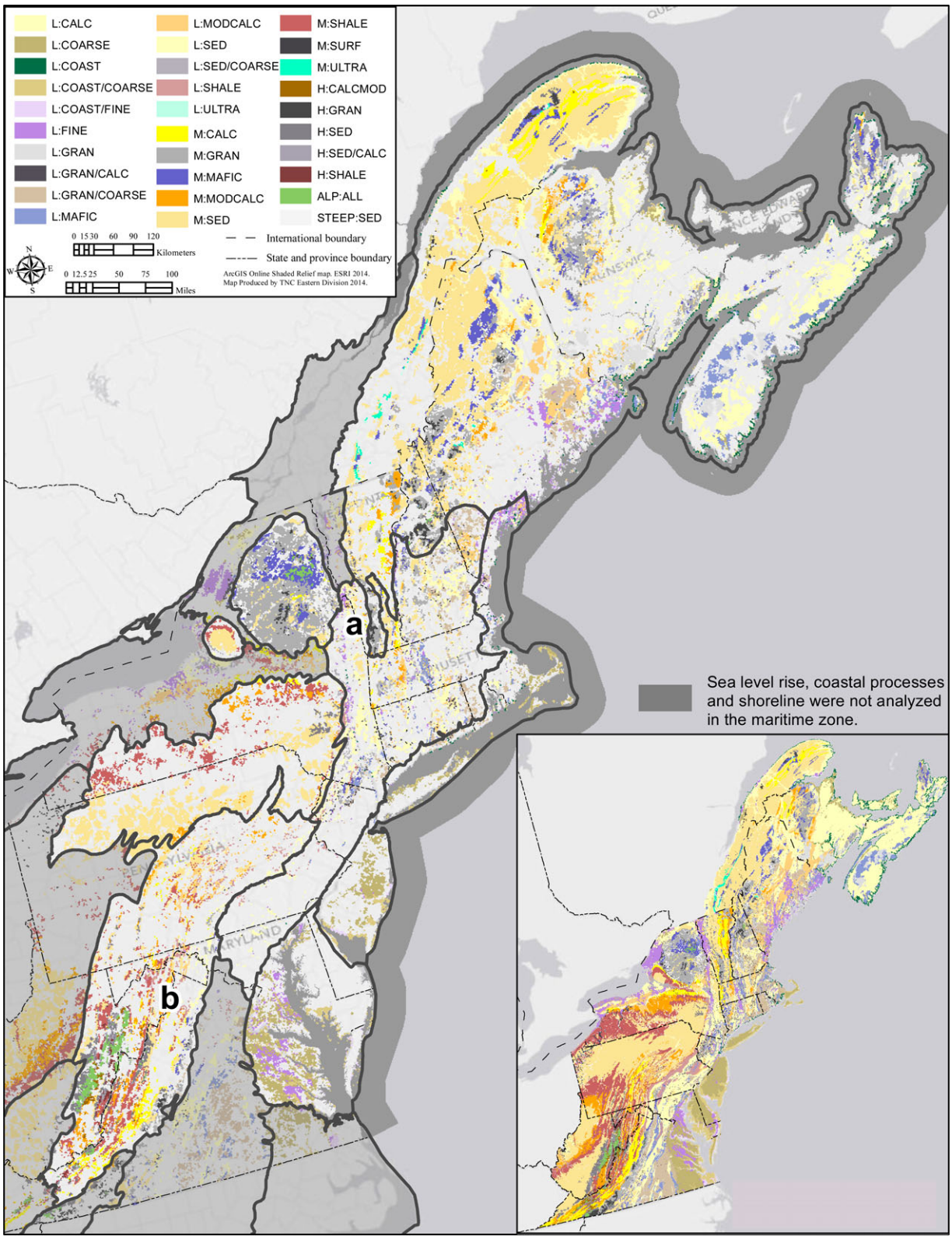


Figure 3. Examples of each geophysical setting with the highest estimated score for relative resilience to climate change. This map shows the hexagons that scored >0.5 SD above the mean with respect to setting and ecoregion and hexagons (405 ha) that scored >0.5 SD above the mean for the entire region. Each hexagon is colored based on its corresponding geophysical setting, and the inset map shows the full distribution of each setting. Abbreviations in the figure legend are defined in Table 1. Ecoregions that were only partially assessed are gray. Site (a) is Blueberry Hill, Vermont, and site (b) is Smoke Hole, West Virginia (adapted from Anderson et al 2012).

the places most valued and used by people; a pattern that may be universal (Pressey et al. 2002). Settlement in northeastern North America has occurred in landscapes with moderate topography and productive soils suitable for farming and development. As a result, low elevation floodplains and limestone valleys are more fragmented by human use and naturally less complex topographically. The high-scoring sites we identified for these geophysical settings have rougher topography and less direct human use than most sites in these settings. To sustain the diversity of these lands, conservation will likely need to focus more on land management than procurement of land for conservation. Certainly, establishing large reserves has been a successful strategy on poor soils, steep slopes, or at high elevations, but networks of small connected reserves seem more practical in the productive, underprotected settings.

Our method also identified low-scoring vulnerable sites, places where natural processes have become disrupted and fragmented and diversity may be depleted. We expect that these sites will increasingly favor opportunistic weedy species adapted to high levels of disturbance and anthropogenic degradation. Although, climate change is expected to exacerbate the degradation of vulnerable sites, these sites may still perform many important natural services, such as buffering storm effects or filtering water.

The correspondence of important biodiversity sites with sites of high estimated site resilience was reassuring. TNC's set of high-quality biodiversity sites was developed independently, but landscape context (similar to local connectedness) was used as one of three selection criteria, and this could explain some correspondence. Alternatively, it may be that topographically diverse and connected areas within each geophysical setting simply contain most of the remaining biodiversity. This is an important area for further research, but in either case, sites that have both significant current biodiversity and high site resilience are worthy places for conservation action, with the understanding that their specific biota may change with the climate.

This analysis identifies real places for conservation action. An example of a site identified both as a resilient example of a geophysical setting and as an important biodiversity site is the large Blueberry Hill—Bald Mountain area in Vermont (Fig. 3a). This site had a mean resilience score of SD 1.6 above the mean, the fifth highest scoring in the region, and 78% of its component hexagons were confirmed by current biodiversity features. In total, the site currently supports 32 natural community types and 147 different rare species. A second, smaller example from the Central Appalachians is the Smoke Hole area of West Virginia, a site that scored above the mean for both diversity and connectedness (average = 0.97, Fig. 3b); it is a hilly complex of calcareous and shale settings. The site currently contains 57 types of rare species and communities. Both of these sites were identified and mapped using the geophysical approach but corresponded to places previously identified for their extant biological features.

It is difficult or impossible to test our hypothesis outright. However, experiments to quantify the temperature difference between micro-climates and study how they are used by species (such as Weiss et al. 1988) could be extended to a wide range of species and habitats and would greatly improve our ability to predict site resilience. Many other questions could be addressed by researchers. Are species near the edge of their climate ranges more restricted to specific microclimates? In areas experiencing large temperature changes, are species persisting longer in microclimatic settings? Was there a geophysical basis for why certain sites acted as refuges during previous periods of rapid climate change? What modification to these methods would be needed for regions with a greater range of aridity and elevation? Due to data limitations, we did not address sea level rise or past land uses that might have altered geophysical structure, but how do these factors affect future resilience? The answer to these questions could improve and refine understanding of how site characteristics buffer the effects of climate change. Given the immediacy of climate change, we hope our approach provides new and useful guidance for conservation planning.

Acknowledgments

We thank J. Dunscomb, J. Fargione, C. Ferree, L. Hanners, M. Hunter, P. Kareiva, B. McRae, M. Miller, D. Ray, B. Vickery, A. Weinberg, and 3 anonymous reviewers for helpful comments on this paper. We thank the Doris Duke Charitable Foundation for support of this research.

Literature Cited

Ackerly, D. D., S. R. Loarie, W. K. Cornwall, S. B. Weiss, H. Hamilton, R. Branciforte, and N. J. B. Kraft. 2010. The geography of climate change: implications for conservation biogeography. Diversity and Distributions **16:**476–487.

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, Boston, Massachusetts.

Anderson, M. G., and C. Ferree. 2010. Conserving the stage: climate change and the geophysical underpinnings of species diversity. PLoS ONE **5**(7)**:**E11554. DOI:10.1371/journal.pone.0011554

Anderson, M. G., and A. Olivero Sheldon. 2011. Conservation status of fish, wildlife and natural habitats in the northeast landscape: implementation of the northeast monitoring framework. The Nature Conservancy, Boston. Available from https://www.conservationgateway.org/ConservationByGeography/NorthAmerica/UnitedStates/edc/reportsdata/stateofnature/Pages/default.aspx.

Beier, P., and B. Brost. 2010. Use of land facets to plan for climate change: conserving the arenas, not the actors. Conservation Biology **24:**701–710.

Compton, B. W., K. McGarigal, S. A. Cushman, and L. G. Gamble. 2007. A resistant-kernel model of connectivity for amphibians that breed in vernal pools. Conservation Biology **21:**788–799.

Conacher, A. J., and J. B. Darymple. 1977. The nine unit land-surface model: an approach to geomorphic research. Geoderma **18:** 1–154.

Dobrowski, S. Z. 2010. A climatic basis for microrefugia: the influence of terrain on climate. Global Change Biology DOI:10.1111/j.1365-2486.2010.02263x

Faith, D. P., and P. A. Walker. 1996. Environmental diversity: on the best-possible use of surrogate data for assessing the relative biodiversity of sets of areas. Biodiversity and Conservation **5:**399–415.

Fels, J. E., and K. C. Matson. 1996. A cognitively based approach for hydro-geomorphic land classification using digital terrain models. In 3rd International Conference on Integrating GIS and Environmental Modeling. National Centre for Geographic Information and Analysis, Santa Barbara, California. CD-ROM.

Gesch, D. B. 2007. The national elevation dataset. Pages 99–118 in D. Maune, editor. Digital elevation model technologies and applications: the DEM users manual. 2nd edition. American Society for Photogrammetry and Remote Sensing, Bethesda, Maryland.

Groves, C. 2003. Drafting a conservation blueprint: a practitioners guide to planning for biodiversity. Island Press, Washington, D.C.

Gunderson, L. H. 2000. Ecological resilience–in theory and application. Annual Review of Ecology and Systematics **31:**425–439.

Heller, N. E., and E. S. Zavaleta. 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. Biological Conservation **142:**14–32.

Hunter, M. L., G. L. Jacobson, and T. Webb. 1988. Paleoecology and the coarse-filter approach to maintaining biological diversity. Conservation Biology **2:**375–385.

Keys, J., Jr., C. Carpenter, S. Hooks, F. Koenig, W. H. McNab, W. Russell, and M. L. Smith. 1995. Ecological units of the eastern United States – first approximation (CD-Rom). U.S. Department of Agriculture, Forest Service, Atlanta, Georgia.

Krosby, M., J. Tewksbury, N. M. Haddad, and J. Hoekstra. 2010. Ecological connectivity for a changing climate. Conservation Biology **24**(6)**:**1686–1689.

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:**1052–1055.

Luoto, M., and R. K. Heikkinen. 2008. Disregarding topographical heterogeneity biases species turnover assessments based on bioclimatic models. Global Change Biology **14**(3)**:**483–494.

McCune, B., and M. J. Mefford. 1999. PC-ORD. Multivariate analysis of ecological data, Version 5.0, MjM Software, Gleneden Beach, Oregon.

Meiklejohn, K., R. Ament, and G. Tabor. 2010. Habitat corridors & landscape connectivity: clarifying the terminology. Center for Large Landscape Conservation, New York.

NLCD (National Landcover Database). 2001. U.S. Department of the Interior, U.S. Geological Survey.

Pachauri, R. K., and A. Reisinger. 2007. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Core Writing Team, R. K. Pachauri, and A. Reisinger, editors. IPCC, Geneva, Switzerland.

Pressey, R. L., M. Cabeza, M. E. Watts, R. M. Cowling, and K. A. Wilson. 2007. Conservation planning in a changing world. TRENDS in Ecology and Evolution **22**(11)**:**583–592.

Pressey, R. L., G. L. Whish, T. W. Barrett, and M. E. Watts. 2002. Effectiveness of protected areas in north-eastern New South Wales: recent trends in six measures. Biological Conservation **106:**57–69.

Randin, C. F., R. Engler, S. Normand, M. Zappa, N. Zimmermann, P. B. Pearman, P. Vittoz, W. Thuiller, and A. Guisani. 2008. Climate change and plant distribution: local models predict high-elevation persistence. Global Change Biology **15**(6)**:**1557–1569.

Rodrigues, A. S. L., and T. M. Brooks. 2007. Shortcuts for biodiversity conservation planning: the effectiveness of surrogates. Annual Review of Ecology, Evolution, and Systematics **38:**713–737.

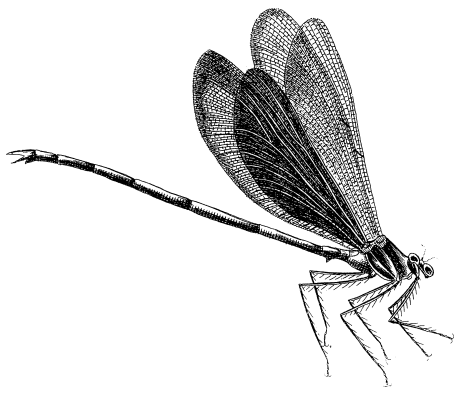
Schloss, C. A., J. J. Lawler, E. R. Larsron, H. L. Paperndick, M. J. Case, D. M. Evanse, J. H. DeLap, J. G. R. Landgon, S. A. Hall, and B. H. McRae. 2011. Systematic conservation planning in the face of climate change: bet-hedging on the Columbia Plateau. PLoS One **6** DOI: 10.1371/journal.pone.0028788.

Tele Atlas North America, ESRI. 2012. U.S. and Canada streets cartographic. Redlands, California.

TNC (The Nature Conservancy). 2012. Eastern U.S. Ecoregional Assessments: Central Appalachian Ecoregion (2003), Chesapeake Bay Lowlands Ecoregion (2003), High Allegheny Ecoregion (2003), St. Lawrence Ecoregion (2003), Lower New England Ecoregion (2003), Northern Appalachian/Acadian Ecoregion (2006), North Atlantic Coast Ecoregion (2006). The Nature Conservancy, Eastern Conservation Science, Boston, Massachusetts. Available from https://www.conservationgateway.org/ConservationByGeography/NorthAmerica/UnitedStates/edc/reportsdata/terrestrial/ecoregional/Pages/default.aspx (accessed January 2012).

USFW (U.S. Fish and Wildlife Service). 2012. National Wetlands Inventory website. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C. Available from http://www.fws.gov/wetlands.

Wiens, J. A., and D. Bachelet. 2010. Matching the multiple scales of conservation with the multiple scales of climate change. Conservation Biology **24**(1)**:**51–62.

Weiss, S. B., D. D. Murphy, and R. R. White. 1988. Sun, slope, and butterflies: topographic determinants of habitat quality for *Euphydryas editha bayensis*. Ecology **69:**1486–1496.

Willis, K. J., and S. A. Bhagwat. 2009. Biodiversity and climate change. Science **326:**806–807.