

LETTER

Forest turnover rates follow global and regional patterns of productivity

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Abstract

Using a global database, we found that forest turnover rates (the average of tree mortality and recruitment rates) parallel broad-scale patterns of net primary productivity. First, forest turnover was higher in tropical than in temperate forests. Second, as recently demonstrated by others, Amazonian forest turnover was higher on fertile than infertile soils. Third, within temperate latitudes, turnover was highest in angiosperm forests, intermediate in mixed forests, and lowest in gymnosperm forests. Finally, within a single forest physiognomic type, turnover declined sharply with elevation (hence with temperature). These patterns of turnover in populations of trees are broadly similar to the patterns of turnover in populations of plant organs (leaves and roots) found in other studies. Our findings suggest a link between forest mass balance and the population dynamics of trees, and have implications for understanding and predicting the effects of environmental changes on forest structure and terrestrial carbon dynamics.

Keywords

Carbon dynamics, forest dynamics, forest turnover, mortality, net primary productivity, permanent sample plots, recruitment, temperate forest, tropical forest.

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INTRODUCTION

In the absence of significant disturbance or environmental changes, mature plant assemblages experience little net change in living mass through time. That is, their rate of gain of new plant mass [net primary productivity (NPP)] is closely matched by the rate of loss of plant mass to death (e.g. Peet 1992). However, the relationship between this mass balance and plant population dynamics is poorly understood. On more productive sites, is the higher rate of mass turnover driven by a higher rate of turnover of plant organs (leaves, roots, etc.), a higher rate of turnover of individuals (whole plants), or both? The answer will affect our understanding of forest carbon storage and dynamics.

Available evidence suggests that turnover rates of at least some plant organs (leaves and roots) do indeed broadly follow global and regional patterns of NPP (e.g. Reich *et al.* 1992, 1995; Gill & Jackson 2000). However, comparably extensive data have not been used to determine whether similar patterns exist in turnover rates of individuals. Some of the clearest results so far come from forests of the New World tropics, where tree turnover rate (mortality and recruitment) has been shown to increase with increasing soil fertility (and more weakly with decreasing seasonality of

precipitation) (Phillips *et al.* 2004), and, at least in Panama, with increasing mean annual precipitation (Condit *et al.* 2004). Additionally, over the last several decades both tropical tree turnover rates and aboveground forest biomass apparently have increased (Phillips & Gentry 1994; Baker *et al.* 2004; Lewis *et al.* 2004a; Phillips *et al.* 2004). While the authors reporting these changes suspect that they are a consequence of increasing resource supply rates (resulting in increased NPP), the causes have not yet been identified.

We sought to provide a first systematic, global analysis aimed at testing the hypotheses that broad-scale patterns exist in turnover rates of forest trees (the average of tree mortality and recruitment rates, hereafter simply referred to as 'forest turnover rates'), and that turnover rates follow broad-scale patterns in NPP. To reach this end, we assembled a global database of forest turnover rates and used it to test the following four predictions.

- (1) Forest turnover rates should be higher in tropical than in temperate forests. This prediction arises because temperate forests are, on average, less productive (Saugier *et al.* 2001; Pregitzer & Euskirchen 2004), partly because their long winter dormant season limits potential for NPP.

- (2) Within a given latitudinal zone or forest type, forest turnover rates should be higher on more fertile soils than on less fertile soils, paralleling associated patterns in NPP (e.g. Malhi *et al.* 2004).
- (3) Within the temperate zone, turnover rates of angiosperm forests (mostly broad-leaved deciduous trees) should be higher than those of gymnosperm forests (mostly needle-leaved evergreen trees). Temperate angiosperm forests are more productive than temperate gymnosperm forests (Zheng *et al.* 2003), and these forest types segregate sharply according to annual actual evapotranspiration, a measure of climatic potential for NPP (Stephenson 1990, 1998).
- (4) Within a single forest type in a region of relatively uniform precipitation regime and soils, turnover rate should be positively correlated with mean annual temperature, because temperature should in turn be positively correlated with NPP (cf. Runyon *et al.* 1994).

Our analyses support all four predictions, revealing up to three- and fourfold differences in turnover rates among and within forest types. These results suggest that a significant amount of the notoriously high site-to-site variation in forest turnover rates may reflect differences related to site potential for NPP, similar to the results of broad-scale analyses of leaf and root turnover rates (Reich *et al.* 1992, 1995; Gill & Jackson 2000). Further, our results have implications for understanding and predicting the effects of environmental changes on forest structure and terrestrial carbon dynamics. For example, all else being equal, environmental changes that result in higher turnover rates will result in forests dominated by proportionally more small trees (Condit *et al.* 1998), potentially affecting total forest carbon storage.

METHODS

Data

Our global database of turnover rates (Appendix S1 in Supplementary Material) was compiled largely from published results. Extensive bibliographical and internet searches identified > 200 candidate publications, which we then examined in detail. After excluding publications that duplicated data, 47 of those remaining were associated with data meeting our criteria [which broadly followed those of Phillips *et al.* (2004)]. Among our most important criteria were: (i) forests were old-growth or otherwise described as late-successional, multi-aged, and not heavily manipulated by humans (such as by heavy livestock grazing or extensive thinning or selective logging), (ii) forests had not experienced a major disturbance within the last several decades (although we included sites for which chronic frequent disturbances, such as high winds, were normal),

(iii) mortality and recruitment rates were determined through repeated censuses of individually identified trees, (iv) minimum tree size was < 15 cm diameter at breast height (dbh) (if data were available for several different minimum dbh, we chose the minimum dbh that was both < 15 cm and closest to 10 cm), and (v) the species sampled comprised $\geq 85\%$ of all trees at a site (all but four of our sites sampled 100% of trees). Sources presented data at different levels of resolution (i.e. individual forest plots or averages of several plots), which we collectively refer to as 'sites.' We compiled data at the level of resolution given in the original sources; in some cases, each of several closely clustered plots would therefore be called a site. If data were given for several non-overlapping time periods at a site, we averaged across the periods.

The near absence of adequate data from sites at > 50° absolute latitude meant that we limited our analyses to tropical and temperate forests. Data from 242 sites met our criteria: 158 for tropical forests (absolute latitude 0–21°, mean = 8°), and 84 for temperate forests (absolute latitude 28–50°, mean = 41°). At least some data came from every forested continent, although the New World dominated (81 and 64% of tropical and temperate sites, respectively).

To test our fourth prediction (see Introduction), we wished to have intensive data from a region of relatively uniform forest physiognomy, soils, and precipitation regime, yet with a steep temperature gradient. Such data are quite rare; we therefore used our largely unpublished data from a network of 22 gymnosperm forest plots (0.9–2.5 ha) arrayed along a steep elevational gradient (1500–3400 m) in the Sierra Nevada, California (36–38° N, 118–120° W). Forest physiognomy is effectively uniform across the gradient, being overwhelmingly dominated by needle-leaved evergreen conifers (mostly *Abies*, *Pinus* and *Calocedrus*; Rundel *et al.* 1977). With one exception, all plots were on relatively young soils (mostly inceptisols) derived from granitic parent materials. Mean annual precipitation varies little with elevation (from *c.* 1100 mm at 1500 m, peaking at *c.* 1400 mm at about 2000 m elevation, then declining slightly with increasing elevation beyond 2000 m; Stephenson 1988). In contrast, mean annual temperature declines sharply [*c.* 5.2 °C for every 1 km increase in elevation (Stephenson 1988), yielding a roughly 10 °C difference between our lowest and highest plots], suggesting that site potential for primary production also decreases with increasing elevation. Mortality and recruitment were measured over periods of 7–21 years. In each plot, recruitment was measured every 1–6 years, whereas with a few exceptions, mortality was measured annually (see van Mantgem *et al.* 2004 for a further description of methods). As we wished to avoid overwhelming our global data for temperate gymnosperm forests with data from a single small

region, these Sierra Nevada plots were not included in our global database.

Ideally, each of our sites would also be associated with a site-specific measurement or estimate of NPP, or at least a reliable surrogate. However, forest NPP is difficult to measure (Clark *et al.* 2001), and the majority of our data sources were associated with neither a site-specific estimate, nor the data needed to produce such an estimate. Additionally, we judged the resolution of global data sets of estimated NPP or terrestrial climate (e.g. 0.5°; Zheng *et al.* 2003) – especially when combined with sometimes substantial uncertainty in forest site locations – to be too coarse to provide site-specific values of NPP or climatic surrogates of NPP, particularly in mountainous regions where NPP and climate can change radically over distances of a few kilometres. We therefore chose to analyse turnover rates relative to broad forest classes associated with published values of NPP.

Relationships among mortality, recruitment and turnover

In the absence of significant disturbance or environmental changes, old-growth forests should experience little or no long-term change in tree density, with losses of individuals (mortality) equalling gains of individuals (recruitment) (e.g. Oliver & Larson 1990). Thus, rather than analyse mortality and recruitment rates separately (which, in theory, would yield identical results), some authors have simplified their presentations by analysing turnover rate, the average of mortality and recruitment rates (e.g. Phillips & Gentry 1994; Lewis *et al.* 2004a,b; Phillips *et al.* 2004). Confirming that such a simplification was justified, we found that for the 183 sites in our global data set that had both mortality and recruitment data, mean mortality and recruitment rates (1.64 and 1.62% year⁻¹, respectively) did not differ ($P = 0.80$, paired randomization test with 10 000 iterations; Manly 1997). Additionally, when we analysed mortality and recruitment rates separately, we found that they yielded the same conclusions regarding our four predictions as analysing turnover rates alone.

We therefore present analyses and results for turnover rates alone. For the 59 sites for which recruitment rates were not available, we followed convention by using mortality rate as our best estimate of turnover rate (Phillips 1996; Phillips *et al.* 2004).

Potential sources of bias

Conclusions drawn from comparisons of published forest turnover rates can be influenced by several sources of error or bias (Sheil 1995). We considered the three sources of bias that potentially could have the greatest influence on our analyses: census-interval bias, census-year bias, and minimum-dbh bias.

Census-interval bias arises because different subpopulations of trees at a site usually have different turnover rates, leading to a decline in calculated turnover rate with increasing census interval (Sheil & May 1996; Lewis *et al.* 2004b). Thus, if calculated mean turnover rates of two groups of sites differ, the lower of the two rates might be an artefact of that group having longer average census intervals. For tropical forests, census-interval bias for a site can be addressed using $r_s = r_u t^{0.08}$, where r_s is turnover rate standardized to a 1-year census interval, r_u is unstandardized turnover rate, and t is length of census interval in years (Lewis *et al.* 2004b). No equivalent correction has been derived for temperate forests.

Tropical forest turnover rates have increased over the last several decades (Lewis *et al.* 2004a,b; Phillips *et al.* 2004). Thus, a difference in calculated turnover rates between two groups of sites might be an artefact of when the data were collected (census-year bias), with the group having the oldest average census midpoint also having the lower turnover rate. For tropical forests, census-year bias of a site can be addressed by adding $0.0261g$ to its calculated turnover rate (in % year⁻¹), where g is the mean census midpoint year of the entire data set minus the site's census midpoint year (Lewis *et al.* 2004b). This correction is applied after correction for census-interval bias has been applied. No correction for census-year bias has been derived for temperate forests, or is it even known whether one is needed.

Minimum-dbh bias might arise because, in both temperate and tropical forests, small trees usually have higher turnover rates (mortality, and recruitment into the size class) than large trees (e.g. Nakashizuka 1991; Condit *et al.* 1999). Additionally, small trees numerically dominate most forests, meaning that the smallest trees measured have great weight in determining forest-wide turnover rates. Thus, if two groups of sites have different calculated mean turnover rates, this could be an artefact of the group with the lower turnover rate having a larger minimum dbh. No correction, tropical or temperate, has yet been derived for minimum-dbh bias.

Given that correction factors have only been derived for tropical forests (and none for minimum-dbh error), we chose to present results in terms of raw (uncorrected) data. (For some tropical comparisons, we were also able to evaluate corrected results.) However, the nature of our data was such that any biases because of any of the three potential sources almost certainly either would be small, or would be conservative – likely to have diminished rather than accentuated the differences we found (see Results).

Analyses

To determine whether New World sites (which dominated our data set) could be pooled with Old World sites, we tested for a difference between New World and Old World

mean forest turnover rates, by forest type (tropical, temperate angiosperm, temperate mixed and temperate gymnosperm). We compared means using two-tailed randomization tests with 10 000 iterations each (Manly 1997). Unless otherwise stated, all other comparisons of means used equivalent randomization tests. Randomization tests are nonparametric, making no assumptions about underlying distributions (Manly 1997).

Finding no difference between New World and Old World sites, we used the full global data set to test our first prediction, seeking a difference in mean annual turnover rates between tropical and temperate forests. We next sought differences in turnover rates associated with soil fertility. However, most of our data sources did not give adequate information to consistently classify soil fertility. We therefore chose to re-analyse data from Phillips *et al.* (2004) [eliminating a single site (CEL-08) that did not meet our minimum-dbh criterion, and using randomization rather than *t*-tests], who segregated sites in Amazonia into those with richer soils (alfisols, eutrophic histosols, ultisols, clay-rich entisols, and alluvial and basaltic inceptisols) and poorer soils (oxisols, oligotrophic histosols, and spodsols and other white sands).

To test our third prediction, we segregated temperate forests according to taxonomic class (and thus effectively by physiognomy): angiosperm forests (dominated mostly by broad-leaved deciduous trees), gymnosperm forests (dominated mostly by needle-leaved evergreen trees), and mixed forests [which we defined as forests in which neither angiosperms nor gymnosperms comprised $\geq 70\%$ of trees (or basal area)]. If precise numbers or basal areas for angiosperms and gymnosperms were not available, forest composition was estimated based on the authors' written descriptions, or the reported composition of nearby sites.

Finding that turnover rates of temperate angiosperm and gymnosperm forests differed, we wished to determine whether the difference was likely the result of direct environmental effects, or indirect effects mediated by intrinsic phylogenetic or life-form differences between angiosperms and gymnosperms. We therefore used a paired randomization test (Manly 1997) to compare mean mortality rates for angiosperms and gymnosperms growing together at the same sites, hence experiencing similar local environments. To qualify for this analysis, the minority taxonomic class of a site had to include > 100 tree-years of observation (e.g. > 20 trees observed for ≥ 5 years; the average of our qualifying sites was > 2500 tree-years of observation for the minority group). If angiosperms and gymnosperms growing together at the same sites had similar turnover rates, it would suggest that turnover rates were controlled directly by environment, rather than indirectly through phylogenetic affinity or life form.

Finally, to test our fourth prediction we linearly regressed turnover rates of our 22 gymnosperm forest plots in the Sierra Nevada against elevation.

RESULTS

As found by Lewis *et al.* (2004b) for a smaller sample, after correction for possible census-interval and census-year biases we could find no difference between mean turnover rates of New World and Old World tropical forests ($P = 0.19$). Additionally, we could find no differences between uncorrected mean turnover rates of New World and Old World temperate angiosperm forests ($P = 0.90$), mixed forests ($P = 0.71$), or gymnosperm forests ($P = 0.96$). We therefore pooled New World and Old World sites for the remaining analyses.

Although much overlap occurred in the distributions of values, uncorrected mean annual turnover rate of tropical forest (1.74%, SE = 0.06) was greater than that of temperate forest (1.19%, SE = 0.07) ($P < 0.0001$) (Fig. 1). The trop-

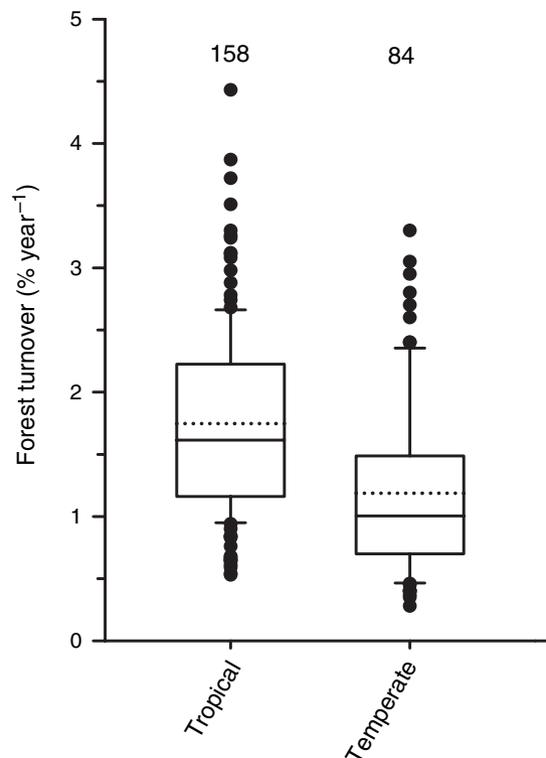


Figure 1 Tropical and temperate forest turnover rates. Each box encompasses the 25th through 75th percentiles; the other solid horizontal lines indicate the 10th, 50th (median), and 90th percentiles. Dotted horizontal lines indicate the mean. The number above each box plot indicates the number of sites in the sample. The tropical and temperate means are significantly different (randomization test, $P < 0.0001$).

ical and temperate samples had nearly identical mean census intervals (9.1 and 9.4 years, respectively) and census midpoints (1984 and 1986), suggesting that significant bias from these sources was unlikely. (Additionally, when we applied the tropical corrections for census-interval and census-year biases to both forest zones, the difference in mean turnover rates remained significant at $P < 0.0001$.) The mean minimum dbh of temperate samples (7.2 cm) was somewhat less than that of tropical samples (9.5 cm), suggesting that any minimum-dbh bias would have diminished, not accentuated, the difference in turnover rates.

As recently demonstrated by Phillips *et al.* (2004), mean annual turnover of tropical Amazonian forest was greater on richer soils (2.26%, SE = 0.08) than on poorer soils (1.39%, SE = 0.09) ($P < 0.0001$) (Fig. 2). Mean minimum dbhs of forests on richer and poorer soils were indistinguishable (10.0 cm). When corrections were applied for census intervals (means of 5.9 and 6.5 years for richer and poorer soils, respectively) and census years (mean midpoint years of 1993 and 1991), the difference remained significant ($P < 0.0001$).

In temperate latitudes, mean annual turnover was highest in angiosperm forest (1.71%, SE = 0.14), intermediate in

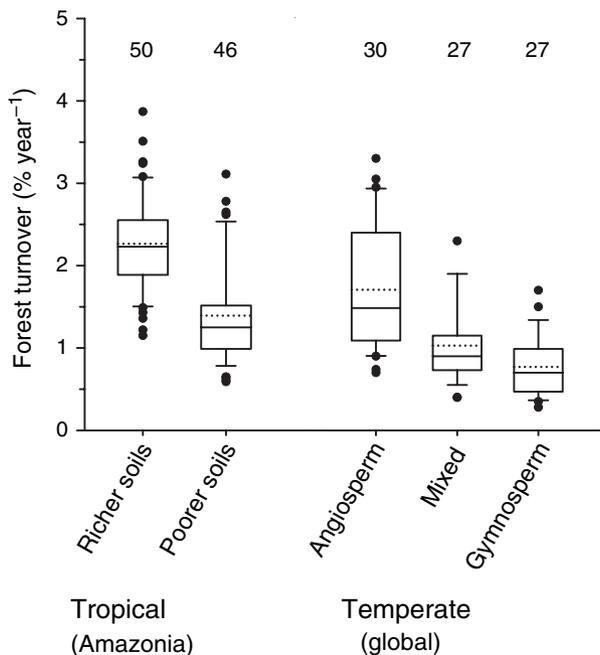


Figure 2 Turnover rates in different tropical and temperate forests. Interpretation of the box plots is as in Fig. 1. Tropical forests of Amazonia are segregated according to soil fertility (Phillips *et al.* 2004), and global temperate forests according to taxonomic class (see Methods). All possible pairwise comparisons of mean turnover rates in the figure are significantly different (randomization tests, $P < 0.05$ to 0.0001).

mixed forest (1.03%, SE = 0.09), and lowest in gymnosperm forest (0.77%, SE = 0.07) ($P < 0.05$ to 0.0001 for all pairwise comparisons) (Fig. 2). In all but one case, differences among the temperate forest types in mean census interval (10.5, 10.4, and 7.0 years respectively), census midpoint year (1984, 1988 and 1988), and minimum dbh (7.9, 8.0 and 5.8 cm) would be expected to have no effect or to have diminished rather than accentuated the differences in turnover rates. For the one exception (7.9 and 8.0 cm minimum dbhs for angiosperm and mixed forests, respectively), the difference was so small that any significant bias is extremely unlikely.

Fifteen temperate sites had adequate data for calculating turnover rates separately for angiosperms and gymnosperms growing at the sites (Appendix S1 in Supplementary Material). When they grew at the same sites, mean annual turnover rates of angiosperms (1.12% year⁻¹, SE = 0.16) and gymnosperms (0.85% year⁻¹, SE = 0.15) did not differ significantly (paired randomization test, $P = 0.23$). Angiosperms had the highest turnover rates at eight of the sites, gymnosperms at seven.

As our sample in the preceding analysis was relatively small (15 pairs), we wished to explore the chance that a similarly small sample from the global data set would have produced a difference in turnover rates of $\leq 0.27\%$ year⁻¹ (which is the difference between the means of the samples in the preceding paragraph). We randomly drew 15 angiosperm and 15 gymnosperm forest sites from our global data set (without replacement; 10 000 iterations), and calculated this chance to be quite small ($P < 0.0001$), consistent with the notion that environment is contributing to the differences in the global data set.

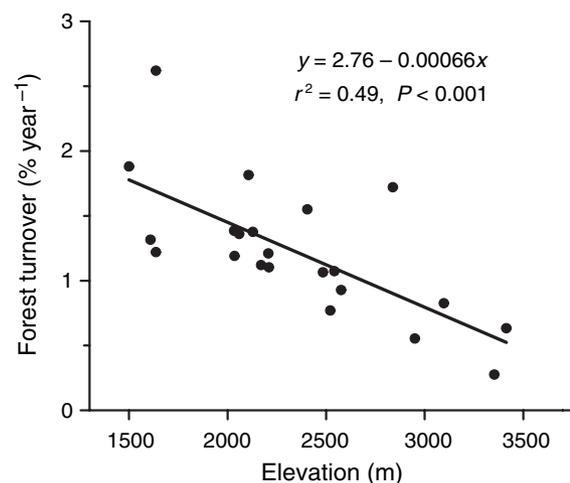


Figure 3 Relationship between forest turnover rate and elevation for coniferous forests of the Sierra Nevada, California. Minimum dbh sampled was 0 cm. Turnover rate declines significantly with increasing elevation (decreasing temperature).

In the gymnosperm forests of the Sierra Nevada, turnover declined significantly with increasing elevation ($r^2 = 0.49$, $P < 0.001$) (Fig. 3), and therefore with decreasing temperature. At lower elevations, turnover rates in the Sierra Nevada were high relative to gymnosperm forests in the global data set (Fig. 2). This difference is partly because of the much smaller mean minimum dbh for the Sierra Nevada sites: 0 cm vs. 5.8 cm for the global sample.

DISCUSSION

Our analyses revealed significant broad-scale patterns in turnover rates of forest trees, both between and within tropical and temperate latitudes. At the extremes, the mean turnover rate of tropical forests growing on fertile soils was nearly three times greater than that of temperate gymnosperm forests. Over a 1900 m elevational gradient in a relatively small region (the Sierra Nevada), coniferous forest turnover rates varied by almost a factor of four. While the notoriously high plot-to-plot and site-to-site variation in forest turnover rates often has been attributed to such things as small samples, random spatial and temporal variation, differences in plot methods and analyses, differences in species composition, and site history (e.g. Sheil 1995; Lugo & Scatena 1996; Hall *et al.* 1998), our results suggest that a significant amount of that variation may also reflect differences that are intrinsic to the local environment.

Consistent with the hypothesis that NPP is positively correlated with turnover rates of individuals in plant populations, each of our four predictions was met. First, tropical forests had higher turnover rates than temperate forests, for which production usually is limited by a cold winter season (Saugier *et al.* 2001; Pregitzer & Euskirchen 2004). Second, as recently demonstrated by Phillips *et al.* (2004), forests of tropical Amazonia that grew on more fertile soils had higher turnover rates than those on less fertile soils. Malhi *et al.* (2004) have demonstrated that Amazonian forests on more fertile soils are also more productive. Third, temperate angiosperm forests had higher turnover rates than temperate gymnosperm forests (with mixed forests falling in between). Temperate angiosperm forests are more productive than temperate gymnosperm forests (e.g. Zheng *et al.* 2003), and angiosperm forests also distinctly occupy sites with higher climatic potential for primary production, as estimated by actual evapotranspiration (Stephenson 1990, 1998). Finally, within a single forest physiognomic type (coniferous forest) in the Sierra Nevada, turnover rate declined significantly with elevation, and therefore with temperature. While we did not have complementary data on NPP along the elevational transect, a climatically similar portion of the 'Oregon Transect', *c.* 900 km to the north, shows a distinct

decline in coniferous forest NPP with increasing elevation (Runyon *et al.* 1994).

Further supporting the case for direct environmental controls, turnover rates appeared to be little influenced by forest phylogenetic affinity or life-form. We could find no differences in turnover rates of New World and Old World forests, or could we find differences in turnover rates of angiosperms and gymnosperms growing at the same sites (hence experiencing similar environments).

We offer three non-mutually exclusive mechanisms that might explain the correlation between NPP and forest turnover rate. The first might be considered the bottom-up mechanism. On intrinsically productive sites, faster tree growth might simultaneously lead to increased fecundity, more intense competition, and quicker outcomes of competition (i.e., tree death), translating to higher turnover rates (Phillips *et al.* 1994; Phillips 1996; Lewis *et al.* 2004a). Second (the top-down mechanism), sites with high potential for primary production will usually also have high potential for secondary production. For example, the warm, moist, aseasonal environments that best favour rapid plant growth also best favour the organisms that attack plants (such as insects, fungi and nematodes), potentially leading to higher death rates (Givnish 1999). [Indeed, rates of herbivory appear to be higher in tropical than in temperate forests, in spite of greater plant defences in the tropics (Coley & Aide 1991).] These higher death rates translate to frequent creation of forest openings and local reductions in competition, leading to higher recruitment rates. Third (the tradeoffs mechanism), trees may face significant tradeoffs between allocating resources towards growth or towards persistence. Specifically, rapid growth may come at the expense of reduced defences or structural integrity, and the abiotic environment may directly or indirectly select for a particular balance between the two (Grime 1979). For example, nutrient-poor soils might select for species that allocate significant resources towards anti-herbivore defences, simultaneously reducing both growth rates and mortality rates (Fine *et al.* 2004).

Particularly in the case of top-down control of turnover rates, increased NPP might be a consequence, not a cause, of increased mortality rates. That is, herbivores and pathogens would cause tree mortality to be higher, which in turn would result in proportionally more forest area being maintained in younger forest patches. As NPP is generally highest in young forest patches (Pregitzer & Euskirchen 2004), the forest as a whole would express higher NPP.

The results we have presented have potentially broad implications for understanding and predicting the effects of environmental changes on forests, hence on terrestrial carbon storage and dynamics. Perhaps most important among these is that environmental changes that increase site productivity (e.g. increasing insolation, nitrogen deposition,

or certain climatic changes) also might be expected to increase forest turnover rates. [Indeed, this argument has been invoked to explain the apparent parallel increases in aboveground live biomass and turnover rates in Amazonian forests over the last several decades (Lewis *et al.* 2004a)]. Simultaneous changes in tree growth rates and turnover rates in turn can be expected to affect forest size structure and age structures (Condit *et al.* 1998), with potentially complex and non-intuitive effects on forest carbon storage. For example, more rapid turnover might also be associated with changes in wood density and tree stature (e.g. Sheil 1996).

Our findings point to several possible directions for future research. First, environmental correlates of forest turnover rates should be explored in greater detail. For example, for those forest sites for which adequate data are available (particularly in the little-examined temperate latitudes), quantitative relationships should be elucidated among site-specific soil properties, climatic parameters, production and forest turnover rates. Second, analyses should be expanded beyond old-growth forests. Do early-successional forests show similar patterns? Third, potential mechanisms driving the relationships should be explored. For example, can data on tree growth rates, fecundity, defences, and causes of mortality be used to estimate the relative influences of the three possible mechanisms described earlier (bottom-up, top-down, or tradeoff controls of turnover rates)? How do mechanisms driving turnover of whole trees compare with those driving turnover of plant organs (Reich *et al.* 1992, 1995; Gill & Jackson 2000)? Fourth, for a number of different forest types and environmental scenarios, forest dynamics models should be used to explore the possible consequences of changing turnover rates on forest carbon storage and dynamics. What forest structural differences are associated with variation in turnover and productivity? Finally, metabolic theory, which predicts that both NPP and turnover rates should be positively correlated with temperature (Brown *et al.* 2004), should be explored as a broader framework for these lines of inquiry.

Our analyses would have been impossible without the results of numerous long-term monitoring efforts conducted worldwide. In the tropics, the extent and intensity of long-term forest monitoring has increased greatly in recent decades, and has included the establishment of extensive networks using common protocols (e.g. Malhi *et al.* 2002; Losos & Leigh 2004). Equivalent efforts have lagged somewhat in temperate latitudes (but see, e.g. Gillespie 1999; Greene *et al.* 2004). Our ability to understand and predict the effects of environmental changes on forests, hence on terrestrial carbon dynamics, depends in part on the diligent establishment and maintenance of such networks.

SUPPLEMENTARY MATERIAL

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/ELE/ELE746/ELE746sm.htm>

Appendix S1 Data for the 242 sites.

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