

## Deviations on a theme: Peat patterning in sub-tropical landscapes

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### ABSTRACT

Patterned landscapes have long been a popular setting to test hypotheses about the effects of processes on ecosystem structure. The combination of scale-dependent and positive feedback theory is one of the most well-supported in current literature, each explaining separate aspects of patterned peatlands. These theories have been developed from dynamics in boreal peatlands and tested in boreal systems, but the mechanisms that control peat patterning in a sub-tropical system have yet to be acknowledged in theory. Statistical evidence for different mechanisms are present in the biophysical features of sub-tropical patterned peatlands, such as the ridge and slough landscape (RSL) within the greater Everglades wetland system. We use data from the RSL to test whether features of a sub-tropical, patterned peatland conform to positive and scale-dependent feedback patterning theories developed in boreal peatlands and use dynamic simulation to explain our results. The analysis of surface elements and nutrient differences within the RSL and our dynamic simulations indicate that positive and scale-dependent feedback may not be appropriate theories for sub-tropical peat patterning. Decomposition, rather than production, appears to be more important for abrupt microtopographical elevation differences, and differential nutrient concentrations are due to vegetation types, rather than increased evapotranspiration from greater vascular plant growth. Our model expands on the current theories for RSL maintenance, incorporating vegetation types and life history traits into differential peat deposition, which create the signature microtopographical differences found in the Everglades, and demonstrates that the underlying ecological patterning processes in sub-tropical peatlands are likely very different from boreal peatlands and require further discussion and study.

### 1. Introduction

Patterned landscapes have long been a popular setting to test hypotheses about the effects of processes on ecosystem patterning (Couteron and Lejeune, 2001; Eppinga et al., 2008; Klausmeier, 1999; Rietkerk and Van de Koppel, 2008). Specifically, research in patterned peatlands has introduced a set self-organization theories to explain how regularly patterned microtopography exists on the landscape (Belyea and Lancaster, 2002; Couwenberg and Joosten, 2005; Rietkerk et al., 2004; Swanson and Grigal, 1988). These include scale-dependent feedback (Eppinga et al., 2008; Rietkerk et al., 2004), differences in hydraulic conductivity between hummocks and hollows (Couwenberg and Joosten, 2005; Foster et al., 1983; Glaser, 1992), uplift by frost heaving (Brown, 1970; Eppinga et al., 2008; Moore and Bellamy, 1974), and the role of seasonal flooding (Sakaguchi, 1980; Seppälä and Koutaniemi, 1985).

Two different mechanisms within the scale-dependent feedback theory, nutrient accumulation and peat accumulation, are the most

well-supported in current literature (Eppinga et al., 2009a; Watts et al., 2010), each explaining separate aspects of patterned peatlands. The peat accumulation mechanism assumes that sharp microtopographical differences between ridges and hollows are reinforced by greater plant production on drier ridges, primarily from the increased presence of vascular plants (Belyea and Clymo, 2001; Hilbert et al., 2000; Rietkerk et al., 2004; Swanson and Grigal, 1988). Plant productivity, which determines the input of biomass to peat production (Belyea and Clymo, 2001; Eppinga et al., 2009a; Hilbert et al., 2000), is a function of peat thickness, a proxy for water stress on productivity (Eppinga et al., 2009a). Net peat accumulation in this mechanism is primarily a function of plant production and peat decomposition, both driven by water table depth. Evidence for this mechanism, expressed as sharp microtopographical differences, is a bimodal “frequency distribution of surface elements (vascular plant biomass or acrotelm thickness)” (Eppinga et al., 2008) and is well documented in boreal peatlands (Eppinga et al., 2009a). This feedback has been studied along a climactic gradient (Eppinga et al., 2010) and focused on the evapotranspiration (ET) and

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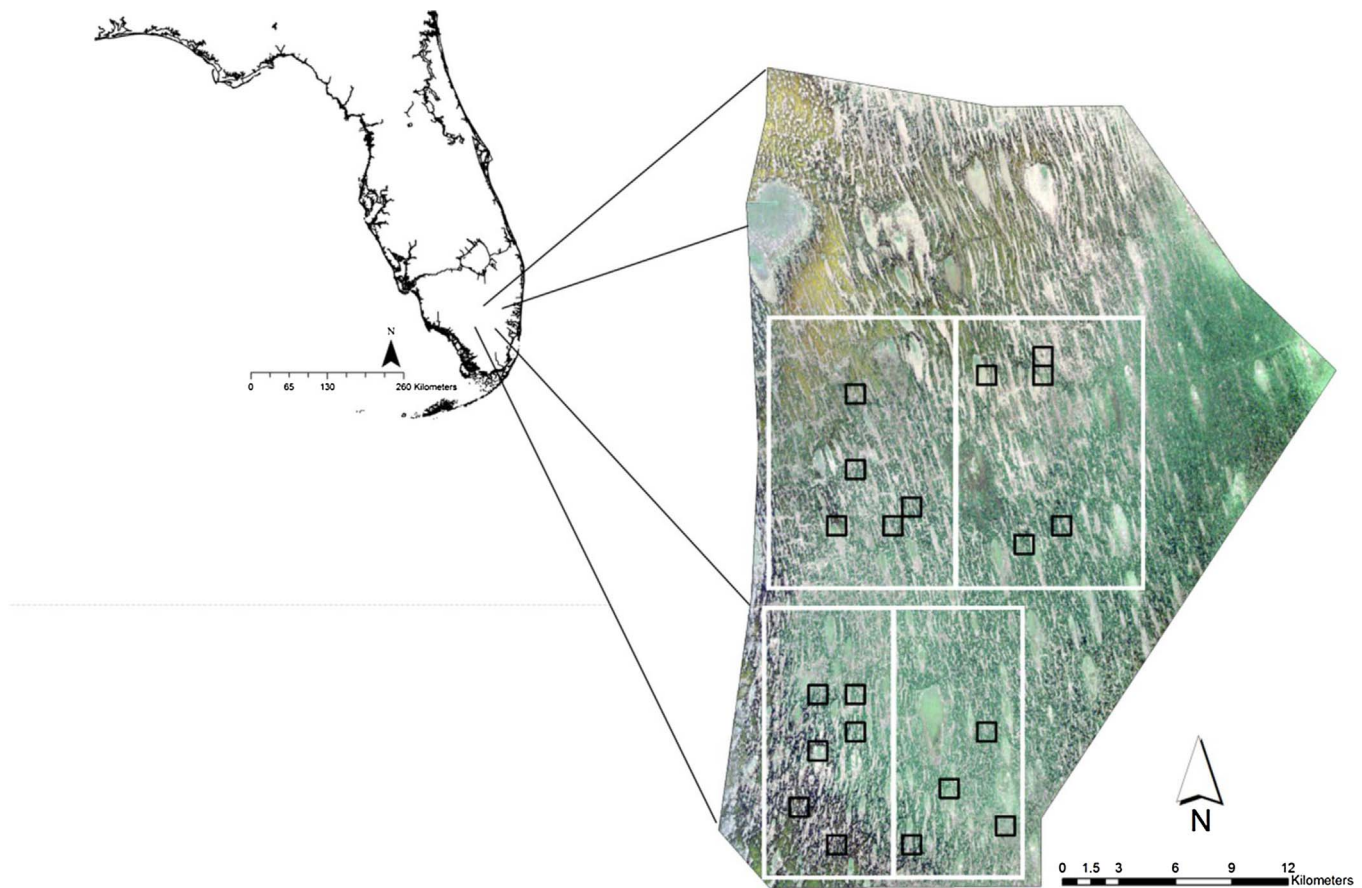


Fig. 1. Study sites for elevation and biomass data within Water Conservation Area 3A South (WCA3AS), FL USA. Small squares are 1 km<sup>2</sup> study plots and large, white rectangles indicate the plots used in each quadrant analysis.

precipitation ratio in sites dominated by temperate and sub-arctic climates (Scotland, Sweden, and Siberia).

The nutrient accumulation mechanism, on the other hand, explains landscape patterning; particularly regular string or maze patterning, from the directed flow of water and nutrients into ridges by increased ET of vascular plants (Rietkerk et al., 2004). As nutrients accumulate within ridges from plant uptake and recycling, vascular plant growth should increase and pull more water and nutrients by ET, reinforcing the nutrient accumulation cycle (Eppinga et al., 2008). This occurs at a local scale within the ridge, creating a negative effect for plants growing further from the ridge and generating a scale-dependent feedback (Eppinga et al., 2008; Rietkerk et al., 2004).

These mechanisms have been developed from dynamics in boreal peatlands and tested as mathematical models or empirical models in temperate or boreal systems (Belyea and Clymo, 2001; Couwenberg and Joosten, 2005; Eppinga et al., 2008; Hilbert et al., 2000; Rietkerk et al., 2004). A limited number of studies have discussed non-boreal microtopography (Cheng et al., 2011; Couwenberg and Joosten, 2005; McVoy et al., 2011; Nungesser, 2003) and some aspects of scale-dependent patterning theories have been applied to the sub-tropical Everglades (Heffernan et al., 2013; Larsen and Harvey, 2010; Watts et al., 2010), including nutrient accumulation effects (Larsen et al., 2007; Larsen et al., 2015). These models were mainly theoretical studies, but one data-based analysis suggested that sub-tropical peatlands do conform to boreal-based peat accumulation mechanisms through elevation bimodality (Watts et al., 2010). However, we hypothesize that the mechanisms that control peat patterning in a sub-tropical system should be different because increased temperatures, longer photoperiod, lack of seasonality, and distinct vegetation communities contribute to differences in structuring processes through changes in

decomposition and plant production (Aerts, 1997; Meentemeyer, 1978). Boreal-based models include production and decomposition as a function of water stress, and do not explicitly use temperature or differences in species' attributes (Eppinga et al., 2009a; Eppinga et al., 2009b; Rietkerk et al., 2004), which are likely important in a sub-tropical climate. Statistical evidence for these differences between boreal and sub-tropical processes would be present in the biophysical features of sub-tropical patterned peatlands, such as the ridge and slough landscape (RSL) within the greater Everglades.

The Everglades RSL is an example of a patterned peatland with parallel drainage topography whose patterning has been relatively stable on the landscape scale for thousands of years (Bernhardt and Willard, 2009) until water management for flood control and water supply was initiated in the early 20th century. The historical RSL was a dominant landscape type of the central portion of the Everglades and is a focus of the current restoration strategy. The RSL consists of long, linear ridges of sawgrass (*Cladium jamaicense* Crantz.); longer hydroperiod sloughs—open water areas with submerged aquatic plants and water lilies; and occasional tree islands oriented parallel to the slow-moving flow of water from northwest to southeast. The RSL also includes a wet prairie community, a short-statured emergent community that is sometimes considered a result of over-draining (McVoy et al., 2011), but is a stable and important community for critically endangered wildlife (Zweig and Kitchens, 2014). This landscape has been fragmented by compartmentalization, impoundment, and reduced flows (Ogden, 2005) and is now in a degraded state (Nungesser, 2011; Wu et al., 2006; Zweig et al., 2011).

We use data from the RSL, explicitly considering wet prairie habitat, to test whether features of a sub-tropical, patterned peatland do, in fact, conform to two patterning mechanisms of scale dependent feedback:

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