

How global biodiversity hotspots may go unrecognized: lessons from the North American Coastal Plain

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ABSTRACT

Biodiversity hotspots are conservation priorities. We identify the North American Coastal Plain (NACP) as a global hotspot based on the classic definition, a region with > 1500 endemic plant species and > 70% habitat loss. This region has been bypassed in prior designations due to misconceptions and myths about its ecology and history. These fallacies include: (1) young age of the NACP, climatic instability over time and submergence during high sea-level stands; (2) climatic and environmental homogeneity; (3) closed forest as the climax vegetation; and (4) fire regimes that are mostly anthropogenic. We show that the NACP is older and more climatically stable than usually assumed, spatially heterogeneous and extremely rich in species and endemics for its range of latitude, especially within pine savannas and other mostly herbaceous and fire-dependent communities. We suspect systematic biases and misconceptions, in addition to missing information, obscure the existence of similarly biologically significant regions world-wide. Potential solutions to this problem include (1) increased field biological surveys and taxonomic determinations, especially within grassy biomes and regions with low soil fertility, which tend to have much overlooked biodiversity; (2) more research on the climatic refugium role of hotspots, given that regions of high endemism often coincide with regions with low velocity of climate change; (3) in low-lying coastal regions, consideration of the heterogeneity in land area generated by historically fluctuating sea levels, which likely enhanced opportunities for evolution of endemic species; and (4) immediate actions to establish new protected areas and implement science-based management to restore evolutionary environmental conditions in newly recognized hotspots.

Keywords

Biodiversity, conservation planning, endemism, hotspot, prioritization.

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INTRODUCTION

Biodiversity is not distributed randomly or uniformly on Earth. Regions richer in biodiversity (hotspots) often are considered conservation priorities, especially when they are centres of endemism and thus irreplaceable. High endemism is often combined with a measure of vulnerability, such as habitat loss, to identify hotspots (Mittermeier *et al.*, 2011). As defined by Myers *et al.* (2000), a hotspot has at least 1500 endemic vascular plants and has lost 70% or more of its historic vegetation cover. The 25 global hotspots recognized by Myers *et al.* (2000) have been expanded to 35 hotspots, which collectively contain > 50% of the earth's vascular plants as single-hotspot endemics within 23.7 million km²,

16% of Earth's land surface (Mittermeier *et al.*, 2011). Interestingly, protecting centres of endemism captures more species than protecting centres of overall species richness, apparently because centres of endemism sample a broader range of biogeographic diversity (Orme *et al.*, 2005; Jenkins *et al.*, 2013).

True hotspots may go unrecognized. First, no one may have organized data that identify them as hotspots. Second, systematic biases may exist regarding historical or modern biogeography. For example, the latitudinal gradient of species richness and endemism is well established, with tropical regions generally being richer for most taxa than higher-latitude regions (Rosenzweig, 1995). Thus, conservationists look to the tropics for hotspots; indeed, most identified hotspots

are in the tropics and secondarily in Mediterranean regions (Mittermeier *et al.*, 2011). Third, misconceptions may exist about some regions. Regions with exceptional biodiversity may be missed because they are not expected to be rich or because much of their richness has been lost. Even within the tropics, 'grassy biomes' have garnered much less conservation attention than forests due to misconceptions about the ecology of these ecosystems (Parr *et al.*, 2014).

In this paper, we explore how biases and misconceptions can preclude scientific recognition of biodiversity hotspots. We focus on the North American Coastal Plain (NACP), a region that meets the Myers *et al.* (2000) criteria. We include as Supporting Information the primary data (on endemic taxa and habitat loss) that establish the NACP as a global hotspot (B. Sorrie *et al.*, unpublished data). We use our study of the NACP to illustrate criteria potentially useful for recognizing other overlooked hotspots world-wide.

STUDY REGION

The NACP is a long, often narrow and geologically unified region (Fenneman, 1938; Thorne, 1993). Late Cretaceous to Holocene coastal marine and fluvial sediments form a plain located ca. 24° to 42° N latitude and -70° to -99° W longitude along the Atlantic Ocean coast from Massachusetts to Florida, westward along the Gulf of Mexico to northeastern Mexico, and inland along the Mississippi embayment to Missouri and Illinois (Fig. 1). The NACP can be defined using the Geological Coastal Plain (GCP, 1.13 million km²) or the Coastal Plain Floristic Province (CPFP, 1.06 million km²). Takhtajan (1986) considers the CPFP the most sharply

defined of any floristic province in North America. The CPFP excludes southern Florida, with a strong West Indian influence, as well as southern Texas and northeastern Mexico within the Sonoran Floristic Province (Sorrie & Weakley, 2001). Our accounting of NACP biodiversity encompasses both the GCP and the CPFP. The NACP is larger than many hotspots, but not as large as, for example, the Mediterranean Basin (2.09 million km²) or Horn of Africa (1.66 million km²) and is similar to Mesoamerica (1.13 million km²) (<http://www.cepf.net/resources/hotspots/Pages/default.aspx>).

The biological richness of the NACP has been suspected since explorations of 18th and 19th century naturalists. High endemism of plants in some subregions of the NACP is well documented (e.g. James, 1961; Estill & Cruzan, 2001), and tallies of endemic taxa for the entire NACP have proceeded since Sorrie & Weakley (2001). The number of recognized taxa grows continually with new discoveries, with more than 400 new endemic vascular plant species, about 6–7% of the total flora, named over the past half century in the southeastern United States (A. Weakley, unpublished data).

Considerable endemism characterizes the GCP and the CPFP. The GCP contains 6200 native taxa of vascular plants, of which 1816 (29.3%) are endemic. The CPFP contains 5470 native vascular plant taxa (1625 endemic; 29.7%) (Table 1). Although the California Floristic Province, a widely recognized hotspot, contains more endemic plants (1931 full species; Harrison, 2013; Table 5), the GCP contains 56 endemic of 1282 native genera (4.4%), close to the state of California's 59 endemic genera (B. Sorrie *et al.*, unpublished data; Harrison, 2013). Figures for other global hotspots can be found in Mittermeier *et al.* (2011). Amphibians,

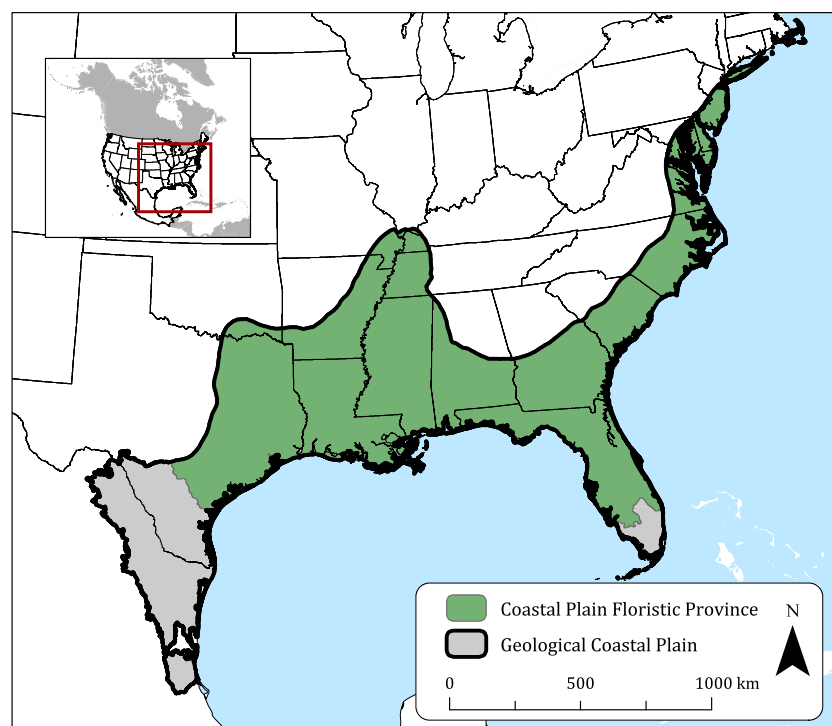


Figure 1 The Geological Coastal Plain (GCP) and the Coastal Plain Floristic Province (CPFP). The CPFP is contained within the GCP. Boundaries adapted from Fenneman (1938), Thorne (1993), and Sorrie & Weakley (2001).

reptiles and freshwater fish in the NACP show exceptional endemism (Table 1). NACP endemics include many ancient lineages and are characterized by strong ecological differentiation within groups and striking patterns of long-distance disjunction (Noss, 2013).

IGNORANCE, BIASES AND MISCONCEPTIONS

Despite appreciation of the biotic richness of the NACP by many regional naturalists for more than a century, recognition of its global hotspot status has been hindered by persistent misconceptions and myths about its ecology and history. We confront these fallacies to provide a more current characterization of this region.

Misconception: The geological youth, unstable climate and frequent inundation of the Coastal Plain precluded development of a rich biota

The NACP has been considered geologically young. According to Thorne (1993), '[B]ecause of repeated Pleistocene inundations, [the Coastal Plain] has a young flora recruited largely from the much more ancient Appalachian Province

Table 1 Richness and endemism of native vascular plants and vertebrates, including infraspecific taxa* and (*in italics*) just full species within the North American Coastal Plain.

GCP = Geological Coastal Plain. CPFP = Coastal Plain Floristic Province. The full lists of vascular plant and vertebrate taxa endemic to the GCP and CPFP are in the Supporting Information (Appendices S1 and S2). Endemic = 90% or more of distribution occurs within the GCP or CPFP.

	Species richness		Endemics (%)	
	GCP	CPFP	GCP	CPFP
Vascular plants	6200	5470	1816 (29.3)	1625 (29.7)
Freshwater fishes (full species only)	424	364	138 (32.5)	83 (22.8)
Amphibians	122	120	57 (46.7)	44 (36.7)
	105	105	45 (42.9)	37 (35.2)
Reptiles	291	230	113 (38.8)	80 (34.8)
	177	123	50 (28.2)	33 (26.8)
Breeding Birds	N/A	N/A	51	43
	274	233	6 (2.2)	5 (2.1)
Mammals	306	204	114 (37.3)	70 (34.3)
	148	85	9 (6.1)	5 (5.9)

*We include subspecies and varieties because we suspect that most are full species by modern taxonomic standards, but have not yet been so recognized due to few taxonomists slowly working through a large backlog. We share the opinion of Gill (2014) that 'Advances in our understanding of the nature of reproductive isolation, the genetics of speciation, the limited role of gene flow, the power of directional selection, and the dynamics of hybridization support a ... null hypothesis for taxonomic decisions ... that places the burden of proof on "lumping" rather than on "splitting" taxa at the species level.'

and to a lesser extent from the West Indian Province to the south and the North American Prairies province to the west'. This view echoes earlier hypotheses of Braun (1955) that vegetation endemic to the NACP originated on Appalachian fluvial peneplains. Nevertheless, Thorne (1993) noted 'several areas of extremely high endemism seem to indicate refugia that were not flooded during the Pleistocene'.

The NACP is not all that young. Terrestrial vegetation has occupied portions of the region continuously since the Late Cretaceous (80–85 Ma), with adjacent regions above the sea for much longer (DiPietro, 2013). Large portions of the NACP remained terrestrial throughout the Cenozoic. Much of the outer NACP was inundated during the last Pleistocene interglacial 120 ka, with sea level 6.6–8.3 m higher than today (Muhs *et al.*, 2011). Perhaps the highest Pleistocene inundation occurred 400 ka, 6–13 m above present (Raymo & Mitrovica, 2012). Still higher levels occurred during the middle Pliocene, when sea level is estimated, with considerable uncertainty, as 35 ± 18 m above present (Dowsett & Cronin, 1990). Fluctuating sea levels repeatedly isolated populations within higher-ground refugia, concurrently preserving relict taxa and fostering allopatric speciation, thereby contributing to high levels of endemism (James, 1961; Sorrie & Weakley, 2001).

Another misconception is that the NACP has been climatically unstable. This misconception is important because centres of endemism generally coincide with climatically stable regions (Sandel *et al.*, 2011). Although Sandel *et al.* (2011) suggest relatively high climate-change velocity for the NACP, their measure is biased against regions with little topographic relief because it is calculated as the ratio of climate change through time (since the Last Glacial Maximum) to the present change in climate over space at a given location. Because the spatial climatic gradient is a function of topographic complexity, relatively flat regions have elevated ratios and are expected to show low endemism, which is not the case for the NACP (Table 1).

Disparate views of climate stability are reflected in postulated Cenozoic vegetation. A long-held view is that boreal vegetation was displaced into the NACP during Pleistocene glaciations (Deevey, 1949; Schmidting & Hipkins, 1998). Recent data indicate primarily temperate vegetation in the region during glacial periods. Although spruce (*Picea*) pollen appears in Late Pleistocene sediments at sites in northern Florida and Louisiana, it is associated with temperate trees (e.g. Watts & Hansen, 1994). Pure boreal vegetation was considerably further north. Continuing palynological investigations in central Florida indicate a Pleistocene flora similar to today's, with no identified northern taxa (Grimm *et al.*, 2006). Moreover, vertebrates associated with savannas are continuously present (except for gaps in the fossil record) in deposits from the Oligocene to the Holocene in Florida (Webb, 1990). Together, these data suggest that the lower NACP, although dynamic with respect to amount and continuity of land area due to changing sea levels, has been climatically stable, serving as a long-term refugium for

temperate and subtropical taxa over tens of thousands to millions of years (Noss, 2013).

Several areas within the NACP are currently the richest in endemic plants in eastern North America. These include the east and west Gulf coastal plains (uplands and lowlands along the Apalachicola River westward to eastern Louisiana, extending into southern Georgia, Alabama, and Mississippi; and western Louisiana and adjacent eastern Texas); central Florida, especially the Lake Wales Ridge; coastal North and South Carolina in the Green Swamp area and inland; extreme southern Texas and adjacent Tamaulipas, Mexico; and extreme southern Florida (Estill & Cruzan, 2001; Sorrie & Weakley, 2001; B. Sorrie and A. Weakley, unpublished data). We infer that portions of these regions constituted climate refugia and were centres of speciation during past high sea-level stands.

Misconception: The modest topography and ostensibly homogeneous environment of the Coastal Plain do not promote high biodiversity

High endemism is often associated with high topographic complexity (Jetz & Rahbek, 2002; Mutke *et al.*, 2011), which is lacking in the NACP. The range of elevations in the NACP (0–250 m) is far less than in any recognized hotspot (Mittermeier *et al.*, 2011), with ca. 40% of the current land surface < 50 m in elevation (Fig. 2). Nevertheless, these low-elevation areas hold many concentrations of endemic taxa. We propose that modest topographic heterogeneity in conjunction with sea-level fluctuations has been a primary source of high endemism within the NACP.

The apparent environmental homogeneity of the NACP is deceptive. As in many hotspots, there is a pronounced range in mean annual precipitation (400 mm in northeastern Mexico/southern Texas to 1700 mm in eastern Louisiana).

Regional vegetation changes from deserts to subtropical and warm-temperate savannas and forests along longitudinal/latitudinal gradients rather than a substantial elevation gradient. Pronounced changes in plant species composition occur along very subtle topographic gradients in the NACP (Platt, 1999).

Frequent lightning-producing thunderstorms, especially during transitions between pronounced dry and wet seasons, historically ignited fires that, promoted by flammable fuels, burned through pine savannas and into surrounding vegetation across most of the lower NACP (Fig. 3). Frequent fires maintain open space in the ground layer by removing litter, cropping dominant grasses and top-killing trees and shrubs, and local variation in post-fire microenvironmental conditions facilitates high plant species richness and turnover along microtopographic gradients (Platt, 1999; Peet, 2006). Heterogeneity in fire effects along these gradients provides fire microrefugia, resulting in local co-occurrence of fire-dependent and fire-sensitive species (e.g. Crandall & Platt, 2012). Moreover, topographically protected or lowland areas (e.g. slope forests and swamps) burn less frequently or patchily, generating variation in fire regimes and producing landscapes with refugia for fire-sensitive species (Platt & Schwartz, 1990; Hctor *et al.*, 2006).

Despite limited elevation diversity, the NACP has high diversity of soils. Nine of twelve global soil orders, with soil pH ranging from 3 to 8.5, as well as a diversity of soil textures (e.g. loess, clays, coarse sands, calcareous and siliceous rocks, and peats) and moisture levels promote a broad variety of plant communities, both regionally (Peet, 2006) and along subtle elevation gradients (e.g. Drewa *et al.*, 2002). The most species-rich vegetation, especially in areas with high endemism, occurs on well-drained or wet silty soils low in organic and nutrient content (Peet, 2006). Thus, high plant

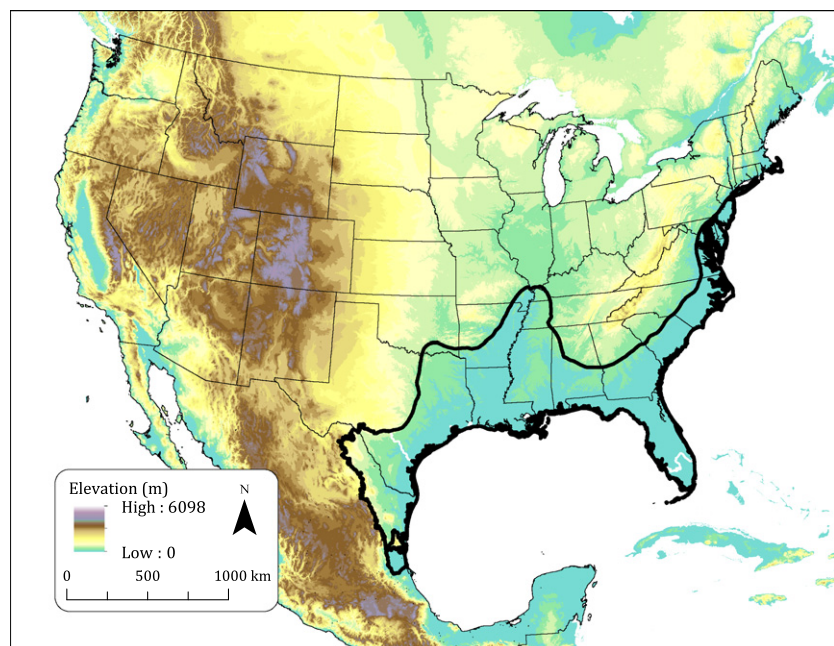


Figure 2 Elevation of the conterminous United States, with the boundary of the Geological Coastal Plain (GCP) indicated by the black line and the Coastal Plain Floristic Province (CPFP) by the white lines. Some 40% of the GCP is < 50 m elevation above mean sea level.

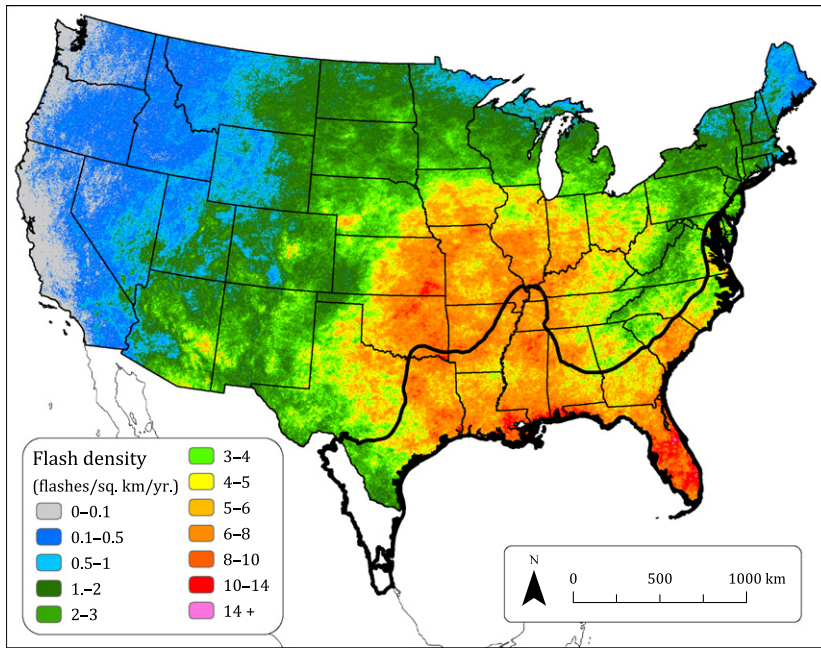


Figure 3 Cloud-to-ground lightning flash density in the 48 conterminous states, expressed as flashes per sq. km per year, 2005–2012. The Geological Coastal Plain boundaries are indicated by the black line. Data from the National Lightning Detection Network owned and operated by Vaisala Inc.

species richness in the NACP conforms to the general pattern of high richness on relatively low-nutrient soils (Pekin *et al.*, 2012; Laliberté *et al.*, 2013), but edaphic conditions across the region are far from homogeneous.

Myth: The Coastal Plain is naturally dominated by closed forest (the climax vegetation)

Estimates of habitat loss require knowledge of historic vegetation. Frequently burned communities occurred over more than half of the NACP prior to the arrival of Europeans (Table 2). Savannas with longleaf pine (*Pinus palustris*) and warm season (C₄) grasses (e.g. *Schizachyrium*, *Aristida*) were most widespread, especially on the most fire-exposed portions of the landscape (Platt, 1999; Frost, 2006). Until recently, however, the prevalent view was that closed hardwood forest constituted the climax vegetation and that pine savannas with low tree diversity were successional stages (e.g. Gano, 1917; Wells, 1928; Quarterman & Keever, 1962). Küchler (1964), in his influential classification of potential natural vegetation, followed Braun (1955) and mapped much of the NACP as ‘southern mixed forest (*Fagus-Liquidambar-Magnolia-Pinus-Quercus*)’. Küchler (1964) defined potential

natural vegetation as ‘the vegetation that would exist today if man were removed from the scene and if the plant succession after his removal were telescoped into a single moment’. Küchler assumed fire in the NACP was anthropogenic. Hence, if humans were removed, savannas and grasslands would transition to hardwood forests.

An important consequence of the emphasis on succession and the concept that hardwood forest is the climax in the NACP is that the true extent of habitat loss was masked. Hardwood forests that developed when fire was excluded from pine savannas, or when agricultural land was abandoned, were falsely considered natural communities. New analyses show that more than 85% of all historic vegetation and 96% of savannas and woodlands in the NACP have been converted to anthropogenic vegetation or are highly departed from natural condition (Table 2 and Supporting Information). Considering that ca. 57% of the endemic plant species in the region are associated with pine savannas, and an additional 28% with small-patch communities embedded in these savannas (A. Weakley and B. Sorrie, unpublished data), actual losses of biodiversity greatly exceed what would be expected on the basis of overall area conversion.

Table 2 Estimates of habitat alteration and conversion for the North American (Geologic) Coastal Plain and three major vegetation classes: Forests; Grasslands, Marshes, and Glades; and Savannas/Woodlands. See Supporting Information (Appendix S3 and Table S3.1) for methods and more information on results.

Habitat	Area (km ²)	Highly altered (%)	Converted (%)	Highly altered plus converted (%)
Forests	46494.25	29.04	43.47	72.50
Grasslands, Marshes, and Glades	11991.88	46.31	51.29	97.60
Savannas/Woodlands	43710.27	55.00	41.08	96.07
All Habitats (excluding water and sparsely vegetated areas)	102196.40	42.20	43.40	85.50

Myth: Fires in the Coastal Plain prior to European settlement were anthropogenic

Fire is a fundamental ecological driver in the NACP. A few astute field biologists [e.g. Harper (1911), Chapman (1932)] notwithstanding, most early authorities assumed fire in the NACP was anthropogenic and occurred mostly outside the growing season (Frost, 2006). More recent studies in the southeastern NACP indicate that pine savannas and associated ecosystems are maintained by frequent surface fires (typically every 1–3 years, based on fire scars in tree rings; Huffman, 2006; Stambaugh *et al.*, 2011). Such fires are ignited primarily by lightning strikes (Fig. 3) during the spring to summer transition season when fine fuels are dry and fuelled by fire-facilitating plants such as longleaf pine (Slocum *et al.*, 2010; Ellair & Platt, 2013). Evolutionary association of dominant pine savanna plants with such fires has been proposed based on demography and life cycles of pines (Platt *et al.*, 1988) and on flowering of herbs (Brewer & Platt, 1994) and grasses (Streng *et al.*, 1993; Fill *et al.*, 2012). Fire adaptations are also evident among species associated with communities that burn on longer intervals than pine savannas (Cavender-Bares *et al.*, 2004; Menges, 2007).

Lightning-ignited fires were likely an evolutionary force in the NACP for millions of years. The first fire-adapted trait (thick bark) in the genus *Pinus* arose during the early Cretaceous, 126 Ma, in association with low-intensity surface fires (He *et al.*, 2012). Fire-dependent ecosystems have analogues in the fossil record of the NACP as far back as the Eocene (Graham, 1999). Endemism in the NACP further supports antiquity of pyrogenic vegetation. High endemism, especially of palaeoendemics (relicts), and the association of most endemic taxa in the NACP with pine savannas and embedded communities suggest these ecosystems evolved with and were maintained by lightning fire rather than by fires set by humans, who have inhabited the region for less than 15,000 years (Noss, 2013).

Despite ample evidence that lightning fire was a primary ecological driver in the NACP, the myth persists that most fires before the arrival of Europeans were set by Native Americans. For example, Mann (2005; 361) provides a map that shows essentially the entire pre-Columbian NACP, including the lightning-riddled Gulf coast and Florida peninsula (Fig. 3), as 'dominated by anthropogenic fire' or with 'widespread forest clearing for agriculture'. No evidence is offered to support these claims. One problem that such representations pose to conservation is that the antiquity of fire and its key role in shaping biodiversity is obscured (Noss, 2013). Regions such as the NACP will not be recognized as hotspots when their natural vegetation is assumed to be an artefact of human actions.

CONCLUSION

Our case study of the NACP underscores the under-representation of certain regions as global conservation priorities. Between our efforts and those of Parr *et al.* (2014), ancient,

fire-dependent biomes with high endemism of herbaceous plants and associated animals are finally becoming recognized as biologically significant. Persistent misconceptions about their age and supposed lack of continuity over evolutionary time, their postulated origin as a result of human activity rather than through a long evolutionary association with lightning-ignited fires and their putative environmental homogeneity have previously imposed blinders.

We suspect systematic biases and misconceptions about biogeographic history and ecology, in addition to paltry information, obscure the existence of other conservation-significant regions world-wide. Particular biases will likely vary by region. We suggest that regions whose major vegetation types are dependent on frequent disturbance by fire, flood or other natural agents are especially likely to be overlooked. Human disruption of disturbance regimes obscures former disturbance-dependent ecosystems, resulting in underestimated habitat loss. We offer four recommendations for enhancing recognition of overlooked hotspots and for improved conservation, which may be especially relevant to regions similar in character to the NACP:

1. Increase field biological surveys and taxonomic determinations of species. New species are being discovered most rapidly within hotspots (Joppa *et al.*, 2011). The NACP conforms to this pattern; we suspect other neglected hotspots also will. Grassy biomes that burn frequently and regions with low soil fertility are excellent candidates for overlooked biodiversity and endemism, especially of poorly surveyed groups (e.g. fungi, invertebrates).
2. Explore the climate refugium role of hotspots. Centres of endemism generally coincide with mountainous regions with low velocity of late Quaternary climate change (Sandel *et al.*, 2011). The high endemism and refugium role of the NACP (and similarly relatively flat hotspots, like south-west Australia) have been unappreciated.
3. In low-lying coastal regions, consider heterogeneity generated by historically fluctuating sea levels, which separated and isolated populations. Such natural fragmentation would have facilitated speciation and promoted endemism, especially if the region (such as the lower NACP) concomitantly served as a long-term climatic refugium for relict taxa.
4. Restore evolutionary environmental conditions within hotspots via science-based management of disturbance-adapted vegetation. In the NACP, prescribed fire that mimics historical fire regimes in such systems as pine savannas and embedded communities is particularly needed. Models for maintaining ecological conditions involved in the evolution of fire-adapted traits need to be integrated with on-the-ground practical management.

In summary, we present two sets of reasons why the NACP is an overlooked hotspot: (1) misconceptions about its age, climate stability and regional/local habitat heterogeneity, and (2) myths related to its ecology, particularly the fire ecology of pine savannas and associated communities that are extraordinarily species-rich at small scales and packed with local and regional endemics. In reality, the

NACP and similar regions world-wide are much more closely aligned with tropical forests and coral reefs than with old-fields in terms of biodiversity, endemism and conservation significance. By exposing myths and misconceptions about the NACP, we not only attempt to improve understanding of this region and promote its recognition as a hotspot but also to promote appreciation and improved conservation of ecologically and evolutionarily similar regions globally.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Endemic vascular plant taxa of the Atlantic and Gulf Coastal Plains of North America.

Appendix S2 Endemic vertebrate taxa of the Atlantic and Gulf Coastal Plains of North America.

Appendix S3 Assessing vegetation modification in the Coastal Plain.

Table S3.1 Classification of ecosystems (biophysical settings) into general habitat types.

BIOSKETCHES

Reed F. Noss is an ecologist and conservation biologist with interests in natural history, biogeography, disturbance ecology and the reconciliation of species and ecosystem conservation.

William J. Platt, Bruce A. Sorrie, Alan S. Weakley and Robert K. Peet are botanists and plant ecologists with

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D. Bruce Means is a zoologist and ecologist with broad interests in the ecology and natural history of the Coastal Plain, with particular expertise in reptiles and amphibians.

Jennifer Costanza is a landscape ecologist interested in land-use change and vegetation dynamics.

Author contributions: R.F.N. took the lead in conceptualizing and writing this paper; W.J.P. gathered the current group of authors together and organized the symposium on the NACP hotspot at the Botany 2013 meeting, as well as being the main author, after R.F.N., of this paper; B.A.S. and A.S.W. initiated efforts to document the richness and endemism of plants in the NACP and contributed to the writing of this paper; D.B.M. compiled the lists of vertebrate taxa indigenous and endemic to the NACP and contributed to the writing of this paper; R.K.P. contributed to the writing of this paper; J.C. contributed to the writing of this paper, led the analysis of vegetation change, and produced the colour figures.

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