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Intraspecific leaf economic trait variation partially explains coffee performance across agroforestry management regimes

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ABSTRACT

The leaf economics spectrum (LES) refers to a suite of correlated leaf-level physiological, morphological, and chemical traits that can be used to describe life-history strategy among plant species. Documenting LES trait variation across environmental gradients has been important for understanding natural plant community dynamics in response to environmental change. However few studies have examined how LES traits covary within crops, or how the LES is correlated with farm-level management practices or goals, especially for important tree-crops such as coffee. We analyzed within-species variation in eight leaf traits in 60 *Coffea arabica* plants, across four management treatments differing in shade-tree species composition, to test (i) if hypothesized LES patterns also describe within-species trait variation, and (ii) if LES traits vary in response to management regimes, or are correlated with reproductive output. Leaf traits varied widely across coffee plants with photosynthetic rates (A_{mass}) and leaf area showing especially high variation. In bivariate and multivariate analyses, coffee leaf traits covaried in patterns consistent with the LES, suggesting shifts between leaf-level resource acquisition and conservation traits among plants may also underpin coffee responses to agroforestry management. The position of a coffee plant along the LES (as described by a principal component analysis score) was best explained by light availability, but did not vary systematically with shade tree composition. LES traits were weakly but significantly related to plant-level reproductive output: coffee plants associated with lower A_{mass} and leaf N values, and higher leaf mass per area were associated with greater reproductive output. In showing that the LES describes resource capture and/or conservation strategies among coffee plants, our study represents a novel adoption of the LES to address applied questions in managed systems. Since within species differences in leaf traits partially explain differences in coffee yield, we also suggest that trait-based research in agroecology can contribute to an applied and comprehensive understanding of crop functional biology, and ultimately, agroecosystem structure and function.

1. Introduction

Diverse agroecosystems are increasingly being recognized as environmentally and economically sustainable alternatives to biologically simplified, conventional agricultural systems (García-Barrios and Ong, 2004; Malézieux et al., 2009). Evidence suggests that diversity in agroecosystems, in particular the integration of perennial crops or trees (agroforestry), augments nutrient capture and cycling processes; processes that in turn lead to reduced reliance on nutrient or water inputs, air and water pollution abatement, and enhancement of other ecosystem services across multiple spatial and temporal scales (Jose, 2009 and references therein). To date, the relationship between perennial planting configurations and crop performance in agroecosystems have typically been evaluated as a suite of isolated parameters (namely growth and reproduction), that vary in relation to site-specific manipulations in environmental conditions (Malézieux et al., 2009). In comparison, relatively few studies have explicitly examined how variation in suites of multiple crop functional traits (*sensu* Violle et al., 2007) – the physical, chemical, anatomical, or phenological characteristics of individual

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plants or plant organs that underpin growth, survival, and reproduction – respond concurrently to management regimes, or are in turn correlated with management goals. This despite important management-related insights that might be gained from such analyses (*e.g.* Fried et al., 2012; Garnier and Navas, 2012; Damour et al., 2014; Gaba et al., 2014).

Ecologists have shown considerable interest in understanding the basis for differences in realized plant performance (*i.e.*, growth, mortality, and reproduction rates) across species, with several hypotheses proposed to explain such differences (*e.g.* Bazzaz, 1979). Subsequent efforts evaluating species differences in functional traits have emerged as a key means to elucidate the mechanistic basis for these differences. While several dimensions of important traits have emerged – including reproductive traits (*e.g.* Moles et al., 2004), wood traits (*e.g.* Chave et al., 2009), and maximum plant size metrics (*e.g.* Thomas, 1996) – the 'leaf economics spectrum' (LES) has received arguably the most extensive attention in studies of plant community dynamics (Wright et al., 2004; Osnas et al., 2013). On one end of the LES are fast-growing, short-lived species that exhibit "resource acquiring" trait syndromes consisting of high leaf-level photosynthetic rates and nitrogen (N) concentrations, and low leaf mass per area (LMA). At the opposite end of the LES are slow-growing, long-lived species that exhibit "resource conserving" trait syndromes including low leaf-level photosynthetic rates and N concentrations and high LMA (Wright et al., 2004).

Evidence supporting the existence of the LES is derived from comparative analyses of bivariate or multivariate covariation in traits across >1000 species (Wright et al., 2004). Although debate has recently emerged regarding the LES (see Poorter et al., 2014), this literature has generally been interpreted to suggest that (i) all vascular plants fall along the global LES somewhere between the two endpoints described above; (ii) data on key LES traits can be used to place a species along the spectrum; and ultimately (iii) a species' position along the LES can be used to describe (or hypothesize) the growth, survival, and reproduction (*i.e.*, the life-history) strategy of a given species. In natural systems, the LES has provided an important framework for understanding critical ecological processes, many of which are highly relevant to agroecological management including soil nutrient availability (*e.g.* Ordonez et al., 2009) and light requirements for plant growth and survival (*e.g.* Baltzer and Thomas, 2007).

Despite extensive studies on LES traits in natural systems, few have extended analyses of LES traits to managed systems (Garnier and Navas, 2012), particularly in common agroforestry systems such as shade coffee. A study by Okubo et al. (2012) has shown how LES trait data conveys more ecologically meaningful descriptions of plant agrodiversity, as compared to conventional metrics such as species richness. Others have used certain LES traits to describe weed or cover crop communities in agroecosystems (Fried et al., 2012; Damour et al., 2014; Gaba et al., 2014). Yet to our knowledge no studies have explicitly examined how LES traits of crops might describe crop responses to agricultural practices, or are correlated with key management goals such as crop yield.

A key aspect limiting applications of the LES concept to such questions is that the LES was devised to describe life-history strategy across species (Wright et al., 2004). Only recently have researchers begun to critically assess the causes and consequences of within-species variation in LES traits (Albert et al., 2010b): a main consideration when applying the LES concept to agro-ecosystems. Some studies on within-species LES trait variation have tested questions in community ecology, evaluating how trait differences across and within species influence plant community assembly or species coexistence (Albert et al., 2010a, 2012; Messier et al., 2010; de Bello et al., 2011; Violle et al., 2012). Others have evaluated the influence of intraspecific variation in LES traits on certain ecological processes such as decomposition (Jackson et al., 2013). Intraspecific variation in LES traits can be evaluated with respect to multiple factors, including differences across similarly sized-conspecifics owing to genetic differences (Ackerly et al., 2000), or plasticity across leaves differing in canopy position or leaf age (Wright et al., 2006); a few studies have examined how LES traits vary within species across plants of different sizes (Martin and Thomas, 2013) or provenance (Robson et al., 2012). No studies have explicitly examined how LES traits vary within crops, directly in response to on-farm management decisions.

This is particularly true for some of the most common agroforestry systems including shade coffee in Central and South America. Shade coffee is largely considered to be a more environmentally benign practice that confers greater ecological and socio-economic benefits, as compared to traditional open-grown coffee monocultures (reviewed by Tejeda-Cruz et al., 2010). Declines in prices for conventionally grown coffee, coupled with certification schemes and price premiums for shade coffee, have made this management approach appealing to a large number of farmers in Latin America (Perfecto et al., 2005).

A critical research need associated with transitioning from traditional to shade coffee, is understanding the causes and consequences of variation in yield between these management practices: differences that are likely to be at least partially moderated by changes in LES traits. C*offea arabica* is widely considered a shade-tolerant plant species that expresses strong plastic leaf-level responses to environmental variability (*e.g.* DaMatta, 2004; Chaves et al., 2008; Matos et al., 2009; Jaramillo-Botero et al., 2010; Cavatte et al., 2012; Rodríguez-López et al., 2014). If the LES also describes ecological strategy in coffee plants, it is possible that these differences may influence reproductive output; though there is relatively little data to support clear predictions on these relationships (Lienin and Kleyer, 2011). Explicit support for how shade tree composition *per se* might affect these expected patterns is scarce, since much of the research on coffee has examined how individual traits differ between a "sun leaf *vs*. shade leaf" dichotomy (DaMatta, 2004). While this dichotomy has been important in understanding coffee leaf traits across broad management regimes (*i.e.*, sun *vs*. shade), this literature does not provide a clear picture on how shade tree species composition affects coffee leaf traits, and potentially, yield.

Addressing some of these uncertainties are critical in understanding how important concepts in trait-based ecology can be used to guide management decisions in agroecosystems. This study was designed to assess four main research questions regarding LES trait variation of coffee in agroforestry systems: (1) do patterns of covariation among LES traits also describe variation in leaf-level resource acquisition/conservation strategies in coffee? If so, then (2) are changes in leaf trait expression systematically associated with shade tree management practices? and (3) across coffee plants, what local-scale environmental variables best predict multivariate leaf trait "syndromes" (*sensu* Reich et al., 1999)? Lastly, (4) do coffee leaf trait syndromes correlate with reproductive output in coffee plants?

2. Methods

2.1. Site description and study design

Our study was based at the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE) located in Turrialba, Costa Rica (09°53′44″ N, 83°40′7″ W). CATIE is situated at 685 m a.s.l. and receives an average of 3200 mm of rainfall year^{-1}, distributed roughly evenly throughout the year as 8 mm day^{-1} with only a mild dry season between February and March (Haggar et al., 2011; Mora and Beer, 2013). Mean annual temperature at CATIE is 23.4 °C