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Joseph A. LaManna

R Travis Belote

Laura A. Burkle

Christopher P. Catano

Jonathan A. Myers
jamyers@wustl.edu

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Negative Density Dependence Mediates

Biodiversity-Productivity Relationships Across Scales

Authors: Joseph A. LaManna^{1*}, R. Travis Belote², Laura A. Burkle³, Christopher P. Catano¹,
and Jonathan A. Myers¹

Author affiliations:

¹ Washington University in St. Louis, Department of Biology & Tyson Research Center, St. Louis, Missouri 63130 USA

² The Wilderness Society, Bozeman, Montana 59717 USA

³ Department of Ecology, Montana State University, Bozeman, Montana 59717 USA

* Corresponding author

Keywords: Beta-diversity, biodiversity, biogeography, community assembly, diversity-environment relationships, diversity maintenance, Forest Inventory and Analysis, large-scale diversity gradients, natural enemies, negative density dependence, productivity, niches, regional species pools, species interactions, species sorting, temperate forest, western North America

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

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36 The relationship between biodiversity and net-primary productivity is one of the most prominent
37 and well-studied biological patterns on Earth¹⁻⁶. Species richness generally increases linearly
38 with productivity across regions^{7,8}, but the relationship is weaker and highly variable at smaller
39 spatial scales^{2,5,9,10}. Increases in regional species richness relative to local species richness
40 across productivity gradients could be explained by greater site-to-site variability in species
41 composition, known as β -diversity, in more productive regions^{3,4,11-14}. Yet β -diversity does not
42 generally increase with productivity¹⁵⁻¹⁹, leaving the mechanisms that might account for scale-
43 dependent changes in species diversity with productivity unclear. These mechanisms are critical
44 to understand given that global climate change is predicted to cause dramatic changes in net
45 primary productivity²⁰, potentially leading to loss of species and ecosystem function²¹.

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

58 In addition to regional mechanisms, shifts in the strength of local density-dependent

59 interactions within and among species may explain changes in β -diversity with productivity, but
60 this mechanism remains unexamined. Stronger interspecific competition or pressure from
61 generalist natural enemies can result in heterospecific negative density dependence (HNDD),
62 where individual recruitment and survival decline with increasing local densities of
63 heterospecifics²⁶⁻²⁸. Stronger HNDD, in turn, can reduce local diversity (or α -diversity) via
64 competitive exclusion or apparent competition²⁶⁻²⁸. Stronger HNDD can also cause greater
65 habitat partitioning (i.e. species sorting) along environmental gradients, as species become more
66 locally abundant and exclude others from habitats where they have higher fitness²⁶⁻²⁹. Both
67 reductions in local diversity and increased habitat partitioning from stronger HNDD are expected
68 to increase β -diversity (Fig. 1c)^{23, 29, 30}. Theoretical and empirical studies suggest that higher
69 densities may intensify interspecific competition in more productive environments³¹⁻³³, in which
70 case β -diversity may also increase with productivity if HNDD mediates diversity-productivity
71 relationships. However, evidence for stronger interspecific competition in more productive
72 environments is mixed^{2, 10}, and competition among species may be greater in less productive
73 environments where limiting resources are scarce²⁸. Therefore, increases in productivity across
74 regions might increase or decrease β -diversity if productivity increases or decreases the strength
75 of HNDD, respectively.

76 In addition, local density-dependent interactions among conspecifics may influence
77 changes in β -diversity with productivity. Stronger conspecific negative density dependence
78 (CNDD), caused by greater intraspecific competition or increased pressure from host-specific
79 predators or pathogens³⁴⁻³⁷, should limit local abundances of dominant species, thereby
80 providing space for other species and increasing local diversity relative to regional diversity^{35, 38-}
81⁴¹. This has led to the prediction that stronger CNDD should homogenize community

82 composition among sites (i.e. decrease β -diversity; Fig. 1d)³⁰, but this prediction remains
83 untested. Moreover, recent studies have found that CNDD can be stronger in wetter regions and
84 resource-rich environments^{36, 42}, suggesting that the strength of CNDD may increase with
85 productivity⁴³. If so, stronger CNDD might cause β -diversity to be lower in more productive
86 regions. In summary, β -diversity may increase or decrease with productivity depending on the
87 relative influence of regional processes as well as how productivity changes the relative strength
88 of local density-dependent interactions within and among species.

89 Here, we untangle the relative importance of these regional- and local-scale mechanisms
90 to changes in β -diversity of tree species across a subcontinental productivity gradient. We used
91 US Forest Service (USFS) Forest Inventory and Analysis (FIA) data comprising over a quarter
92 million trees in 9,592 plots that span 18 ecoregions in western North America (Fig. 2a).
93 Ecoregions (hereafter, regions) were defined by the USFS and delineated by elevation and other
94 physical components including climate, physiography, lithology, and soils⁴⁴. This productivity
95 gradient ranges from temperate rainforests to semi-arid juniper-sagebrush ecosystems
96 (Supplementary Table 1), covering substantial variation in net-primary productivity (NPP) while
97 minimizing the potentially confounding influence of latitude on diversity⁴⁵. The gradient also
98 has a large enough extent (576,000 km²) to appropriately test the influence of processes that act
99 across regions, and a spatial-grain size small enough (one plot covers ~0.24 ha) to test the
100 influence of local-scale species interactions on diversity⁴¹. We first examine relationships
101 between productivity and diversity at the regional and local scales, and assess whether β -
102 diversity changes with productivity across regions. Second, we evaluate the degree to which
103 differences in regional-species pools (i.e., number and relative abundance of species in a region)
104 explain changes in β -diversity across regions using null-models²² (Fig. 1a). Third, we evaluate

105 the degree to which differences in environmental heterogeneity (variation in climate,
106 productivity & topography within regions) explain changes in β -diversity across regions (Fig.
107 1b). Fourth, we assess if the strength of CNDD and/or HNDD change with productivity across
108 regions, and whether any differences in CNDD and/or HNDD across regions explain changes in
109 local species diversity, habitat partitioning along environmental gradients, and variation in β -
110 diversity unexplained by regional processes (e.g. Fig. 1c, 1d). Finally, we discuss broader
111 implications of our study for understanding the mechanisms underlying variation in diversity-
112 productivity relationships.

113

114 **RESULTS AND DISCUSSION**

115 Diversity at local and regional scales increased along the subcontinental-productivity gradient.
116 Linear regressions revealed that regional ($r^2 = 0.61$, $P < 0.001$) and mean local ($r^2 = 0.39$, $P =$
117 0.006) species richness increased with mean annual NPP across regions (Fig. 2b, Supplementary
118 Fig. 1). Examination of species accumulation curves for all regions revealed that sampling of
119 regional richness did not systematically change across the productivity gradient (Supplementary
120 Fig. 2). Mean local species evenness also increased with NPP across regions ($r^2 = 0.37$, $P =$
121 0.007), indicating that more productive regions had more equal relative abundances of species in
122 each FIA plot. Likewise, the mean local effective number of species (or inverse Simpson
123 diversity index), which is similar to rarefied species richness and insensitive to sample grain or
124 extent ⁴⁶, increased with NPP across regions ($r^2 = 0.36$, $P = 0.009$), indicating that increases in
125 mean species richness with productivity were not simply due to the spatial scale of FIA plots or
126 increases in density.

127 Differences in the composition of regional-species pools were associated with differences

128 in NPP across regions (permutational multivariate ANOVA test: $F_{1,16} = 4.9$, $P = 0.001$; Fig. 2c),
129 suggesting that productivity may influence β -diversity via changes to regional-species pools.
130 However, linear regressions of median β -diversity ($r^2 = 0.36$, $P = 0.008$; Fig. 3a) and median β -
131 diversity standardized effect sizes ($r^2 = 0.20$, $P = 0.061$; Fig. 3b), which reflect β -diversity not
132 accounted for by differences in regional-species pools (hereafter β_{SES}), declined with NPP across
133 regions. The relationship between productivity and β_{SES} was slightly weaker than the
134 relationship between productivity and β -diversity, suggesting that differences in regional-species
135 pools may partially contribute to—but are not a dominant mechanism causing— β -diversity to
136 decline with productivity. Moreover, median β_{SES} was significantly positive in each region
137 (Supplementary Table 1), indicating that β -diversity was generally higher than would be
138 expected if community composition was only determined by stochastic assembly from regional-
139 species pools. Differences in environmental heterogeneity (variation in climate, productivity &
140 topography within a region) were unrelated to NPP across regions (linear regression: $r^2 = 0.01$, P
141 $= 0.65$; Fig. 3c), indicating that regional differences in available niche space had a limited
142 influence on β -diversity. Other differences among regions that might have influenced β -diversity
143 include: the number of FIA plots, region area, mean nearest-plot distance, total number of trees
144 in a region, mean local-community size (i.e., the average number of tree individuals per FIA
145 plot), and the contribution of spatial distances among plots to changes in species composition.
146 These were all unrelated to NPP across regions and, thus, had little influence on the observed
147 decline in β -diversity with productivity (Supplementary Table 2).

148 The relative strength of local conspecific and heterospecific negative density dependence
149 largely accounted for declines in β -diversity with productivity. Negative effects of
150 heterospecific trees on focal sapling densities (hereafter HNDD) were strongest in low-

151 productivity regions (linear regression weighted by the error around HNDD estimates for each
152 region: $r^2 = 0.42$, $P = 0.004$; Fig. 4a, Supplementary Fig. 3). Contrary to the expectation that
153 stronger HNDD would erode diversity and reduce species richness²⁶⁻²⁸, stronger HNDD was not
154 associated with lower mean local species richness ($r^2 = 0.03$, $P = 0.49$) or diversity (i.e. Shannon
155 diversity index; $r^2 = 0.08$, $P = 0.25$). Instead, two patterns suggest that stronger HNDD in low-
156 productivity regions is associated with increased habitat partitioning. First, variation in species
157 composition associated with the environment declined with NPP ($r^2 = 0.24$, $P = 0.04$),
158 suggesting that species in low-productivity regions exhibit greater habitat partitioning than
159 species in high-productivity regions despite encountering similar or lower environmental
160 heterogeneity (Fig. 3c). Second, variation in species composition associated with the
161 environment increased with HNDD ($r^2 = 0.42$, $P = 0.003$; Fig. 4b), supporting the idea that
162 strong interspecific competition or pressure from generalist enemies (e.g., apparent competition)
163 promotes habitat partitioning^{26-29, 47}. Stronger HNDD was also associated with higher β_{SES} ($r^2 =$
164 0.25 , $P = 0.033$; Fig. 4c), indicating that increases in habitat partitioning from stronger HNDD
165 contribute to higher β -diversity in less productive regions.

166 In contrast, stronger CNDD in high-productivity regions was associated with increased
167 mean local diversity and lower β -diversity (Fig. 4d-4f). Stronger CNDD in high-productivity
168 regions (linear regression weighted by the error around CNDD estimates for each region: $r^2 =$
169 0.41 , $P = 0.004$; Fig. 4d, Supplementary Fig. 3) is consistent with other recent findings of
170 stronger CNDD in wetter regions and resource-rich environments^{36, 42}. Our analyses cannot
171 determine whether CNDD was due to intraspecific competition, pressure from host-specific
172 predators and pathogens, or a combination of both processes. However, our results indicate that
173 HNDD, which reflects the strength of interspecific competition, is weak in productive regions

174 (Fig. 4a). If the strength of competition among tree species is indicative of the strength of
175 competition within tree species, then weaker HNDD combined with stronger CNDD in
176 productive regions (Fig. 4a, 4d) suggests that specialized enemies may contribute to increases in
177 CNDD with productivity. Indeed, evidence is mounting that activities of host-specific enemies,
178 and not intraspecific competition, are largely responsible for CNDD³⁴⁻³⁷. Stronger CNDD in
179 more productive regions was associated with higher mean local species evenness ($r^2 = 0.66$, $P <$
180 0.001 ; Supplementary Fig. 4), richness ($r^2 = 0.39$, $P = 0.005$; Fig. 4e), and diversity ($r^2 = 0.42$, P
181 $= 0.004$), supporting the hypothesis that CNDD limits the dominance of locally-abundant species
182 and increases local diversity^{35,38-42}. Stronger CNDD in more productive regions was also
183 associated with decreased β_{SES} ($r^2 = 0.37$, $P = 0.007$; Fig. 4f), suggesting that stronger CNDD
184 decreases β -diversity by homogenizing community composition among sites. β -diversity also
185 declined as the ratio of CNDD to HNDD increased ($r^2 = 0.32$, $P = 0.014$; Supplementary Fig. 5),
186 indicating that the relative strength of local conspecific to heterospecific density-dependent
187 interactions may largely determine changes in β -diversity with productivity.

188 Changes in the strength of local interactions within and among species trumped potential
189 regional influences on β -diversity across the productivity gradient (Fig. 3, 4). This result
190 challenges recent conceptual models that deemphasize the importance of local-species
191 interactions to community assembly and patterns of biodiversity, particularly at biogeographic
192 scales⁴⁸. While we examined a broad-scale productivity gradient that was largely decoupled
193 from the potentially confounding influences of latitude on diversity, our study area provided only
194 a moderate gradient in regional-species richness (11-41 species). Vast differences in
195 biogeography and evolutionary history across even larger gradients in regional-species richness
196 (e.g., 10-1000 species) might have a stronger influence on β -diversity, and biodiversity in

197 general, than local-species interactions⁴⁹. However, effects of local-species interactions on
198 diversity have been largely neglected at global scales due to lack of appropriate data to test them.

199 Our results indicate that changes in local diversity and β -diversity along a large-scale
200 productivity gradient are largely mediated by shifts in the relative strength of local-scale species
201 interactions (Fig. 4). Specifically, stronger HNDD in low-productivity regions was associated
202 with greater habitat partitioning and higher β -diversity, likely because species become more
203 abundant in favourable environmental conditions. In contrast, stronger CNDD in high-
204 productivity regions was associated with greater mean local diversity, more equal relative
205 abundances of species, and lower β -diversity, likely because CNDD limited abundances of
206 dominant species and homogenized community composition among sites. While a handful of
207 previous studies have found that stronger CNDD increases local diversity^{35, 40-42}, none, to our
208 knowledge, have examined the relative importance of conspecific and heterospecific density-
209 dependent effects on β -diversity. These findings provide support for the idea that increases in
210 CNDD (e.g. pressure from specialized enemies) enhance local diversity within sites but
211 homogenize community composition among sites (decrease β -diversity) and reduce the relative
212 importance of competitive interactions among species³⁰. Our results further advance this
213 framework by demonstrating that shifts in the relative strength of CNDD and HNDD may
214 underlie relationships between primary productivity and diversity (Fig. 4).

215 These findings have important implications for understanding why local diversity and β -
216 diversity often show variable relationships with primary productivity. Studies have found that
217 both local diversity (species richness) and β -diversity can increase, decrease, or have a unimodal
218 relationship with productivity^{2-6, 11, 16, 19, 22, 50}. Previous explanations for these variable
219 relationships include differences in spatial scales, geographic extents, and ranges of productivity

220 over which diversity is measured ¹⁶. Our results suggest that the shape of these relationships
221 may also depend on how the strength of CNDD changes relative to the strength of HNDD along
222 productivity gradients. Positive relationships between diversity (β -diversity or species richness)
223 and productivity may reflect stronger self-limitation of dominant species (i.e. stronger CNDD) in
224 productive environments, as indicated by our results. However, in some cases (e.g. smaller
225 spatial extents or smaller ranges of productivity), increases in CNDD with productivity may be
226 modest or offset by relatively stronger increases in HNDD. In such cases, greater habitat
227 partitioning or competitive exclusion in productive environments may lead to unimodal or
228 neutral diversity-productivity relationships. Changes in productivity ^{4, 8}, and potentially CNDD
229 ^{36, 41}, accompany other prominent large-scale biodiversity gradients, such as the latitudinal-
230 diversity gradient. Therefore, systematic shifts in the relative strength of density-dependent
231 interactions within and among species at local scales might generally contribute to some of the
232 most striking gradients in global biodiversity.

233

234 **METHODS**

235 **Data**

236 We used tree species-abundance data from the United States Forest Service (USFS) Forest
237 Inventory and Analysis (FIA) project. These data are freely available at
238 <http://www.fia.fs.fed.us/tools-data> and were accessed for this study on November 28, 2015.

239 Since 2000, FIA has used a nationally-standardized sampling design with outstanding sampling
240 intensity (an average of one plot per 2,428 ha). FIA plots consist of four 7.3-m-radius subplots
241 with centres spaced ~36-63 m apart to cover an area approximately equal to 0.24 ha. We used
242 data from all forested (> 10% canopy cover) and natural (non-plantation and non-disturbance)

243 FIA plots within ecoregions that at least partially lay between 42° N and 49° N latitude and west
244 of 105° W longitude. These values of latitude and longitude capture substantial orographically-
245 generated east-west variation in net-primary productivity (NPP) while minimizing the potentially
246 confounding influence of latitude and vast differences in biogeographic and evolutionary
247 histories across the continental USA on species diversity⁴⁵. This area includes all ecoregions
248 from the coast of Washington and Oregon to the Rocky Mountain front on the boundary of the
249 North American great plains (east of which forests become very sparsely distributed). Forests in
250 this latitudinal belt from eastern North America also have very different biogeographic histories
251 from forests in our study area. For example, eastern forests at this latitude were recolonized
252 from glacial refugia in the southeastern United States, whereas western forests were recolonized
253 from glacial refugia in the Cascade mountain ranges and along the west coast^{51, 52}.

254 We excluded FIA plots that reported any natural or human-caused disturbance (e.g. fire,
255 logging; FIA protocol requires reporting any disturbances in the 10 years prior to plot
256 measurement on western US plots, as this is the time between subsequent measurements).
257 Because disturbance was largely concentrated on private land, we only included FIA plots from
258 public lands (USFS lands, national parks, state parks and other state-held lands). Another
259 important reason for excluding private land from our analysis is that geographic locations are
260 swapped among private FIA plots within counties to protect landowner privacy, up to 220 km
261 (largest distance between FIA plots within a county; in Idaho County, Idaho) away from the
262 original location. This is not done for public FIA plots, and accurate geographic coordinates are
263 essential for variation-partitioning analyses (see below). Ecoregions used in our analysis were
264 defined by the USFS ('ECOSUBCD' in FIA database)⁵³. We only included regions that were
265 defined by FIA as 'mountainous' because publicly-owned as well as non-plantation and non-

266 disturbed forested FIA plots are heavily concentrated in these regions⁵³. We only included
267 regions that had at least 150 publicly-owned FIA plots to have a minimum appropriate sample
268 size at which to precisely estimate β -diversity (Supplementary Table 1).

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

277 Environmental variables were provided with FIA data or obtained from publicly-
278 available satellite-based datasets. Topographic variables (slope, aspect, and elevation) are
279 provided for each FIA plot. Where multiple slope and aspect values were reported, we used the
280 slope and aspect values that reflect the majority of the FIA plot. We calculated the cosine and
281 sine of aspect as measures of north-south-facing and east-west-facing slopes, respectively.
282 Heterogeneity in soil characteristics among sites is likely an important environmental variable to
283 consider, but soils data were only available for 219 of the 9,592 plots (2.2%) used in our
284 analyses. However, topography is known to strongly influence soil formation⁵⁴, and was used as
285 a proxy. We obtained measurements for each FIA plot (mean values within a 1 km buffer
286 around each FIA plot) of mean annual net primary productivity (NPP) during 2000-2014 from
287 MODIS satellite-based data operated by the National Aeronautics and Space Administration
288 (NASA)⁵⁵. We also obtained mean annual temperature ($^{\circ}\text{C}$), mean temperature of the warmest

289 month ($^{\circ}\text{C}$), mean temperature of the coldest month ($^{\circ}\text{C}$), mean annual precipitation (mm), mean
290 summer precipitation (mm), number of degree-days above 18°C , precipitation as snow (mm),
291 extreme maximum temperature over 30 years ($^{\circ}\text{C}$), and mean annual relative humidity (%)
292 during 1981-2010 for each FIA plot from the AdaptWest Project ⁵⁶. Other available climatic
293 variables from AdaptWest (e.g., number of frost-free days) were highly correlated ($r > 0.95$) with
294 variables listed above and were not included. Locations of FIA plots on public land are
295 perturbed up to 1.67 km but typically within a 0.8 km of the actual location. Slope, aspect, and
296 elevation are provided for the actual plot location, and the spatial resolution of the NPP and
297 climate data (1-km resolution) is similar to that of the FIA perturbed plot locations. Thus, we
298 used the perturbed plot locations to match FIA plots with NPP and climate data as in other recent
299 studies using FIA data ⁵⁷.

300

301 **Analyses**

302 *Diversity measures*

303 For each region, we calculated the total number of species (regional species richness), the mean
304 number of species per FIA plot (mean local species richness), mean local effective number of
305 species (i.e. the inverse Simpson diversity index, which is similar to rarefied species richness and
306 insensitive to spatial grain and extent⁴⁶) per FIA plot, and mean local species diversity (Shannon
307 diversity index) per FIA plot. We calculated mean local-species evenness for each region by
308 first calculating the relative abundance and abundance rank of each species in each FIA plot. We
309 then used a mixed model to calculate the mean slope of these local rank-abundance curves for
310 each region, which is a measure of species evenness ⁵⁸. Species relative abundances were log-
311 transformed for these relationships ⁵⁸. We also calculated the median pairwise Bray-Curtis

312 dissimilarity among FIA plots (hereafter, β -diversity) for each region using the package ‘vegan’
313 in R^{59,60}. While Whittaker’s β -diversity partition ($\frac{\text{regional richness}}{\text{local richness}}$) increased with productivity
314 (Fig. 2a), this measure of β -diversity is mathematically dependent on regional and local richness
315 and does not capture dissimilarities in the presence/absence or relative abundance of species
316 across sites. The Bray-Curtis dissimilarity index incorporates information about the relative
317 abundances of species (a fundamental component of diversity) in addition to presences/absences
318 of species, and is a recommended measure of β -diversity when composition and relative
319 abundance data are available⁶¹. Thus, we measured β -diversity as the median dissimilarity in
320 the composition and relative abundances of species among FIA plots within each region.

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

335 better at detecting deterministic processes than deviations using incidence-based β -diversity
336 metrics⁶⁵.

337 We used simple linear regression models to test for changes in these measures of
338 diversity with mean annual NPP across regions. Variation in NPP was much greater across
339 regions than within regions (Supplementary Fig. 6), as ecoregion identity explained 72.7% of
340 total variation in NPP across all 9,592 FIA plots used in this analysis. Mean regional NPP was
341 log-transformed in all analyses due to a right-skewed distribution. To evaluate if regional-
342 species pools (i.e., the number and relative abundances of species in a region) differed among
343 regions or if assemblages in some regions were nested within assemblages of other regions, we
344 used nonmetric-multidimensional scaling (NMDS) in the ‘vegan’ package to plot species
345 composition of regions in NMDS space and the ‘adonis’ function to test for significant
346 differences in species composition as a function of mean NPP across regions⁶⁰. To examine
347 other potential regional or sampling influences on β -diversity, we also tested if the number of
348 FIA plots per region, area of a region (ha), total number of individuals in a region, mean local
349 community size per region, or the mean nearest-neighbour FIA plot distance within each region
350 changed systematically with mean regional NPP (Supplementary Table 2).

351

352 *Null-model analysis*

353 To evaluate if differences in regional-species pools contributed to differences in β -diversity with
354 NPP across regions, we performed null-model analyses^{22, 64}. Individuals from each regional-
355 species pool (preserving the regional species-abundance distribution) were randomly distributed
356 among FIA plots in that region while preserving the total number of individuals in each plot^{22, 64}.
357 Thus, these null local assemblages were only the product of stochastic assembly from the

358 regional-species pool, and all other mechanisms that might cause additional spatial aggregation
359 of individuals (e.g., habitat partitioning, local interactions among species, dispersal limitation)
360 were removed. The pairwise dissimilarities of these simulated communities within each region
361 (β_{SIM}) were then compared to the observed dissimilarities (β_{OBS}) relative to the standard
362 deviation of β_{SIM} (σ_{SIM}) after 1,000 iterations, and a standardized effect size of the difference was
363 calculated as: $\beta_{SES} = (\beta_{OBS} - \beta_{SIM}) / \sigma_{SIM}$. Therefore, β_{SES} represents β -diversity that remains
364 unexplained by stochastic assembly from the regional-species pool²². We also tested if median
365 β -diversity in each region was significantly greater than median β -diversity expected from
366 stochastic assembly from the regional-species pool by assessing if fewer than 5% of median β_{SIM}
367 values were greater than or equal to median β_{OBS} (i.e. one-tailed test of significance).

368

369 *Environmental heterogeneity among regions*

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

378

379 *Partitioning variation in species composition*

380 To assess the degree to which species partition habitat in each region (i.e. species sorting), we
 381 calculated the proportion of variation in species composition among localities associated with
 382 environmental heterogeneity in each region using the ‘vegan’ package⁶⁰. Variation partitioning
 383 produces four terms: β -diversity associated with the environment only (i.e., not associated with
 384 spatial distance), β -diversity associated with spatial distance only, β -diversity associated with
 385 both spatial distance and the environment, and β -diversity unexplained by the environment or
 386 spatial distance. To test if habitat partitioning (i.e. species sorting) was greater in more
 387 productive regions or regions with stronger HNDD, we tested for a positive relationship between
 388 the variation in species composition purely associated with the environment and regional NPP or
 389 HNDD, respectively. We also evaluated if variation in species composition associated with
 390 spatial distance changed systematically with NPP to test if differences in dispersal limitation or
 391 other spatial factors might explain changes in β -diversity across regions (Supplementary Table
 392 2).

393

394 *Conspecific and heterospecific density dependence*

395 We estimated the strength of CNDD and HNDD following previously-published methods^{40, 42}.

396 For each region, we used the following hierarchical model to estimate the mean strength of

397 CNDD and HNDD:

$$398 \ln(S_{ij} + 1) = r_j + \text{CNDD}_j \times \ln(A_{ij} + 1) + \text{HNDD}_{\text{tree}_j} \times a_{ij} + \text{HNDD}_{\text{sap}_j} \times s_{ij} + \text{NPP}_j \times \text{npp}_i + \varepsilon_{ij}$$

$$399 \varepsilon_{ij} \sim N(0, \sigma^2) \quad (1)$$

400 Where S_{ij} is the observed number of saplings of species j in plot i , r_j is the per-capita recruitment

401 rate for species j at low conspecific tree densities, CNDD_j is the per-capita effect of conspecific

402 tree density on sapling recruitment for species j , A_{ij} is the observed number of conspecific trees

403 of species j in plot i , HNDDtree_j is the per-capita effect of heterospecific tree density on sapling
404 recruitment for species j , a_{ij} is the observed number of heterospecific trees (i.e. not species j) in
405 plot i , HNDDsap_j is the per-capita effect of heterospecific sapling density on sapling recruitment
406 of species j , s_{ij} is the observed number of heterospecific saplings in plot i , NPP_j is the per-capita
407 effect of NPP on sapling recruitment for species j , npp_i is the observed value of NPP in plot i ,
408 and ε_{ij} is normally-distributed error. We began with a full random effects structure (i.e. random
409 species-specific effects for r_j , CNDD_j , HNDDtree_j , HNDDsap_j , and NPP_j), and then removed
410 random effects that were either correlated ($r \geq 0.7$) with the random intercept or whose standard
411 deviation was estimated to be at or near zero ($\text{SD} \leq 0.1$). This approach avoids over-
412 parameterization of models^{67,68}. However, results were similar if all random effects were
413 included in the model. These models were run in R (package ‘lme4’)^{59,69}. Thus, for each
414 region, we quantified the mean effects of conspecific tree density on focal sapling density
415 (CNDD), and two measures of HNDD: (1) effects of heterospecific tree density on focal sapling
416 density (HNDDtree) and (2) effects of heterospecific sapling density on focal sapling density
417 (HNDDsap; Supplementary Table 3, Supplementary Fig. 3).

418 Conspecific tree and sapling densities were log-transformed for all forest plots to estimate
419 the proportional (and not additive) change in sapling densities with increasing conspecific tree
420 densities^{40,42}. Negative relationships between heterospecific densities and focal sapling density
421 represent HNDD^{40,42}. Reductions in per-capita recruitment with increasing conspecific tree
422 density represent stronger CNDD (Supplementary Fig. 7)^{40,42}. Sapling density may also depend
423 on variation in NPP within a region (e.g., species-specific habitat preferences), so we included
424 mean annual NPP in our models of sapling density, as well as a random slope of NPP for each

425 species to account for potentially different effects of NPP on sapling densities across species, i.e.,
426 equation (1).

427 We used numerical abundances to quantify densities (trees/ha) for conspecific trees and
428 all saplings to maintain consistency and comparability with previous studies that quantified stem
429 densities with numerical abundances^{40, 42}. Nonetheless, our reported estimates of CNDD were
430 highly correlated with estimates of CNDD that used basal area to quantify conspecific and
431 heterospecific densities ($r = 0.93$; $P < 0.0001$). Likewise, our reported estimates of HNDDsap
432 were highly correlated with estimates of HNDDsap that used basal area to quantify conspecific
433 and heterospecific densities ($r = 0.99$, $P < 0.0001$). We used basal area to quantify densities of
434 heterospecific trees because tree-size distributions can vary extensively across species, and basal
435 area provides a way to standardize the spatial influence of older age classes across species⁴².
436 Nonetheless, our reported estimates of HNDDtree were highly correlated with estimates of
437 HNDDtree that used numerical abundances to quantify conspecific and heterospecific densities
438 ($r = 0.90$, $P < 0.0001$).

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

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

448 0.802) nor tree ($r = 0.04$, $P = 0.884$) densities varied with NPP across regions (Supplementary
449 Table 2). Furthermore, the scale at which CNDD and HNDD were measured did not influence
450 estimates for each region. Density-dependent interactions (e.g. CNDD) are known to occur at
451 small spatial scales. Evidence from temperate and tropical forests indicates that these effects are
452 strongest between 10 m to 30 m from a focal tree, but can extend up to 50 m away from focal
453 trees^{72,73}. Thus, individuals in particular FIA subplots, which are ~7 m in radius and spaced
454 ~36-63 m apart, may influence density-dependent recruitment or survival in neighbouring
455 subplots. Moreover, two previous studies have used FIA data from the eastern and central US to
456 estimate CNDD (but have not linked changes in CNDD to changes in β -diversity or
457 productivity). Both studies used the entire FIA plot to estimate the strength of CNDD^{41,57}.
458 Thus, we used the entire FIA plot to estimate the strength of local density-dependent interactions.
459 Nonetheless, CNDD measured at the subplot scale was highly correlated with reported measures
460 of CNDD, regardless of whether subplot CNDD was calculated using basal area ($r = 0.90$; $P <$
461 0.0001) or numerical abundance ($r = 0.86$; $P < 0.0001$). Similarly, HNDD for heterospecific
462 trees and saplings, each measured at the subplot scale, were highly correlated with reported
463 measures of HNDD regardless of whether subplot HNDD was calculated using basal area
464 (heterospecific trees: $r = 0.84$; $P < 0.0001$; heterospecific saplings: $r = 0.77$; $P = 0.0002$) or
465 numerical abundance (heterospecific trees: $r = 0.73$; $P = 0.0006$; heterospecific saplings: $r =$
466 0.81 ; $P < 0.0001$).

467 Finally, we examined hypothesized relationships between the strength of HNDD, NPP,
468 habitat partitioning, and β -diversity after accounting for regional influences (i.e., median β_{SES}).
469 We also examined hypothesized relationships between the strength of CNDD, NPP, local-species
470 evenness, local-species richness and diversity (Shannon-diversity index), and β_{SES} . These

471 regressions were weighted by the inverse error variance around estimates of either HNDD or
472 CNDD for each region.

473

474 **Data availability**

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

479

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637
638 **Supplementary Information** is linked to the online version of the paper at www.nature.com.

639

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644

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646 and R.T.B. obtained the funding. J.A.L. executed the statistical analyses and wrote the first draft
647 of the manuscript, and J.A.L., J.A.M., R.T.B., L.A.B., and C.P.C. contributed to revisions.

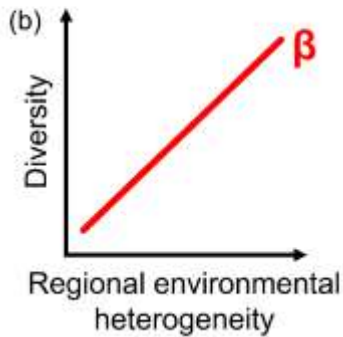
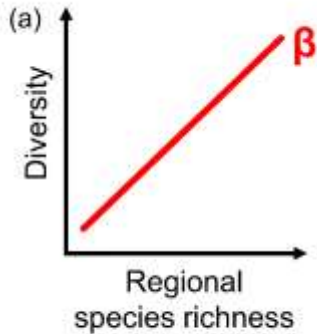
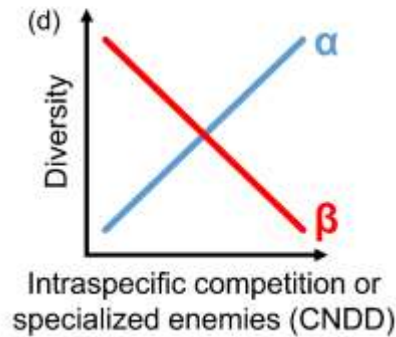
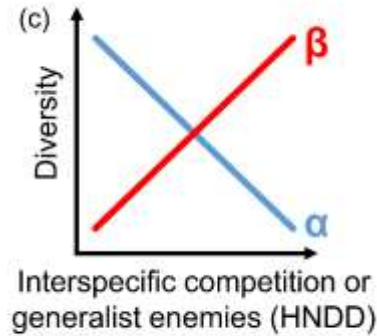
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649 **Author Information:** Data are available at <http://www.fia.fs.fed.us/tools-data>. Reprints and
650 permissions information is available at www.nature.com/reprints. We declare no conflicts of
651 interest. Correspondence and requests for materials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

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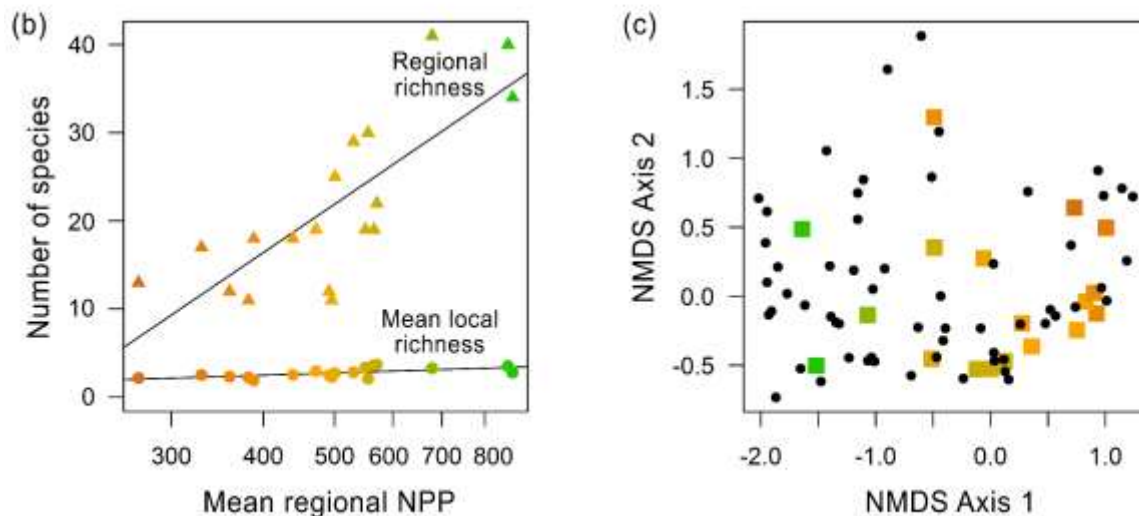
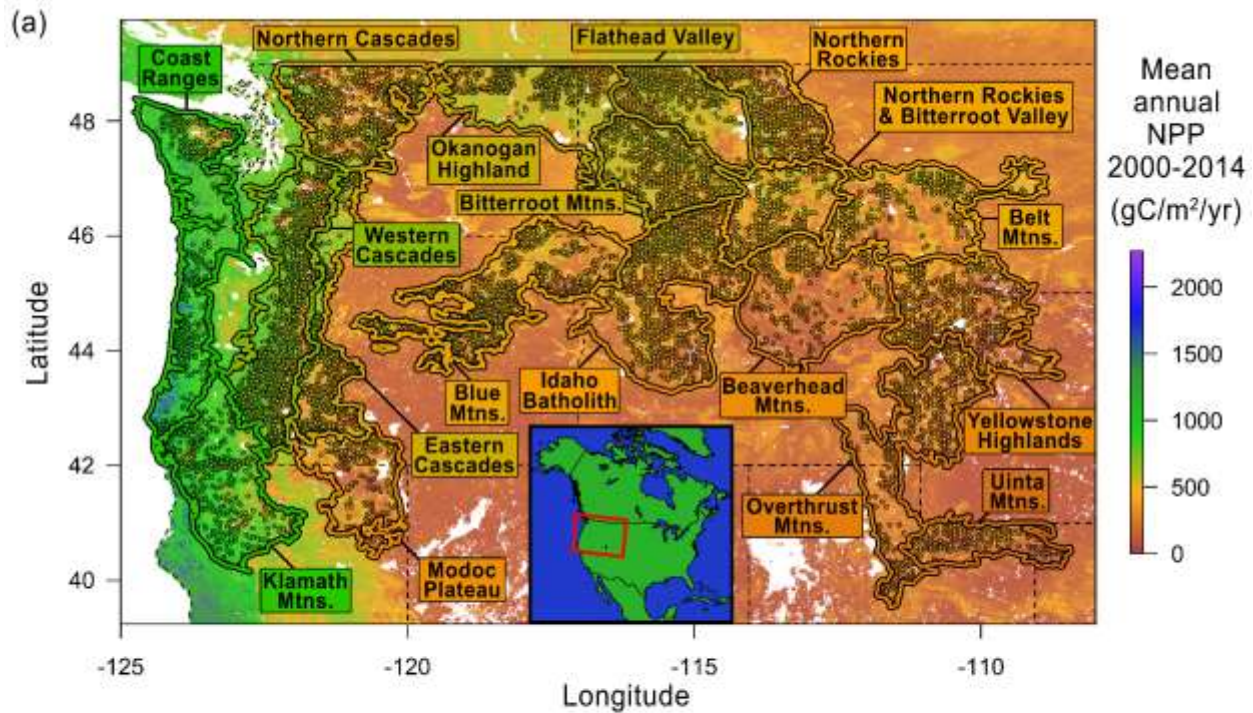
654 **Competing interests**

655 The authors declare no competing financial interest.

Regional processes**Local processes**

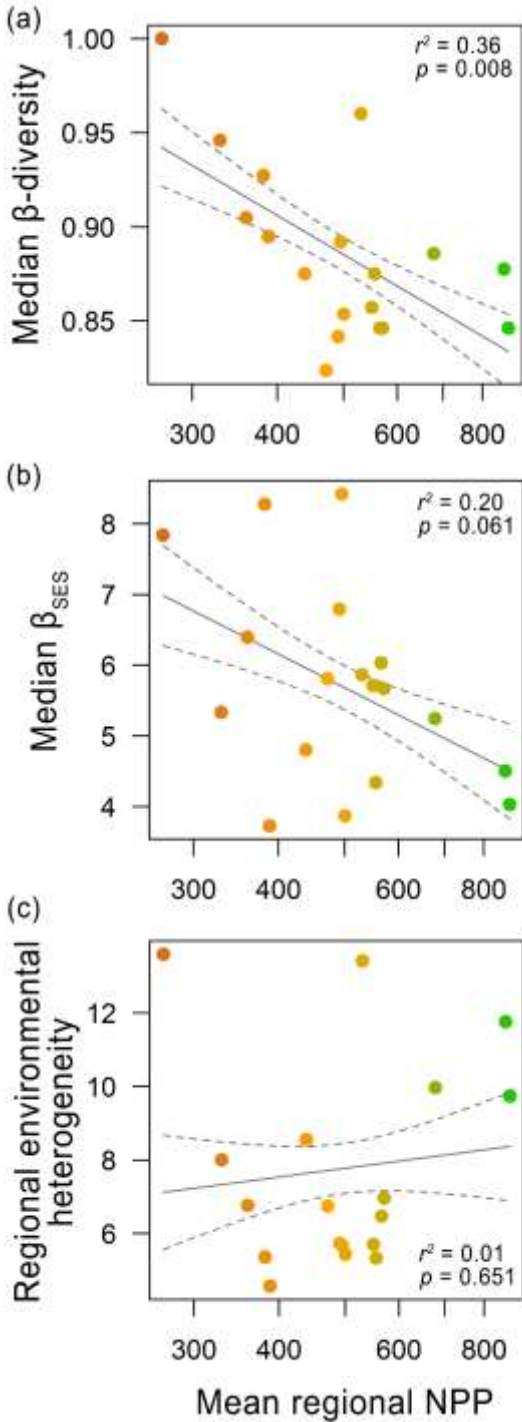
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657 **Fig. 1. Hypothesized influences of regional and local processes on patterns of biodiversity**
 658 **across regions that vary in primary productivity.** (a-b) Regional hypotheses predict that site-
 659 to-site variation in community composition (β -diversity) increases with (a) regional species
 660 richness (number of species in a region) and (b) environmental heterogeneity (variation in
 661 environmental conditions within a region). If more productive regions have greater/lower
 662 regional species richness or environmental heterogeneity, then productive regions might have
 663 higher/lower β -diversity, respectively. (c-d) Local hypotheses predict that β -diversity and mean
 664 local diversity (α -diversity) vary systematically with the strength of local density-dependent
 665 interactions within and among species. (c) Stronger interspecific competition or pressure from
 666 generalist enemies (which cause heterospecific negative density dependence, or HNDD) is
 667 predicted to reduce mean α -diversity via competitive exclusion or apparent competition.
 668 Stronger HNDD can also increase habitat partitioning (i.e. species sorting) along environmental
 669 gradients. Reductions in α -diversity and greater habitat partitioning are each expected to
 670 increase β -diversity. (d) In contrast, stronger intraspecific competition or pressure from
 671 specialized enemies (which cause conspecific negative density dependence, or CNDD) is
 672 expected to increase mean α -diversity and decrease β -diversity. Effects of productivity on β -
 673 diversity across regions, therefore, might depend on whether productivity strengthens or weakens
 674 CNDD and/or HNDD. See text for details.
 675



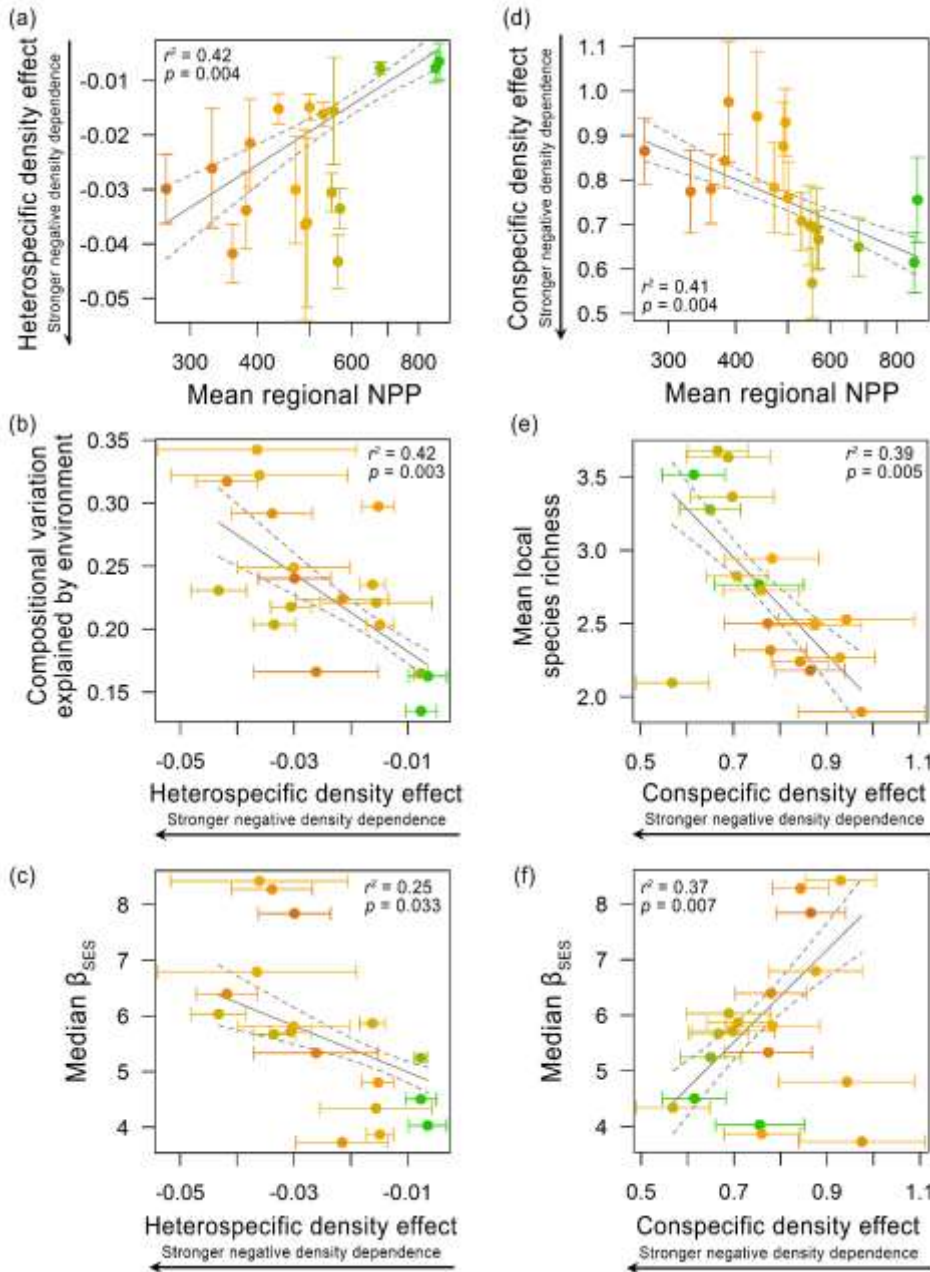
676

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



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



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