

Evidence of biogeomorphic patterning in a low-relief karst landscape

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ABSTRACT: Patterned landscapes are often evidence of biotic control on geomorphic processes, emerging in response to coupled ecosystem processes acting at different spatial scales. Self-reinforcing processes at local scales expand patches, while self-inhibiting processes, operating at a distance, impose limits to expansion. In Big Cypress National Preserve (BICY) in southwest Florida, isolated forested wetland depressions (cypress domes) appear to be evenly distributed within a mosaic of short-hydroperiod marshes and pine uplands. To test the hypothesis that the apparent patterning is regular, we characterized frequency distributions and spatial patterns of vegetation communities, surface and bedrock elevation, and soil properties (thickness and phosphorus content). Nearest neighbor distances indicate strongly significant wetland spatial overdispersion, and bedrock elevations exhibited periodic spatial autocorrelation; both observations are consistent with regular patterning. Bedrock elevations and soil P were clearly bimodal, suggesting strong positive feedbacks on wetland patch development. Soil-surface elevations exhibited weaker bimodality, indicating smoothing of surface morphology by some combination of sediment transport, mineral reprecipitation, and organic matter production. Significant negative autocorrelation of bedrock elevations at scales similar to wetland spacing suggest the presence of distal negative feedbacks on patch expansion. These findings support the inference of regular patterning, and are consistent with the presence of local positive feedbacks among hydroperiod, vegetation productivity and bedrock dissolution. These processes are ultimately constrained by distal negative feedbacks, potentially induced by landscape scale limitations on the water volume required to enable this biogeomorphic mechanism. Copyright © 2014 John Wiley & Sons, Ltd.

KEYWORDS: biogeomorphology; carbonate dissolution; ecological drill; karst; overdispersion; pattern; reciprocal feedbacks

Introduction

Biogeomorphic landscape patterning

Biota play an essential role in shaping the surface of the Earth (Dietrich and Perron, 2006; Corenblit *et al.*, 2011). Biogeomorphology studies have expanded upon the 'ecological engineer' concept (Jones *et al.*, 1997) to explore bidirectional interactions between biota and geomorphology in processes such as the weathering of rock to produce soil (Sterflinger, 2000) and the accretion of carbonate to form reefs (Spencer and Viles, 2002). These reciprocal interactions can locally amplify biotic regulation of geomorphic processes (Corenblit *et al.*, 2008), influencing spatial arrangement of landforms and aggregations of species (Cutler, 2011). They may thus cause the emergence of landscape-scale patterns in the arrangement of vegetation, or in the topography of the substrate (Klausmeier, 1999;

Rietkerk and van de Koppel, 2008; Watts *et al.*, 2010; Larsen and Harvey, 2011).

Scale-dependent feedbacks arise from resource availability at close spatial proximity but generate long-range inhibition (Rietkerk and van de Koppel, 2008), promoting clustering of biotic communities (Corenblit *et al.*, 2011) and yielding a pattern of patches on the landscape. These coupled, reciprocal feedbacks result in spatial patterns of species or habitat types in a wide variety of settings including mussel beds in the Netherlands (van de Koppel *et al.*, 2008), ridge-slough landscapes in the Florida Everglades (Larsen and Harvey, 2011), and patterned xeric shrublands such as Tiger Bush (Lefever and Lejeune, 1997; Klausmeier, 1999), among many other diverse ecosystems. Although regular landscape pattern alone is not diagnostic of their presence (D'Odorico *et al.*, 2006), where clear abiotic drivers (e.g. geologic structure, hydrology) are absent, regular patterning does generally imply coupled feedbacks that produce or reinforce landscape pattern (Eppinga *et al.*, 2009).

Patterning in Karst landscapes

Karst landscapes form in response to feedbacks between drainage and dissolution. Most karst occurs in carbonate rocks where dissolution is controlled by CO_2 derived from the atmosphere or organic matter mineralization, and delivered to reaction sites by flowing water. In short, dissolved CO_2 from atmospheric sources and organic matter respiration creates weakly acidic water that is buffered along a hydrologic flowpath by carbonate dissolution. The CO_2 hydrates to carbonic acid and dissolves morphologic features, including connected flow conveyances (conduits) in settings with highly permeable geology. The dissolution is self-regulating, as under-saturated water expands conveyances via dissolution – thereby further enhancing dissolution. In carbonate karst systems that are poorly drained due to low relief and/or presence of a confining unit, prolonged surface inundation in landscape depressions supports aquatic respiration of organic matter, which may amplify biotic influence on dissolution and karst feature (e.g. sinkhole, doline) expansion. Biotically mediated carbonate dissolution, along with the action of acidified rainwater, is one proposed mechanism for the formation of depressional wetlands in areas with low topographic relief and shallow limestone bedrock (Odum, 1984; Cohen *et al.*, 2011).

Processes that reinforce dissolution (e.g. increased inundation, focused conveyance), and the degree to which those processes are limited by resource availability, control the geometry of karst development. Absence of inhibitory mechanisms would create power-law distributions of karst void features. Regular patterning could arise in karst settings, however, if negative feedbacks occur at intermediate spatial scales. Such feedbacks might arise from limited local availability of water

necessary to enable continued dissolution (e.g. when the landscape becomes over-drained). Alternatively, the deposition of insoluble material after dissolution could form a confining barrier between surface waters and the aquifer, inhibiting continued carbonate dissolution.

The karst landscape of Big Cypress National Preserve (BICY) in southwest Florida (Figure 1(A)) is characterized by discrete depressional wetlands interspersed among pine and prairie mosaics in a seemingly regular pattern (Figure 1(B)–(D)). The depressions appear visually to be spatially overdispersed, i.e. distributed more uniformly than expected by chance (Diggle, 2002). Cohen *et al.* (2011) proposed that such patterning could arise from locally positive hydrologic and biogeochemical feedbacks that are constrained by negative feedbacks arising from water volume (Figure 2). In that conceptual model, small incipient depressions attract and hold rainwater, which promotes dissolution, depression expansion, and wetland development as relatively impermeable surfaces act as local catchments and subsidize water delivery to them. As wetlands develop, organic matter production and processing further enhance dissolution, expanding wetland basins and potentially mobilizing nutrients (especially phosphorus [P], which is limiting in this system; Noe *et al.*, 2001) that increase primary production (and, by extension, organic matter mineralization). Wetland expansion, however, reduces the ratio of local catchment to wetland area, thus reducing the water subsidy from the local catchment that helps to maintain long hydroperiods, water storage, and enhanced dissolution in the depression. At the landscape scale, rainfall volume and thus water limitation are thought to impose a constraint on total wetland extent (pathway #7, Figure 2), and resulting distal negative feedbacks could produce relatively uniform spacing

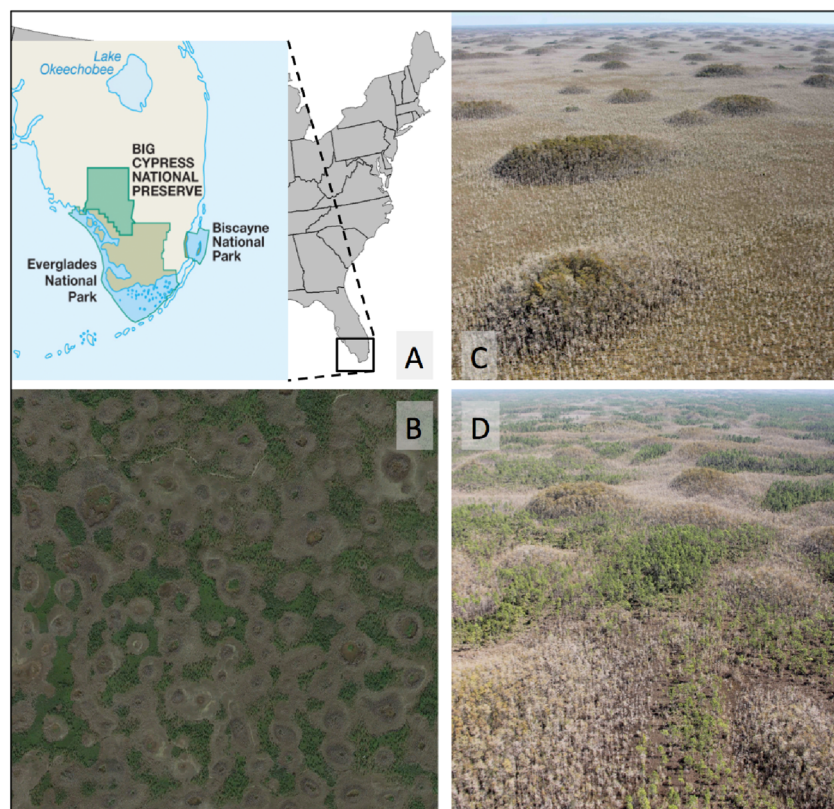


Figure 1. (A) Big Cypress National Preserve occupies 295 000 ha in southern Florida, USA, contiguous with Everglades National Park. (B) Circular depressional wetlands occur commonly in Big Cypress and throughout southern Florida. This SPOT image from Google Earth (Google, Inc., Mountain View, CA USA) shows a 3 km² area from the central portion of the Preserve. The dome-shaped profiles of pondcypress (*Taxodium distichum* var. *imbricarium*) swamp patches are distinctive in a landscape consisting of alternative long-hydroperiod wetland and prairie (C) or pineland (D) communities.

of dissolution features (as opposed to random or clustered spacing) across a landscape. Under these circumstances any given point on the landscape would tend to be located within the spatial domain of a locally positive feedback to bedrock dissolution, or a distally negative inhibitory feedback to dissolution. Assuming uniform initial elevations and similar rates of dissolution across the landscape by the above mechanisms, the frequency distributions of elevations for randomly chosen points across such a landscape would tend to be distributed bimodally: falling either within a zone of active dissolution and therefore at lower elevations, or at the relatively higher elevations found in the negative-feedback zones. Soil building processes, including deposition of insoluble particles transported via overland flow, accumulation of organic matter under flooded (and thus likely anaerobic) conditions, and re-precipitation of dissolved calcium carbonate would act to moderate the effects of these feedbacks on soil surface elevations (i.e. thicker soils would be found within depressions).

Specifically, we tested the following predictions:

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Materials and Methods

Site description

Big Cypress National Preserve (BICY) is located in southwest Florida (USA) and is a large (295 000 ha), low-relief landscape with carbonate bedrock at or very near the land surface (Figure 1). Pleistocene deposits (carbonate rocks of the Tamiami and Fort Thompson formations) are relatively thin (c. 50 m) and highly permeable, contain approximately 20% insoluble residual material (principally quartz sand and apatite ($\text{Ca}_5(\text{PO}_4)_3(\text{OH}, \text{F}, \text{Cl})$), and are bounded below by a thick clay confining unit (MacPherson, 1974). Depressions in the formation create wetlands, with ~20 cm thick layers of organic-rich muck (i.e. histic epipedon), which overlay deeper (up to 3 m) sediments containing mixed quartz sand (dissolution residue), calcareous mud (marl/micrite) and humified organic matter. Surrounding these wetlands, the Tamiami Formation is exposed or near the land surface as it has been since the last glacial maximum (LGM) 130 000 years before present (ybp). During the early Holocene, sea-level rise slowed between 5 and 7 kypb at an elevation similar to the base of wetland sediments (~3–4 m below the land surface), suggesting modern genesis. Where it is exposed, the Tamiami Formation has been locally dissolved and re-cemented into a discontinuous but highly impermeable layer (cap-rock) that induces surface runoff (Miller *et al.*, 2004). Because the geologic formations under BICY are slightly mounded in relation to the surrounding landscapes (the central Everglades to the east, Everglades National Park to the south), the terrestrial and wetland systems are entirely rain-fed, with hydrology driven by strong seasonality in precipitation (c. 70% of rainfall occurs between June and September, Duever *et al.*, 1986). Extremely shallow relief (mean landscape slope from north to south is c. 5 cm/km) and abundant rainfall leads to prolonged periods of surface inundation, particularly in depressional wetlands, which may experience annual hydroperiods > 300 d (Watts *et al.*, 2012).

Vegetation in BICY responds strongly to subtle variation in elevation, which has large effects on hydrology, with marked shifts in community composition evident over less than a meter of local surface relief. Elevation differences also tend to correspond to the frequency with which vegetation communities experience lightning-ignited fires at the onset of the region's rainy season; fire frequency also exerts control over vegetation community composition and ecosystem attributes such as soil organic matter content (Watts *et al.*, 2012). In higher elevation settings, slash pine (*Pinus elliottii* [Engelm.]) rockland or flatwoods and hardwood hammock communities dominate. Marl prairie, commonly dominated by *Muhlenbergia capillaris* or *M. sericea*, or cypress prairie with sparse short-stature pondcypress (*Taxodium distichum* var. *imbricarium* [Nutt.]) occurs at slightly lower elevations and is maintained by frequent fires (fire return interval c. 2–3 y, Gunderson and Snyder, 1994). Interspersed within both forested and prairie portions of the landscape are either small circular swamps (called *domes*) dominated by pondcypress, or wetland marsh communities primarily composed of such emergent herbaceous species as sawgrass (*Cladium jamaicense* Crantz), cattail (*Typha domingensis* Pers.), fire flag (*Thalia geniculata* Lin.), or arrowhead (*Sagittaria latifolia* [Willd.]). While these forested wetland patches remain inundated for much of the year, occasional droughts create conditions conducive to periodic surface fires or even severe smoldering fires in their desiccated organic soils.

Spatial analysis

We selected three 1.5 km × 1.5 km blocks (Deep Lake, DL; Low Site, LS; and Raccoon Point, RP; Figure 3) within BICY, where

we measured spatial patterning of landform features. Sampling sites were chosen to represent typical configurations of common vegetation communities within BICY. We used 2.5 m resolution images from 2010 SPOT (Satellite Pour l'Observation de la Terre) imagery (geo-referenced and accessed via Google Earth, Google, Inc., Mountain View, CA) to locate the sampling blocks, measure wetland depression area (i.e. patch area), and determine the location of wetland depression centers. In two of the sampling blocks (LS and RP), the boundary of depressional features was defined as the outer extent of the nearly monotypic communities of pondcypress. In the third sampling block (DL), depressions were occupied by marsh communities instead of forest patches; here, the boundary between prairie dominated by muhly grass (*Muhlenbergia capillaris* Lam. or *M. sericea* Michx.) and marsh composed primarily of sawgrass, cattail, or other emergent obligate wetland species (e.g. fire flag) was delineated as the depression boundary. In both cases, species were chosen based on (1) their characteristic occurrence in wetlands of the region, (2) ease of identification from satellite imagery as signals of depressions, and (3) their ubiquity among all depressions in the sampling blocks in which they occurred. Heads-up digitization of satellite imagery verified by ground observations revealed 45 to 60 depressions in each of the three 225 ha sampling blocks.

To test the prediction that depressions are non-randomly dispersed, we used nearest-neighbor analysis (Diggle, 2002) to discriminate between overdispersion (i.e. regular spacing) or underdispersion (clustering) against the null hypothesis of complete spatial randomness (CSR). The mean nearest-neighbor distances (μ_{NN}) across wetland depressions (i.e. between depression centers) is compared with the expected nearest neighbor distance between randomly-dispersed pairs ($\mu_{\text{E}} = 0.5/\sqrt{(n/D)}$) based on the size of the domain ($D = 2.25 \text{ km}^2$) and the number of wetlands (n). Values of the ratio of μ_{NN} to μ_{E} greater than 1 indicate overdispersion, while values below 1 indicate clustering. A z-score to evaluate the significance of overdispersion or clustering (z_{ANN}) is computed from the difference between μ_{NN} and μ_{E} scaled by the standard error ($0.26/\sqrt{(n^2/D)}$). We evaluated the probability distribution of observed nearest neighbor distances to further visualize the dispersion of wetlands in the landscape.

To test the prediction that patch sizes are truncated by distal negative feedbacks (i.e. there is a limit to wetland expansion), we plotted the cumulative probability density – that is, the $\text{Pr}(A > a)$, where A is the area of the patches and a is an area threshold – and plotted that versus wetland area. Patch areas were obtained by analyzing the radius of individual patches in SPOT imagery and assuming they were circular. This approach was verified in comparison with field measurements of area based on delineation of wetland perimeters, with strong agreement (i.e. within 4–7% error) between methods. We compared the cumulative density distribution with power-law scaling [$\text{Pr}(A < a) = \alpha a^B$], which is observed where patterns are controlled globally, and not by scale-specific inhibitory feedbacks (Scanlon *et al.*, 2007) and with exponential scaling [$\text{Pr}(A < a) = \alpha e^{B^A}$], which is observed when patch sizes are constrained by scale-specific feedbacks (Kefi *et al.*, 2010).

Soil and bedrock characterization

We selected 40–70 spatially-randomized sampling points within each of the three sampling blocks to serve as the centers of sampling clusters, in which five measurements of soil and bedrock elevations were made (one in each cardinal direction at random distances of 1–25 m, and one at the center). Elevation measurements were made during August–October 2011,

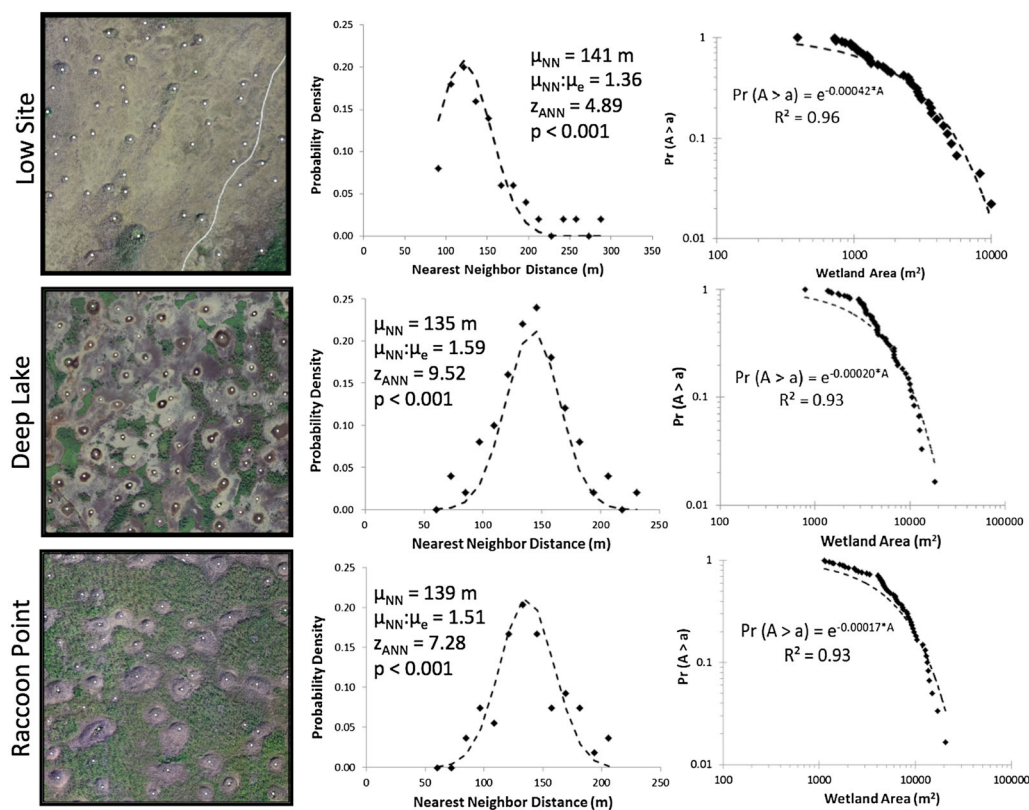


Figure 3. Digital ortho-quad images from 2009 of sampling locations (left column from top to bottom: low site, LS; Deep Lake, DL; Racoon Point, RP) with wetland centers (white dots). Wetland nearest-neighbor distances (center column) are normally distributed in all three blocks, with mean distances significantly larger than values expected given random placement; results from statistical tests confirming spatial overdispersion are reported. Distributions of wetland area follow exponential scaling for each site (right column); other functional forms (power and cumulative normal) yielded significantly worse fits and are not shown.

late in the region's rainy season when seasonally high water tables inundate most of the local landscape (including upland areas). Soil elevation measurements were obtained by measuring water depth and benchmarking to nearby USGS Everglades Depth Estimation Network (Telis, 2006) sites. Given extremely low surface water slopes in BICY and continuous surface water connections between our sites and nearby EDEN gages, we assumed that water elevations (relative to mean sea level, MSL, at NAVD88 datum) recorded at EDEN gages were equal to water-surface elevations at measurement locations. This assumption allowed soil elevation relative to MSL to be estimated from measured water depth, EDEN water depth data, and EDEN gage elevations. Steel tile probes (Forestry Suppliers, Inc., Jackson, MS USA) were used to measure depth to bedrock and soil thickness; these depths and soil elevations yielded bedrock elevations. Ground elevations of sampling points that were not inundated were benchmarked to nearby inundated areas using a laser level (Johnson Level and Tool, Mequon, WI USA).

We obtained soil P concentrations from a previous survey of soil characteristics across the greater Everglades (including BICY; Osborne *et al.*, 2011). Soil samples were collected at 208 randomly determined locations within BICY, and analyzed for total soil P using the ashing procedure of Anderson (1976) and inorganic P using 1.0 M HCl extraction followed by measurement of soluble reactive P using standard colorimetric techniques. While the spatial footprint of soil samples differs from other data in this study, it nonetheless allows us to evaluate the prediction that positive feedbacks on dissolution and plant growth should produce bimodal distributions of P concentrations.

To test predictions that regular depression patterning occurs consistent with hypothesized elevation-affecting processes

(Cohen *et al.*, 2011), we used spatial autocorrelation measurements of landform elevation to compare the relationship between elevation at a given sampling point and elevation at increasing distances. We used GS+ software (Gamma Design Software LLC, Plainwell, MI USA) to calculate and construct correlograms for soil surface and underlying bedrock elevations measurements from each block using a lag spacing (h) of 10 m, a range of 500 m, and an angular tolerance of 22.5° . Soil P data, collected as part of another effort, were not of appropriate density and spatial distribution for comparable analysis.

To test the prediction that distributions of bedrock and soil elevations and soil P concentrations are bimodal, we compared goodness-of-fit metrics between a single-normal model and a mixed-normal (bimodal) model (Wolfe, 1970). Model selection (uni- vs. bi-modal) used Bayes's Information Criterion (BIC). Models were implemented and evaluated using the software program R (R Development Core Team, 2005).

Results

Spatial distribution and patch size

Each of the three blocks had strong visual evidence of patterning, with small circular wetlands embedded in a mosaic of uplands or prairie (Figure 4(a)). Nearest-neighbor distances between depression centers are much larger (1.36 to 1.59 times larger) than would be expected given complete spatial randomness. Overdispersion (i.e. $z_{ANN} > 1.96$) was observed in all sampling blocks (Table I). This overdispersion is further illustrated by the apparent normality and tight clustering of the distribution of nearest neighbor distances (Figure 4(B)) at

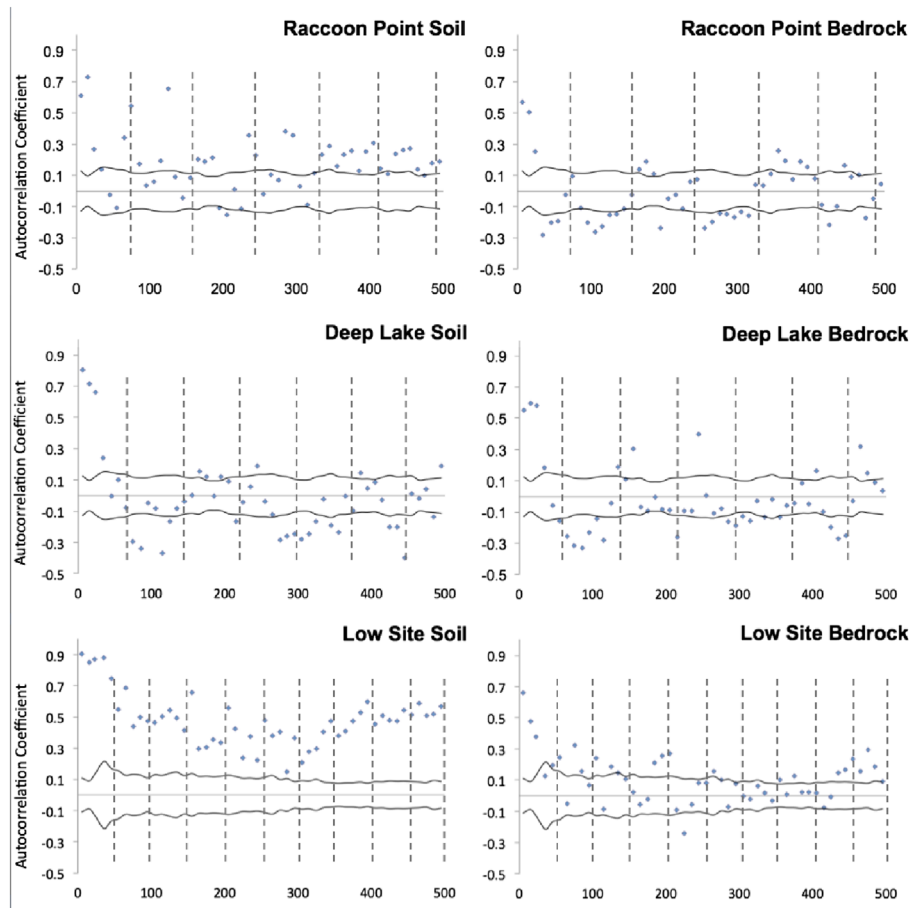


Figure 4. Correlograms showing spatial autocorrelation of soil and limestone bedrock elevation with lag distance of 10 m and range of 500 m. Solid black lines indicate 95% confidence intervals for significant non-zero autocorrelation at each lag distance. Dashed vertical lines indicate mean diameter (m) of depressional landscape features estimated from satellite images. This figure is available in colour online at wileyonlinelibrary.com/journal/espl

Table I. Characterization of the depressional landscape features observed in three 1.5 km × 1.5 km landscape sampling blocks. While average depression size and percentage of landscape occupied by depressional features varied, nearest-neighbor analysis indicated nonrandom, even distribution of landform depressions

Site name	Number of depressions	Mean (s.d.) depression size, ha	Mean (s.d.) depression dia., m	Depression area, ha (%)	Z-score
DL	64	0.47 (0.31)	74 (24)	28.1 (12.5%)	9.52*
LS	46	0.25 (0.35)	50 (25)	11.0 (4.9%)	4.89*
RP	59	0.58 (0.42)	81 (29)	34.9 (15.5%)	7.26*

*Indicates significant overdispersion (i.e. regular or even spatial distribution, as opposed to random or clustered distribution), $\alpha \leq 0.05$.

all sites. Depressions were generally < 1 ha in size, and comprised 11% – 28% of the area of the sampling blocks (Table I). Wetland area clearly follows exponential scaling (Figure 4(C)), which fit wetland size distributions far better than a power function in each block ($r^2 = 0.72$, 0.67 and 0.64 for LS, RP and DL, respectively); we observed a similar exponential scaling parameter in RP and DL, but an exponent value roughly double in LS, indicating smaller patches.

Soil and bedrock characterization

At each site, upland vegetation communities generally occurred on thin layers of soil, with bare limestone outcrops common in the transitional pine rockland communities at the RP site. On the other hand, long-hydroperiod, depressional pond cypress swamps and marshes had deeper soils characterized by sandy, calcareous clay or granules under a thin mantle of organic horizon (histic or fibric epipedon, muck, or peat)

ranging from a few cm at depression edges to ~1 m in their centers. Soil surface elevations in depressions ranged from 233 cm above MSL (NAVD88) at the RP site to 384 cm at the DL site. Underlying limestone bedrock reached a maximum elevation of 361 cm above MSL (NAVD88) and a minimum of 72 cm, in both cases at the DL site. Equipment limitations prevented measurement of deeper bedrock, but this was limited to 9 (out of > 500) sampling points. The layer of soil overlying limestone bedrock was typically thinnest at the highest bedrock elevations observed.

Correlograms of elevation measurements (Figure 4) indicated significant positive spatial autocorrelation at close distances (i.e. similar to mean depression diameters; Table I) for both soil and bedrock elevations ($P < 0.05$ for all cases). While soil elevation did not have significant negative autocorrelation at RP and LS sites, alternating positive and negative autocorrelation was apparent at the DL sites. In contrast, significant negative autocorrelation was observed at increased distances for DL and RP bedrock measurements ($P < 0.05$); in both

cases, alternating positive and negative autocorrelations occurred with pseudoperiodicity roughly corresponding to mean depression diameters estimated from satellite imagery (Table I; Figure 4).

Comparisons of single-normal and mixed-normal models for distributions of soil and bedrock elevation and thickness of the overlying layer of soil (Figure 5, Table II) indicated bimodal distributions were the best fit model in all cases except for soil-surface elevation at RP, which was best fit with a unimodal distribution. At all three sites, bimodal distributions were more strongly evident in limestone bedrock elevation observations than for soil-surface measurements. Difference in means

between higher-elevation vs. lower-elevation modes were greater for bedrock than for soil elevations at both DL (120.7 cm vs 25.6 cm) and the LS locations (71.6 vs 9.2 cm). Soil thickness was significantly correlated with bedrock elevation at all three sites (RP $r^2=0.93$, $P<10^{-15}$; DL $r^2=0.98$, $P<10^{-15}$; LS $r^2=0.97$, $P<10^{-15}$; Figure 6), helping to explain the stronger bimodality in bedrock compared to soil surface elevations.

Soil inorganic P (TP_i) and total P (TP) were also bimodally distributed (Table II), exhibiting similar patterns to bedrock elevation distributions with a large peak at low values (33.7 $\mu\text{g TP}_i \text{ kg}^{-1}$ and 176.3 $\mu\text{g TP kg}^{-1}$; Figure 7) and less abundant (mixture coefficients of 0.90 and 0.85 for TP_i and TP,

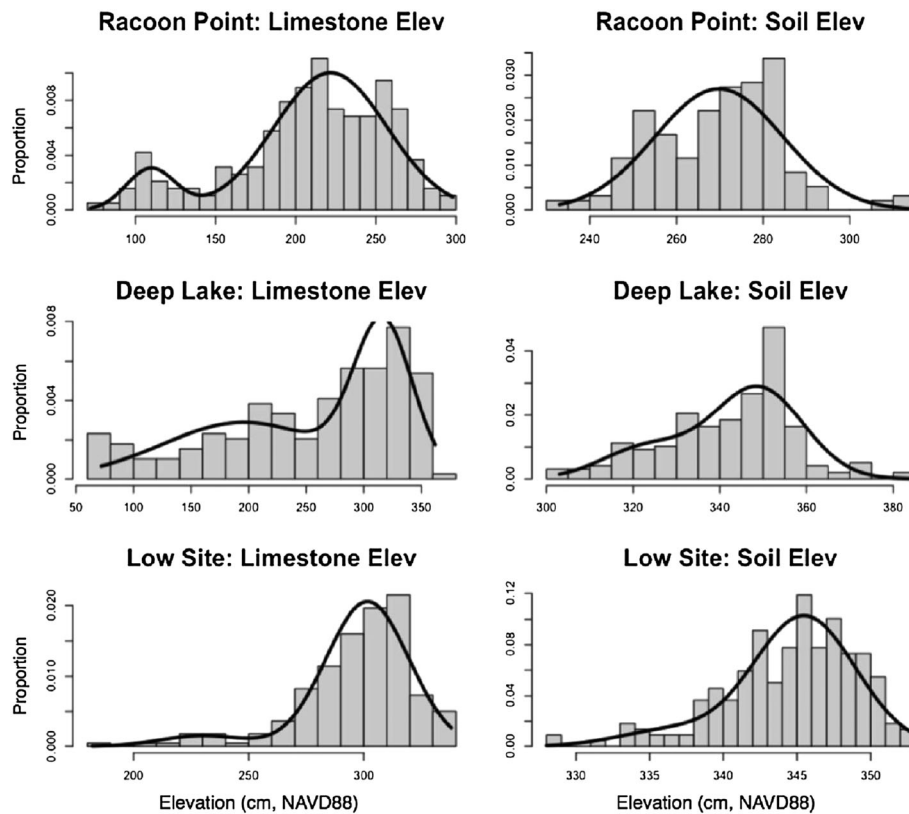


Figure 5. Distributions of measured soil and bedrock elevation are bimodal in all cases except for RP soil elevations, which were unimodal except where extreme values were omitted. Fitted models (solid lines) suggest stronger bimodality in limestone bedrock elevation than in soil elevation at all sites.

Table II. Means and standard deviations for best-fit models of bedrock and soil surface elevation and soil thickness based on BIC comparisons within three sampling blocks (RP, DL, and LS), and soil P measurements made across the Preserve (BICY)

Site	Measurement	Model parameters (BIC best-fit model)				
		X_1	X_2	σ_1	σ_2	q
RP	Bedrock Elevation	109.6	221.7	15.2	35.2	0.12
	Soil Surface Elevation	269.8	NA	14.8	NA	1.00
	Soil Thickness	47.0	132.3	23.8	23.8	0.84
DL	Bedrock Elevation	196.0	316.7	71.8	71.8	0.52
	Soil Surface Elevation	323.3	348.9	10.3	10.3	0.26
	Soil Thickness	32.7	139.2	20.5	20.5	0.48
LS	Bedrock Elevation	230.0	301.6	18.1	18.1	0.07
	Soil Surface Elevation	336.3	345.5	3.5	3.5	0.11
	Soil Thickness	43.2	108.9	16.8	16.8	0.93
BICY	Soil Total P (mg/kg)	176.3	491.5	54.8	49.7	0.86
	Soil Inorganic P (mg/kg)	33.7	109.7	16.2	12.5	0.90

X_1 is mean at the first mode for bimodal distributions (or where greater maximum Bayes Information Criterion (BIC) values indicated unimodal model was more appropriate); X_2 is mean of second mode for bimodal distributions; σ_1 and σ_2 are standard deviations of first and second (if applicable) distributions; q is weight of first distribution; NA = not applicable in cases of unimodal model offering better fit.

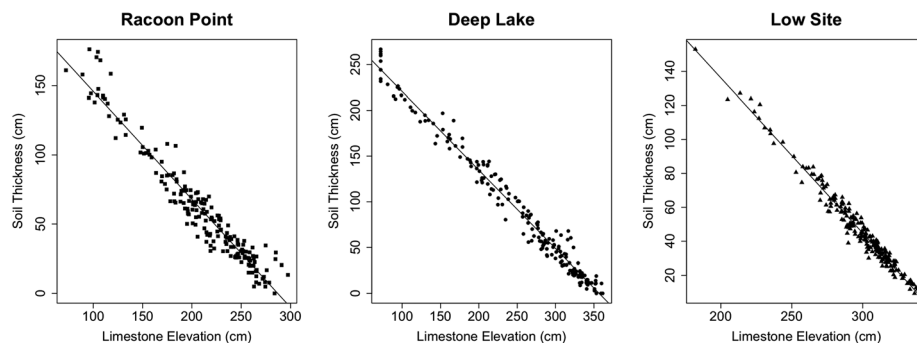


Figure 6. Thickness of soil, the distance between soil surface and underlying bedrock, was greatest at the lowest bedrock elevations observed in all three sampling locations; soils became thinner at locations with decreasing bedrock depth. Elevation of limestone bedrock are in cm above mean sea level. R-squared values for linear-regression models of these relationships (not shown) are 0.93 for RP; 0.97 for DL and LS ($P < 0.01$ in each case); slope is -0.53 , -0.71 , and -0.40 , respectively.

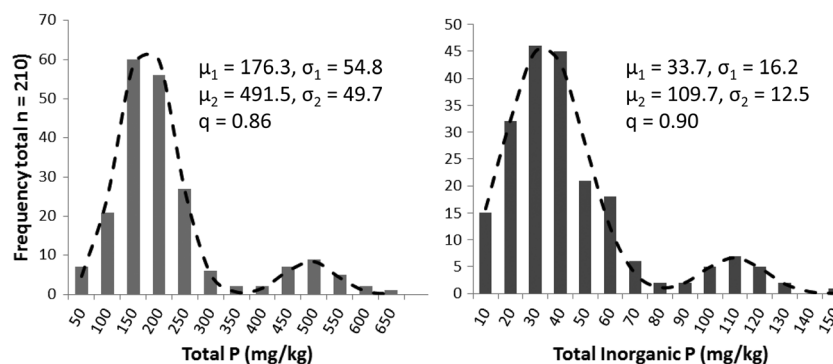


Figure 7. Distributions of total P and inorganic P in samples from BICY in 2003 ($n = 210$). Bimodality suggests patch-scale feedbacks mobilize P; the high P mode is from sites with high soil organic content and predominantly wetland taxa.

respectively) but clearly distinct peaks at higher values ($109.7 \mu\text{g TP}_i \text{ kg}^{-1}$ and $491.5 \mu\text{g TP kg}^{-1}$) associated with deeper wetland sites.

Discussion

Regular spatial distribution of wetland depressions

Our results suggest that the BICY landscape exhibits regular spatial patterning of vegetation and bedrock elevation. Wetland depressions exhibited significant spatial overdispersion in all three sampling blocks, indicating a uniform distribution (patterning) as opposed to random or clumped distribution (Table I; Figure 3). Additionally, alternating positive and negative autocorrelations were observed for bedrock and, to a lesser extent, soil elevations (although this trend is not evident in the LS data, possibly due to underlying bedrock slope and low prevalence of depressions observed in the random sampling scheme; Figure 4). The apparent periodicity in autocorrelation corresponded with approximate boundaries of vegetation communities, consistent with a mechanism of pattern formation that links vegetation and bedrock elevation.

The observation of evenly distributed depressions confirmed the strong visual suggestion of patterning observed from satellite imagery for RP and DL sites; and also confirmed uniform spacing of depressions at the LS site despite their low prevalence in that area ($<5\%$ of surface area; Table I). Truncated size distributions of wetland patches (Figure 4) indicate that wetland size is relatively constant; this pattern is consistent with the operation of negative feedbacks that inhibit patch expansion, though we note that the distribution of sizes is not normal, as would strictly be expected under regular patterning, but rather exponential. Given the number of recent studies that have

observed power law distributions of wetland patch sizes (Foti *et al.*, 2012) and even landscape depressions (Le and Kumar, 2014), the strong evidence against power law scaling strongly underscores that patterning in BICY is controlled by spatial feedbacks that constrain local patch expansion.

Regular patterning has been observed in a variety of landscapes, including string and maze fens, banded and spotted vegetation patterns in drylands, and in estuarine mussel beds and algae-covered mudflats (Rietkerk and van de Koppel, 2008). To our knowledge, this study is the first to demonstrate coupled, regular patterning in bedrock and vegetation within a single landscape. Despite the novelty of this observation, we suggest that the basic processes that shape the BICY landscape are likely to be similar to those that form patterned landscapes elsewhere.

Hydrologic processes are integral to regular pattern formation in wetlands, drylands, and other landscapes, through a diverse array of mechanisms (Sponseller *et al.*, 2013). Scale-dependent feedbacks create regular pattern via interactions between vegetation growth and soil moisture (Scanlon *et al.*, 2007), or through transport and accumulation of nutrients (Rietkerk *et al.*, 2004; Kefi *et al.*, 2010). In wetlands and other shallow aquatic systems, hydroperiod interacts with organic matter production and decomposition to shape microtopography (Eppinga *et al.*, 2009; Sullivan *et al.*, 2011; Heffernan *et al.*, 2013). Vegetation effects on hydrodynamics (van der Heide *et al.*, 2010; Kaplan *et al.*, 2012) and sediment erosion and deposition can also produce regular patterns. In this light, it is highly probable that the pattern forming mechanisms in BICY are hydrologic in nature, but could involve one or more geomorphic and biogeochemical processes.

The bimodal bedrock elevation distributions at all three sites (Table II; Figure 5), and the differences among those sites, suggest that the primary patterning feedbacks operate primarily

on bedrock dissolution, and are consistent with the hypothesis that basin volume is involved in feedbacks that produce regular patterning of depressional wetlands (Figure 2). Bimodality was most pronounced at the RP site, where cypress domes occupied a higher fraction of the landscape (15.5%). Yet bimodality of soil elevations was clear even at the LS site, with relatively rare occurrence of depressional vegetation communities. The presence of bimodal elevation distributions in bedrock despite a lack of significant negative spatial autocorrelation at the LS site may have been due in part to the low areal extent of depressions compared with RP and DL sites. Differences in prevalence of depressions may be due to differences in hydrology driven by elevation: mean bedrock elevations at the LS site (297 cm) are substantially higher than those at the DL site (254 cm) or the RP site (209 cm).

The bimodal distribution of P in BICY soils (Table II, Figure 7) provides additional evidence that basins form through carbonate weathering, and suggest an additional mechanism by which dissolution and biotic production may feedback on one another. Since carbonate minerals readily remove P from solution during precipitation (Tunesi *et al.*, 1999), it is likely that the mode of elevated soil P reflects P-rich bedrock dissolution within wetland depressions. No studies have assessed whether P limits growth of trees or algae in BICY, but low P availability is a severe constraint on plant and algal growth in the nearby peatlands of the Everglades (Noe *et al.*, 2001; Gaiser *et al.*, 2005), and P availability is positively associated with litter production in cypress strands elsewhere in Florida (Brown, 1981). Increased P availability and its effects on organic matter production and processing may further enhance dissolution, amplifying biotic influence on landscape patterning (Figure 2) via the stimulation of respiration and subsequent alterations to dissolution potential.

Soil building and surface smoothing

The influences of biotic processes on geomorphology may be difficult to detect when masked by the signature of physical processes (Dietrich and Perron, 2006). Divergence in landform signature between pattern-generating biota-environment interactions and abiotic processes (e.g. erosion) occur in some riverine systems (Francis *et al.*, 2009; Corenblit *et al.*, 2011) and has also been demonstrated at small scales in a coastal mudflat (Weerman *et al.*, 2011). In BICY, variation in soil surface elevations are muted compared with the variation in the underlying bedrock (Figure 5) and soil thickness is strongly correlated with bedrock elevation (Figure 6). For LS and DL sites, soil-surface elevation measurements also displayed bimodal distributions, but with lower differences between local-relative low- and high-elevation modes compared with bedrock elevation distributions. At RP, where basins are least abundant, soil surface elevations were unimodally distributed despite bimodal bedrock elevations. From these patterns we infer that patterning formation in bedrock from dissolution is obscured by soil formation and accumulation that occurs more quickly in depressions than at higher elevations.

The slope of the relationship between soil thickness and bedrock elevation (Figure 6) may be diagnostic of the relative strength of pattern-forming processes versus pattern-smoothing ones. In this instance, a more negative slope (i.e. thicker soils at lower bedrock elevations) would indicate a higher degree of surface 'smoothing' of any subsurface spatial patterning, and would be expected where greater subsurface relief provides greater potential for soil transport from higher areas to depressions. Indeed, this is seen in our study areas, where

the DL site's difference between bedrock modes (Table II) and patterning z-score (Table I) were greatest of the three, followed by RP and LS; DL site's bedrock:soil relationship slope was steepest, followed by those for RP and DL (Figure 6).

A variety of processes may contribute to soil accumulation in wetland depressions. First, insoluble particles (e.g. quartz sand) may accumulate in depressions as residuals of dissolution of the carbonate matrix, and through sediment advection via overland flow. High rates of biomass production by wetland vegetation, in conjunction with anaerobic conditions under long hydroperiods, would favor rapid accumulation of production of organic matter. Finally, aquatic primary production in depressions can raise water column pH and foster re-precipitation of amorphous carbonate minerals (i.e. marl, Figure 2). The variation in soil-building processes evident across our study sites is likely to both reflect and influence the biogeochemical and hydrologic mechanisms that produce the BICY landscape.

Biogeomorphic feedbacks and pattern formation in karst landscapes

Bimodal bedrock elevations suggest the possibility that some process constrains lateral expansion of basins when they achieve a particular depth. For example, in the nearby ridge-slough landscape, soil elevations are bimodally distributed (Watts *et al.*, 2010). (Heffernan *et al.*, 2013) showed that greater rates of peat production in higher elevation sawgrass (*Cladium jamaicense* [Crantz]) ridges could be counteracted by shorter hydroperiods and thus greater organic matter decomposition, preventing divergence of ridges from less productive, lower elevation sloughs. In the absence of similar constraints in BICY, positive feedbacks between drainage and dissolution would produce deep dissolution features, such as the cenotes observed in the higher-elevation carbonate platforms of the Yucatan peninsula produced by sea level variation (Schmitter-Soto *et al.*, 2002). One possible explanation is that a confining layer on the BICY platform inhibits vertical infiltration of water and thus dissolution at the bottom of the basin, and thereby promotes dissolution and lateral expansion along depression edges (Cohen *et al.*, 2011). In similar wetland depressions in N. Florida, head differences and frequent lateral groundwater exchange between open water and upland water table have been observed due to differences in evapotranspiration and specific yield between uplands and wetlands (McLaughlin and Cohen, 2013); similar groundwater exchange is likely in BICY and could promote basin widening along those flowpaths.

Changes in soil properties during wetland development may also influence the magnitude and direction of groundwater exchange and thereby influence rates and spatial patterns of dissolution and the geometry of wetland depressions. The deposition of insoluble residues after dissolution, or the precipitation of marl at the soil surface, could form a confining barrier between surface waters and the aquifer below, preventing vertical groundwater flux. Limitation of vertical hydrologic fluxes would act to focus groundwater exchange and dissolution at the basin edge, leading to lateral, rather than vertical, expansion of wetland depressions. The occurrence of continuously connected cypress strands (rather than domes) in other portions of the BICY landscape may reflect the outcome of these processes under conditions (e.g. shallower water table, greater slope) that are even more favorable to wetland expansion via lateral dissolution.

Conclusion

The non-random spatial arrangement of depressional features in the low-relief carbonate landscape of Big Cypress Preserve supports a conceptual model for biogeomorphic landform development driven by spatially coupled feedbacks. A local positive feedback on dissolution drives wetland formation via this 'ecological drill', but is counteracted by a negative feedback on basin expansion as catchment hydrologic subsidies necessary to create the positive feedback become limiting. Our findings provide preliminary evidence of reciprocal feedbacks operating directly on bedrock, in opposition to processes at the soil surface. Bimodal distributions of bedrock elevation are evidence of a constraint on vertical dissolution that may arise from regional hydrologic drivers or from changes in hydrologic exchange as wetland depressions fill with dissolution residue material. Mechanistic, process-based studies are clearly needed to more directly assess the feedbacks hypothesized to create landscape pattern in BICY. Such studies could provide insight not only into the formation of this particular patterned landscape, but also provide a model for understanding the role of biota in shaping the evolution of karst landscapes more broadly.

The BICY landscape, represents a novel type of regular, seemingly self-organized spatial pattern (Rietkerk and van de Koppel, 2008), and may represent a particularly long-lived example of niche creation (Corenblit *et al.*, 2011). Dissolution processes likely proceed at very slow rates relative to the lifespans of the species whose members participate in their creation. This study therefore provides a compelling example of a system in which biogeomorphologic change can proceed and persist at particularly long timescales, with ecological 'footprints' left directly on bedrock despite the pattern smoothing influence of other surface processes.

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