2009

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Abstract:

Major shifts in many ecosystem-level properties of tropical forests have been observed,

3   but the processes driving these changes are poorly understood. The forest on Barro

Colorado Island exhibited a 20% decrease in the number of trees and a 10% increase in

average diameter. Using a metabolism-based zero-sum framework, we show that

6   increases in per capita resource use at BCI, caused by increased tree size and increased

temperature, compensated for the observed declines in abundance. This trade-off between

abundance and average resource use resulted in no net change in the rate resources are

9   fluxed by the forest. Observed changes in the forest are not consistent with other

hypotheses, including changes in overall resource availability and existing self-thinning

models. The framework successfully predicts interrelated changes in size, abundance, and

12   temperature, indicating its utility for understanding changes in the structure and dynamics

of ecosystems.

15

Introduction

The assumption that the abundance, distribution, and diversity of species are due primarily to resource limitation is a cornerstone of ecological and evolutionary theory (Van Valen 1973; Hubbell 2001; Brown *et al.* 2004). Fundamental to this assumption is the idea that the rate of supply of usable energy or material to an ecosystem limits the carrying capacity, which can be defined as the total resource use or metabolism of the biota. At steady state, when the total rate of resource use by organisms equals the rate of limiting resource supply, an ecosystem is subject to a zero-sum metabolic constraint; any increase in resource use by some organisms must be balanced by decreases in resource use by other organisms (Van Valen 1973; Charnov 1993; Ernest & Brown 2001; Hubbell 2001). Such zero-sum dynamics impose simple rules on ecosystem-level properties (Enquist *et al.* 1998; Ernest & Brown 2001; Hubbell 2001; Enquist *et al.* 2003; White *et al.* 2004, Ernest et al. 2008). For example, changes in the overall rate of resource supply (R) will be reflected in changes in the overall rate of resource use (U_{tot}) by the community of organisms that share requirements for the same limiting resource (i.e., energy and/or materials).

The rate of energy and material use by an individual organism is related to its whole-organism metabolic rate (B_i) and the total rate of resource use of an ecological guild, community, or ecosystem will be related to the sum of the resource use of the component individuals (Enquist *et al.* 1998; Ernest & Brown 2001; Enquist *et al.* 2003; White *et al.* 2004), so,

$$R \propto U_{tot} = \sum_{1}^{N} U_i \approx \sum_{1}^{N} B_i = N\overline{B} \tag{1}$$

where i indexes the individuals constrained by a common resource and the

proportionality indicates that the group in question does not have to use all of the

3   available resource, just a constant proportion. In Eqn 1, we have made $\sum_1^N U_i \approx \sum_1^N B_i$ to

denote the approximate relationship between metabolic rate and actual organism resource

use. Because the metabolic rate of an individual is related to its size (Brown *et al.* 2004),

6   a given rate of resource supply can support many small individuals or fewer larger

individuals. Specifically, under zero-sum dynamics (i.e., if R equals a constant) Eq. 1

implies a tradeoff between the number of organisms and their average individual

9   metabolic rate (Enquist *et al.* 1998; White *et al.* 2004)

$$R \propto N\overline{B}$$
$$\Rightarrow N \propto \overline{B}^{-1}$$

(2)

and changes in the size distribution of individuals (White *et al.* 2007) should result in

12   specific, quantifiable, changes in abundance.

Studies of tropical forests have documented a variety of dynamic changes,

including shifts in biomass (Phillips *et al.* 1998; Chave *et al.* 2008), individual growth

15   rates (Clark *et al.* 2003; Laurance *et al.* 2004; Feeley *et al.* 2007b), abundance (Losos &

Leigh 2004; Pitman 2005), size structure (Condit *et al.* 1996), and species composition

(Condit 1998a; Laurance *et al.* 2004). These shifts could have multiple causes, including

18   climate change (e.g., long-term shifts in temperature, light availability), increased CO_2,

or other abiotic or biotic effects on population dynamics (Condit *et al.* 1996; Graham *et

al.* 2003; Laurance *et al.* 2004; Pitman 2005; Feeley *et al.* 2007a). Changes in the

21   ecosystem-level properties of tropical forests have been interpreted as implying that

climate change has altered overall rates of primary production through changes in light

availability and/or CO_2 enrichment (Clark *et al.* 2003; Graham *et al.* 2003; Laurance *et al.* 2004; Feeley *et al.* 2007b). A long-term study of trees on Barro Colorado Island

3   (BCI), Panama (Condit 1998b; Hubbell *et al.* 1999; Condit *et al.* 2005) provides an excellent case study for evaluating alternative hypotheses for changes documented in this tropical forest. The BCI 50-ha plot has been repeatedly and intensively censused since

6   1981. Documented changes include: altered species composition (Condit *et al.* 1996; Condit 1998a), large decreases in the numbers of small trees (Condit *et al.* 1996), smaller increases in the numbers of large trees (Condit *et al.* 1999), and, consequently, an overall

9   decrease in the abundance of trees (Condit *et al.* 1999; Losos & Leigh 2004). Many of these changes are similar to changes documented in other tropical forests (Clark *et al.* 2003; Losos & Leigh 2004; Feeley *et al.* 2007b).

12   Here we use a metabolic zero-sum framework to evaluate whether changes observed at BCI reflect 1) the reallocation of resources due to the tradeoff between individual resource use and abundance, 2) self-thinning processes caused by geometric

15   packing constraints as trees grow larger, or 3) whether they result from a reduced carrying capacity due to decreased resource supply. These alternative hypotheses make clear predictions: 1) Zero-sum dynamics – If overall resource supply rate has remained

18   effectively constant (see Supplementary Results), and the changes in forest structure reflect a metabolic tradeoff between the number of individuals and the metabolic rates of those individuals, we should observe no directional change in total forest-level energy

21   flux, and N and $\bar{B}$ should be inversely related, so $N \propto \bar{B}^{-1}$, 2) Self-thinning – as a forest recovers from disturbance, large numbers of young, small trees grow larger creating packing constraints, which lead to increased mortality and decreases in tree abundance.

Different models for self-thinning suggest a variety of relationships between N and

diameter (D), with the extremes represented by the 3/2 and the 4/3 thinning models

3   (Enquist et al. 1998, Pretzsch 2006) which, properly accounting for Jensen's inequality

(see appendix), result in the predictions: $N \propto \overline{D^2}^{-1}$ or $N \propto \overline{D^{16/9}}^{-1}$, respectively. 3)

Reduced carrying capacity – If the decrease in the total number of trees reflects a

6   decrease in the overall carrying capacity of the environment for trees, then the estimated

rate of energy flux should have decreased over the 20-year period and the slope of the

relationship between abundance and average metabolic rate should differ from -1.

9   Furthermore, a potentially limiting resource would need to exhibit a significant decline

over the period of the study.

12   **Methods**

Research Site – Data for this study come exclusively from the Smithsonian Tropical

Research Institute's research station at Barro Colorado Island. Barro Colorado Island is

15   an artificial island formed when the Panama Canal was flooded and has been part of a

protected biodiversity reserve since 1923. The 1500 ha island contains a moist lowland

tropical forest community. This forest was disturbed by human activities – by both pre-

18   and post-Columbian societies - through forestry and clearing for agricultural land until

1923 (Leigh *et al.* 1996).

Forest Data – All data on trees were obtained from the online database for the 50 ha

21   Forest Dynamic Plot on Barro Colorado Island. This forest plot has been completely

censused approximately every 5 years since 1980. Detailed methods for the census are

available at http://ctfs.si.edu/datasets/bci/. Here we only discuss census methodology

relevant for this study.

3   For each forest census, all stems greater than or equal to 10 mm were identified

and diameter at breast height (DBH) was measured. Because there is no data for

individuals < 10 mm, our forest-level estimates and subsequent analyses are only valid

6   for that component of the forest ≥ 10 mm DBH. DBH is defined as diameter at 1.3 meters

unless the tree contained buttresses or stilts in which case DBH is taken immediately

above these structural components. Each individual in the census is given a unique tag

9   number. If an individual has multiple stems, a DBH is taken for all stems ≥ 10 mm.

Methodology is consistent across censuses except that in the 1980 and 1985 census the

DBH for all trees less than 50 mm was rounded down to the lowest 5 mm increment.

12   Because of the importance for this study of having comparable size estimates across all

censuses, we follow (Muller-Landau *et al.* 2006) and do not use the data from the first

two censuses.

15   Because theoretical models linking the diameter of a tree with its metabolic rate

are based on the diameter of the basal stem (West *et al.* 1999), basal stem diameter had to

be estimated for individuals with multiple stems at breast height. We used the pipe

18   model, an area preserving model used since Leonardo da Vinci, to back calculate the

basal diameter from the number of stems at breast height (*n*) and the diameter each of

those stems (*D*).

21
$$D_{basal} = \sqrt{\sum_i^n D_i^2}$$

Temperature data – Long-term climate data has been collected at Barro Colorado Island

on an hourly basis since 1983 at the field station (clearing weather station) and since

1984 at the Lutz canopy tower. Temperature data (and all other abiotic datasets for BCI described in this paper) are available at:

3   http://striweb.si.edu/esp/meta_data/index_metadata_terr.htm. Temperature data for this study was obtained from the clearing weather station due to large gaps in data collection at the Lutz tower. Recent activities around the clearing weather station may have

6   influenced recent temperature readings (http://striweb.si.edu/esp/physical_monitoring/descrip_bci.htm). However, comparisons of the daily average temperature readings for both stations reveals that these data are well

9   correlated with each other (r = 0.7942) and this correlation has not decayed since 1999 (r = 0.8416).

For studying temperature trends at the site, we calculated an average temperature

12   for each year of the study. Data were averaged by calculating monthly averages of hourly temperatures (day and night) and then averaging the monthly averages within each year. This reduces the impact of the timing of missing data on the averages.

15   ***Estimating Metabolic Rates*** - To estimate metabolic rate for each tree, we used a previously published relationship (West *et al.* 1999; Gillooly *et al.* 2002; Allen *et al.* 2005) that incorporates both the size of the individual and the temperature:

18   $$B \propto D^{\lambda} e^{-E/kT} \tag{3},$$

where λ is a constant (≈ 2) relating basal stem diameter (D) to metabolic rate (West *et al.* 1999), E is the average activation energy of C_3 photosynthesis (≈ 0.32 eV; Allen *et al.*

21   2005), k is Boltzmann's constant (8.6×10^{-5} eVK), and T is air temperature in Kelvins (K). Our results are not sensitive to a reasonable range of variation in values of either E or λ (see *Diameter exponent and activation energy*, below). This equation assumes that

all species can be characterized by this same relationship. Eqn 3 was used to estimate the

metabolic rate for an individual tree, which was then used to calculate both estimated

3   mean individual metabolic rate (i.e., averaged across individuals) and estimated total

stand metabolic flux (i.e., summed over all individuals). When λ=2, our model is an

extension of resource-based self-thinning rules (e.g., Enquist et al. 1998).

6   Because temperature varies at multiple timescales, the effect of temperature on

metabolic rate is more complicated than simply inserting an average temperature into the

temperature term for the metabolic equation. Therefore, temperature terms were

9   calculated for each hourly data point, which were then used to calculate monthly averages

of the temperature term. An average temperature term was determined for each census

period by averaging 5-year blocks of monthly terms consisting of the 4 years prior to

12   each census and the year in which the census began. As a result, the exact form of the

relationship we are testing is: $N \propto \dfrac{1}{\overline{D^2} \times <e^{-E/kT}>}$,where $<e^{-E/kT}>$ denotes that the

average of the temperature term is taken across time, not across individuals as is the case

15   with diameter ($\overline{D^2}$) .

Finally, it should be noted that we have no measure of the scaling constant

required to calibrate the metabolic rate for these trees. While the constant would allow us

18   to comment on absolute metabolic flux of the forest, the proportional values are sufficient

to evaluate the above hypotheses. Finally, we quantified the compensatory dynamics

among size classes by calculating total metabolic flux for eight equal-width logarithmic

21   bins to assess whether decreases in flux for small size classes due to decreasing numbers

of small trees were matched by increases in flux for large size classes due to increasing

numbers of large trees.

Diameter exponent and activation energy - The resource use exponent ($\lambda = 2$) and

activation energy (0.32 eV) we used have been suggested as the theoretical expectations

3   for these values (West *et al.* 1999; Allen *et al.* 2005), and have some empirical support

(Enquist *et al* 1998; Allen *et al* 2005; Meinzer *et al* 2005). However, the specific values

for both of these exponents are controversial (Muller-Landau *et al.* 2006; Enquist *et al.*

6   2007). However, the general functional form of this relationship is, at least, a reasonable

statistical description of the relationships between diameter, temperature, and resource

use or related responses (Clarke & Fraser 2004; Muller-Landau *et al.* 2006). Therefore, in

9   order to test the sensitivity of our analysis to our specific choice of exponent and

activation energy we varied these exponents and refit the exponent of the abundance-

metabolic rate tradeoff (eq. 2) to determine if this caused it to deviate from the predicted

12   value of -1.

Long-term dynamics of potential limiting resources - Recent studies have suggested that

changes in light availability (Graham *et al.* 2003), nitrogen availability (Magnani *et al.*

15   2007), or CO_2 (Phillips *et al.* 1998) might be driving changes in tropical forests. Each of

these possibilities was explored using either local data collected at BCI or the results of

recent regional scale analyses.

18   *Light availability*: Photosynthetically available radiation (PAR) has been

measured at BCI since 1990 at the Lutz tower using a LI-COR 190SB (for more details

see: http://striweb.si.edu/esp/meta_data/details_bci_sun.htm). Daily Total PAR values

21   (measured in Einsteins/m^2) were summed for each year to obtain yearly total PAR.

     Nitrogen Availability: Recent papers have suggested that increased nitrogen

deposition could increase nitrogen availability in forests (Magnani *et al.* 2007). However,

a recent study suggests that nitrogen deposition rates in Central America have not

changed substantially since the late 1800s (Galloway *et al.* 2004). To the best of our

3   knowledge, there is no long-term monitoring of nitrogen availability in soils on the 50-ha

plot. Nitrogen availability could either be increasing or non-changing at BCI. There is no

reason to suspect that nitrogen levels have declined.

6   *CO$_2$*: Global CO$_2$ levels have increased over the past few decades (Forster *et al.*

2007), which would imply that CO$_2$ available to trees should also have increased.

          Water availability: Annual precipitation for BCI was taken from the data

9   collected at the Clearing near the field station from 1990-2005 (for more details see:

http://striweb.si.edu/esp/meta_data/details_bci_rain.htm). We used the daily data file and

summed these values for each year to determine annual precipitation (measured in mm).

12   Potential evapotranspiration at BCI was also measured at the field station clearing (for

more details see: http://striweb.si.edu/esp/meta_data/details_bci_evap.htm). Daily values

of PET (measured in mm) were summed for each year to determine annual PET.

15   **Results and Discussion**

          The dynamics of the forest on BCI clearly support hypothesis (1), and are

consistent with a metabolic zero-sum dynamic without directional changes in resource

18   availability (Figs 1 & 2). The total metabolic flux of all trees exhibited no directional

trend over time, while other forest-level properties (i.e., abundance, biomass, total basal

area) changed directionally (see Supplementary Results). Total stand metabolic flux did

21   not change directionally due to the tradeoff between increased average metabolic rates of

individual trees (resulting from increased average diameter and increased temperature)

and decreased average abundance (Fig 2). While the data support an inverse relationship

between N and $\bar{B}$, the data do not support either of the self-thinning models (Table 1).

Furthermore, all biological measures of the forest either do not change directionally or

3   decrease through time, while potential limiting resources appear to either increase or

remain stable (Fig 3). As such, the weight of evidence is consistent with a metabolic

zero-sum dynamic and rejects both packing constraints and shifts in resource availability

6   as drivers of the observed declines in abundance at BCI.

The sensitivity analyses indicate that our results are robust to reasonable variation

in the form of the temperature and body size dependence of metabolic rate (Fig 4A). The

9   range of reasonable activation energy values includes those estimated in recent work

purporting that the activation energy will be shallower than expected due to acclimation

(Enquist *et al.* 2007). The range of diameter exponents includes those equivalent to the

12   growth rate allometries recently estimated for BCI (Muller-Landau *et al.* 2006) and

therefore our results are robust to potential differences in scaling exponents due to size-

biased light competition. We also examined whether our results were sensitive to the

15   spatial scale of our analysis. By dividing the 50 ha plot into smaller and smaller subplots

(see Supplemental Methods), we determined whether the observed relationship between

abundance and average individual metabolic rate changed as the spatial scale of analysis

18   decreased. We found that behavior predicted by a metabolic zero-sum dynamics was

observed until the size of a subplot equaled approximately 6 ha (Fig 4B). Below this size,

slopes were significantly shallower than expected. This same type of pattern has been

21   observed in estimates of biomass (Keller *et al.* 2001; Chave *et al.* 2003) and biomass

accumulation (Feeley *et al.* 2007) and was interpreted in those studies as indicating that

below 6 ha the idiosyncrasies of gap-phase dynamics dominate and the signal of forest-

level dynamics is weaker.

3   Our results are also consistent with previous studies documenting that the

numbers of trees with small diameters decreased dramatically, while the numbers of large

trees increased only modestly (Condit *et al.* 1996; Condit *et al.* 1999). Because size-

6   related differences in metabolic rate means not all trees will contribute equally to

resource use, small changes in the abundance of larger size classes have a much greater

influence on total metabolic flux than much larger changes in abundance in smaller size

9   classes (Fig 5). Our results also indicate that increases in per capita metabolic rate due to

temperature played an important role in maintaining the metabolic zero-sum dynamic.

Without this temperature effect, the small increase in the number of larger trees was not

12   sufficient to balance the losses in the small size classes (Fig 5). This supports the

necessity of our extension of previous self-thinning models (e.g., Enquist et al. 1998) for

understanding the observed dynamics of this system.

15   Because we only have four data points suitable for our analyses, some caution

should be used in interpreting our results. Obviously, further tests of a metabolic zero-

sum dynamic involving longer time-series and/or experimental tests are needed.

18   However, because we are still able to clearly distinguish among models we feel that our

conclusions are reasonably robust and warrant further investigation of this concept in

forests. Furthermore, the importance of tropical forests to conservation and global carbon

21   budgets makes it necessary to make use of existing, though sometimes limited, time-

series (Condit *et al.* 1996; Condit 1998a; Laurance *et al.* 2004; Losos & Leigh 2004;

Feeley *et al.* 2007b; Chave *et al.* 2008). Despite the short nature of the time-series our

framework successfully describes the observed behavior of the system in response to

changes in average tree size. The processes driving this shift in size-structure are not yet

3   well understood. One reasonable possibility is that simply that natural growth of

individual trees has been compensated for by increased mortality in the smaller size

classes. Alternatively, some studies have implicated climate change as the driver of

6   declines in small trees (Condit *et al.* 1996), while others have suggested that succession,

in response the anthropogenic activities, may be occurring in this forest (Sheil & Burslem

2003). While self-thinning based successional mechanisms are insufficient for describing

9   the overall dynamics of the forest (Table 1), succession may still be responsible for the

increase in average individual size. The success of the metabolic zero-sum framework

suggests that in order to predict future dynamics of abundance (and biomass; see

12   Supplementary Information) of tropical trees it will be necessary to understand the

processes that affect the individual size distribution. Finally, our results highlight the

importance of incorporating the effects of temperature on the rates of biological processes

15   (Enquist *et al.* 2003; Allen *et al.* 2005), because both size and temperature played

important roles in the dynamics of this forest.

    Further testing will be necessary to assess the general utility of a zero-sum

18   approach for understanding the long-term dynamics of ecosystems. Previous work has

shown that the long-term dynamics of a desert rodent community also exhibit metabolic

zero-sum dynamics, with maintenance of relatively constant rates of resource use due to a

21   similar tradeoff between metabolic rate and abundance of small and large individuals

(White *et al.* 2004, Ernest et al. 2008). That the long-term dynamics of tropical forests

and desert rodents can be explained using this relatively simple framework suggests that

it may apply more generally across habitat types and taxonomic groups. The extent of

generality likely depends on how often the two key assumptions – that overall resource

3   supply does not change directionally over time and that organisms tend to use a constant

fraction of available resources – are met in different ecosystems. Obviously, the zero-sum

does not apply when resources are not limiting, such as immediately following major

6   disturbance events. The fact that it appears to apply to both tropical trees and desert

rodents suggests that the long-term rates of limiting resource supply that impose the zero

sum may be more constant than the environmental variables that cause temporal variation

9   in body size and species composition.

The utility of the zero-sum framework arises in large part from the fact that it

synthesizes important components from two influential and general theories in ecology:

12   the zero-sum constraint from the unified neutral theory of biodiversity (Hubbell 2001)

and differences between individuals and species in resource use from the metabolic

theory of ecology (Brown *et al.* 2004). The resulting simple mathematical framework not

15   only combines the role of community and ecosystem-level constraints and the importance

of differences among individuals and species in their rates of resource use, but is easily

applied to both plants and animals and is equally relevant to tropical and desert systems.

18

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Supplemental Information file includes: Supplementary Methods, Results, Analyses,

Figures, and Discussion

3

Table 1. Tests of predictions of metabolic zero-sum and self-thinning models against

observed trends at Barro Colorado Island. All three models predict a -1 slope for the

3   relationship between abundance (N) and either $\overline{D^2} \times <e^{-E/kT}>$, $\overline{D^2}$, or $\overline{D^{16/9}}$. All fits

were performed using reduced major axis regression [31] on log-transformed data. Only

the metabolic zero-sum framework is consistent with the observed data.

6

Model Name	Model Tested	Observed Slope	Lower 95% Confidence Interval	Upper 95% Confidence Interval
Metabolic Zero-Sum	$N \propto \dfrac{1}{\overline{D^2} \times <e^{-E/kT}>}$	-0.93	-1.14	-0.72
4/3 Self-thinning	$N \propto \dfrac{1}{\overline{D^2}}$	-1.22	-1.36	-1.08
3/2 Self-thinning	$N \propto \dfrac{1}{\overline{D^{16/9}}}$	-1.25	-1.36	-1.13

Figure Legends

Figure 1. Long-term trends on the 50-ha forest dynamics plot at BCI, Panama. A) total

3   abundance of trees (individuals/50 ha) decreases through time ($r^2 = 0.96$; p = 0.018), B)

total stand metabolic flux (proportional to the true total stand metabolic flux) does not

change directionally ($r^2 = 0.06$; p = 0.94), C) average diameter of a tree (mm) increases

6   ($r^2 = 0.94$; p = 0.031), and D) average temperature (Celsius) increases ($r^2=0.18$; p=0.042);

regression calculated on yearly temperature averages (see Supplementary Information)

but displayed here as 5-year averages. Y-axis extents of 20% of the mean value were

9   used to facilitate proper visual comparison of relative variability across variables.

Figure 2. Relationship between average estimated resource use of an individual

12   ($\frac{1}{N}\sum_{i=1}^{N} D^2 < e^{-E/kT} >$) and the total number of individuals (N) occurring on the BCI 50 ha

plot. The exponent, fitted using reduced major axis regression on log-transformed data, is

-0.93 (se: 0.10), which is not significantly different from the predicted value of -1

15   (similar results are obtained using both ordinary and non-linear least squares). Points are

labeled with the year of the census.

18   **Figure 3.** Time-series of PAR (a), precipitation (b), and PET (c), at BCI from 1990 to

2005. PAR did not change directionally from 1990-2005 ($r^2=0.0062$; p=0.77).

Precipitation did not exhibit any directional changes ($r^2 = 0.0006$; p = 0.93). PET data

21   was only available starting in 1994 making it difficult to determine the trend over the

period of the study, but it appears that during the second half of the study PET was

increasing, resulting in an overall increase from 1994-2005 ($r^2 = 0.44$; p = 0.018). The

combined precipitation and PET results suggest that water use by plants either remained

constant or may have increased during the study period. All potential resources for which

3   we have a time series appear to have either remained stable or increased slightly, at least

since 1990. These data are consistent with the long-term stability of total metabolic flux,

suggesting that rates of resource supply to this forest have remained stable.

6

Figure 4. Parameter and spatial scale sensitivity analyses. (A) Results from the

sensitivity analysis examining effects of varying the values of the diameter exponent (λ)

9   and activation energy (E_a). The shaded area indicates combinations of λ and E_a where the

95% confidence interval of the RMA regression between abundance and average

metabolic rate still contains -1, the value predicted by a metabolic zero-sum dynamic.

12   The solid lines indicate $\lambda = 2$ and $E_a = 0.32$, the values used in the analyses presented in

this paper. The black circle shows the location of the combination of λ and E_a used in this

study, relative to the shaded area. The dashed line represents the value of λ that results

15   from converting a diameter growth allometry based on size-dependent light competition

(Muller-Landau *et al* 2006) into a metabolic rate. The large area of parameter space over

which our results are maintained indicates that they are robust to the details of the

18   metabolic rate equations. (B) Effects of spatial scale on observed tradeoff between

abundance and individual metabolic rate. Plot of the mean estimated exponent and 95%

confidence intervals for Eqn 2 across subplots plotted against the spatial scale of the

21   subplots. The estimated exponent for the entire plot and its 95% confidence interval

based on RMA regression (Isobe et al. 1990, Warton et al. 2006) is included to illustrate

that the exponent is approximately scale invariant at scales of 6 ha and above.

Figure 5. Changes within size classes of metabolic flux (A) and abundance (B) between

1990 and 2005. X-axis: center of the size class in logarithmic space. Y-axis: Size classes

3   with increased abundance or metabolic flux since 1990 are positive, decreases are

negative. A) Difference in resource use (U) between 2005 and 1990 across size classes (i)

expressed as the proportion of the total resource use in a given year:

6      $\dfrac{U_{i,2005}}{\sum\limits_{i} U_{i,2005}} - \dfrac{U_{i,1990}}{\sum\limits_{i} U_{i,1990}}$. Squares: metabolic flux if temperature is assumed constant across

years; circles: metabolic flux with observed temperature changes. Increases in metabolic

flux by medium trees provide partial compensation for decreases in smaller and larger

9   trees. With observed temperature changes included, medium trees compensate for

decreases in other size classes. B) Difference in abundance between 2005 and 1990

normalized as for metabolic flux. Inset: close-up of four largest size classes, showing

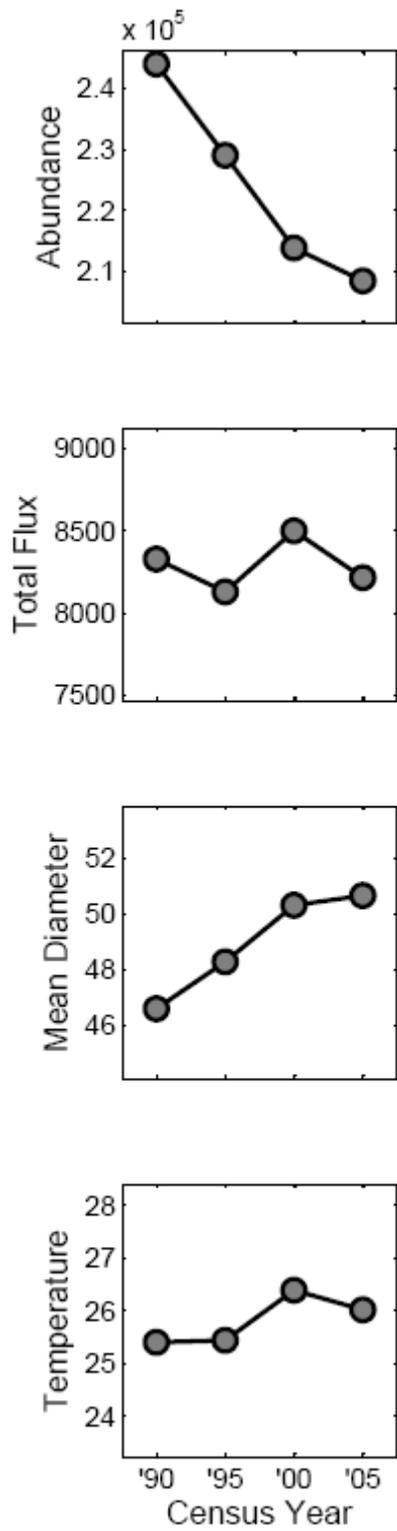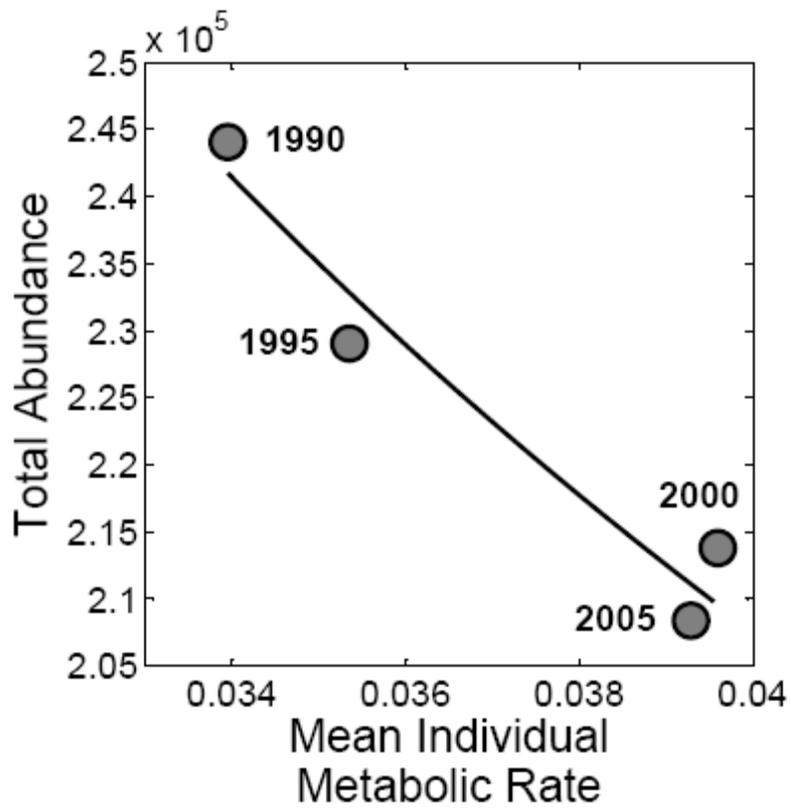12   small increase in medium-sized trees.

15

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Figure 1.

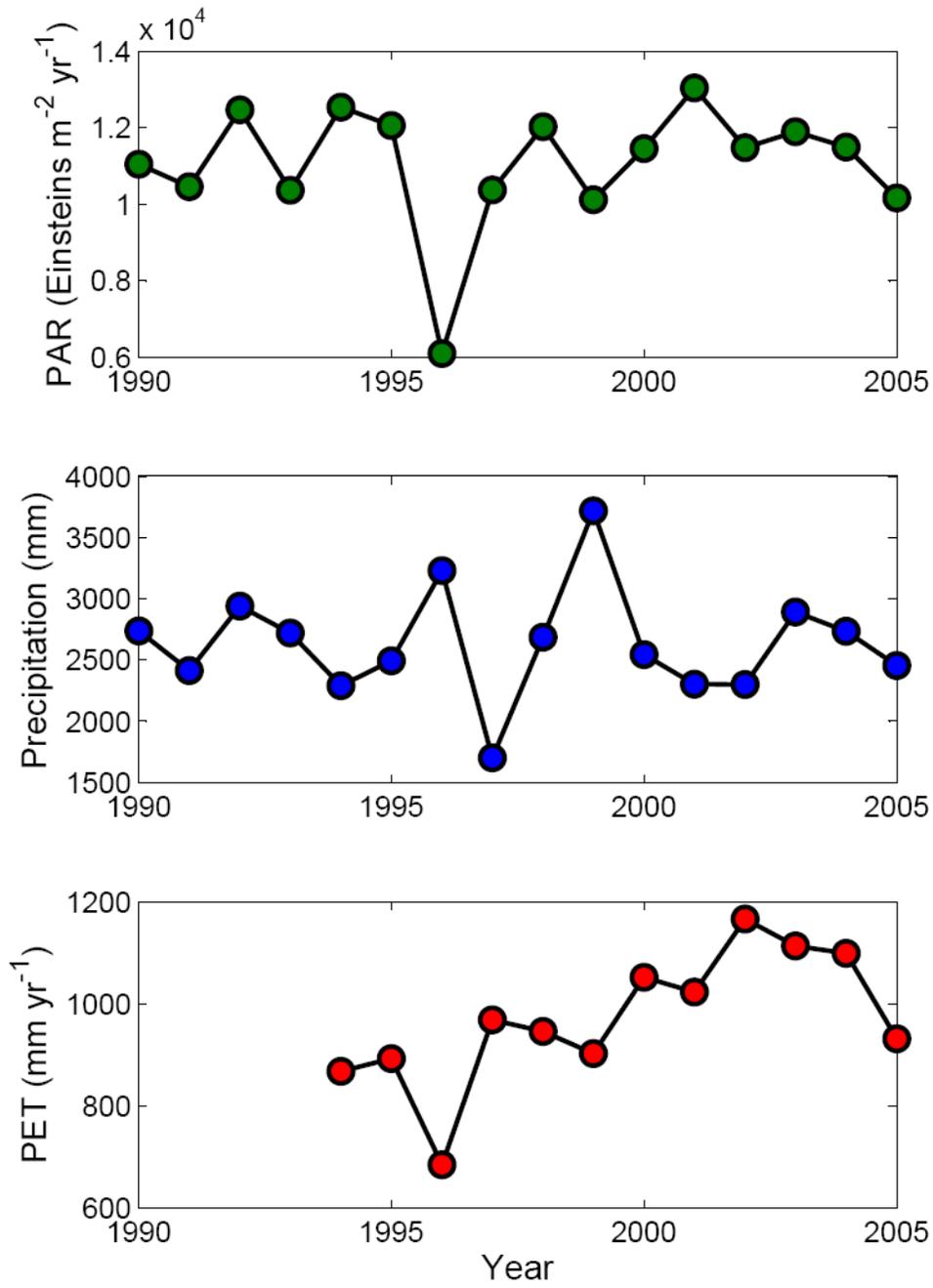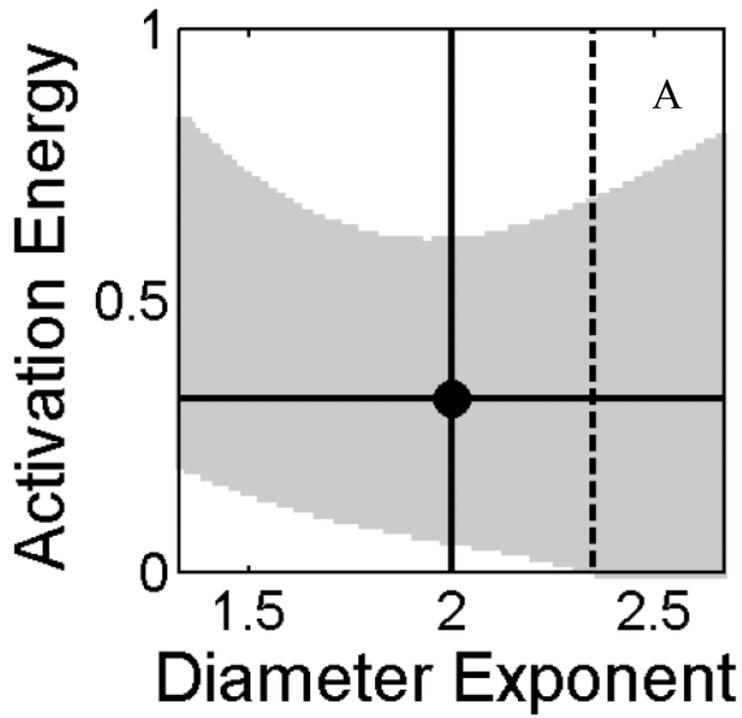**Figure 2**

3   **Figure 3**

3

Figure 4

Fig 5