Supporting Information

Methods

Study sites

Our forest plots were located in Sarapiquí County, Heredia Province, Costa Rica (Table S1). The regional life zone is tropical wet forest with annual temperature and rainfall averaging 26° C and ~3800 mm, respectively (1). Soils in the study areas are derived from weathered basalt and are primarily classified as ultisols (2). Conditions at plots prior to abandonment were largely consistent although plots varied in the abundance of remnant trees and surrounding vegetation (3).

Trait data

Whenever possible we sampled fully expanded sun-lit leaves with low levels of herbivory or epiphyll cover. For each tree, we collected small branches from the field and transported them to the lab in plastic bags. In the lab, we re-cut the stems and stored them in water to ensure that all tissues were equally hydrated. Samples were stored in the dark at 4°C until measurements were made. Fresh weight, leaf size, leaf thickness and leaf toughness were measured within 24 hr. Leaf size was measured on a digital leaf area meter (LI-3100, LiCor Environmental, Lincoln, Nebraska). Leaf thickness was measured with a digital micrometer, and we used a leaf penetrometer to measure leaf toughness (punch force; Chatillion push-pull gauge, Chatillion, USA). Dry leaf weight was measured after drying for ~72 hours at 60°C. Leaf density was calculated as the inverse of leaf thickness*leaf dry matter content*specific leaf area (4). Trait values were measured on two leaves per tree, and averaged prior to analyses. We measured wood specific gravity (WSG) on 1-51 individuals of 176 study species. We used a 5.15 mm increment borer (Suunto, Finland) to core each tree from the bark to the pith. Samples were transported to the lab in plastic bags. After removing the bark, we measured wood core volume with the water displacement method and dry weight after ~72 hrs at 105°C (5).

Leaf traits were measured on a total of 1,984 individuals (Table S2). Wood specific gravity (WSG, unitless) was measured on 1,281 individuals of 176 species. We log-transformed leaf size, leaf density, SLA, leaf thickness, and leaf toughness because all were strongly right-skewed.

Demographic models

Diameter effects

In order to control for spurious correlations between species identity and mean

DBH variation among species we standardized DBH to the mean for each species.

Change in neighborhood trait diversity (NTD)

In the main text we presented results on total change in NTD, i.e. change in diversity due to growth, mortality and recruitment. To further investigate the potential causes of changes in NTD, we also partitioned NTD into that arising from growth and stem turnover. NTD change due to neighbor growth is calculated as (*NCIS* / *NCI* for a stems' neighbors at time $t + 1$) - (*NCIS* / *NCI* for a stems' neighbors at time t), restricted to those neighbors surviving the interval. Thus when growth of neighbors increases neighbor trait diversity, NTD change is positive. Change in NTD due to growth was averaged for all stems in each plot, and plot averages were then averaged across years. Thus the unit of observation in the t-test was each plot. Change in NTD due to stem turnover was computed similarly, with the exception that it was calculated as (*NCIS* / *NCI* for a stems' neighbors recruiting between time t and $t + 1$) - (*NCIS* / *NCI* for a stems' neighbors dying between time t and $t + 1$). Thus a negative value for change in NTD due to turnover indicates that recruiting stems were less functionally diverse (standardized to their *NCI*) than dying stems.

Results

Survival model overview – We fit survival models for each of the traits (see Methods). Mean annual stem survival varied between 96.1 and 96.4%, depending on the species included for each trait model. Posterior predictions had 93.4–94.0% accuracy in predicting survival vs. mortality, predicting survival accurately in 96.6–96.9% of cases (Table S3). Survival was significantly greater for large DBH individuals of a species compared to small individuals in all models (Table S4). Survival also tended to be greater for individuals in less crowded neighborhoods (Table S5)

1. Trait relationships with average survival

Species with high leaf toughness and low leaf size had significantly greater average survival while other traits were not significant (Table S6).

2. Neighborhood crowding and changes in trait relationships with survival

No additional traits of focal trees significantly influenced species response to crowding (β_2 parameter, Table S7).

3. Trait-mediated competitive dominance hierarchy

Other traits did not show significant hierarchical dominance effects (Table S8, β_3 parameter).

4. Traits and niche variation among neighbors

Two other traits exhibited significant evidence for niche-based neighbor interactions. Focal trees exhibited significantly greater survival as *absolute* trait differences with neighbors (*NCIS*: trait difference weighted by *NCI*) increased for leaf size and leaf thickness (β_4 parameter, Table S9). Neighbor differences for other traits had no significant effects on survival. However, estimates for the effect of *NCIS* on survival were positive in all cases.

5. Successional differences in trait diversity

Neighborhood trait diversity (*NTD*) increased with stand age for the remaining functional traits. Leaf size (linear mixed effects model; $t=5.8$, $p<0.0001$), leaf thickness ($t = 5.0$, $p<0.0001$), leaf toughness ($t = 6.6$, $p<0.0001$) and leaf density ($t=3.9$, $p=0.0002$) all showed significant increases in NTD from early- to mid-successional stands to old-growth stands.

Sources of change in neighborhood trait diversity (NTD)

Increases in NTD with stand age were partly due to annual growth of surviving neighbors, with leaf size and thickness showing significant annual increases in NTD due to growth (one sample t-tests, see Table S10, Figure S2). In contrast, no traits showed significant positive annual change in NTD due to stem turnover, and NTD for LDMC and WSG showed significant annual decreases due to stem turnover (Table S10, Figure S2).

References

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4. Vile D et al. (2005) Specific Leaf Area and Dry Matter Content Estimate Thickness in Laminar Leaves. *Annals of Botany* 96:1129–1136.

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Tables

Table S1. Stand characteristics of eight 1-ha monitoring plots in northeastern Costa Rica. The number of unique stems whose survival was modeled is included. This table is modified from Table 1 of Chazdon *et al.* (2010).

Plot name (abbreviation)	Year abandoned	Year sampling initiated	Location	Latitude/ Longitude	Surrounding landscape	Unique stems modeled
El Bejuco (EB)	1995	2005	Chilamate	10.46°N/ 84.06°W	Pasture, old-growth and second-growth forest	603
Juan Enriquez (JE)	1995	2005	Chilamate	10.46°N/ 84.07°W	Pasture, old-growth and second-growth forest	619
Lindero Sur (LSUR)	1985	1997	La Selva	10.41°N/ 84.03°W	Old-growth and second-growth forest	765
Tirimbina (TIR)	1982	1997	La Virgen	10.40°N/ 84.11°W	Pasture, plantations, and second-growth forest	641
Lindero El Peje secondary (LEPS)	1977	1997	La Selva	10.43°N/ 84.03°W	Old-growth and second-growth forest	802

Cuatro Rios (CR)	1972	1997	La Virgen	10.39°N/ 84.13°W	Pasture, second-growth and old-growth forest	736
Lindero El Peje primary (LEPP)	Old-growth	2005	La Selva	10.42°N/ 84.04°W	Old-growth forest	497
Selva Verde (SV)	Old-growth	2005	Chilamate	10.44°N/ 84.07°W	Pasture, second-growth and old-growth forest	602

Table S2. Summary statistics for traits and number of individuals and species sampled.

	N individuals	*N species*	*N species w/ at least 4 individuals*	*Mean*	*Minimum*	*Maximum*	*Standard deviation*
Leaf size (cm^2)	1982	213	153	253.821	4.442	9464.399	878.598
LDMC ($g\ g^{-1}$)	1985	214	153	0.337	0.136	0.590	0.079
SLA ($mm^2\ mg^{-1}$)	1982	213	153	16.363	4.607	38.424	5.887
Leaf thickness (mm)	1979	213	152	0.205	0.106	0.511	0.055
Leaf toughness ($N\ mm^{-1}$)	1902	212	150	0.359	0.057	1.198	0.180
Leaf density ($mg\ mm^{-3}$)	1979	213	152	1.079	0.699	2.480	0.225
WSG (unitless)	1281	176	110	0.513	0.139	0.806	0.138

Table S3. Accuracy of posterior predictive simulations of survival (averaged across posterior simulations). Accuracy is further split into proportion of surviving trees predicted accurately and proportion of dying trees predicted accurately. Trait abbreviations: LDMC = leaf dry matter content, SLA = specific leaf area, WSG = wood specific gravity.

	Prediction accuracy	*Surviving trees prediction accuracy*	*Dying trees prediction accuracy*
Leaf size	0.939	0.968	0.143
LDMC	0.940	0.969	0.159
SLA	0.940	0.969	0.157
Leaf thickness	0.937	0.967	0.179
Leaf toughness	0.934	0.966	0.143
Leaf density	0.935	0.966	0.147
WSG	0.936	0.967	0.136

Table S4. The slope of DBH effect on survival for the full model (eqn. 1 in the main text), incorporating different traits, and showing median of posterior distributions with 95% CI in parentheses. β_5 is the average DBH effect across species; note that in our model the DBH effect varied randomly across species [$\beta_{5s} \sim N(0, \sigma^2)$]. Also note that DBH effects were not modeled as a function of traits, or neighbors, so that similar DBH effects were expected across models. DBH values were standardized within species. Note that all 95% CIs exclude zero. Trait abbreviations: LDMC = leaf dry matter content, SLA = specific leaf area, WSG = wood specific gravity.

Model	*β_5 survival DBH effect*
Leaf size	0.184 (0.012, 0.338)
LDMC	0.206 (0.056, 0.382)
SLA	0.207 (0.038, 0.347)
Leaf thickness	0.215 (0.065, 0.357)
Leaf toughness	0.205 (0.042, 0.355)
Leaf density	0.206 (0.07, 0.344)
WSG	0.229 (0.073, 0.367)

Table S5. The slope of *NCI* effect, $\beta_{2.0}$ (see eqn. 4), on survival for models incorporating different traits, showing median of posterior distributions with 95% CI in parentheses. Entries in bold indicate 95% CIs that exclude zero. Trait abbreviations: LDMC = leaf dry matter content, SLA = specific leaf area, WSG = wood specific gravity.

Model	$\beta_{2.0}$ *survival NCI effect*
Leaf size	**-0.136 (-0.243, -0.029)**
LDMC	**-0.097 (-0.203, -0.008)**
SLA	**-0.155 (-0.258, -0.041)**
Leaf thickness	**-0.098 (-0.205, -0.001)**
Leaf toughness	-0.063 (-0.166, 0.045)
Leaf density	**-0.103 (-0.208, -0.014)**
WSG	-0.077 (-0.196, 0.038)

Table S6. Effect of interspecific trait variation on average survival rates β_1 (see eqn. 2). Posterior medians and 95% CIs are shown. Entries in bold indicate 95% CIs that exclude zero. Trait values were standardized to mean zero and unit standard deviation. Trait abbreviations: LDMC = leaf dry matter content, SLA = specific leaf area, WSG = wood specific gravity.

Model	*β_1 survival intercept*trait effect*
Leaf size	**-0.285 (-0.515, -0.068)**
LDMC	**0.293 (0.037, 0.53)**
SLA	-0.048 (-0.277, 0.186)
Leaf thickness	-0.065 (-0.303, 0.178)
Leaf toughness	**0.373 (0.142, 0.596)**
Leaf density	-0.23 (-0.435, 0.02)
WSG	**0.531 (0.279, 0.768)**

Table S7. Effect of the interaction between NCI and traits on survival rates, β_2 (see eqn. 4). Negative values indicate greater sensitivity to NCI, *i.e.* reduced performance as NCI and the trait increase or reduced performance as NCI increases for specific habitat groups. Posterior medians and 95% CIs are shown. Entries in bold indicate 95% CIs that exclude zero. Trait values were standardized to mean zero and unit standard deviation. Trait abbreviations: LDMC = leaf dry matter content, SLA = specific leaf area, WSG = wood specific gravity.

Model	*β_2 survival NCI sensitivity*
Leaf size	0.028 (-0.053, 0.131)
LDMC	-0.103 (-0.216, 0.02)
SLA	0.013 (-0.089, 0.115)
Leaf thickness	-0.006 (-0.098, 0.089)
Leaf toughness	-0.008 (-0.097, 0.08)
Leaf density	-0.016 (-0.103, 0.075)
WSG	0.054 (-0.047, 0.155)

Table S8. Effect of crowding mediated by trait hierarchy of neighboring trees (*NCIH*), β_3 (see eqn. 1). Positive values indicate that as a neighbor's value of the trait decreases relative to the focal tree, the effect of crowding is reduced. Posterior medians and 95% CIs are shown. Entries in bold indicate 95% CIs that exclude zero. Trait values were standardized to mean zero and unit standard deviation. Trait abbreviations: LDMC = leaf dry matter content, SLA = specific leaf area, WSG = wood specific gravity.

Model	β_3 *survival NCIH effect*
Leaf size	-0.018 (-0.091, 0.069)
LDMC	0.103 (-0.021, 0.194)
SLA	-0.082 (-0.16, 0.001)
Leaf thickness	0.025 (-0.066, 0.109)
Leaf toughness	0.067 (-0.042, 0.171)
Leaf density	0.044 (-0.031, 0.136)
WSG	**0.171 (0.028, 0.324)**

Table S9. Effect of crowding mediated by trait similarity of neighboring trees (*NCIS*), β_4 (see eqn. 1). Positive values indicate that as neighbor trait differences increase, the effect of crowding is reduced. Posterior medians and 95% CIs are shown. Entries in bold indicate 95% CIs that exclude zero. Trait values were standardized to mean zero and unit standard deviation. Trait abbreviations: LDMC = leaf dry matter content, SLA = specific leaf area, WSG = wood specific gravity.

Model	β_4 *survival NCIS effect*
Leaf size	**0.157 (0.03, 0.301)**
LDMC	**0.166 (0.035, 0.328)**
SLA	**0.184 (0.075, 0.308)**
Leaf thickness	**0.147 (0.041, 0.262)**
Leaf toughness	0.056 (-0.039, 0.169)
Leaf density	0.098 (-0.008, 0.228)
WSG	0.052 (-0.041, 0.164)

Table S10. Average plot change in NTD due to neighbor growth or turnover tested versus a null expectation of zero (one sample t-test, N = 8 plots, df = 7). NTD change due to neighbor growth is calculated as: (*NCIS* / *NCI* for a stems' neighbors at time *t* + 1) - (*NCIS* / *NCI* for a stems' neighbors at time *t*), restricted to those neighbors surviving the interval. Thus when growth of neighbors increases neighbor trait diversity, NTD change is positive. Change in NTD due to growth was averaged for all stems in each plot, and plot averages were then averaged across years. Thus the unit of observation in the t-test was each plot. Change in NRD due to stem turnover was computed similarly, with the exception that it was calculated as: (*NCIS* / *NCI* for a stems' neighbors recruiting between time *t* and *t* + 1) - (*NCIS* / *NCI* for a stems' neighbors dying between time *t* and *t* + 1). Thus a negative value for change in NTD due to turnover indicates that recruiting stems were less functionally diverse (standardized to their *NCI*) than dying stems. Entries in bold indicate significant results. Trait abbreviations: LDMC = leaf dry matter content, SLA = specific leaf area, WSG = wood specific gravity

	Change in NTD due to neighbor growth		*Change in NTD due to stem turnover*	
Trait	*t*	*p*	*t*	*p*
Leaf size	**2.55**	**0.0383**	-0.13	0.8974
LDMC	-0.23	0.8219	**-3.46**	**0.0105**
SLA	-1.16	0.2857	-0.88	0.4087
Leaf thickness	**3.07**	**0.0182**	0.60	0.5671
Leaf toughness	1.22	0.2619	-0.61	0.5624
Leaf density	1.03	0.3385	-1.50	0.1766
WSG	0.10	0.9200	**-3.98**	**0.0053**

Figures

Figure S1. Relationship between species traits and survival. Each species is represented by a dot with size proportional to the square root of number of observations. A) Species (N=176) mean survival increases (y-axis) as WSG increases (x-axis). B) As leaf dry matter content (LDMC) increases (shown as dot color), species (N=214) mean survival increases (x-axis). Parameter values are plotted in model units. Lines show 95% CI for each species parameter, which is drawn from a hyperdistribution.

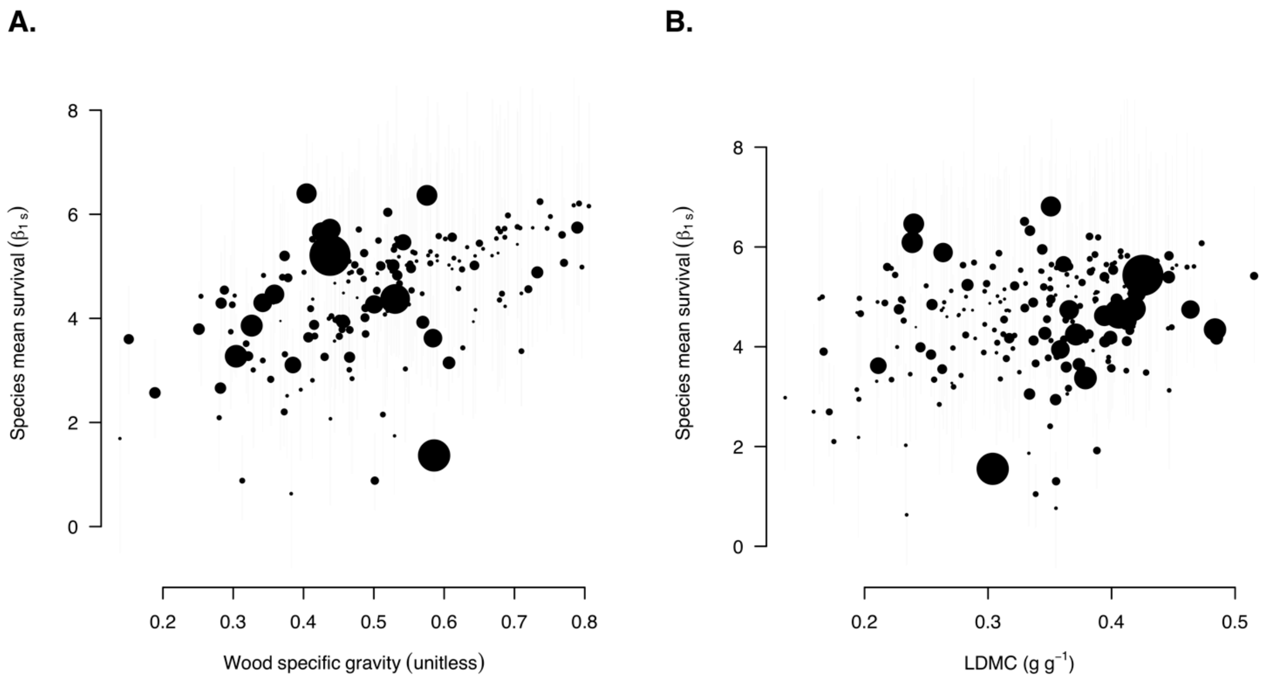
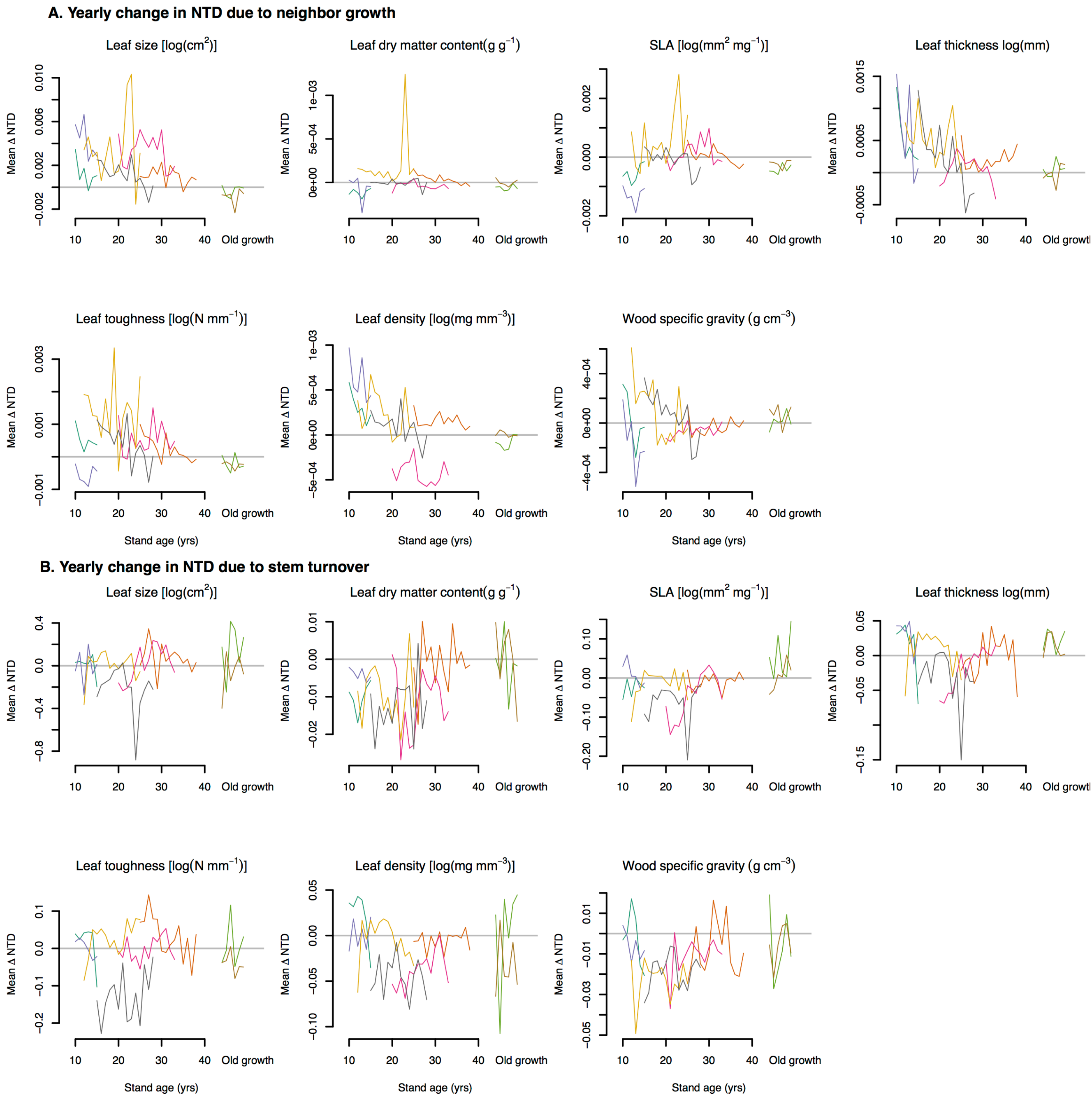


Figure S2. The change in NTD due to (A) the growth of surviving neighbors or (B) replacement of dying neighbors by recruiting neighbors. NTD change due to neighbor growth is calculated as (*NCIS* / *NCI* for a stems' neighbors at time $t + 1$) - (*NCIS* / *NCI* for a stems' neighbors at time t), restricted to those neighbors surviving the interval. Thus when growth of neighbors increases neighbor trait diversity, NTD change is positive. Change in NTD due to growth was averaged for all stems in each plot, and plot averages were then averaged across years. Thus the unit of observation in the t-test was each plot. Change in NRD due to stem turnover was computed similarly, with the exception that it was calculated as (*NCIS* / *NCI* for a stems' neighbors recruiting between time t and $t + 1$) - (*NCIS* / *NCI* for a stems' neighbors dying between time t and $t + 1$). Thus a negative value for change in NTD due to turnover indicates that recruiting stems were less functionally diverse (standardized to their *NCI*) than dying stems.


A. Yearly change in NTD due to neighbor growth
Leaf size [log(cm2)]
Leaf dry matter content(g g−1)
SLA [log(mm2 mg−1)]
Leaf thickness log(mm)
Leaf toughness [log(N mm−1)]
Leaf density [log(mg mm−3)]
Wood specific gravity (g cm−3)
B. Yearly change in NTD due to stem turnover
Leaf size [log(cm2)]
Leaf dry matter content(g g−1)
SLA [log(mm2 mg−1)]
Leaf thickness log(mm)
Leaf toughness [log(N mm−1)]
Leaf density [log(mg mm−3)]
Wood specific gravity (g cm−3)
Mean Δ NTD
Stand age (yrs)
10
20
30
40
Old growth