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Inferring ecological disturbance in the fossil record: A case study from the late Oligocene of Ethiopia

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ABSTRACT

Environmental disturbances profoundly impact the structure, composition, and diversity of modern forest communities. A review of modern studies demonstrates that important characteristics used to describe fossil angiosperm assemblages, including leaf margin type, plant form, plant diversity, insect herbivore diversity and specialization, and variation in herbivory among plant species, differ between early and late successional forests. Therefore, sequences of fossil floras that include a mix of early and later successional communities may not be appropriate to study long-term temporal trends or biotic effects of climate, latitude, or other variables.

We conducted sedimentological, paleobotanical, and insect damage analyses at two contemporaneous late Oligocene (27–28 Ma) leaf localities in the Chilga Basin, northwest Ethiopia, to test the hypothesis that successional stage explains variation between the assemblages. The Guang River and Bull's Bellow fossil plant localities are stratigraphically equivalent and only 1.5 km apart, but they have no plant species in common. Sedimentary structures at Bull's Bellow suggest multiple episodes of deposition and a more disturbed environment than the single, featureless mudstone that composes the Guang River fossil unit. Bull's Bellow has a significantly higher percentage of plant species with toothed margins, lower plant and insect herbivore damage diversity, and less specialized herbivore damage than Guang. Furthermore, the nearest living relatives of many of the Bull's Bellow plant species are associated with early successional forests, whereas the Guang River plants are a mix of early and late successional species. Thus, the physiological and ecological attributes of the Guang flora are consistent with a more mature forest community, and the differences between the two floras emphasize the importance of collecting multiple floras from the same stratigraphic level in order to account for landscape-level ecological processes. More specifically, accurate estimates of diversity and feeding specialization in tropical, angiosperm-rich fossil assemblages are essential to address adequately the origin and persistence of relatively high species diversity in the modern tropics, and diversity differences between regions such as modern tropical Africa and South America.

1. Introduction

Disturbances like fires, hurricanes, floods, and volcanic eruptions play an integral role in structuring forest communities and may even be essential to maintaining that structure (e.g. Connell, 1978; Denslow, 1987; Hubbell et al., 1999). The process of community recovery following a disturbance is called succession (Harper, 1977), and forest communities often go through a series of compositional and structural changes following disturbances, recognized as successional stages, each with different plant and insect herbivore diversity, composition, and life habits. The fundamental structural and taxonomic differences among stages of forest recovery emphasize the importance of determining the successional stage (or stages) represented by a fossil leaf assemblage. Complete sequences of forest succession are rarely preserved in the plant macrofossil record because of its limited temporal and spatial resolution (Behrensmeyer and Hook, 1992; Burnham et al., 1992). Instead, the macrofloral record preserves either isolated leaf floras representing a single successional stage or time-averaged floras that mix early and later successional stages, although there are exceptions (García Massini et al., 2010). Sampling a mix of early and later successional communities in a stratigraphic sequence may mask true long-term temporal trends, create spurious trends, or obscure correlations with climate (Cross and Taggart, 1982; Burnham, 1994), latitude, or other variables. Furthermore, extracting the deep–time record of alpha and beta diversity accurately, especially at tropical paleolatitudes, is critical for identifying drivers of biodiversity change through time

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(e.g., Wing and Dimichele, 1995; Burnham, 2008), and is relevant to understanding modern differences between regions, for example Africa and South America. Most individual paleobotanical sites sample at the community scale, and thus pertain to alpha diversity, which must be understood in light of successional stage.

Spatial heterogeneity in plant composition and insect herbivory within a forest can be assessed in the paleobotanical record through lateral sampling (e.g., Burnham et al., 1992; Wing et al., 1993; Burnham, 1994; Davies-Vollum and Wing, 1998; DiMichele et al., 2007; Currano, 2009). Several paleobotanical studies have attributed abrupt taxonomic changes across a landscape or through time to post-disturbance succession (e.g., Cross and Taggart, 1982; Taggart and Cross, 1990; Frank and Bend, 2004; Samant and Mohabey, 2009; Bashforth et al., 2010; García Massini et al., 2010; Bashforth et al., 2011). For example, Bashforth et al. (2010, 2011) demonstrated succession in Carboniferous macrofossil deposits by linking sedimentological data to plant taxa. Cross and Taggart's (1982) work on the Miocene Succor Creek palynofloras used analogies to nearest living relatives to conclude that progression through distinct post-disturbance successional stages caused abrupt taxonomic shifts.

Here, we focus on non-taxonomic approaches that can be used to recognize post-disturbance succession in angiosperm-rich fossil assemblages. We first review the ecological literature on plant and insect herbivore responses to disturbance in order to determine what (and whether) structural and functional attributes characterize early vs. late successional angiosperm-dominated tropical forests (Table 1). We then apply these characters to the Oligocene fossil record of the Chilga Basin, northwest Ethiopia. We focus on two stratigraphically equivalent paleofloras that are 1.5 km apart but have no plant species in common. We hypothesize that sedimentological, taxonomic, and paleoecological differences between the two paleofloras will be consistent with communities in different, earlier and later, forest successional stages. This is one of the few paleobotanical studies to attribute physiognomical and paleoecological variations in contemporaneous macrofossil assemblages to succession, and the first to apply insect herbivore damage data to issues involving disturbance and succession.

2. Non-taxonomic approaches to recognizing disturbance in modern settings

2.1. Plant physiology and morphology

The first plants to occupy an area following a disturbance generally have rapid resource acquisition, high growth rates, and a life strategy that maximizes seed production (Grime, 1974). Their leaves often have low leaf mass per area, short leaf lifespan, high nutrient concentrations, and high rates of photosynthesis and respiration (Wright et al., 2004), all of which make them highly palatable to insect herbivores (Coley et al., 1985; Wright et al., 2004). Late successional species display a much wider range of life strategies and leaf traits. Some species invest most of their energy in growth and little in anti-herbivore defenses, making them vulnerable to both generalist and specialist herbivores. Others are adapted to maximize nutrient retention by having a long leaf lifespan, low nutrient concentrations in the leaves, and low photosynthetic and respiration rates (Wright et al., 2004). These species, which are more likely to invest in chemical defenses, should be less palatable to generalist herbivores and display a high percentage of specialized damage.

A variety of studies suggest that plant species with toothed margins are more abundant in early successional forests than in later successional forests. In upper montane Costa Rican forests, about 60% of plant species in early successional forests had toothed margins, versus ~50% in late successional and ~30% in primary forests (Kappelle and Leal, 1996). Subsequent studies in Ecuador, Australia, and North America have demonstrated that plant species with toothed leaves are more common in riparian habitats than distal floodplain or terra firma sites (Burnham, 1994; Burnham et al., 2001; Kowalski and Dilcher, 2003; Greenwood, 2005; Royer et al., 2009). The studies referenced above have proposed three main explanations for the abundance of toothed species in riparian and disturbed habitats: increased availability of water (Bailey and Sinnott, 1915; Wolfe, 1993; Kowalski and Dilcher, 2003; Royer et al., 2009), higher diversity of toothed lianas (Burnham et al., 2001), and selection against untoothed species in disturbed environments (Kappelle and Leal, 1996; Burnham et al., 2001). Higher rates of transpiration, respiration, and photosynthesis have been measured in toothed margins than in untoothed margins (Wolfe, 1993; Royer and Wilf, 2006), interpreted as advantageous in places where rapid leaf expansion would be beneficial. Rapid leaf growth could provide toothed pioneer and ruderal species a competitive advantage in disturbed habitats, especially where water availability is high and can support high rates of transpiration and photosynthesis. Although the mechanism driving the pattern may vary based on geography, phylogeny, and the presence/absence of a well-defined successional sequence (Royer et al., 2009; Little et al., 2010), these data overwhelmingly support a higher percentage of toothed angiosperm species in riparian and disturbed habitats.

Table 1
Key characters for recognizing early versus late successional tropical forests.

Character	Early successional forest	Late successional forest
Leaf margin	Higher percentage toothed species	Lower percentage toothed species
Plant form	Abundant lianas, shrubs, herbs, and ruderal species	Abundant canopy trees and understory vegetation
Plant diversity	Lower	Higher, many rare species
Insect herbivore diversity	Lower	Higher, echoing the higher plant taxonomic and structural diversity
Insect herbivore specialization	Lower percentage of specialized feeders; wider niche breadth	Higher percentage of specialized feeders; narrower niche breadth
Variation in herbivory among plant species	Low. Most species have a lot of damage.	High. Some species have very little damage, whereas others have many types and occurrences of damage.

2.2. Plant ecology

Ecological studies of disturbance and succession in neotropical ecosystems have focused on forest regeneration following timber harvesting, clear-cutting, and hurricanes. Guariguata and Ostertag (2001) review the literature and propose a four stage sequence for tropical terra firma forest recovery. Initial colonization by grasses, herbs, and ferns occurs during the first five years following the disturbance. Years 5–20 are characterized by early forest development, as short-lived pioneers create a closed canopy forest. Lianas, shrubs, and herbs are also an important component of the forest (Guariguata et al., 1997; Pena-Claros and De Boo, 2002; Capers et al., 2005). Species richness steadily increases, and age since disturbance is the best predictor of plant diversity (Aide et al., 1996; Letcher and Chazdon, 2009). Over roughly the next hundred years, long-lived successors replace the short-lived pioneers. Plant species richness can reach pre-disturbance levels in as few as forty years (Aide et al., 1996; Barberena-Arias and Aide, 2003), and richness in late successional forests often exceeds that in primary forests because of the mixing of early successional, late successional, and mature forest tree species (e.g. Vandermeer et al., 2000; Urquhart, 2009). The final stage of recovery is the return to old growth forest composition. The nature and rate of this process depends on seed bank dynamics, soil characteristics, frequency and intensity of disturbance, and distance