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SPECIAL INVITED PAPER—GLOBAL BIOLOGICAL CHANGE

# DIFFERENCES IN FOREST PLANT FUNCTIONAL TRAIT DISTRIBUTIONS ACROSS LAND-USE AND PRODUCTIVITY GRADIENTS[1]

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- *Premise of study:* Plant functional traits are commonly used as proxies for plant responses to environmental challenges, yet few studies have explored how functional trait distributions differ across gradients of land-use change. By comparing trait distributions in intact forests with those across land-use change gradients, we can improve our understanding of the ways land-use change alters the diversity and functioning of plant communities.
- *Methods:* We examined how the variation and distribution of trait values for seven plant functional traits differ between reference natural forest and three types of land-use conversion (pasture, old-field, or "legacy" sites—regrowth following logging), landscape productivity (NPP) and vegetation strata (tree or non-tree "understory"), in a meta-analysis of studies from 15 landscapes across five continents.
- *Key results:* Although trait variation often differed between land-uses within a landscape, these patterns were rarely consistent across landscapes. The variance and distribution of traits were more likely to differ consistently between natural forest and land-use conversion categories for understory (non-tree) plants than for trees. Landscape productivity did not significantly alter the difference in trait variance between natural forest and land-use conversion categories for any trait except dispersal.
- *Conclusions:* Our results suggest that even for traits well linked to plant environmental response strategies, broad classes of land-use change and landscape productivity are not generally useful indicators of the mechanisms driving compositional changes in human-modified forest systems.

**Key words:** community assembly; forest regeneration; functional trait variation; land-use change; net primary productivity; secondary forest; trait distributions.

Most of the world's natural ecosystems are under pressure from land-use change, species invasions and habitat destruction (Chapin et al., 2000; Davis, 2003; Martin et al., 2012). Land-use change in particular has been identified as one of the greatest threats to biodiversity worldwide (Sala et al., 2000), largely due to the role it plays in habitat loss, fragmentation, isolation, and degradation across most terrestrial ecosystems (Novacek and Cleland, 2001). A pressing research need is to identify how species and communities respond to land-use change and drive changes in biodiversity across human-impacted landscapes (Mayfield et al., 2010); however, the inherent complexity of natural ecosystems makes such research extremely challenging. One way to manage this complexity is to view ecosystems from a functional trait perspective (Garnier et al., 2007) because functional traits are more direct predictors of the role species play in ecosystems than is their taxonomic origin (McGill et al., 2006).

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Functional traits are any measureable feature of an individual that has the potential to impact fitness (Cadotte et al., 2011). The functional traits of most interest for studies of plant communities are those with clear roles in determining where species can live (what environmental conditions they can tolerate), how they acquire resources, grow, reproduce, and how they interact with other species (Westoby et al., 2002; Westoby and Wright, 2006). For example, within a community, species from distinct taxonomic groups may share traits such as leaf size and nitrogen-fixing ability, reflecting life-history strategies that are successful in their specific environment. Hence, by comparing the functional traits present in intact ecosystems with those across land-use change gradients, we can better understand the specific ways that land-use change alters the environment, diversity and the functioning of plant communities (Díaz et al., 2007a; Garnier et al., 2007; Flynn et al., 2009; Laliberté et al., 2010).

Two types of tools are commonly used for studying plant communities from a functional perspective: univariate statistics of trait distributions and multivariate indices of functional diversity (Cadotte et al., 2011). Univariate approaches, such as those used in this study, focus on the distributions of trait values and are useful for identifying the mechanisms driving differences among land-use categories (e.g., Grime, 2006; Messier et al., 2010; Violle et al., 2012). When the distribution of an individual functional trait shifts, contracts, or expands along environmental gradients or among land-use categories, it reflects significant changes in the abiotic and/or biotic processes structuring communities (Cornwell and Ackerly, 2009). It is important when using this approach to look at a range of traits, as each trait relates to a different aspect of plant ecological strategies (Weiher et al., 1999). For instance, differences in the distribution of specific leaf area (SLA) values between primary and selectively logged forests will reflect which resource acquisition and growth strategies are most successful in each of these forest types as well as which types of species were selected for extraction from forests during logging (Lavorel and Garnier, 2002; Wright et al., 2004); differences in the distribution of maximum height values will indicate the role of vertical light gradients in plant competition, and/or the role of disturbance in limiting potential lifespan. Multivariate tools are frequently used because the ecology of species inherently relates to a combination of many traits. For this reason, researchers seeking to capture an overall sense of how communities are impacted by land-use change may identify ecologically similar types of species (based on groups of functional traits) that are lost or negatively impacted by land-use conversion activities (e.g., Laliberté et al., 2010; Cadotte et al., 2011). In this paper, we focus on the former approach, i.e., identifying how specific traits are affected by particular land-use changes. We take this approach because, as detailed later, the distributions of individual traits can provide valuable information about the processes driving community compositional differences, and we thus wished to assess whether shifts in ecologically important traits were consistent across diverse landscapes and productivity gradients.

Work on community assembly (sensu Keddy, 1992) posits that species from a regional species pool pass through a series of "ecological filters," which determine which species are able to establish and persist in a given community. These filters involve dispersal limitations, environmental tolerances, and biotic interactions (HilleRisLambers et al., 2012). Though this filtering idea has further led to the conception of constraints on trait distributions (Shipley, 2010; Laughlin et al., 2011), little is known about what processes actually determine the details of trait distributions. For instance, species can be lost from one end of a trait distribution representing increased pressure on one "type" of species, such as the loss of large-leaved species due to increased water stress, or loss of large-seeded species through the loss of large vertebrate dispersers. Such changes would result in a shift in the trait mean. Other changes in trait distributions, however, would not be evident in the mean. If, for example, both large- and small-seed species were lost, the mean of the distribution might not change appreciably, whereas the dispersion of trait values probably would (i.e., variance would decrease). Alternatively, trait values can be lost (or gained) randomly across the distribution, particularly if an environmental change acts independently of a given trait, e.g., if light becomes more available at all canopy levels, allowing more species of many types to colonize the forest. Such changes may have little effect on the mean but would increase trait variation. Despite the importance of trait distributions in identifying mechanisms driving community differences (Fraterrigo and Rusak, 2008; Messier et al., 2010), many comparative studies of trait–environment relationships only report on community-weighted means (Wright et al., 2001; Garnier et al., 2007; Quétier et al., 2007; Harrison et al., 2010; Feeley et al., 2011, but see Ackerly, 2004 and Cornwell and Ackerly, 2009 for exceptions).

There is a growing literature documenting changes in multivariate functional diversity and univariate trait distributions across gradients of land-use change in grazed (Diaz et al., 2001, 2007b; Vesk et al., 2004; Dorrough and Scroggie, 2008; Laliberté et al., 2012), urban (Thompson and McCarthy, 2008; Duncan et al., 2011) and logged sites (Mayfield et al., 2006; Mabry and Fraterrigo, 2009), but few studies have identified generalizable patterns of trait distributions associated with land-use change across regions. Differences in the trait distributions observed across land-use categories may be complex, partly because land-use intensification is a multifaceted phenomenon. Species and functional differences among communities associated with land-use change are well known to vary widely among ecosystems that differ in their biota and physical environments (Diaz et al., 2007b; Garnier et al., 2007; Dorrough and Scroggie 2008; Laliberté et al., 2010), yet it remains unclear whether trait changes are always associated with certain types of land-use, regardless of differences among sites and ecosystems. Identifying generalizable patterns of functional trait variation among common land-use conversion categories will advance our understanding of the processes driving community changes in heavily used areas and help identify how best to prioritize conservation efforts in human-modified landscapes (Suding and Goldstein, 2008; Mayfield et al., 2010; Douma et al., 2012).

To this end, we examined the distribution and variation of seven plant functional traits in 15 forest landscapes across the planet (Fig. 1, Table 1). These forest landscapes have all undergone extensive land-use changes associated with selective logging and clearing in the last century. We focus on three common types of forest land-use change: (1) conversion of forest to grazed pasture ("pasture"); (2) conversion of forest to agricultural fields, which were maintained and subsequently abandoned ("old-field") and; (3) logging, in which trees are cut but the land is immediately allowed to return to a forested state, leaving a biological legacy of the former forest ("legacy"). We also investigate if landscape productivity influences the relative impacts of land-use change on trait variation. Productivity is known to drive patterns of species diversity at multiple spatial scales (Grime, 1973; Huston, 1997; Chase, 2010) and may

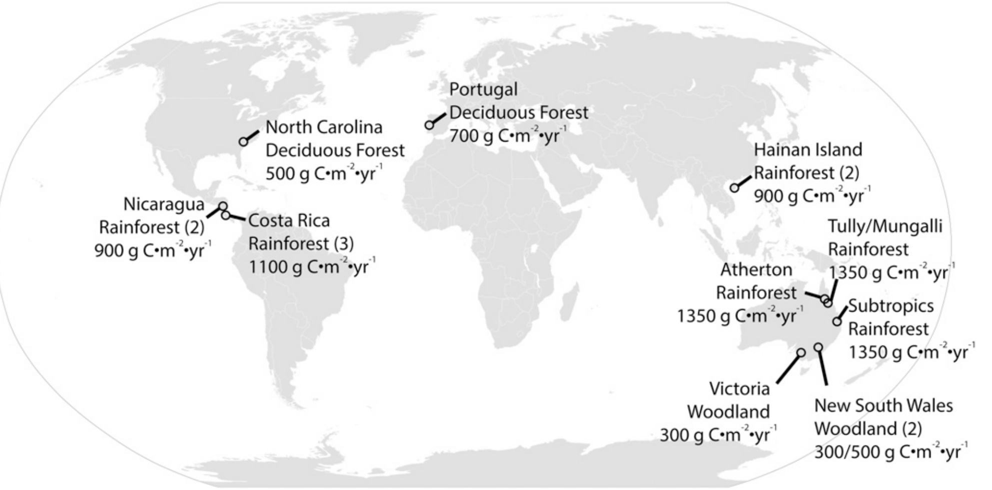

Fig. 1. Map of landscapes used in this study. Landscapes are shown by country and region, along with the ecosystem type for each landscape (deciduous temperate forest: "Deciduous Forest"; subtropical or tropical rainforest: "Rainforest"; or temperate woodland: "Woodland"). If there were data from more than one landscape in a region, the number of landscapes in that region is listed in parentheses following the ecosystem type. The final number listed under each location is the estimated NPP in g carbon·m$^{-2}$·yr$^{-1}$ (if landscapes within a region had different NPP estimates, they are listed separated by a "/"). More information about the original studies is presented in Table 1.

influence the responses of trait distributions to land-use change (Mayfield et al., 2010). For all analyses, we consider trees and non-tree plant species (henceforth called "understory", even in pasture, for consistency) separately, as land-use changes to forest systems may impact these vegetation layers ("vegetation strata") in very different ways (Guariguata and Ostertag, 2001; Chazdon, 2003).

The specific questions we asked were: (1) Are there generalizable patterns in the species diversity and functional trait variation found in similar types of human-modified forests, regardless of global region or forest type? (2) Does trait variation in different land-use conversion categories differ between tree and understory components of forest communities? (3) Can differences in trait variation patterns observed across land-use conversion categories be explained by regional-scale productivity (NPP)?

## MATERIALS AND METHODS

***Data sets***—In this study, we examined how the variation and distribution of seven plant functional traits differ across 15 distinct landscapes in Australia, Costa Rica, Nicaragua, China, Portugal, and the United States (Fig. 1, Table 1). As the goal of the study was to identify generalizable changes in commonly measured, ecologically important functional traits across common human-modified forest types, our analyses were all conducted at a landscape scale, with comparisons made between land-use categories within landscapes rather than across distinct landscapes or studies. This approach ensured that we accounted for, rather than conflated, the inevitable and important differences among the diverse landscapes included in this meta-analysis.

Landscapes included in our analyses represent three broad forest biomes: tropical/subtropical rainforest, temperate deciduous forest, and temperate evergreen woodlands (Fig. 1). In each landscape, plant communities were surveyed across sites representing relatively undisturbed "natural" forest systems (Portuguese "natural forests" are the exception, being old regrowth; C. Queiroz, Stockholm University and the University of Lisbon; personal communication) and one to three land-use conversion categories: pasture, old-field, or legacy (Table 1). The inclusion of "natural forest" sites provides a reference with which to compare trait variation patterns observed for land-use conversion categories in each landscape. "Pasture" sites were logged and converted to permanently grazed cattle pasture between 25 and 100+ years prior to survey (some sites having a history of cropping followed by pasture) and hence, represent the most extreme land-use conversion category. "Old-field" sites were logged and used for crops or pasture, then abandoned between 5 and 65 yr before the survey, meaning they were no longer subject to management at the time the sites were surveyed, thus representing an intermediate level of land-use modification. "Legacy" sites were logged 25–80 yr previously (either semi-selectively or clear-felled) but left to regrow immediately thereafter. Due to the brevity of disturbance and the presence of biological legacies in these sites (seeds and resprouts), this category represents the least intensive land-use change. Though the specific conditions in each study vary, these categories capture major differences in disturbance histories as documented by each study's authors (see author list, Acknowledgments and Table 1).

Vegetation in each landscape was surveyed in one to 24 sites per land-use category, depending on the study. Some studies included all vascular plant species, whereas others only examined trees or understory vegetation (where "understory" refers to non-tree plants and includes pasture; Table 1). Standardized sampling methods were used for all land-use categories within each study and landscape (see original studies for sampling details; Table 1). Sampling effort did, however, vary substantially among studies (Table 1).

***Site productivity***—Site productivity was not directly measured in any of the original studies used here. Hence, we used coarse estimates of net primary productivity (NPP) in g C·m$^{-2}$·yr$^{-1}$ (based on S1, fig. 3 in Haberl et al., 2007) for each landscape. These are potential productivity estimates that vary by whole landscape, not land-use conversion category within landscapes. Estimates ranged from 300–1350 g C·m$^{-2}$·yr$^{-1}$ (Fig. 1). Because we aimed to understand the importance of productivity in driving patterns of trait variation across the globe, these estimates are sufficiently precise for our purposes.

***Functional traits***—We selected seven functional traits for analysis, including four continuous traits: maximum height (height), specific leaf area (SLA), leaf lamina area (LLA), and seed mass, and three categorical traits: growth form (23 categories), pollination mechanism (12 categories), and dispersal mode (7 categories). These traits are a subset of plant functional traits previously suggested to be important for species responses to ecological challenges (Weiher et al., 1999) that were also available for our data sets and have been shown to be responsive to land-use change in other studies (e.g., Garnier et al., 2007). Though some of these traits are related to species responses to the same ecological challenges (such as competition), none provide completely redundant information. For instance, dispersal mode is a frequently used proxy for dispersal ability. Seed mass is a related trait, but it fundamentally represents the trade-off between producing many small propagules able to reach safe sites, and few large propagules able to withstand hazards of seedling establishment (Leishman et al., 2000; Levine and Murrell, 2003). Likewise, SLA and LLA are both related to establishment and competitive ability, while SLA also represents the trade-off between resource acquisition and resource conservation (Wright et al., 2004).

TABLE 1. Details of landscapes examined in this study. “Country” indicates the country in which that landscape is located and “Landscape” identifies the location (either the nearest town or general region) within the country of the study. “Land-use categories” shows which land-use categories are represented in a given dataset (landscape): “N” = natural forest, “P” = pasture, “OF” = old-field, and “L” = legacy forest. “Trees/Understory (data type)” indicates whether surveys recorded trees, understory plants or both: “T” = trees and “U” = understory and “data type” describes the type of data collected: “PA” = presence/absence, “Abnd” = abundance, and “% cover” = percentage cover. “Plot size (no. of plots)” shows the size of sampled plots within a given landscape in hectares (ha) for trees (or both trees and understory) and in meters ($m^2$) for understory plant sampling, and the total number of plots sampled in that landscape is given in parenthesis. (T) or (U) next to plot size is listed in cases where trees and understory plants were surveyed with different plot sizes. Within a landscape, the sample plot size was always consistent. “Total no. of species” is the total number of species recorded for a given landscape. References for the original studies of each landscape are listed under “Study reference”.

| Country | Landscape location | Land-use categories | Trees/Understory (data type) | Plot size (no. of plots) | Total no. of species | Study reference |
|---|---|---|---|---|---|---|
| Australia | Tully, Queensland | N; OF; L | T/U (PA) | 0.1 ha (8) | 285 | Butler et al., in press |
| Australia | Mungalli, Queensland | N; OF | T/U (Abnd) | 0.25 ha (6) | 162 | J. A. Wells (unpublished data) |
| Australia | Atherton, Queensland | N; P; OF | T/U (PA) | 0.039 ha (35) | 309 | Kanowski et al., 2003;<br>Catterall et al., 2004;<br>Wardell-Johnson et al., 2005 |
| Australia | Subtropical Queensland | N; P; OF | T/U (PA) | 0.039 ha (35) | 336 | Kanowski et al., 2003;<br>Catterall et al., 2004;<br>Wardell-Johnson et al., 2005 |
| Australia | New South Wales | N; L | T/U (% cover) | 0.04 ha (39) | 52 | Thompson and Eldridge, 2005a, b |
| Australia | New South Wales | N; L | T/U (% cover) | 0.04 ha (20) | 52 | Thompson and Eldridge, 2005a, b |
| Australia | Victoria | N; L | T/U (% cover) | 1.0 ha (T) 30 $m^2$ (U) (20) | 88 | Morgan (unpublished data) |
| Costa Rica | Las Cruces, Puntarenas | N; P; L | U (Abnd) | 20 $m^2$ (17) | 388 | Mayfield and Daily, 2005;<br>Mayfield et al., 2006 |
| Costa Rica | La Palma, Puntarenas | N; P; L | U (Abnd) | 20 $m^2$ (17) | 366 | Mayfield and Daily, 2005;<br>Mayfield et al., 2006 |
| Costa Rica | Pt. Jimenez, Puntarenas | N; P; L | U (Abnd) | 20 $m^2$ (17) | 348 | Mayfield and Daily, 2005;<br>Mayfield et al., 2006 |
| Nicaragua | Rivas | N; P; OF | T (Abnd) | 4.0 ha (4) | 146 | Sánchez et al., 2005a |
| Nicaragua | Matiguas | N; P; OF | T (Abnd) | 4.0 ha (4) | 173 | Sánchez et al., 2005b |
| China | Hainan Island | N; OF; L | T (Abnd) | 1.0 ha (8) | 378 | Ding et al., 2012 |
| China | Hainan Island | N; OF; L | T (Abnd) | 1.0 ha (6) | 311 | Ding et al., 2012 |
| Portugal | Minho | N; P; OF | T/U (PA) | 0.13 ha (T) 64 $m^2$ (U) (18) | 108 | Queiroz and Pereira (unpublished data) |
| United States | North Carolina | N; OF; L | T/U (% cover) | 4 ha (T) 40.0 $m^2$ (U) (13) | 35 | Pearson et al., 1998 |

We compiled functional trait data for all data sets included in this meta-analysis (though not all traits were available for all data sets), ensuring that consistent definitions, units, and measurement methods were applied. For any traits that were not measured using comparable methods in the original studies (Table 1), new trait data were collected or collated (from published sources or herbarium specimens) according to standard protocols. For principal data sources and references for each study, see Table S4 in Laliberté et al. (2010).

***Data analysis—****Functional variation*—For all analyses, functional variation was calculated as standard deviation (SD) for continuous traits and as Shannon’s index (Magurran, 1988) for categorical traits. Both Shannon’s index and SD incorporate abundance data; thus, all of our variation estimates account for dominance of particular trait values where abundance data are available (Table 1; Diaz et al., 2007a). Shannon’s index was calculated for categorical traits using the number of species (or individuals if abundance data were available) with each functional type.

We also ran all analyses of continuous trait variation using functional dispersion (FDis, Laliberté and Legendre, 2010). When applied to single traits, FDis is highly correlated with SD and produced very similar results. FDis is not appropriate for characterizing the variation of categorical traits in this context and thus was not calculated for these traits (E. Laliberté, The University of Western Australia, personal communication). For brevity, we only present results based on SD for continuous traits.

*Differences in species diversity and functional variation across land-use change categories*—We used mixed-effects meta-ANOVAs to assess across-study changes in species richness and trait variation associated with conversion of forest to other land-uses. We expressed pairwise differences (between natural forest and each land-use conversion category) using log response ratios (Hedges et al., 1999). For a given landscape within a study, the natural forest plots were treated as “controls”, and the other land-uses were treated as “treatments”. For example, when comparing trait variation of natural forest to that of legacy forest within a particular landscape, the response ratio was quantified as $\mathrm{RR} = \ln\left(\bar{x}_{\mathrm{nat}} / \bar{x}_{\mathrm{leg}}\right)$, where $\bar{x}_{\mathrm{nat}}$ and $\bar{x}_{\mathrm{leg}}$ are the mean values for trait variation (or species richness) for the natural forest and legacy plots respectively. Positive values indicate trait variation that is greater in natural forest and negative values indicate the opposite. Values around zero indicate equivalent trait variation to natural forest. In all but one study there were multiple plots per land-use per landscape, so it was possible to calculate the variance associated with each RR value, as $s^2_{\mathrm{RR}} = \left[ s^2_{\mathrm{nat}} \middle/ \left( n_{\mathrm{nat}} \cdot \bar{x}^2_{\mathrm{nat}} \right) \right] + \left[ s^2_{\mathrm{leg}} \middle/ \left( n_{\mathrm{leg}} \cdot \bar{x}^2_{\mathrm{leg}} \right) \right]$, where $s^2_{\mathrm{nat}}$ and $s^2_{\mathrm{leg}}$ are the respective sample variances for the natural forest and legacy plots and $n_{\mathrm{nat}}$ and $n_{\mathrm{leg}}$ are the respective number of replicate plots in natural forest and legacy forest. We calculated response ratios and associated variances separately for tree and understory strata. RR values for “trees in pasture” were available for only one study and thus were omitted from this analysis.

Mixed-effects meta-ANOVAs (and meta-regressions) do not treat each $\mathrm{RR}_i$ as fixed, but rather they are drawn from their own distributions with variance equal to $s^2_{\mathrm{RR}i}$ (i.e., the variation among replicates for a given treatment). Fixed effect explanatory variables can be included within this framework to test whether RR values vary systematically along covariates of interest or within particular groupings (factors). This approach is appealing because it incorporates variation among study replicates while estimating overall effects of variables of interest. We did not include landscape as an additional random effect because such “three-level” meta-analyses have not yet been fully implemented in the statistical package we used (*Metafor*, by Viechtbauer, 2012), in the R-language, and we were hesitant to consider overly complex models given the sample size issues discussed. Refer to Hedges et al. (1999) for a detailed explanation of used meta-analytical models and their application in ecology.

For this particular analysis, the single explanatory variable in all meta-ANOVA models was a factor with five levels: legacy (tree stratum), old-field (tree stratum), legacy (understory), old-field (understory), and pasture (understory). Pasture (tree stratum) was omitted due to a lack of data. We fit all models without an intercept so that each factor level was compared to zero, with zero being the reference value equivalent to natural forests on the RR scale. The Knapp & Hartung adjustment (Knapp and Hartung, 2003) for testing the significance of coefficients was applied in all cases.

*Differences in trait distributions among land-use conversion categories*—To determine how the distribution of trait values differed between natural forest and each land-use conversion category, we examined differences in the 10th, 50th, and 90th percentiles of trait values for each continuous trait. We first calculated the percentiles for natural forest and each land-use conversion category for each landscape separately (averaging across replicate plots within each landscape and separating tree and understory strata). For each land-use conversion (e.g., from forest to legacy), we then tested if percentile changes were consistent across study landscapes using paired two-tailed Wilcoxon signed-rank tests. We used paired tests to ensure that comparisons were maintained within study landscapes. To present these results graphically, we calculated the proportional change in percentiles from forest to each of the other land-use categories, as shown in Fig. 2.

*Trait variation across an NPP gradient and land-use conversion categories*—For this analysis, we used similar mixed-effects meta-analysis models as those described already. The main difference was that we included NPP as a continuous covariate in the models to test whether the effects of land-use change on trait variation vary with NPP. Once again, the response variables were the RRs for each trait (RRs for species richness were not considered in this analysis). Twelve candidate models with different combinations of explanatory variables were fit for each trait (Appendix S1). Candidate models varied in complexity from a simple model with just an overall intercept to models with multiple two-way interaction terms. Three-way interaction terms were not tested in the most complex models because of sample size limitations. As a conservative measure, data type (presence/absence, abundance) was included as a covariate in all but the simplest candidate models. Models were compared using the second order Akaike information criterion corrected for small sample sizes (AICc, Burnham and Anderson, 2002). All AICc values were calculated using the unrestricted likelihood because our interest was in comparing models with different fixed effects. All tested models for each trait are shown in full in Appendix S1.

All analyses were completed in R (R Development Core Team, 2012). All mixed-effects meta-analysis models were fit using the *Metafor* library (Viechtbauer, 2012).

## RESULTS

***Differences in species richness and trait variation between natural forest and land-use conversion categories*—**We found only one concomitant decline in species richness and trait variation in our analysis. Tree species richness was significantly lower in old-fields compared to natural forest, as was SLA variation (Table 2). Other than this, species richness and trait variation did not differ significantly between natural forests and either legacy forests or old-fields. Pastures however, showed a greater number of differences in trait variation compared to natural forests. Specifically, we found significantly greater variation in the dispersal modes and leaf sizes (LLA) represented in pasture compared with natural forest understories and significantly less variation in plant heights, seed masses, and pollination mechanisms in pasture compared with forest understories (Table 2).

***Differences in trait distributions across land-use conversion categories*—**The distribution of all four continuous traits varied extensively in individual landscapes (individual results not shown) but showed few consistent significant changes with any land-use conversion type (Fig. 2, Appendix 1). The distributional patterns that did change consistently across all examined landscapes were almost all in the understory stratum (Fig. 2A). Understory vegetation showed more significant changes in trait distributions for seed mass, leaf area, and plant height, including significant declines in the size of seeds and leaves in pastures compared to natural forests, and a shift of the leaf lamina area (LLA) distribution to lower values in legacy forests compared with natural forests. Understory plant heights generally declined in conversions of forest to pasture and legacy forests, but this was not significant across all studies (Fig. 2A). Heights only declined significantly in understory plants for natural forest conversions to old-fields (Fig. 2A). The only significant distributional change in the tree stratum was a significant decline in maximum height with the conversion of natural forest to old-fields (Fig. 2B). This change is consistent with a decline in taller tree heights (significant declines in the median and 90th percentile; Fig. 2B) without much change in the height of the shortest trees (10th percentile).

***NPP, land-use conversion categories, and trait variation*—**We found very little evidence that landscape-scale NPP, land-use conversion category or vegetation stratum are important for driving differences in functional trait variation between natural forests and land-use conversion categories (Fig. 3; Table 3; Appendix S1). In fact, we found almost no evidence for any change in trait variation with land-use conversion for the majority of traits (clustering of RR points around the 0 line in Fig. 3). There was significantly less trait variation in pasture than natural forest for height and seed mass variation (height and seed mass panels in Fig. 3; and land-use was included in the best model for height and seed mass in Table 3 and Appendix S1). NPP was only a significant factor for explaining how variation in dispersal modes differed between natural forest and all other land-uses combined (a positive slope for the fitted line in the dispersal panel of Fig. 3, Table 3, and Appendix S1). Specifically, we found that as landscape-scale NPP increased, dispersal mode variation increased in all land-use conversion categories compared to natural forest (Fig. 3). We also found that regardless of land-use conversion type, variation in understory leaf area was higher in modified than natural forest (shown with the two separate fitted lines in the leaf area panel of Fig. 3.)

## DISCUSSION

In this meta-analytical study, we found scant evidence that the type of land-use conversion or the productivity of the landscape (NPP) led to consistent differences in the trait distributions observed in human-altered compared to natural forests. This lack of evidence is surprising given that all of the traits we examined have well-established links to species' responses to environmental challenges associated with deforestation and environmental degradation (Laliberté et al. 2010).

In a recent conceptual paper on this topic, various mechanisms were described for why trait distributions may expand or contract following land-use change (Mayfield et al., 2010). For instance, environmental filters can reduce trait variation, while the removal of a competitive dominant may increase trait variation. The lack of consistent differences in trait distributions among land-uses and across our diverse set of study landscapes may occur for two quite different reasons. First, chance plays a key role in driving trait distributions. Second, systematic (non-random) processes vary in their importance across distinct forest systems. In other words, the ecological, biogeographic, evolutionary, and land-use histories of landscapes are more important for determining which processes drive changes in forest

TABLE 2. Changes in species richness and trait variation resulting from conversion of natural forest to different land-uses. Values shown are estimated changes with associated standard errors and the *t* values used in significance testing. Significant changes (declines or increases) in species richness and trait variation are in boldface and indicated with the level of significance as: *** $P < 0.001$, ** $0.001 > P < 0.01$, * $0.01 > P < 0.05$. Results are from mixed-effects meta-ANOVAs; one model was fit for species richness and separate models were fit for each trait. Changes (from forest to other land-uses) were expressed as log response ratios (RR), each with an associated variance term capturing variation among replicates (within studies). To test for changes due to land-use conversion, models were parameterized to compare coefficients for each combination of land-use and vegetation stratum to zero (zero indicates no change from forest). The Knapp and Hartung 2003 adjustment for testing the significance of coefficients was applied in all cases. LLA = leaf area, SLA = specific leaf area, Poll mechanism = pollination mechanism.

| | Tree stratum: Estimated change (SE), *t* | | Understory stratum: Estimated change (SE), *t* | | |
|---|---|---|---|---|---|
| Character (*n*) | Forest to Legacy | Forest to Old-field | Forest to Legacy | Forest to Old-field | Forest to Pasture |
| Species richness (34) | −0.01 (0.23), −0.05 | **-0.51* (0.19), −2.64** | −0.02 (0.19), −0.13 | −0.26 (0.22), −1.19 | −0.14 (0.21), −0.66 |
| Trait variation | | | | | |
| Height (26) | −0.01 (0.12), −0.06 | −0.09 (0.09), −1.00 | −0.02 (0.13), −0.14 | −0.01 (0.11), −0.13 | **-0.51** (0.15), −3.43** |
| LLA (31) | −0.03 (0.09) −0.28 | −0.04 (0.07), −0.57 | 0.14 (0.07, 2.01) | 0.03 (0.08), 0.37 | **0.24** (0.07), 3.44** |
| SLA (18) | −0.11 (0.15), −0.72 | **-0.28* (0.12), −2.29** | 0.11 (0.12), 0.94 | 0.004 (0.45), 0.01 | −0.10 (0.13), −0.76 |
| Seed mass (32) | 0.05 (0.19), 0.25 | −0.09 (0.12), −0.69 | −0.30 (0.15), −1.98 | −0.24 (0.13), −1.78 | **-1.05*** (0.18), −5.98** |
| Growth form (29) | 0.05 (0.13), 0.36 | −0.06 (0.08), −0.75 | 0.001 (0.09), 0.01 | 0.01 (0.09), 0.13 | −0.15 (0.08), −1.85 |
| Dispersal mode (33) | 0.15 (0.15), 0.97 | 0.08 (0.13), 0.57 | 0.06 (0.09), 0.68 | 0.18 (0.10), 1.91 | **0.30* (0.11), 2.70** |
| Poll mechanism (29) | −0.008 (0.16), −0.05 | −0.04 (0.09), −0.42 | −0.13 (0.08), −1.70 | −0.13 (0.07), −1.80 | **-0.26** (0.08), −3.47** |

communities following land-use change (and thus the trait values found in those communities) than the broad type of disturbance or the productivity of the system.

Alongside the lack of consistent differences in trait distributions across land-use conversion categories, two consistent patterns are worth noting. First, the variation of functional traits of trees and understory plants (including non-tree pasture plants) differs between land-use conversion categories and natural forest in distinct ways (Table 2, Fig. 2), suggesting that different traits are important for defining community responses to land-use change in forest canopies and forest understories. These contrasting results for trees and understory plants are noteworthy because studies of forest communities, in the context of land-use change, generally focus on trees only or, in a few cases, understory species but not trees (Benítez-Malvido and Martínez-Ramos, 2003; Mayfield et al., 2006, 2005). Few studies, however, acknowledge the importance of examining understory forest vegetation separately or with different traits for trees and understory vegetation, selected based on the distinct impacts land-use changes have on these vegetation strata. Our results suggest that such an approach is important for understanding how land-use change fully impacts forest communities.

Second, there is limited evidence that species richness and trait variation decline concomitantly following conversion from natural forests and other land-uses (Table 1). This pattern supports the suggestion of Mayfield et al. (2010) that land-use conversion leads to changes in trait distributions via modifications in the processes driving community assembly rather than through the reduction of species richness following land-use change.

***Differences between natural forest and pasture***—The only significantly consistent differences in trait variation observed for any traits in this study were between pasture and natural forest (Table 2). We focus here on the processes influencing the understory (non-tree) plants in pastures and forests, because the lack of trees in pastures reflects direct human manipulations rather than ecological processes. Some pastures are actively maintained; the managed flora thus determines trait distributions in such pastures. However, many pasture systems are planted and then left relatively unmaintained, with many native and exotic species colonizing these "open" systems. The majority of the pastures included in this study fit this type.

Mayfield et al. (2010) proposed that changes to the abiotic and biotic environment (environmental filters and competitive dynamics) are likely to determine how species richness and functional trait variation differ in original forest systems compared to land-use conversion categories such as open pasture. When forests are converted to pasture, the most common and immediate changes are an increase in the solar radiation available to surviving and recolonizing plants, the introduction of abundant grass and broadleaf herbaceous species and increased grazing pressure from livestock (Reiners et al., 1994). Annual pasture grasses and associated broad-leaved species generally have high growth rates, high SLA (reflecting high photosynthetic rates per unit of biomass; Garnier, 1992; Shipley et al., 2005), small seeds (reproductive strategies involving many small seeds that disperse and establish widely; Leishman et al., 2000) and are wind-pollinated. All of these traits correspond with life-history strategies involving rapid growth, establishment, and spread. In contrast, traits in forest understories tend toward the opposite end of the life-history spectrum: slower growth, low SLA, and investment in fewer offspring with a wide range of dispersal and pollination strategies (Valladares et al., 2002; Mayfield et al., 2005, 2006). Due to the differences in life-history strategies that typically dominate these distinct communities, the filters created by grazing, and intense competition from pasture grasses, we expected to find significantly lower mean trait values and less trait variation for all continuous traits (except SLA, for which we expected a mean increase, reflecting the values for fast growing annual grasses) in pasture compared to forest. We also expected the number of different dispersal modes in pasture to be higher than in forest due to the influx of species with seeds dispersed through exozoochory (on the outside of animals) into pastures (Mouissie et al., 2005; Manzano and Malo, 2006) without a loss of most dispersal modes also represented in forests (Mayfield et al., 2006).

These patterns are not, however, entirely what we found (Table 2, Fig. 2). Only seed mass was found to be significantly smaller in pastures compared to natural forests (Fig. 2), with a non-significant decline in height values also apparent (Fig. 2). In general, there were surprisingly few significant differences in the distribution of traits in natural forest understory compared

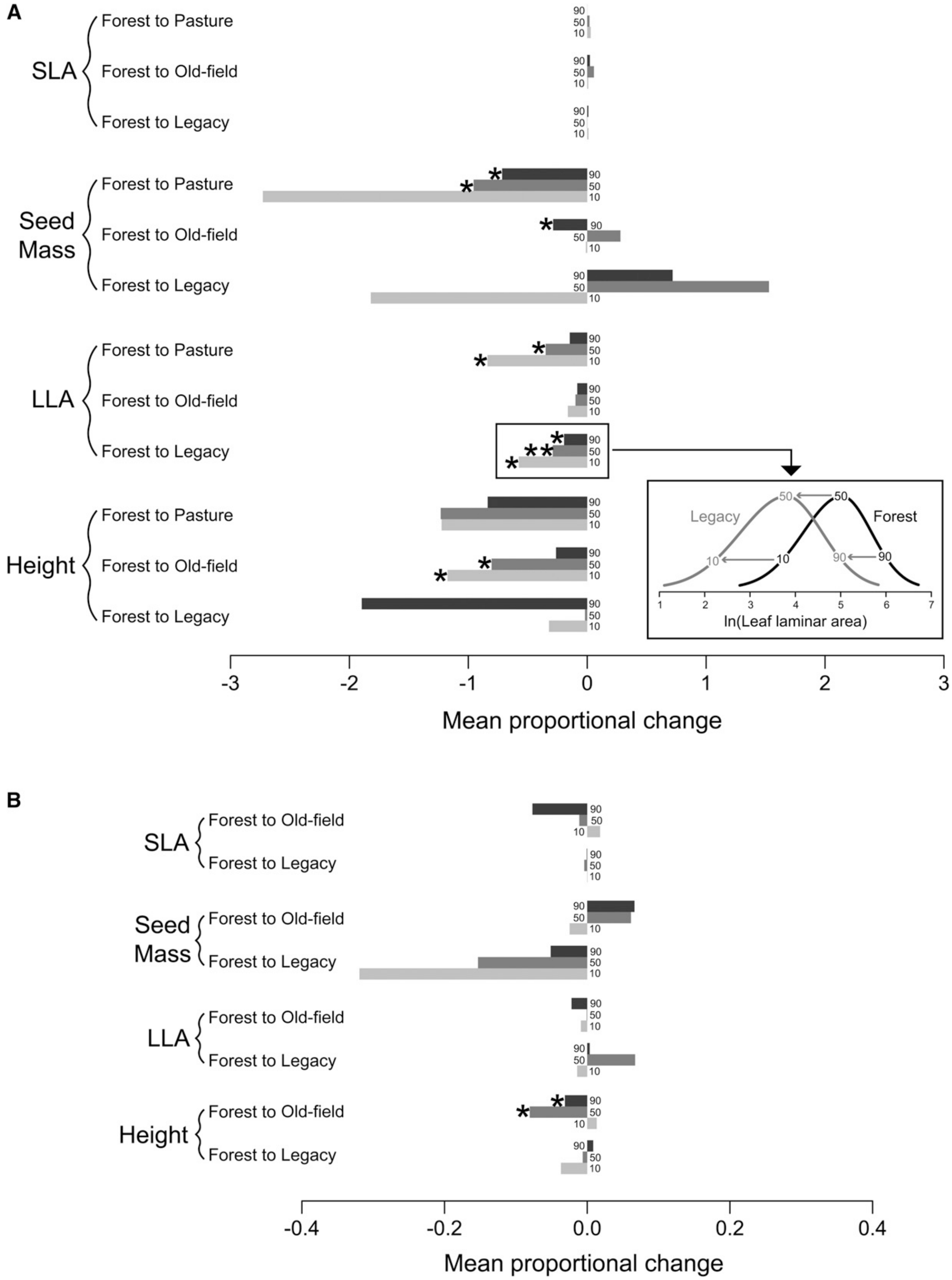

Fig. 2. Changes in the distributions of continuous traits (all ln-transformed) associated with the conversion of natural forest to other land-uses for (A) understory and (B) tree stratum. For each land-use conversion category, bars indicate the proportional change in the 10th, 50th, and 90th percentiles (averaged over the relevant studies). See inset in (A) to assist interpretation. Asterisks indicate significant changes as determined using paired two-tailed Wilcox sign rank tests (refer to methods and Appendix 1 for statistical details). Significant changes are generally those that are consistent (i.e., in the same direction) across all studies.

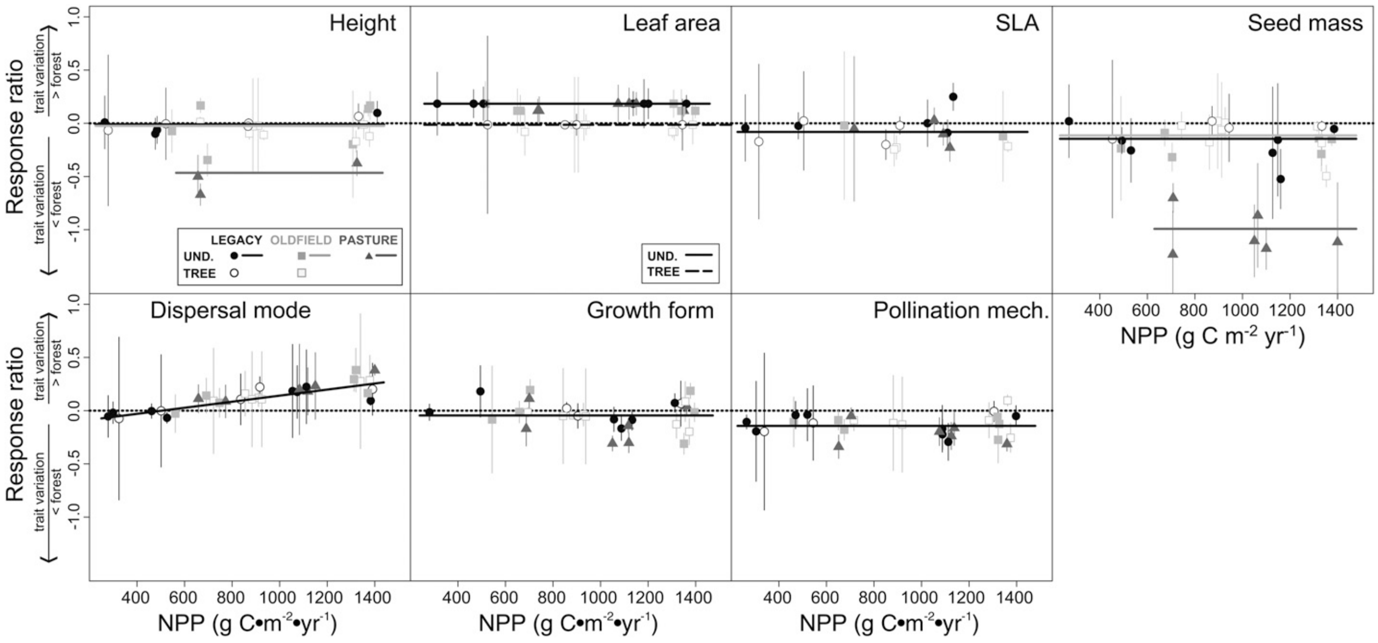

Fig. 3. Plots of net primary productivity (NPP) vs. changes in trait variation for each of the eight traits considered. Positive *y*-values (log response ratios, RR) indicate increases in trait variation compared to natural forests and negative values indicate decreases in trait variation. Fitted relationships are from the most supported mixed-effects meta-regression models for each trait (refer to Table 3 and Appendix S1). Points are modeled RR estimates and bars are standard errors indicating the distribution from which RR values were drawn. As many landscapes had the same coarse NPP estimate, points were jittered around NPP values for clarity of results. Symbols in all plots follow the legend in the height plot. For all traits, RRs are plotted against NPP even if NPP was not included in the "most-supported" model (Table 3). Horizontal fitted lines are shown when the most-supported models did not include NPP (and hence had zero slope). A separate line-type legend is provided for leaf area for which vegetation stratum was a significant factor. As a conservative measure, data type (PA or abundance data) was included as a covariate in all but the simplest candidate models; however, it was not significant for any trait. For models that included data type (height, LLA, seed mass, and dispersal mode), only the fitted lines for abundance data are shown, but these were virtually identical to the lines for PA data.

to pastures (Fig. 2), reflecting a wide range of responses across the landscapes tested here (results for individual studies not shown). The lack of a significant generalizable pattern may result from differences in the details of the environmental filters and competitive dynamics structuring open pasture communities in these different landscapes.

Patterns in trait *variation* (rather than absolute values) were more consistent with our predictions, with significantly less variation in heights, seed masses, and pollination mechanisms and more variation in dispersal modes in pasture compared to natural forest understories (Table 2). The unexpected pattern of higher variation in leaf size in pastures than forests may be due to an influx of pasture grasses combined with new broad-leaved, weedy species and broad-leaved survivors from forest systems (Katovai et al., 2012). From a process perspective, this pattern probably results from a release from strong low-light filters that restrict many small-leaved species from the regional species pool from persisting in forest understories (Mayfield et al., 2010). The relatively high level of trait variation for some traits in pastures may be important for explaining why pastures are often extremely resilient to changes (for instance, restoration back to forest systems; Cramer et al., 2008).

Given that the analyses in this study assess changes in trait distributions relative to reference forests in the same landscape, it is important to note that the species pool supplying both forest and pasture communities is the same within each landscape. Thus, although the pasture environment is clearly very different from forest understory, certain regional filters may already have shaped the trait distributions observed across all vegetation within each landscape. Thus, region-wide restrictions may initially limit the number of species with very different trait values that colonize pastures.

***Differences between mature forests and old-fields—***Tree species richness in old-fields was consistently and significantly lower than in natural forests (Table 2). Numerous studies have examined the diversity of plant species in old-fields compared to natural forests (Reiners et al., 1994; Fujisaka et al., 2000; Mayfield and Daily, 2005 to name a few), with variable results. Unlike these past studies, we analyzed tree and understory species separately and found that species diversity patterns differed for these strata, with significantly lower species richness for trees and no consistent pattern for understory plants. Lower tree species richness in old-fields compared with natural forest may indicate that original climax trees are present only as seedlings and saplings, have not yet recolonized, or are no longer favored in these sites due to a decline in recruitment microsites. Old-fields may thus be slow to return to states similar to predisturbance forest because propagules (seeds or ramets) of many of the original forest tree species have been eliminated or heavily reduced during these systems' agricultural phase, and these species are slower to colonize and/or reach maturity and reproduce in situ (Foster and Tilman, 2000; Standish et al., 2007; Cramer et al., 2008). Though understory diversity was not significantly different from reference forest sites, it is likely that the compositions of these communities do differ, as seen in

TABLE 3. Summaries of the most supported meta-regression models for each trait, as indicated by AICc weights applied to 12 candidate models (refer to Appendix S1). Response variables were log response ratios (RR) indicating deviation from natural forest reference communities in each study landscape. Shown for each model are the estimated coefficients as well as associated standard errors, *t* values and *P* values (the Knapp and Hartung [2003] adjustment for testing the significance of coefficients was applied in all cases). Only those variables included in the most-supported model are shown (land-use [LU], net primary productivity [NPP], data type, and/or stratum). Appendix S1 shows all candidate models tested for each trait. Each of the models summarized here are plotted in Fig. 3, with variation in NPP shown on the abscissa whether NPP was included in the most supported model for each trait.

| Model terms | Estimate | SE | *t* value | *P* value |
|---|---|---|---|---|
| A) Height variation | | | | |
| Model structure: *y* ~ LU + Data type | | | | |
| Intercept (LU = Legacy) | −0.010 | 0.084 | −0.116 | 0.909 |
| Intercept shift when LU = Old-field | −0.015 | 0.130 | −0.116 | 0.908 |
| Intercept shift when LU = Pasture | −0.456 | 0.211 | −2.159 | 0.042 |
| Data type | −0.049 | 0.131 | −0.377 | 0.71 |
| B) Leaf area variation | | | | |
| Model Structure: *y* ~ Strata + Data type | | | | |
| Intercept (Stratum = Tree) | −0.014 | 0.037 | −0.369 | 0.715 |
| Intercept shift when Stratum = Understory | 0.198 | 0.049 | 4.037 | <0.001 |
| Data type | −0.066 | 0.049 | −1.342 | 0.190 |
| C) SLA variation | | | | |
| Model Structure: *y* ~ 1 | | | | |
| Intercept | −0.081 | 0.069 | −1.180 | 0.254 |
| D) Seed mass variation | | | | |
| Model structure: *y* ~ LU + Data type | | | | |
| Intercept (LU = Legacy) | −0.146 | 0.115 | −1.273 | 0.214 |
| Intercept shift when LU = Old-field | 0.033 | 0.172 | 0.19 | 0.851 |
| Intercept shift when LU = Pasture | −0.850 | 0.227 | −3.741 | <0.001 |
| E) Dispersal mode variation | | | | |
| Model structure: *y* ~ NPP + Data type | | | | |
| Intercept | −0.141 | 0.101 | −1.389 | 0.175 |
| NPP | 3.00E-04 | 1.00E-04 | 2.688 | 0.012 |
| Data type | 0.070 | 0.084 | 0.833 | 0.411 |
| F) Growth form variation | | | | |
| Model structure: *y* ~ 1 | | | | |
| Intercept | −0.045 | 0.040 | −1.140 | 0.264 |
| G) Pollination mechanism variation | | | | |
| Model structure: y ~ 1 | | | | |
| Intercept | −0.143 | 0.039 | −3.656 | 0.001 |

individual studies from this analysis (e.g., J. A. Wells, unpublished data) and in light of previous studies showing slow recovery of species composition in old-fields (Standish et al., 2007; Cramer et al., 2008).

Few significant differences in trait distributions were observed between old-fields and natural forest (Fig. 2, Table 2). Variation in SLA in the tree stratum was significantly lower in old-fields, the only trait to differ in a similar way to species richness for the same stratum. This pattern may reflect a dominance of pioneer tree species that are more similar in growth strategies than are found in mature forest.

We also found that the whole distribution of plant heights shifted to lower values for trees and understory plants in old-fields compared with natural forest (Fig. 2). This decline resulted from more short species and fewer tall species in old-fields compared with mature forest both in the understory and the canopy (Fig. 2). This pattern may relate to the combination of poor soil conditions and limited recruitment in many old-fields (Cramer et al., 2008). Given what is known about old-field development, we expected significant differences in dispersal modes and seed masses in old-fields compared with mature forest (Standish et al., 2007; Cramer et al., 2008). However, we observed no significant differences in mean dispersal modes (though differences did occur within some individual studies; results not shown) and seed mass only appeared to change for understory plants, seen as a decline in the 90th percentile (Fig. 2). Therefore, these traits do not appear to show a lasting signal of old-field assembly processes, at least in old-field communities of the ages surveyed in this study. Though height may relate to these processes of old-field assembly, it alone does not provide a clear indication of the mechanism driving differences from natural forests (Standish et al., 2007, Cramer et al., 2008).

***Differences between mature forest and legacy forest—*** Legacy forests were, as expected, the land-use conversion type that was most similar to natural forest, with almost no significant differences in species richness, trait variation, or trait distributions compared with reference forest systems (Costa and Magnusson, 2002; Table 2, Fig. 2). The one significant difference that was observed was significantly smaller leaf sizes in legacy understories compared to understories in natural forests. This change results from a reduction in large-leaved species and a similar increase in the number of small-leaved understory species (Fig. 2). This pattern likely reflects that even after many years of recovery (25–80 yr) the understory environment of legacy forests has more light, resulting in a restriction of understory species adapted to very low light environments and a release of understory species that were restricted to light gaps, edges, and non-forest systems before logging occurred in these landscapes. It is also likely that legacy forest less than 80 yr old have yet to achieve the structural complexity and the associated microclimatic complexity of mature forest, which may be reflected in fewer very large-leaved species (cf. Richards, 1996).

***The role of NPP and land-use conversion category in driving changes in trait variation—*** Though the role of productivity in driving trait variation differences among land-uses have been examined before (Vesk et al., 2004; Diaz et al., 2007b; Laliberté and Tylianakis, 2012), to our knowledge, no studies have reported on whether landscape productivity alters patterns of trait distributions in land-use conversion categories compared with reference natural forest. We predicted such differences would occur due to the growing evidence that system productivity can determine which ecological processes structure community diversity (Chase, 2010). With the exception of dispersal, however, we found no evidence that landscape-scale productivity alters the ways that traits are distributed in land-use conversion categories compared with natural forests. We thus conclude that though productivity may affect the processes involved in community assembly, it does so consistently across land-use types for most traits.

The significant positive relationship between dispersal mode RR (i.e., the change in diversity of modes) and landscape productivity suggests, however, that in high productivity landscapes, there are more dispersal modes in all land-use conversion categories than in natural forest (Fig. 3). In contrast, low productivity landscapes do not show this pattern, which may reflect a greater diversity of dispersal modes represented in the regional species pools of high productivity forested landscapes than in low productivity forest systems. Additionally, more of the dispersal modes represented in high productivity species pools appear to be found in all land-use conversion categories than in reference natural forests. This pattern could indicate that dispersal is a more important structuring process in high productivity land-use conversion categories than in reference natural forests. Another possibility is that forest disturbance, whether logging or clearance, releases a restriction on which dispersal modes are viable, leading to increased variation in this trait when there are additional dispersal modes available in the species pool (a condition found most often in high productivity areas). We therefore suggest that changes in environmental filters and a sampling effect drive this interesting pattern (Mayfield et al., 2010).

***Conclusions***—Understanding how anthropogenic disturbance impacts functional trait variation in plant communities is fundamentally important for elucidating the relationship between land-use and ecosystem function. The most striking pattern that emerges from this study is that the type of land-use conversion and the productivity of the system are generally not good predictors for how trait distributions will respond to land-use changes in forest systems. Landscape-scale productivity did alter the way dispersal modes were distributed in human-altered systems, which probably reflects the larger species pools in more productive landscapes. The other pattern that emerged from this study was that differences in trait variation between natural forest and all land-use conversion categories were largely distinct between the understory and tree stratum. Future studies of how land-use change impacts the ecology of plant communities should therefore account for vegetation stratum, particularly in cases were results are used to direct conservation actions. As with all studies of individual traits, analysis of further traits would certainly add valuable details about how land-use change impacts the functioning and assembly processes structuring secondary forests, old-fields, and open pastures worldwide.

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APPENDIX 1. Tests of shifts in continuous trait distributions (compared to natural forest trait distributions) for each land-use conversion category. Tests were paired two-tailed Wilcoxon signed-rank tests performed for the 10th, 50th, and 90th percentiles. Paired tests were used to ensure that comparisons were maintained within study landscapes. The test statistic, number of pairs and *P* value are shown for each test. Figure 2 graphically presents the results from this analysis.

UNDERSTORY stratum

| Land-use | Trait | Percentile | Wilcox statistic | *n* pairs | *P* value |
|---|---|---|---|---|---|
| Legacy | Height | 10 | 9 | 5 | 0.813 |
| | | 50 | 12 | 5 | 0.313 |
| | | 90 | 13 | 5 | 0.188 |
| | LLA | 10 | 34 | 8 | 0.023 |
| | | 50 | 36 | 8 | 0.008 |
| | | 90 | 35 | 8 | 0.016 |
| | Seed mass | 10 | 17 | 8 | 0.945 |
| | | 50 | 26 | 8 | 0.313 |
| | | 90 | 32 | 8 | 0.055 |
| | SLA | 10 | 5 | 5 | 0.625 |
| | | 50 | 6 | 5 | 0.813 |
| | | 90 | 5 | 5 | 0.625 |
| Old-field | Height | 10 | 21 | 6 | 0.031 |
| | | 50 | 21 | 6 | 0.031 |
| | | 90 | 19 | 6 | 0.094 |
| | LLA | 10 | 19 | 6 | 0.094 |
| | | 50 | 19 | 6 | 0.094 |
| | | 90 | 19 | 6 | 0.094 |
| | Seed mass | 10 | 5 | 6 | 0.313 |
| | | 50 | 19 | 6 | 0.093 |
| | | 90 | 21 | 6 | 0.031 |
| | SLA | 10 | 1 | 2 | 1 |
| | | 50 | 0 | 2 | 0.5 |
| | | 90 | 0 | 2 | 0.5 |
| Pasture | Height | 10 | 6 | 3 | 0.25 |
| | | 50 | 6 | 3 | 0.25 |
| | | 90 | 6 | 3 | 0.25 |
| | LLA | 10 | 21 | 6 | 0.031 |
| | | 50 | 21 | 6 | 0.031 |
| | | 90 | 15 | 6 | 0.059 |
| | Seed mass | 10 | 10 | 6 | 1 |
| | | 50 | 21 | 6 | 0.031 |
| | | 90 | 21 | 6 | 0.031 |
| | SLA | 10 | 0 | 4 | 0.125 |
| | | 50 | 5 | 4 | 1 |
| | | 90 | 4 | 4 | 0.875 |

TREE stratum

| Land-use | Trait | Percentile | Wilcox statistic | *n* pairs | *P* value |
|---|---|---|---|---|---|
| Legacy | Height | 10 | 10 | 5 | 0.625 |
| | | 50 | 4 | 5 | 0.789 |
| | | 90 | 5 | 5 | 0.625 |
| | LLA | 10 | 5 | 4 | 1 |
| | | 50 | 2 | 4 | 0.375 |
| | | 90 | 4 | 4 | 0.875 |
| | Seed mass | 10 | 7 | 4 | 0.625 |
| | | 50 | 9 | 4 | 0.25 |
| | | 90 | 5 | 4 | 1 |
| | SLA | 10 | 3 | 4 | 1 |
| | | 50 | 2 | 4 | 1 |
| | | 90 | 5 | 4 | 1 |
| Old-field | Height | 10 | 10 | 8 | 0.554 |
| | | 50 | 36 | 8 | 0.014 |
| | | 90 | 27 | 8 | 0.035 |
| | LLA | 10 | 18 | 9 | 1 |
| | | 50 | 15 | 9 | 0.402 |
| | | 90 | 31 | 9 | 0.078 |
| | Seed mass | 10 | 22 | 9 | 0.205 |
| | | 50 | 38 | 9 | 0.074 |
| | | 90 | 31 | 9 | 0.360 |
| | SLA | 10 | 2 | 3 | 0.75 |
| | | 50 | 5 | 3 | 0.5 |
| | | 90 | 6 | 3 | 0.25 |