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Negative Density Dependence Mediates Biodiversity-Productivity Relationships Across Scales

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Summary paragraph: Regional species diversity generally increases with primary productivity while local diversity-productivity relationships are highly variable. This scale-dependence of the biodiversity-productivity relationship highlights the importance of understanding mechanisms governing variation in species composition among local communities, known as β-diversity. Hypotheses to explain changes in β-diversity with productivity invoke multiple mechanisms operating at local and regional scales, but the relative importance of these mechanisms is unknown. Here we show that changes in the strength of local density-dependent interactions within and among tree species explain changes in β-diversity across a subcontinental-productivity gradient. Stronger conspecific relative to heterospecific negative density dependence in more productive regions was associated with higher local diversity, weaker habitat partitioning (i.e. less species sorting), and homogenization of community composition among sites (lower β-diversity). Regional processes associated with changes in species pools had limited effects on β-diversity. Our study suggests that systematic shifts in the strength of local interactions within and among species might generally contribute to some of the most prominent but poorly understood gradients in global biodiversity.

The relationship between biodiversity and net-primary productivity is one of the most prominent and well-studied biological patterns on Earth [1-6]. Species richness generally increases linearly with productivity across regions [7, 8], but the relationship is weaker and highly variable at smaller spatial scales [2, 5, 9, 10]. Increases in regional species richness relative to local species richness across productivity gradients could be explained by greater site-to-site variability in species composition, known as β-diversity, in more productive regions [3, 4, 11-14]. Yet β-diversity does not generally increase with productivity [15-19], leaving the mechanisms that might account for scale-dependent changes in species diversity with productivity unclear. These mechanisms are critical to understand given that global climate change is predicted to cause dramatic changes in net primary productivity [20], potentially leading to loss of species and ecosystem function [21].

Mechanisms underlying the relationship between β-diversity and primary productivity have remained elusive because several non-mutually-exclusive community-assembly mechanisms operating at different spatial scales may alter β-diversity along productivity gradients. At regional scales, two mechanisms might influence β-diversity. First, productive regions may have higher β-diversity because more species exist in their regional-species pools (i.e. higher regional species richness; Fig. 1a). In regions with larger species pools, a smaller proportion of the species pool is expected to occur in any one locality wherein only a limited number of individuals can occur, resulting in greater variation in species composition among localities (higher β-diversity) [11, 22]. Second, β-diversity may be higher in regions with more environmental heterogeneity if species sort among more available niches [3, 19, 23-25]. Therefore, changes in β-diversity across regions may reflect changes in environmental heterogeneity across productivity gradients (Fig. 1b).

In addition to regional mechanisms, shifts in the strength of local density-dependent interactions within and among species may explain changes in β-diversity with productivity, but this mechanism remains unexamined. Stronger interspecific competition or pressure from generalist natural enemies can result in heterospecific negative density dependence (HNDD), where individual recruitment and survival decline with increasing local densities of heterospecifics [26-28]. Stronger HNDD, in turn, can reduce local diversity (or α-diversity) via competitive exclusion or apparent competition [26-28]. Stronger HNDD can also cause greater habitat partitioning (i.e. species sorting) along environmental gradients, as species become more locally abundant and exclude others from habitats where they have higher fitness [26-29]. Both reductions in local diversity and increased habitat partitioning from stronger HNDD are expected to increase β-diversity (Fig. 1c) [23, 29, 30]. Theoretical and empirical studies suggest that higher densities may intensify interspecific competition in more productive environments [31-33], in which case β-diversity may also increase with productivity if HNDD mediates diversity-productivity relationships. However, evidence for stronger interspecific competition in more productive environments is mixed [2, 10], and competition among species may be greater in less productive environments where limiting resources are scarce [28]. Therefore, increases in productivity across regions might increase or decrease β-diversity if productivity increases or decreases the strength of HNDD, respectively.

In addition, local density-dependent interactions among conspecifics may influence changes in β-diversity with productivity. Stronger conspecific negative density dependence (CNDD), caused by greater intraspecific competition or increased pressure from host-specific predators or pathogens [34-37], should limit local abundances of dominant species, thereby providing space for other species and increasing local diversity relative to regional diversity [35, 38-41]. This has led to the prediction that stronger CNDD should homogenize community composition among sites (i.e. decrease β-diversity; Fig. 1d) [30], but this prediction remains untested. Moreover, recent studies have found that CNDD can be stronger in wetter regions and resource-rich environments [36, 42], suggesting that the strength of CNDD may increase with productivity [43]. If so, stronger CNDD might cause β-diversity to be lower in more productive regions. In summary, β-diversity may increase or decrease with productivity depending on the relative influence of regional processes as well as how productivity changes the relative strength of local density-dependent interactions within and among species.

Here, we untangle the relative importance of these regional- and local-scale mechanisms to changes in β-diversity of tree species across a subcontinental productivity gradient. We used US Forest Service (USFS) Forest Inventory and Analysis (FIA) data comprising over a quarter million trees in 9,592 plots that span 18 ecoregions in western North America (Fig. 2a). Ecoregions (hereafter, regions) were defined by the USFS and delineated by elevation and other physical components including climate, physiography, lithology, and soils [44]. This productivity gradient ranges from temperate rainforests to semi-arid juniper-sagebrush ecosystems (Supplementary Table 1), covering substantial variation in net-primary productivity (NPP) while minimizing the potentially confounding influence of latitude on diversity [45]. The gradient also has a large enough extent (576,000 km^2) to appropriately test the influence of processes that act across regions, and a spatial-grain size small enough (one plot covers ~0.24 ha) to test the influence of local-scale species interactions on diversity [41]. We first examine relationships between productivity and diversity at the regional and local scales, and assess whether β-diversity changes with productivity across regions. Second, we evaluate the degree to which differences in regional-species pools (i.e., number and relative abundance of species in a region) explain changes in β-diversity across regions using null-models [22] (Fig. 1a). Third, we evaluate the degree to which differences in environmental heterogeneity (variation in climate, productivity & topography within regions) explain changes in β-diversity across regions (Fig. 1b). Fourth, we assess if the strength of CNDD and/or HNDD change with productivity across regions, and whether any differences in CNDD and/or HNDD across regions explain changes in local species diversity, habitat partitioning along environmental gradients, and variation in β-diversity unexplained by regional processes (e.g. Fig. 1c, 1d). Finally, we discuss broader implications of our study for understanding the mechanisms underlying variation in diversity-productivity relationships.

RESULTS AND DISCUSSION

Diversity at local and regional scales increased along the subcontinental-productivity gradient. Linear regressions revealed that regional ($r^2 = 0.61$, $P < 0.001$) and mean local ($r^2 = 0.39$, $P = 0.006$) species richness increased with mean annual NPP across regions (Fig. 2b, Supplementary Fig. 1). Examination of species accumulation curves for all regions revealed that sampling of regional richness did not systematically change across the productivity gradient (Supplementary Fig. 2). Mean local species evenness also increased with NPP across regions ($r^2 = 0.37$, $P = 0.007$), indicating that more productive regions had more equal relative abundances of species in each FIA plot. Likewise, the mean local effective number of species (or inverse Simpson diversity index), which is similar to rarefied species richness and insensitive to sample grain or extent [46], increased with NPP across regions ($r^2 = 0.36$, $P = 0.009$), indicating that increases in mean species richness with productivity were not simply due to the spatial scale of FIA plots or increases in density.

Differences in the composition of regional-species pools were associated with differences in NPP across regions (permutational multivariate ANOVA test: $F_{1,16} = 4.9$, $P = 0.001$; Fig. 2c), suggesting that productivity may influence β-diversity via changes to regional-species pools. However, linear regressions of median β-diversity ($r^2 = 0.36$, $P = 0.008$; Fig. 3a) and median β-diversity standardized effect sizes ($r^2 = 0.20$, $P = 0.061$; Fig. 3b), which reflect β-diversity not accounted for by differences in regional-species pools (hereafter β_{SES}), declined with NPP across regions. The relationship between productivity and β_{SES} was slightly weaker than the relationship between productivity and β-diversity, suggesting that differences in regional-species pools may partially contribute to—but are not a dominant mechanism causing—β-diversity to decline with productivity. Moreover, median β_{SES} was significantly positive in each region (Supplementary Table 1), indicating that β-diversity was generally higher than would be expected if community composition was only determined by stochastic assembly from regional-species pools. Differences in environmental heterogeneity (variation in climate, productivity & topography within a region) were unrelated to NPP across regions (linear regression: $r^2 = 0.01$, $P = 0.65$; Fig. 3c), indicating that regional differences in available niche space had a limited influence on β-diversity. Other differences among regions that might have influenced β-diversity include: the number of FIA plots, region area, mean nearest-plot distance, total number of trees in a region, mean local-community size (i.e., the average number of tree individuals per FIA plot), and the contribution of spatial distances among plots to changes in species composition. These were all unrelated to NPP across regions and, thus, had little influence on the observed decline in β-diversity with productivity (Supplementary Table 2).

The relative strength of local conspecific and heterospecific negative density dependence largely accounted for declines in β-diversity with productivity. Negative effects of heterospecific trees on focal sapling densities (hereafter HNDD) were strongest in low-productivity regions (linear regression weighted by the error around HNDD estimates for each region: $r^2 = 0.42$, $P = 0.004$; Fig. 4a, Supplementary Fig. 3). Contrary to the expectation that stronger HNDD would erode diversity and reduce species richness [26-28], stronger HNDD was not associated with lower mean local species richness ($r^2 = 0.03$, $P = 0.49$) or diversity (i.e. Shannon diversity index; $r^2 = 0.08$, $P = 0.25$). Instead, two patterns suggest that stronger HNDD in low-productivity regions is associated with increased habitat partitioning. First, variation in species composition associated with the environment declined with NPP ($r^2 = 0.24$, $P = 0.04$), suggesting that species in low-productivity regions exhibit greater habitat partitioning than species in high-productivity regions despite encountering similar or lower environmental heterogeneity (Fig. 3c). Second, variation in species composition associated with the environment increased with HNDD ($r^2 = 0.42$, $P = 0.003$; Fig. 4b), supporting the idea that strong interspecific competition or pressure from generalist enemies (e.g., apparent competition) promotes habitat partitioning [26-29, 47]. Stronger HNDD was also associated with higher β_{SES} ($r^2 = 0.25$, $P = 0.033$; Fig. 4c), indicating that increases in habitat partitioning from stronger HNDD contribute to higher β-diversity in less productive regions.

In contrast, stronger CNDD in high-productivity regions was associated with increased mean local diversity and lower β-diversity (Fig. 4d-4f). Stronger CNDD in high-productivity regions (linear regression weighted by the error around CNDD estimates for each region: $r^2 = 0.41$, $P = 0.004$; Fig. 4d, Supplementary Fig. 3) is consistent with other recent findings of stronger CNDD in wetter regions and resource-rich environments [36, 42]. Our analyses cannot determine whether CNDD was due to intraspecific competition, pressure from host-specific predators and pathogens, or a combination of both processes. However, our results indicate that HNDD, which reflects the strength of interspecific competition, is weak in productive regions

(Fig. 4a). If the strength of competition among tree species is indicative of the strength of competition within tree species, then weaker HNDD combined with stronger CNDD in productive regions (Fig. 4a, 4d) suggests that specialized enemies may contribute to increases in CNDD with productivity. Indeed, evidence is mounting that activities of host-specific enemies, and not intraspecific competition, are largely responsible for CNDD [34-37]. Stronger CNDD in more productive regions was associated with higher mean local species evenness ($r^2 = 0.66$, $P < 0.001$; Supplementary Fig. 4), richness ($r^2 = 0.39$, $P = 0.005$; Fig. 4e), and diversity ($r^2 = 0.42$, $P = 0.004$), supporting the hypothesis that CNDD limits the dominance of locally-abundant species and increases local diversity [35, 38-42]. Stronger CNDD in more productive regions was also associated with decreased β_{SES} ($r^2 = 0.37$, $P = 0.007$; Fig. 4f), suggesting that stronger CNDD decreases β-diversity by homogenizing community composition among sites. β-diversity also declined as the ratio of CNDD to HNDD increased ($r^2 = 0.32$, $P = 0.014$; Supplementary Fig. 5), indicating that the relative strength of local conspecific to heterospecific density-dependent interactions may largely determine changes in β-diversity with productivity.

Changes in the strength of local interactions within and among species trumped potential regional influences on β-diversity across the productivity gradient (Fig. 3, 4). This result challenges recent conceptual models that deemphasize the importance of local-species interactions to community assembly and patterns of biodiversity, particularly at biogeographic scales [48]. While we examined a broad-scale productivity gradient that was largely decoupled from the potentially confounding influences of latitude on diversity, our study area provided only a moderate gradient in regional-species richness (11-41 species). Vast differences in biogeography and evolutionary history across even larger gradients in regional-species richness (e.g., 10-1000 species) might have a stronger influence on β-diversity, and biodiversity in general, than local-species interactions [49]. However, effects of local-species interactions on diversity have been largely neglected at global scales due to lack of appropriate data to test them.

Our results indicate that changes in local diversity and β-diversity along a large-scale productivity gradient are largely mediated by shifts in the relative strength of local-scale species interactions (Fig. 4). Specifically, stronger HNDD in low-productivity regions was associated with greater habitat partitioning and higher β-diversity, likely because species become more abundant in favourable environmental conditions. In contrast, stronger CNDD in high-productivity regions was associated with greater mean local diversity, more equal relative abundances of species, and lower β-diversity, likely because CNDD limited abundances of dominant species and homogenized community composition among sites. While a handful of previous studies have found that stronger CNDD increases local diversity [35, 40-42], none, to our knowledge, have examined the relative importance of conspecific and heterospecific density-dependent effects on β-diversity. These findings provide support for the idea that increases in CNDD (e.g. pressure from specialized enemies) enhance local diversity within sites but homogenize community composition among sites (decrease β-diversity) and reduce the relative importance of competitive interactions among species [30]. Our results further advance this framework by demonstrating that shifts in the relative strength of CNDD and HNDD may underlie relationships between primary productivity and diversity (Fig. 4).

These findings have important implications for understanding why local diversity and β-diversity often show variable relationships with primary productivity. Studies have found that both local diversity (species richness) and β-diversity can increase, decrease, or have a unimodal relationship with productivity [2-6, 11, 16, 19, 22, 50]. Previous explanations for these variable relationships include differences in spatial scales, geographic extents, and ranges of productivity over which diversity is measured [16]. Our results suggest that the shape of these relationships may also depend on how the strength of CNDD changes relative to the strength of HNDD along productivity gradients. Positive relationships between diversity (β-diversity or species richness) and productivity may reflect stronger self-limitation of dominant species (i.e. stronger CNDD) in productive environments, as indicated by our results. However, in some cases (e.g. smaller spatial extents or smaller ranges of productivity), increases in CNDD with productivity may be modest or offset by relatively stronger increases in HNDD. In such cases, greater habitat partitioning or competitive exclusion in productive environments may lead to unimodal or neutral diversity-productivity relationships. Changes in productivity [4, 8], and potentially CNDD [36, 41], accompany other prominent large-scale biodiversity gradients, such as the latitudinal-diversity gradient. Therefore, systematic shifts in the relative strength of density-dependent interactions within and among species at local scales might generally contribute to some of the most striking gradients in global biodiversity.

METHODS

Data

We used tree species-abundance data from the United States Forest Service (USFS) Forest Inventory and Analysis (FIA) project. These data are freely available at http://www.fia.fs.fed.us/tools-data and were accessed for this study on November 28, 2015. Since 2000, FIA has used a nationally-standardized sampling design with outstanding sampling intensity (an average of one plot per 2,428 ha). FIA plots consist of four 7.3-m-radius subplots with centres spaced ~36-63 m apart to cover an area approximately equal to 0.24 ha. We used data from all forested (> 10% canopy cover) and natural (non-plantation and non-disturbance)

FIA plots within ecoregions that at least partially lay between 42° N and 49° N latitude and west of 105° W longitude. These values of latitude and longitude capture substantial orographically-generated east-west variation in net-primary productivity (NPP) while minimizing the potentially confounding influence of latitude and vast differences in biogeographic and evolutionary histories across the continental USA on species diversity [45]. This area includes all ecoregions from the coast of Washington and Oregon to the Rocky Mountain front on the boundary of the North American great plains (east of which forests become very sparsely distributed). Forests in this latitudinal belt from eastern North America also have very different biogeographic histories from forests in our study area. For example, eastern forests at this latitude were recolonized from glacial refugia in the southeastern United States, whereas western forests were recolonized from glacial refugia in the Cascade mountain ranges and along the west coast [51, 52].

We excluded FIA plots that reported any natural or human-caused disturbance (e.g. fire, logging; FIA protocol requires reporting any disturbances in the 10 years prior to plot measurement on western US plots, as this is the time between subsequent measurements). Because disturbance was largely concentrated on private land, we only included FIA plots from public lands (USFS lands, national parks, state parks and other state-held lands). Another important reason for excluding private land from our analysis is that geographic locations are swapped among private FIA plots within counties to protect landowner privacy, up to 220 km (largest distance between FIA plots within a county; in Idaho County, Idaho) away from the original location. This is not done for public FIA plots, and accurate geographic coordinates are essential for variation-partitioning analyses (see below). Ecoregions used in our analysis were defined by the USFS (‘ECOSUBCD’ in FIA database) [53]. We only included regions that were defined by FIA as ‘mountainous’ because publicly-owned as well as non-plantation and nondisturbed forested FIA plots are heavily concentrated in these regions [53]. We only included regions that had at least 150 publicly-owned FIA plots to have a minimum appropriate sample size at which to precisely estimate β-diversity (Supplementary Table 1).

We included data from the first complete FIA census since implementation of the nationally-standardized protocol in 2000. This includes data collected during 2000-2014. For analyses of diversity and environmental habitat partitioning (i.e. species sorting), we included all individuals >12.7 cm diameter at breast height, or dbh, of tree species (hereafter, trees). Smaller individuals (2.5 cm ≤ dbh < 12.7 cm) were only surveyed within four smaller 1.83-m radius microplots nested within the larger 7.3-m radius subplots. These smaller individuals (hereafter, saplings) were used in conjunction with trees to calculate the strength of HNDD and CNDD (see below).

Environmental variables were provided with FIA data or obtained from publicly-available satellite-based datasets. Topographic variables (slope, aspect, and elevation) are provided for each FIA plot. Where multiple slope and aspect values were reported, we used the slope and aspect values that reflect the majority of the FIA plot. We calculated the cosine and sine of aspect as measures of north-south-facing and east-west-facing slopes, respectively. Heterogeneity in soil characteristics among sites is likely an important environmental variable to consider, but soils data were only available for 219 of the 9,592 plots (2.2%) used in our analyses. However, topography is known to strongly influence soil formation [54], and was used as a proxy. We obtained measurements for each FIA plot (mean values within a 1 km buffer around each FIA plot) of mean annual net primary productivity (NPP) during 2000-2014 from MODIS satellite-based data operated by the National Aeronautics and Space Administration (NASA) [55]. We also obtained mean annual temperature (°C), mean temperature of the warmest month (°C), mean temperature of the coldest month (°C), mean annual precipitation (mm), mean summer precipitation (mm), number of degree-days above 18°C, precipitation as snow (mm), extreme maximum temperature over 30 years (°C), and mean annual relative humidity (%) during 1981-2010 for each FIA plot from the AdaptWest Project [56]. Other available climatic variables from AdaptWest (e.g., number of frost-free days) were highly correlated ($r > 0.95$) with variables listed above and were not included. Locations of FIA plots on public land are perturbed up to 1.67 km but typically within a 0.8 km of the actual location. Slope, aspect, and elevation are provided for the actual plot location, and the spatial resolution of the NPP and climate data (1-km resolution) is similar to that of the FIA perturbed plot locations. Thus, we used the perturbed plot locations to match FIA plots with NPP and climate data as in other recent studies using FIA data [57].

Analyses

Diversity measures

For each region, we calculated the total number of species (regional species richness), the mean number of species per FIA plot (mean local species richness), mean local effective number of species (i.e. the inverse Simpson diversity index, which is similar to rarefied species richness and insensitive to spatial grain and extent[46]) per FIA plot, and mean local species diversity (Shannon diversity index) per FIA plot. We calculated mean local-species evenness for each region by first calculating the relative abundance and abundance rank of each species in each FIA plot. We then used a mixed model to calculate the mean slope of these local rank-abundance curves for each region, which is a measure of species evenness [58]. Species relative abundances were log-transformed for these relationships [58]. We also calculated the median pairwise Bray-Curtis dissimilarity among FIA plots (hereafter, β-diversity) for each region using the package 'vegan' in R [59, 60]. While Whittaker's β-diversity partition ($\frac{regional\ richness}{local\ richness}$) increased with productivity (Fig. 2a), this measure of β-diversity is mathematically dependent on regional and local richness and does not capture dissimilarities in the presence/absence or relative abundance of species across sites. The Bray-Curtis dissimilarity index incorporates information about the relative abundances of species (a fundamental component of diversity) in addition to presences/absences of species, and is a recommended measure of β-diversity when composition and relative abundance data are available [61]. Thus, we measured β-diversity as the median dissimilarity in the composition and relative abundances of species among FIA plots within each region.

Previous studies of β-diversity-productivity relationships have measured β-diversity using both incidence-based (i.e. based on species presences/absences) and abundance-based (i.e. based on relative species abundances) metrics, and have shown that both types of metrics can increase or decrease with productivity [3, 4, 11, 13, 16, 19, 62]. Thus, the shape of the β-diversity-productivity relationship does not appear to be dependent on the use of incidence- or abundance-based β-diversity metrics. In this study, we focused on an abundance-based metric (i.e. Bray-Curtis dissimilarity) because variation in relative-species abundance is more informative given our hypotheses, which focus on the effects of local species interactions on the relative abundance of species (e.g. effects of CNDD on dominant species). Abundance-based metrics of β-diversity are generally preferred when testing hypotheses involving deterministic processes because incidence-based metrics are more sensitive to random occurrences of rare species [13, 63]. Moreover, one of our key hypotheses concerns the influence of regional species pools on β-diversity, which we test using a null-model approach [22, 64]. Simulations using this null-model approach indicate that null-model deviations using abundance-based β-diversity metrics are better at detecting deterministic processes than deviations using incidence-based β-diversity metrics [65].

We used simple linear regression models to test for changes in these measures of diversity with mean annual NPP across regions. Variation in NPP was much greater across regions than within regions (Supplementary Fig. 6), as ecoregion identity explained 72.7% of total variation in NPP across all 9,592 FIA plots used in this analysis. Mean regional NPP was log-transformed in all analyses due to a right-skewed distribution. To evaluate if regional-species pools (i.e., the number and relative abundances of species in a region) differed among regions or if assemblages in some regions were nested within assemblages of other regions, we used nonmetric-multidimensional scaling (NMDS) in the 'vegan' package to plot species composition of regions in NMDS space and the 'adonis' function to test for significant differences in species composition as a function of mean NPP across regions [60]. To examine other potential regional or sampling influences on β-diversity, we also tested if the number of FIA plots per region, area of a region (ha), total number of individuals in a region, mean local community size per region, or the mean nearest-neighbour FIA plot distance within each region changed systematically with mean regional NPP (Supplementary Table 2).

Null-model analysis

To evaluate if differences in regional-species pools contributed to differences in β-diversity with NPP across regions, we performed null-model analyses [22, 64]. Individuals from each regional-species pool (preserving the regional species-abundance distribution) were randomly distributed among FIA plots in that region while preserving the total number of individuals in each plot [22, 64]. Thus, these null local assemblages were only the product of stochastic assembly from the regional-species pool, and all other mechanisms that might cause additional spatial aggregation of individuals (e.g., habitat partitioning, local interactions among species, dispersal limitation) were removed. The pairwise dissimilarities of these simulated communities within each region (β_{SIM}) were then compared to the observed dissimilarities (β_{OBS}) relative to the standard deviation of β_{SIM} (σ_{SIM}) after 1,000 iterations, and a standardized effect size of the difference was calculated as: $\beta_{SES} = (\beta_{OBS} – \beta_{SIM})/ \sigma_{SIM}$. Therefore, β_{SES} represents β-diversity that remains unexplained by stochastic assembly from the regional-species pool [22]. We also tested if median β-diversity in each region was significantly greater than median β-diversity expected from stochastic assembly from the regional-species pool by assessing if fewer than 5% of median β_{SIM} values were greater than or equal to median β_{OBS} (i.e. one-tailed test of significance).

Environmental heterogeneity among regions

To calculate the multivariate environmental heterogeneity of regions, we first performed a principal component analysis (PCA) on all 14 environmental variables (elevation, slope, NPP, cos(aspect), sin(aspect), and the nine climatic variables) across all 9,592 FIA plots. Variables were standardized for the PCA. We then calculated the multivariate environmental heterogeneity of each region as the mean square of multivariate (Euclidean) distances from each FIA plot in a region to that region's centroid. This is identical to calculating the 'niche space' of each region using outlying mean index (OMI) [66]. We tested for a relationship between environmental heterogeneity and NPP across regions with linear regression.

Partitioning variation in species composition

To assess the degree to which species partition habitat in each region (i.e. species sorting), we calculated the proportion of variation in species composition among localities associated with environmental heterogeneity in each region using the ‘vegan’ package [60]. Variation partitioning produces four terms: β-diversity associated with the environment only (i.e., not associated with spatial distance), β-diversity associated with spatial distance only, β-diversity associated with both spatial distance and the environment, and β-diversity unexplained by the environment or spatial distance. To test if habitat partitioning (i.e. species sorting) was greater in more productive regions or regions with stronger HNDD, we tested for a positive relationship between the variation in species composition purely associated with the environment and regional NPP or HNDD, respectively. We also evaluated if variation in species composition associated with spatial distance changed systematically with NPP to test if differences in dispersal limitation or other spatial factors might explain changes in β-diversity across regions (Supplementary Table 2).

Conspecific and heterospecific density dependence

We estimated the strength of CNDD and HNDD following previously-published methods [40, 42]. For each region, we used the following hierarchical model to estimate the mean strength of CNDD and HNDD:

$$\ln(S_{ij}+1) = r_j + \mathrm{CNDD}_j \times \ln\left(A_{ij}+1\right) + \mathrm{HNDDtree}_j \times a_{ij} + \mathrm{HNDDsap}_j \times s_{ij} + \mathrm{NPP}_j \times npp_i + \varepsilon_{ij}$$

$$\varepsilon_{ij} \sim \mathrm{N}(0,\sigma^2) \qquad (1)$$

Where S_{ij} is the observed number of saplings of species j in plot i, r_j is the per-capita recruitment rate for species j at low conspecific tree densities, CNDD_j is the per-capita effect of conspecific tree density on sapling recruitment for species j, A_{ij} is the observed number of conspecific trees of species j in plot i, HNDDtree$_j$ is the per-capita effect of heterospecific tree density on sapling recruitment for species j, a_{ij} is the observed number of heterospecific trees (i.e. not species j) in plot i, HNDDsap$_j$ is the per-capita effect of heterospecific sapling density on sapling recruitment of species j, s_{ij} is the observed number of heterospecific saplings in plot i, NPP$_j$ is the per-capita effect of NPP on sapling recruitment for species j, npp_i is the observed value of NPP in plot i, and ε_{ij} is normally-distributed error. We began with a full random effects structure (i.e. random species-specific effects for r_j, CNDD$_j$, HNDDtree$_j$, HNDDsap$_j$, and NPP$_j$), and then removed random effects that were either correlated ($r \geq 0.7$) with the random intercept or whose standard deviation was estimated to be at or near zero (SD ≤ 0.1). This approach avoids over-parameterization of models [67, 68]. However, results were similar if all random effects were included in the model. These models were run in R (package 'lme4') [59, 69]. Thus, for each region, we quantified the mean effects of conspecific tree density on focal sapling density (CNDD), and two measures of HNDD: (1) effects of heterospecific tree density on focal sapling density (HNDDtree) and (2) effects of heterospecific sapling density on focal sapling density (HNDDsap; Supplementary Table 3, Supplementary Fig. 3).

Conspecific tree and sapling densities were log-transformed for all forest plots to estimate the proportional (and not additive) change in sapling densities with increasing conspecific tree densities [40, 42]. Negative relationships between heterospecific densities and focal sapling density represent HNDD [40, 42]. Reductions in per-capita recruitment with increasing conspecific tree density represent stronger CNDD (Supplementary Fig. 7) [40, 42]. Sapling density may also depend on variation in NPP within a region (e.g., species-specific habitat preferences), so we included mean annual NPP in our models of sapling density, as well as a random slope of NPP for each species to account for potentially different effects of NPP on sapling densities across species, i.e., equation (1).

We used numerical abundances to quantify densities (trees/ha) for conspecific trees and all saplings to maintain consistency and comparability with previous studies that quantified stem densities with numerical abundances [40, 42]. Nonetheless, our reported estimates of CNDD were highly correlated with estimates of CNDD that used basal area to quantify conspecific and heterospecific densities ($r = 0.93$; $P < 0.0001$). Likewise, our reported estimates of HNDDsap were highly correlated with estimates of HNDDsap that used basal area to quantify conspecific and heterospecific densities ($r = 0.99$, $P < 0.0001$). We used basal area to quantify densities of heterospecific trees because tree-size distributions can vary extensively across species, and basal area provides a way to standardize the spatial influence of older age classes across species [42]. Nonetheless, our reported estimates of HNDDtree were highly correlated with estimates of HNDDtree that used numerical abundances to quantify conspecific and heterospecific densities ($r = 0.90$, $P < 0.0001$).

We found that negative effects of heterospecific trees on sapling recruitment (HNDDtree) were significant in all but two regions and generally stronger than negative effects of heterospecific saplings on sapling recruitment (HNDDsap), which were only significant in five of 18 regions (Supplementary Table 3). This result supports previous findings that negative density-dependent effects of heterospecifics tend to come from older instead of younger age classes [42, 70, 71]. Thus, we report effects of heterospecific trees on sapling recruitment (HNDDtree) as HNDD in the Results and Discussion section (including Fig. 4).

While changes in CNDD and HNDD might have been influenced by systematic changes in sapling and tree densities across the productivity gradient, neither sapling ($r = -0.06$, $P =$

0.802) nor tree ($r = 0.04$, $P = 0.884$) densities varied with NPP across regions (Supplementary Table 2). Furthermore, the scale at which CNDD and HNDD were measured did not influence estimates for each region. Density-dependent interactions (e.g. CNDD) are known to occur at small spatial scales. Evidence from temperate and tropical forests indicates that these effects are strongest between 10 m to 30 m from a focal tree, but can extend up to 50 m away from focal trees [72, 73]. Thus, individuals in particular FIA subplots, which are ~7 m in radius and spaced ~36-63 m apart, may influence density-dependent recruitment or survival in neighbouring subplots. Moreover, two previous studies have used FIA data from the eastern and central US to estimate CNDD (but have not linked changes in CNDD to changes in β-diversity or productivity). Both studies used the entire FIA plot to estimate the strength of CNDD [41, 57]. Thus, we used the entire FIA plot to estimate the strength of local density-dependent interactions. Nonetheless, CNDD measured at the subplot scale was highly correlated with reported measures of CNDD, regardless of whether subplot CNDD was calculated using basal area ($r = 0.90$; $P < 0.0001$) or numerical abundance ($r = 0.86$; $P < 0.0001$). Similarly, HNDD for heterospecific trees and saplings, each measured at the subplot scale, were highly correlated with reported measures of HNDD regardless of whether subplot HNDD was calculated using basal area (heterospecific trees: $r = 0.84$; $P < 0.0001$; heterospecific saplings: $r = 0.77$; $P = 0.0002$) or numerical abundance (heterospecific trees: $r = 0.73$; $P = 0.0006$; heterospecific saplings: $r = 0.81$; $P < 0.0001$).

Finally, we examined hypothesized relationships between the strength of HNDD, NPP, habitat partitioning, and β-diversity after accounting for regional influences (i.e., median β_{SES}). We also examined hypothesized relationships between the strength of CNDD, NPP, local-species evenness, local-species richness and diversity (Shannon-diversity index), and β_{SES}. These regressions were weighted by the inverse error variance around estimates of either HNDD or CNDD for each region.

Data availability

The FIA datasets analysed during the current study are freely available from the United States Forest Service at http://www.fia.fs.fed.us/tools-data. The NPP dataset is available from the University of Montana at http://www.ntsg.umt.edu/project/mod17, and the climate data are available from AdaptWest at https://adaptwest.databasin.org/pages/adaptwest-climatena.

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Supplementary Information is linked to the online version of the paper at www.nature.com.

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Author Information: Data are available at http://www.fia.fs.fed.us/tools-data. Reprints and permissions information is available at www.nature.com/reprints. We declare no conflicts of interest. Correspondence and requests for materials should be addressed to J.A.L. (joe.a.lamanna@gmail.com).

Competing interests

The authors declare no competing financial interest.

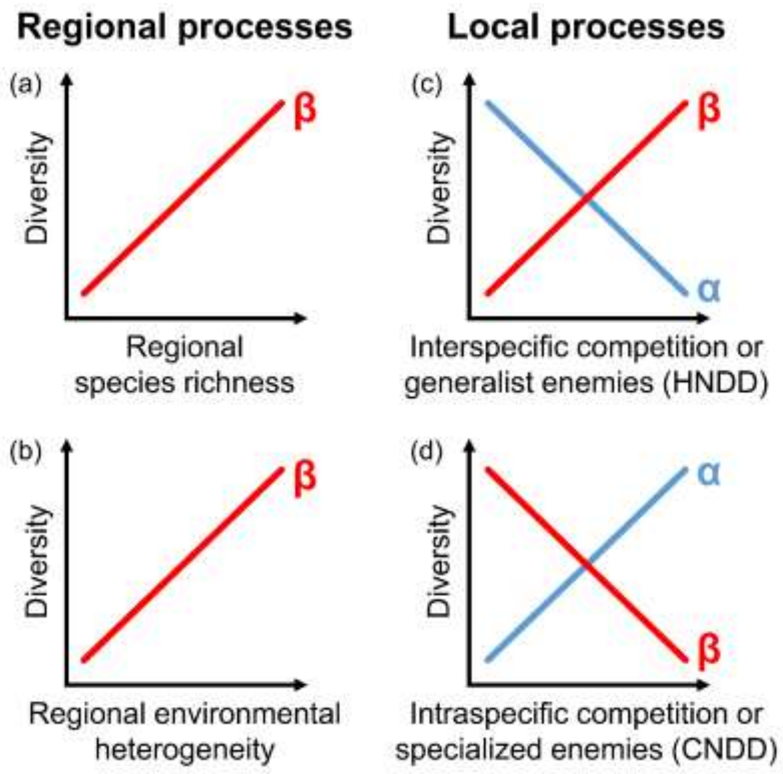

Fig. 1. Hypothesized influences of regional and local processes on patterns of biodiversity across regions that vary in primary productivity. (a-b) Regional hypotheses predict that site-to-site variation in community composition (β-diversity) increases with (a) regional species richness (number of species in a region) and (b) environmental heterogeneity (variation in environmental conditions within a region). If more productive regions have greater/lower regional species richness or environmental heterogeneity, then productive regions might have higher/lower β-diversity, respectively. (c-d) Local hypotheses predict that β-diversity and mean local diversity (α-diversity) vary systematically with the strength of local density-dependent interactions within and among species. (c) Stronger interspecific competition or pressure from generalist enemies (which cause heterospecific negative density dependence, or HNDD) is predicted to reduce mean α-diversity via competitive exclusion or apparent competition. Stronger HNDD can also increase habitat partitioning (i.e. species sorting) along environmental gradients. Reductions in α-diversity and greater habitat partitioning are each expected to increase β-diversity. (d) In contrast, stronger intraspecific competition or pressure from specialized enemies (which cause conspecific negative density dependence, or CNDD) is expected to increase mean α-diversity and decrease β-diversity. Effects of productivity on β-diversity across regions, therefore, might depend on whether productivity strengthens or weakens CNDD and/or HNDD. See text for details.

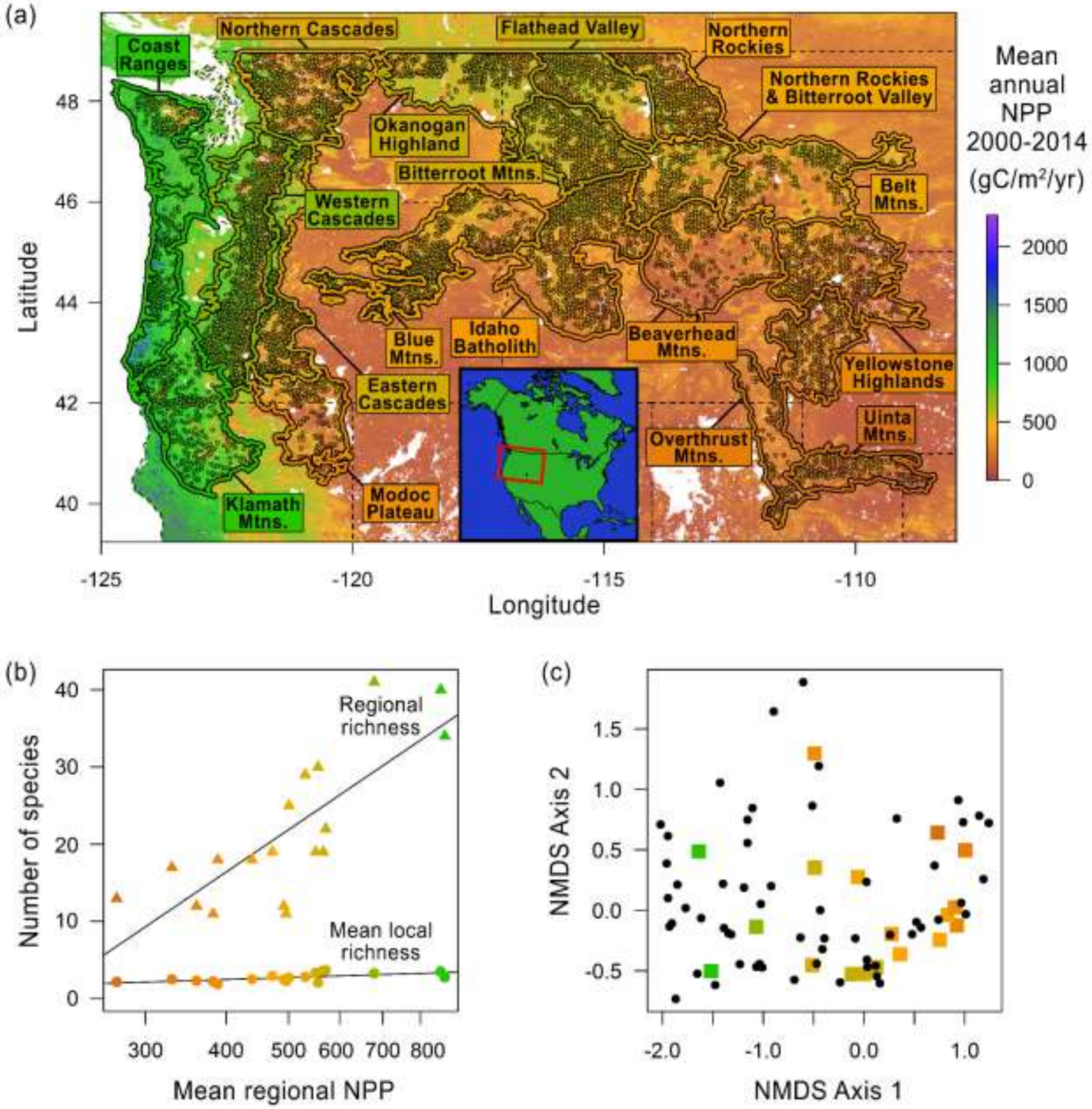

Fig. 2. Study area in western North America and changes in tree species richness and composition with net-primary productivity (NPP). (a) Mean annual NPP (2000-2014) and US Forest Service Forest Inventory and Analysis (FIA) plots used in this analysis (*N* = 9,592) grouped into 18 ecoregions (Supplementary Table 1). Plots are coloured by their individual NPP, and regional boundaries and labels are coloured by their mean NPP. (b) Changes in regional (triangles) and mean-local (circles) species richness with NPP across regions (NPP is on a log scale and regions coloured by mean NPP). (c) The composition of regional-species pools differed among ecoregions (squares coloured by regional NPP) according to nonmetric-multidimensional scaling (NMDS). Each circle in (c) represents a species (*N* = 65 total species).

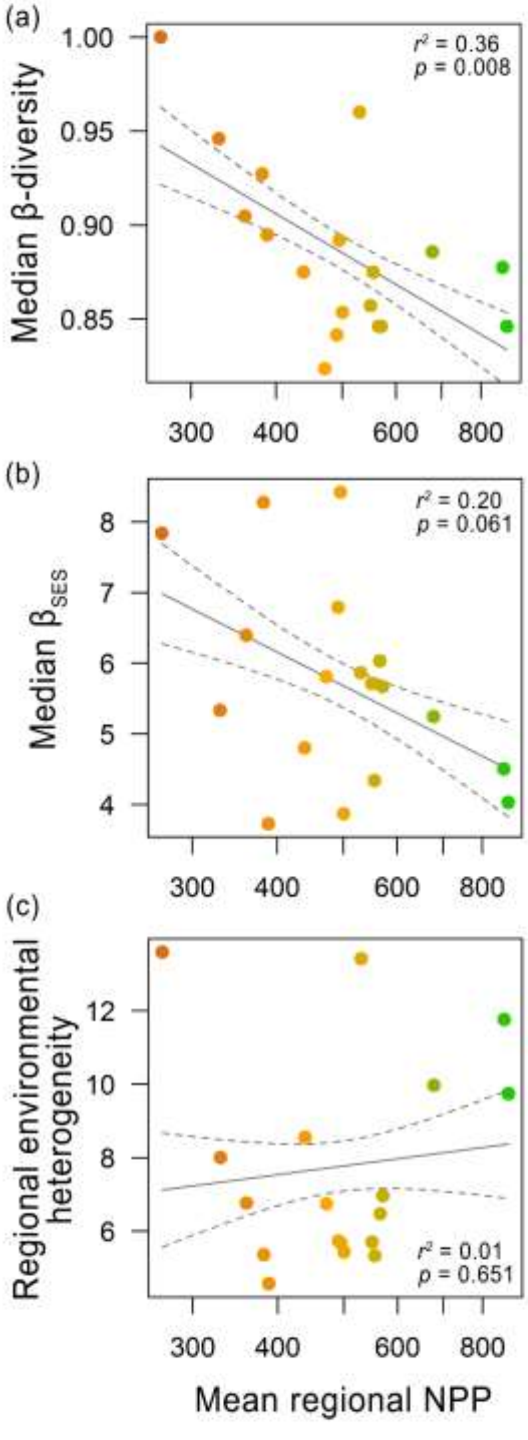

Fig. 3. Relationships between β-diversity, environmental heterogeneity, and net-primary productivity (NPP). (a) Median β-diversity (Bray-Curtis dissimilarity) and (b) median β-standardized-effect size, or β_{SES} (which accounts for regional influences on β-diversity) both decreased with mean annual NPP across regions. (c) Environmental heterogeneity (variation in climate, productivity & topography within a region) was unrelated to NPP across regions. Each point is one of 18 ecoregions coloured by its mean annual NPP. NPP is on a log scale. Best-fit lines (±1 SE) are in grey. Statistics are from linear regression tests.

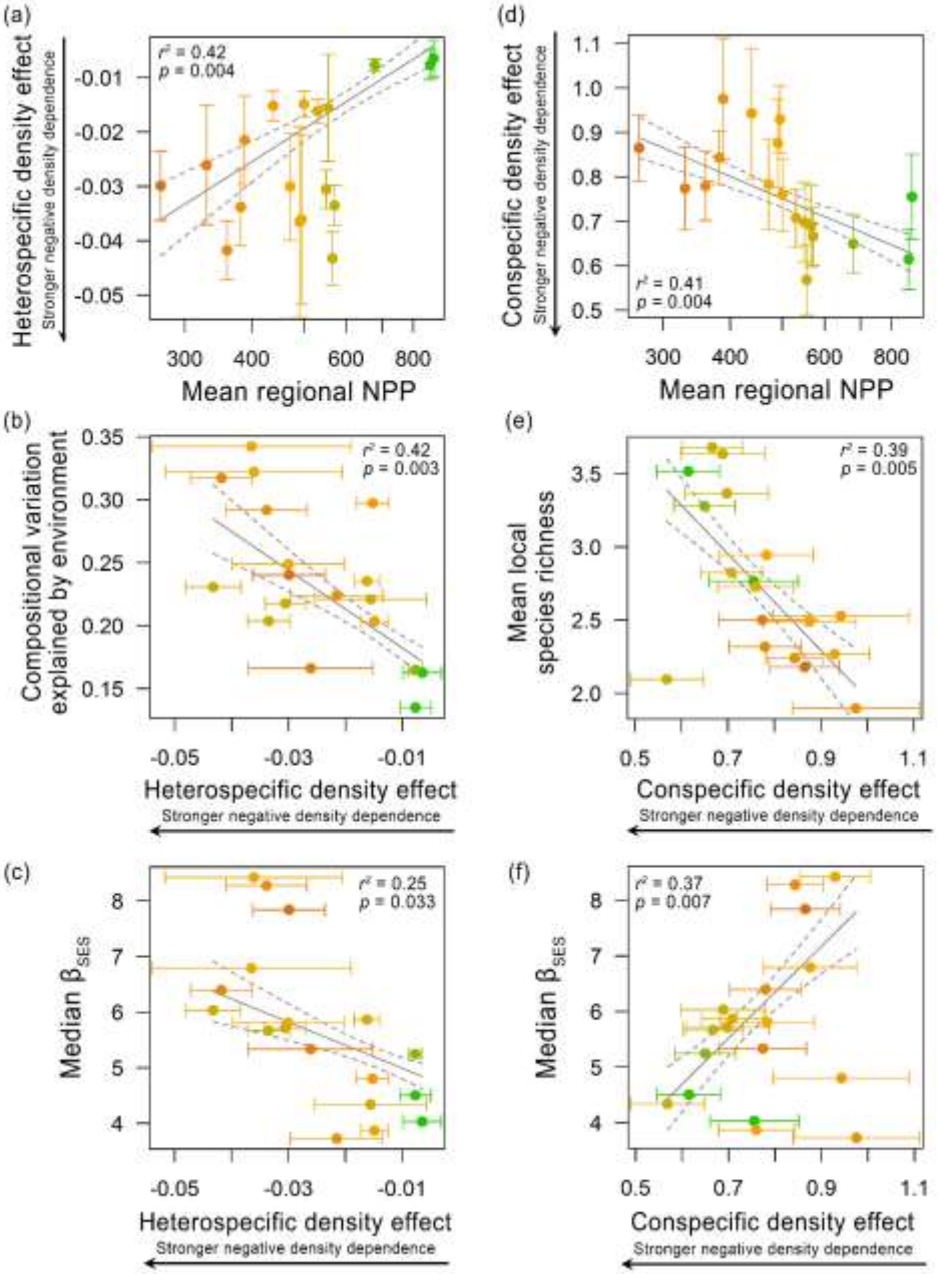

Fig. 4. Conspecific and heterospecific negative density dependence (CNDD and HNDD), net primary-productivity (NPP), and effects on β-diversity. (a) HNDD was weaker in productive regions. (b) Stronger HNDD was associated with greater habitat partitioning (i.e. species sorting), measured as the amount of variation in species composition associated with the environment, and (c) greater β-diversity after accounting for regional influences (β_{SES}). (d) CNDD was stronger in productive regions, and stronger CNDD was associated with (e) greater local species richness and (f) lower β-diversity (β_{SES}). Each point is one of 18 ecoregions coloured by its mean annual NPP. CNDD and HNDD measures represent means across all species in a region, and error bars represent ±1 SE around those estimates. NPP is on a log scale. Best-fit lines (±1 SE) are in grey. Statistics are from linear regression tests weighted by the error around estimates of CNDD or HNDD.