

1 **Latitude influences stability via stabilizing mechanisms in naturally-assembled**
2 **forest ecosystems at different spatial grains**

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33 **Abstract**

34 Ecosystem stability reveals how ecosystems respond to global change over time. Yet,
35 the focus of past research on small spatial grains and extents overlooks scale
36 dependence and how broad-scale environmental gradients shape stability. Here, we use
37 forest inventory data covering a broad latitudinal gradient from the temperate to the
38 tropical zone to examine cross-scale variation in stability of aboveground biomass and
39 underlying stabilizing mechanisms. While stability did not shift systematically with
40 latitude at either spatial grain, we found evidence that species asynchrony increased
41 towards the tropics at the small spatial grain while species stability decreased at both
42 spatial grains. Moreover, latitude stabilized forest communities *via* its effects on both
43 stabilizing mechanisms, which compensated for the weak and destabilizing effects of
44 species richness. Yet, the trade-off in the relative importance of species stability and
45 species asynchrony for stability was not mediated by latitude, suggesting that context-
46 dependent factors - to a greater extent than macroecological ones - underlie large-scale
47 patterns of stability. Our results highlight the crucial role of species asynchrony and
48 species stability in determining ecosystem stability across broad-scale environmental
49 gradients, suggesting that conserving biodiversity alone may not be sufficient for
50 stabilizing naturally-assembled forest ecosystems.

51
52 **Keywords:** forest stability; latitudinal pattern; spatial scale; macroecological process;
53 trade-off

54 **Introduction**

55

56 Given the evidence that diverse communities can buffer environmental fluctuation to a
57 greater extent than less diverse communities¹⁻⁴ and thus stabilize ecosystem function
58 over time (i.e., temporal stability or invariability), the diversity-stability relationship
59 has been one of core research issues in ecology. The stabilizing effects of biodiversity
60 on ecosystem functioning emerge largely due to two complementary, and not mutually
61 exclusive, ecological mechanisms: species asynchrony and species stability⁵. Species
62 asynchrony captures the heterogeneity in the response of co-occurring species to similar
63 environmental conditions^{6,7}, whereas species stability reflects the stabilizing effects of
64 dominant species on temporal stability, whose impacts may – or may not – be mediated
65 by biodiversity⁸⁻¹⁰. Yet, our understanding of diversity-stability relationships in
66 naturally-assembled forest ecosystems comes mostly from studies with a limited
67 geographic extent (i.e., the total area covered by all sampling units; but see: ^{11,12}) and
68 small spatial grains (i.e., the spatial scale of sampling; average spatial grain (or plot
69 size) = 0.04 ha¹³⁻¹⁵). This limits our understanding of how temporal stability and its
70 drivers vary across both aspects of spatial scale, and it remains uncertain whether results
71 from small spatial grains and extents can provide a robust theoretical basis for
72 developing management policies that target large areas for forest conservation.

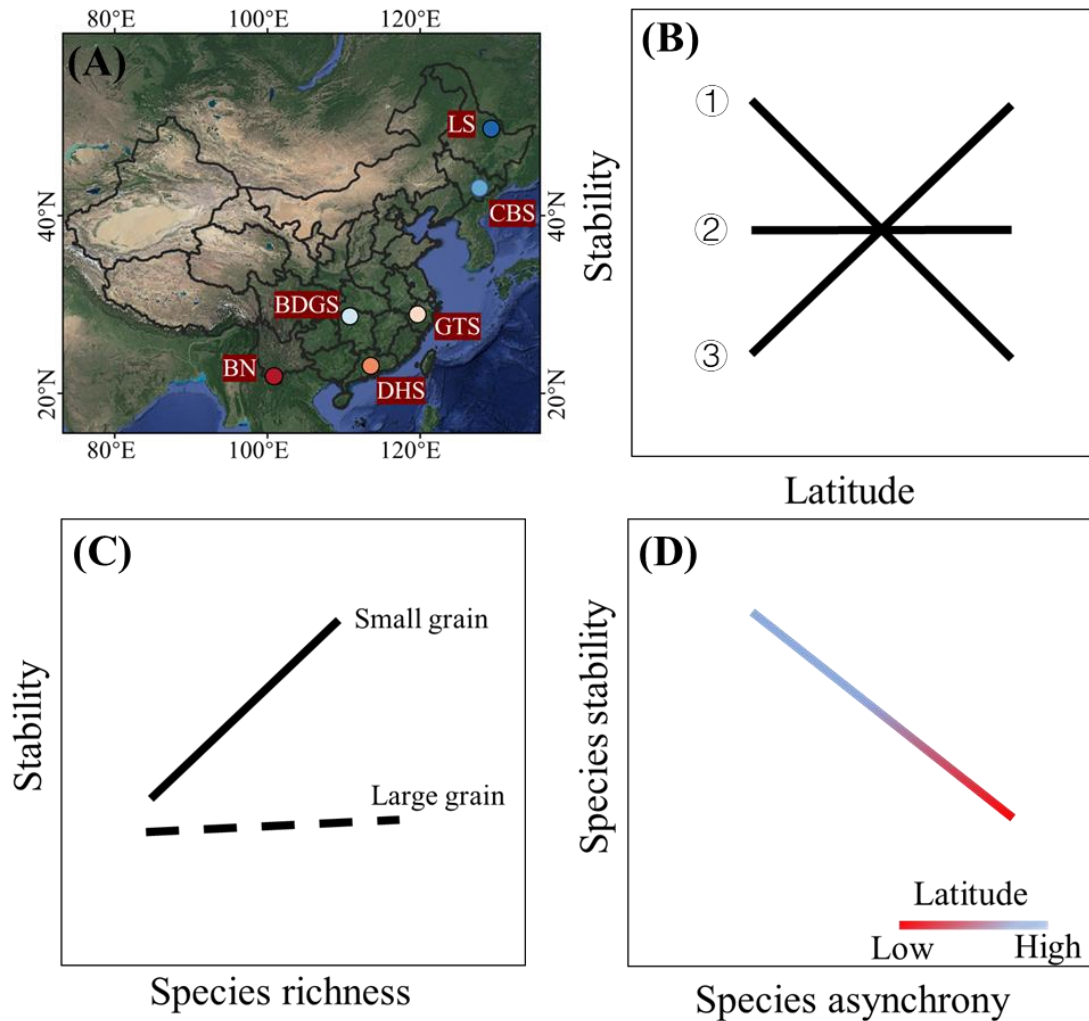
73 With increasing spatial grain, the range and heterogeneity in environmental conditions
74 are expected to increase¹⁶, resulting in a strengthening of biodiversity-ecosystem
75 functioning (BEF) and diversity-stability relationships. For instance, stronger positive
76 biodiversity effects on ecosystem functioning are expected at larger spatial grains since
77 higher environmental heterogeneity and a broader range of environmental conditions
78 provide more opportunities for niche partitioning¹⁷. Yet, an analysis of 25 naturally-
79 assembled forests¹⁸ found that positive BEF relationships emerged mainly at the
80 smallest spatial grain (0.04 ha), while BEF relationships shifted in direction to either
81 neutral or negative at the largest spatial grain (1 ha). However, recent studies reported
82 that biodiversity at large spatial grains could also enhance and stabilize ecosystem
83 functions due to ‘macroecological complementarity’ effects, i.e. that diverse
84 communities’ ability to buffer against environmental fluctuations should be more
85 pronounced at larger spatial grains because more species with different ecological
86 niches accumulate, or ‘spatial insurance’ effects, i.e. higher spatial turnover of
87 biodiversity can stabilize regional community dynamics, implying that similar

88 ecological processes may occur at multiple spatial scales^{19–23}. As such, whether the
89 current understanding of stability from local spatial grains can predict stability patterns
90 and underlying stabilizing mechanisms at larger spatial grains – and whether they
91 generate emergent macroecological patterns – is unclear.

92 Macroecological patterns of stability and shifts in stabilizing mechanisms may emerge
93 due to changes in species richness, tree community properties (i.e. functional
94 composition and stand structure), and environmental conditions. For instance, due to
95 the stabilizing effects of biodiversity, it is expected that stability will change with
96 latitude as is typically the case for species richness, i.e., increasing from the poles
97 towards the equator²⁴. Additionally, because forests can be less even towards the
98 equator²⁵, ecosystem functioning at higher latitudes may be regulated more strongly by
99 dominant species^{26,27}. Consequently, the stabilizing effects of species stability may be
100 stronger at higher latitudes, while species asynchrony may follow the inverse pattern.
101 Beyond biotic factors, latitudinal variation in abiotic factors, such as climate, have been
102 shown to explain not only ecosystem stability^{28,29}, but also the diversity-stability
103 relationship^{30,31}. Variation in climate regulates the spatial pattern of functional
104 composition³², thus influencing ecosystem functions (as predicted by the mass ratio
105 hypothesis³³), such that communities with high biomass stocks and stability are
106 typically dominated by species with trait values associated with resource
107 conservation^{33–36}. Similarly, stem density also varies with climate^{12,13}, and often reflects
108 interactions among individuals within a community, which in turn could influence
109 temporal stability. In areas with fertile soil and warm climate, competition could
110 destabilize ecosystem functioning, while in areas with barren soil and cold climate
111 facilitation could increase temporal stability^{13,37}.

112 To elucidate large-scale patterns of temporal stability and underlying stabilizing
113 mechanisms in naturally-assembled forests, we analyzed a comprehensive census of six
114 plots covering a broad latitudinal gradient (21.61 °N - 47.18 °N) ranging from
115 temperate to tropical forests in the Chinese Forest Biodiversity Monitoring Network
116 over ten years (Fig. 1A). Our dataset contains more than 1,900,000 re-measurements
117 over three censuses with 1,013 species from these six plots, whose area range from 9
118 ha to 25 ha and are divided in quadrants of 0.4 ha (Table S1). To account for differences
119 in plot size, we randomly selected 100 quadrant per plot (4.0 ha) 100 times (Fig S1).

120 We address the following questions: (1) How do stability and stabilizing mechanisms
121 (i.e. species asynchrony and species stability) vary with latitude, and how do latitudinal
122 patterns vary with spatial grain (0.4 ha and 4.0 ha)? (2) What are the principal drivers
123 that underpin stability? (3) Is there a latitudinal trade-off between species stability and
124 species asynchrony in driving ecosystem stability? We hypothesize (H1) that the
125 latitudinal pattern of stability may be either positive, negative, or neutral (Fig. 1B) due
126 to three different opposing mechanisms. A positive relationship may emerge given the
127 potentially destabilizing effects of warmer climates, resulting in stability increasing
128 with latitude^{28,29,38}. A negative relationship may emerge if the stabilizing role of
129 biodiversity is stronger than the destabilizing effects of climate, mirroring the
130 latitudinal diversity gradient³⁹, and resulting in stability decreasing with latitude; or
131 there might not be a directional change in stability with latitude, as biodiversity and
132 stability may be decoupled in naturally-assembled ecosystems^{36,40}. We anticipate that
133 species asynchrony and species stability will decrease and increase with latitude,
134 respectively, and that their stabilizing effects will be stronger at the smaller spatial grain,
135 with weak or neutral effects at the large grain (Fig. 1C). Second, we hypothesize (H2)
136 that both biotic (species richness, species stability, species asynchrony, functional trait
137 composition, and stem density) and abiotic factors (latitude, climate and soil nutrients),
138 directly and indirectly, influence variation in temporal stability across the latitudinal
139 gradient. Finally, while we expect (H3) that both species asynchrony and stability will
140 jointly determine stability, we anticipate that their relative importance will exhibit a
141 trade-off along the latitudinal gradient (Fig. 1D), with stability mainly being driven by
142 species stability at higher latitudes and by species asynchrony at lower latitudes.



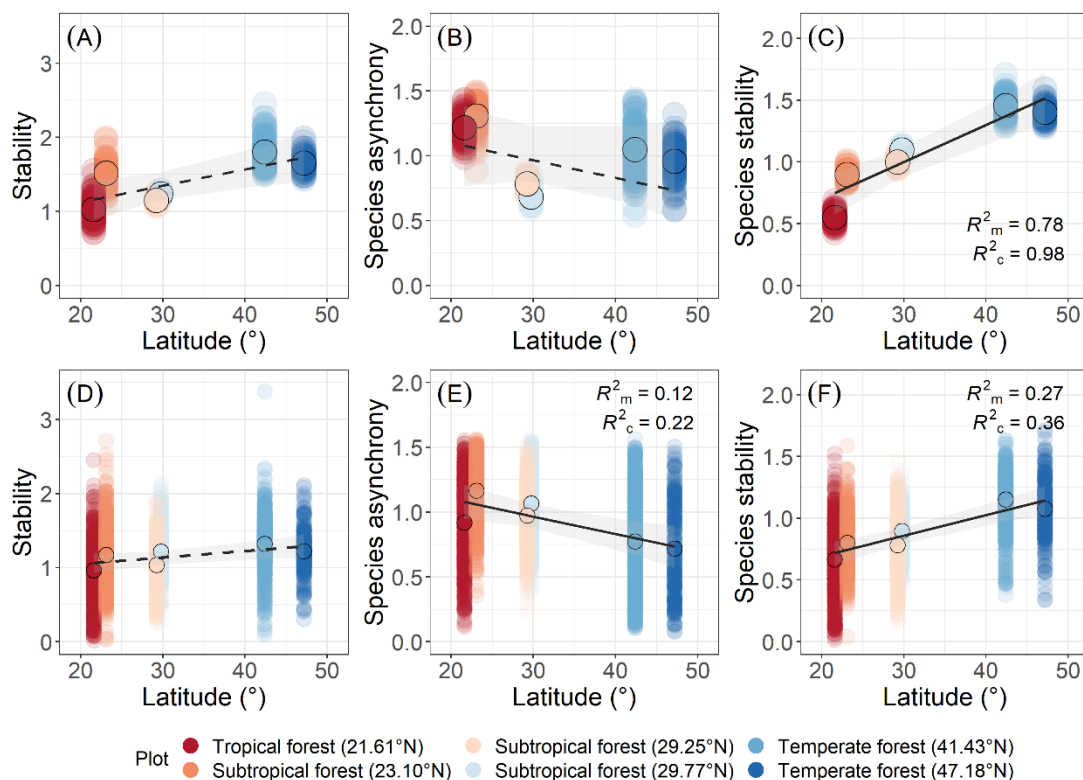
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Fig. 1 The latitudinal gradient used in this study to examine broad-scale patterns and the hypothesized patterns, drivers of ecosystem stability. (A) The spatial distribution of six study sites belonging to three forest ecosystems across China (temperate forest: LS (Liangshui) and CBS (Changbaishan); subtropical forest: BDGS (Badagongshan), GTS (Gutianshan), and DHS (Dinghushan); tropical forest: BN (Banna), Table S1). (B) Hypothesized latitudinal patterns of stability. Given a stabilizing effect of biodiversity, we would expect that stability is higher at lower latitudes, and decreases with increasing latitude (1). However, biodiversity and stability could be decoupled in naturally-assembled ecosystems, resulting in a non-directional relationship between stability and latitude (2). Due to the destabilizing effects of warmer climates, stability also could decrease with latitudinal shifts in temperature (3). (C) Hypothesized relationships between species richness and stability at different spatial grains. The positive effects of species richness on stability at small spatial grain (0.04 ha) could weaken with spatial grain, possibly becoming neutral at the large spatial grain (4.0 ha). (D) The prediction that the relative importance of species stability and asynchrony for ecosystem stability in forest communities may vary across the latitudinal gradient. Species asynchrony could play a more important role in shaping the stability of tropical forests due to their higher biodiversity, while species stability could play a more significant role in determining the stability of temperate forests, which are frequently dominated by fewer species (i.e. they are less even) than tropical forests.

166 **Results**

167 **Latitudinal patterns in temporal stability and stabilizing mechanisms across**
 168 **spatial grains**

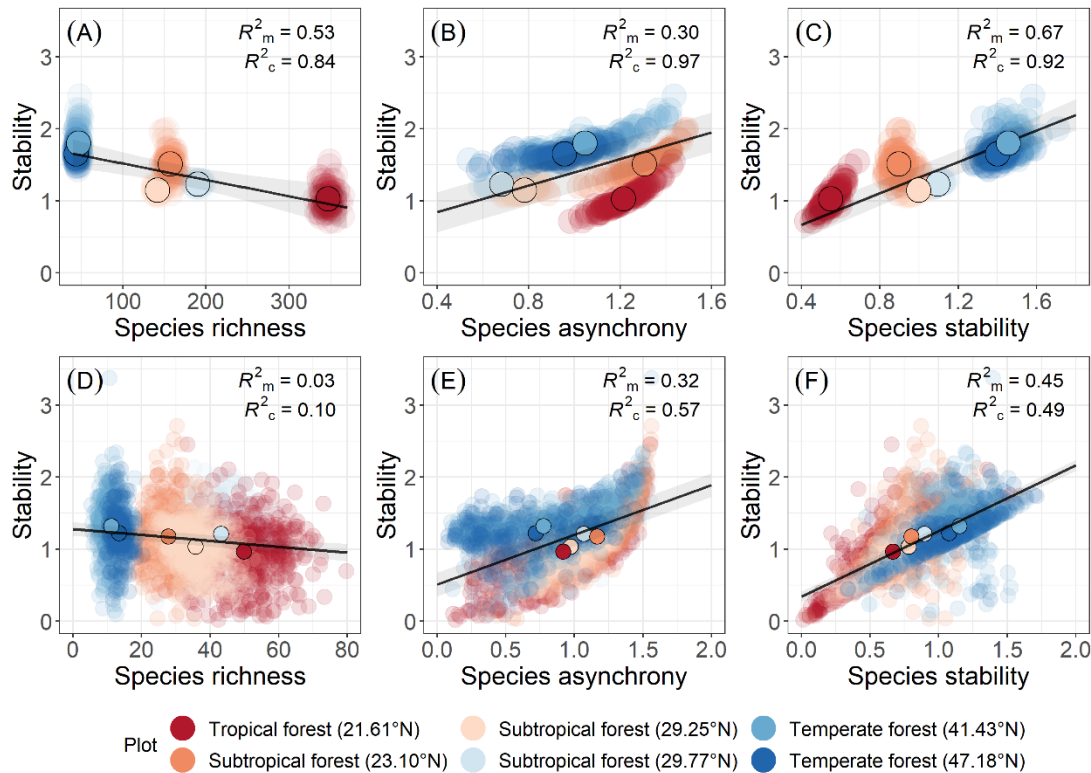
169 Our results indicated that stability did not vary significantly with latitude at either
 170 spatial grain (large grain: $P = 0.08$, small grain: $P = 0.13$, Fig. 2A, D). In contrast, we
 171 found that species asynchrony significantly decreased with latitude at the small, but not
 172 at the large spatial grain (large grain: $P = 0.61$; small grain: $R^2_m = 0.12$, $P = 0.04$, Fig.
 173 2B, E) and that species stability significantly increased with latitude at both spatial
 174 grains (large grain: $R^2_m = 0.78$, $P < 0.01$; small grain: $R^2_m = 0.27$, $P < 0.01$, Fig. 2C,
 175 F).



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Fig. 2 Latitudinal patterns of stability (A, D), species asynchrony (B, E) and species stability (C, F) at two spatial grains (4.0 ha ($n = 600$) and 0.4 ha ($n = 3075$)). Lines are mixed-effects model fits (solid lines: $P < 0.05$; dashed line: $P > 0.05$). Translucent points are plot-level values, while opaque points with black circles are mean values for each of the six study sites. Different colors indicate different study sites. R^2_m and R^2_c represent variation explained by fixed effects and the combination of fixed and random effects in mixed-effects models, respectively. Grey bands represent 95% confidence intervals. Both stability and species stability were log10 transformed, and species asynchrony was angular transformed.

187 Our results showed that species richness destabilized forest communities at both spatial
 188 grains (large grain: $R^2_m = 0.53$; small grain: $R^2_m = 0.03$; Fig. 3A, D; Table S7), while
 189 species asynchrony (large grain: $R^2_m = 0.30$; small grain: $R^2_m = 0.32$; Fig. 3B, E) and
 190 species stability stabilized forest communities at both spatial grains (large grain: $R^2_m =$
 191 0.67 ; small grain: $R^2_m = 0.45$; Fig. 3C, F; Table S7).

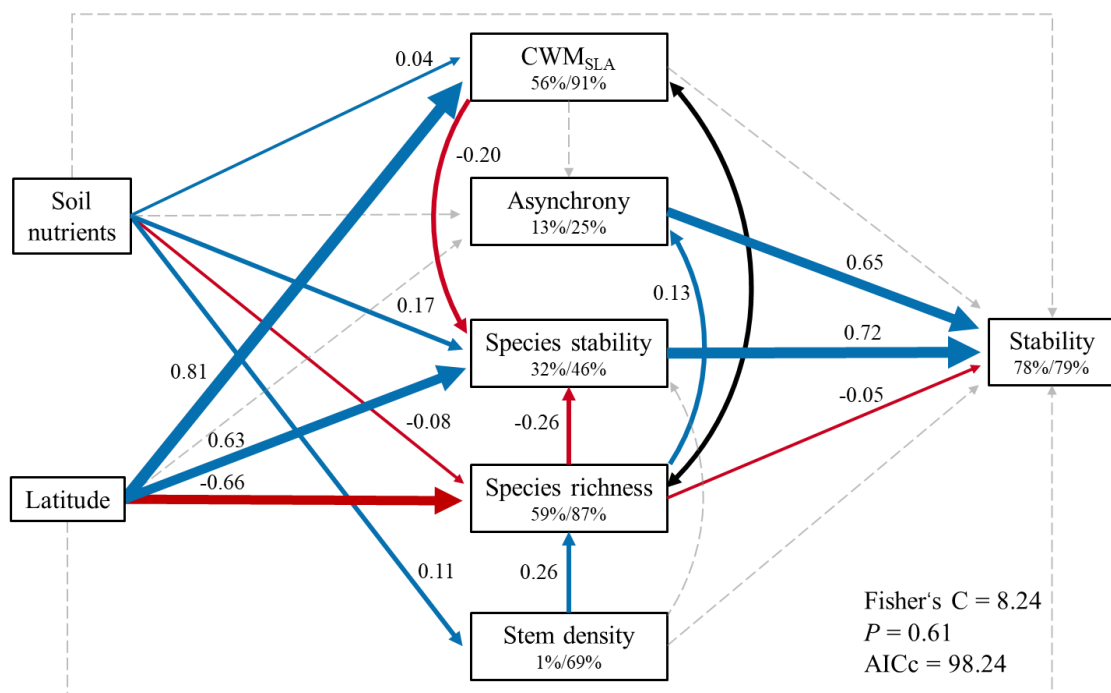


192 **Fig. 3 Relationships between species richness (A, D), species asynchrony (B, E),**
 193 **species stability (C, F) and stability at two spatial grains (4.0 ha (n = 600) and 0.4**
 194 **ha (n = 3075)).** Lines are mixed-effects model fits. Translucent points are plot-level
 195 values, while opaque points with black circles are mean values for each study site.
 196 Different colors indicate different study sites. R^2_m and R^2_c refer to the marginal and
 197 conditional R^2 , which represent variation explained by fixed effects and the
 198 combination of fixed and random effects in mixed-effects models, respectively. Light
 199 grey bands represent 95% confidence intervals. Both stability and species stability were
 200 log10 transformed, and species asynchrony was angular transformed.
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203 Drivers of stability across a latitudinal gradient

204 A piecewise structural equation model explained 78% of the variation in stability
 205 (Fisher's $s = 8.24$, $P = 0.61$, $AICc = 98.24$; Fig. 4, Table S8), with species stability and
 206 species asynchrony being the main drivers of stability at the small grain (standardized
 207 path coefficients = 0.72 and 0.65, respectively). Latitude and soil nutrients influenced
 208 stability indirectly. Specifically, latitude increased stability *via* CWM_{SLA} , species

209 stability, and species richness (total effect: 0.44, Fig. 4); with CWM_{SLA} affecting
 210 stability *via* a negative effect on species stability (standardized path coefficient = -0.14)
 211 and stem density *via* a positive effect on species richness (standardized path coefficient
 212 = -0.04). Forests with lower soil total nitrogen and soil organic carbon increased
 213 stability *via* CWM_{SLA} , species stability and stem density (total effect: 0.12, Fig. 4).
 214 Negative effects of species richness on stability were both direct (standardized path
 215 coefficient = -0.05) and indirect, which operated *via* species stability (standardized path
 216 coefficients = -0.17; Fig. 4). In contrast, species richness increased stability *via* species
 217 asynchrony (standardized path coefficients = 0.08; Fig. 4).

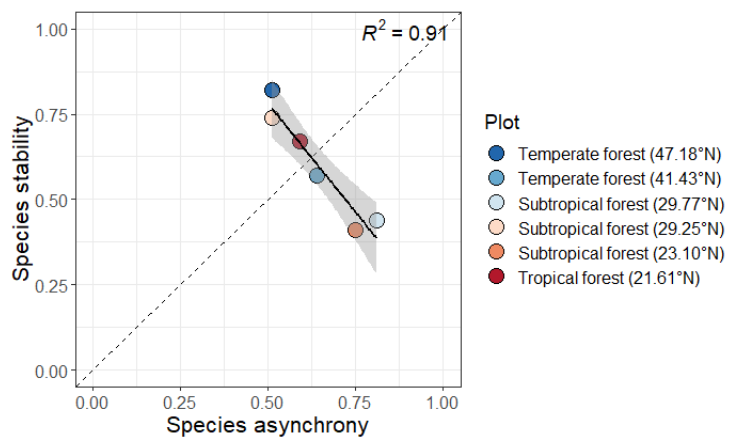


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Fig. 4 Direct and indirect effects of biotic and abiotic factors on stability across a latitudinal gradient at the small spatial grain. The structural equation model includes soil nutrients (the first principal axis, positive values associated with lower total nitrogen and soil organic carbon), latitude (Latitude), functional trait composition (represented by the community-weighted mean of specific leaf area, CWM_{SLA}), species asynchrony (Asynchrony), species stability (Species stability), species richness (Species richness), stem density (Stem density) and stability (Stability). The data fit the model well (Fisher's C = 8.24, P = 0.61; AICc = 98.24). Arrows represent causal relationships between variables. Black bi-directional arrows refer to significant partial pairwise correlations. Solid blue and red lines represent significant ($P \leq 0.05$) positive and negative standardized paths, respectively. Gray dashed lines represent non-significant paths ($P > 0.05$). Standardized path coefficients are represented for each statistically significant path, and path widths are scaled by standardized path coefficients. Numbers within boxes indicate the variance explained by fixed (left, marginal R^2) and the combination of fixed and random effects (right, conditional R^2).

236 Trade-off between species stability and asynchrony in driving stability

237 We observed a trade-off between the relative importance of species stability and species
238 asynchrony in determining stability (slope = -1.27, $P = 0.002$, $R^2 = 0.91$, Fig. 5).
239 However, this trade-off was not related to latitude. Specifically, there were no
240 significant relationships between latitude and the stabilizing effect of species
241 asynchrony and species stability, and their ratio (P value were 0.45, 0.34 and 0.40,
242 respectively. Fig. S6).



243 **Fig. 5 The relative importance of species stability and species asynchrony for**
244 **stability across a latitudinal gradient.** The black line is a linear model fit ($P < 0.05$)
245 for the relationship between the relative importance of both biotic stabilizing
246 mechanisms in determining stability. Each point refers to the direct effect of species
247 stability and asynchrony on stability for each study site.
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250 Discussion

251 In naturally-assembled forest ecosystems, stability and its underlying mechanisms vary
252 in response to biotic and abiotic factors^{12,14,15}, yet it remains uncertain to what extent
253 these factors shape emergent macroecological patterns of stability across spatial scales.
254 Here, we provide unique insights by demonstrating that there is no clear latitudinal
255 pattern of stability at either small or large spatial grains. Yet, we found that latitude
256 influenced stability *via* biotic stabilizing mechanisms, primarily species stability and
257 species asynchrony, at both spatial grains. Our study therefore reveals consistent
258 positive effects of species stability on stability across spatial grains. The trade-off
259 between species asynchrony and species stability in driving stability did not follow a
260 latitudinal pattern, suggesting that context-dependent factors - to a greater extent than
261 macroecological ones - underlie large-scale patterns of stability in naturally-assembled

262 forests.

263 Although there was not a clear latitudinal pattern of stability, we found that latitude
264 influences stability *via* biotic stabilizing mechanisms. Latitudinal patterns of species
265 asynchrony and species stability may arise from latitudinal variation in climate and
266 systematic shifts in the importance of abundant and rare species for stability. Warm
267 regions typically hold more species that differ in their response to environmental
268 conditions^{41,42}, resulting in higher species asynchrony at lower latitudes as observed in
269 this study. Conversely, the increase in environmental stress (i.e., low temperature) with
270 latitude may lead to a convergence of species responses to the environment, which
271 lowered species asynchrony⁴³. One possible explanation for the latitudinal shift in
272 species asynchrony is that it is driven by underlying gradients in species diversity, as
273 suggested by theory that diversity enhance species asynchrony^{5,7}, and as observed in
274 this study (Fig. 4). While theory suggests that species asynchrony should increase with
275 spatial grain and extent^{16,22}, as both factors are associated with larger species pools, we
276 found that the latitudinal pattern of species asynchrony was weaker at the large spatial
277 grain. For the latitudinal pattern of species stability, shifts in the ecological roles of
278 abundance and rare species may be the primary reason⁵. Our results suggest that the
279 impacts of dominant and rare species on stability change with latitude: while dominant
280 species exhibit strong impacts on stability at higher latitudes with lower community
281 evenness, rare species appear to have stronger impacts on stability at lower latitudes
282 with higher community evenness^{5,44}. Furthermore, the contrasting latitudinal patterns
283 for species stability and species richness support growing evidence that species richness
284 has a significantly negative effect on species stability^{9,40,44}.

285 Overall, species richness had neutral or negative effects on stability. This finding
286 suggests that other factors, e.g. climate change, affect biodiversity and stability
287 simultaneously, implying correlation and not causality^{28,45}. For example, warming can
288 reduce stability but increase biodiversity, which may result in a neutral or even negative
289 relationship between biodiversity and stability^{38,45}. At small spatial grain, , our results
290 support the idea that the impacts of species richness on stability are highly context-
291 dependent in naturally-assembled ecosystems^{28,40}. On the one hand, species-rich
292 communities increase the likelihood that asynchronous responses among species to
293 environmental conditions increase stability^{15,36}. On the other hand, higher functional

294 redundancy in species-rich communities may enhance competition, thereby decreasing
295 stability^{28,46}. Therefore, the balance between the diversity of ecological strategies and
296 their redundancy may shape the overall effect of species richness on stability in
297 naturally-assembled forests. At the large spatial grain, the negative effects of species
298 richness on stability are inconsistent with patterns found in grasslands⁴⁷. The
299 destabilizing effects of species richness we observe adds to the growing empirical
300 evidence¹⁸ that the expected positive effects of macroecological complementarity on
301 ecosystem functioning may not manifest at "small" spatial grains (< 10 ha), a scale at
302 which demographic stochasticity may overwhelm spatial insurance effects⁴⁸.

303

304 The trade-off between species stability and asynchrony in driving stability was not
305 driven by latitude, suggesting that the relative importance of different stabilizing
306 mechanisms is not determined uniquely by macroecological drivers. Biotic and abiotic
307 factors operating at smaller spatial scales may shape the relative importance of
308 stabilizing mechanisms. For instance, García-Palacios et al.³⁰ found that diversity-
309 stability is mediated by climate and soil nutrients, which were equally as important in
310 stabilizing ecosystem functioning as biotic factors. We found that soil nutrients
311 influenced stability *via* species stability, CWM_{SLA}, species richness, and stem density.
312 Soils associated with lower soil organic carbon (SOC), total nitrogen (TN), available
313 phosphorus (AP) and pH had, overall, higher species stability, CWM_{SLA}, and stem
314 density, but lower species richness. Yet, when zooming in, the relative importance of
315 soil nutrients on stabilizing mechanisms fluctuated inconsistently across the latitudinal
316 gradient (Supplementary results), likely influencing the overall observed trade-off in
317 the relative importance of species stability and species asynchrony. Therefore,
318 understanding the trade-off between stabilizing mechanisms requires not only the
319 integration of climatic factors and species richness, but also other abiotic conditions
320 and biotic dimensions that operate at different ecological scales⁴⁹.

321 In conclusion, our study provides fundamental empirical evidence that latitude
322 influences stability in naturally-assembled forest ecosystems *via* stabilizing biotic
323 mechanisms. Furthermore, we show that results from small spatial grains can provide
324 valuable insights for understanding stability and underlying stabilizing mechanisms at
325 spatial extents that are relevant for conservation and forest management. Moreover, our

326 results suggest that ecological processes that alter the functional composition and stem
327 density, like secondary succession, anthropogenic disturbance, or forest management
328 may also play a key role in driving nature's contributions to people over time.

329

330 **Methods**

331

332 **Study sites and data collection**

333 The dataset used in this study was compiled from CForBio Network
334 (<http://www.cfbiodiv.cn>), which contains six forest dynamic plots, belonging to three
335 forest ecosystems (temperate forest: LS, CBS; subtropical forest: BDGS, GTS, DHS;
336 tropical forest: BN), whose area ranged from 9 ha to 25 ha (Fig. 1A; Table S1) and that
337 are located across a latitudinal gradient (spanning from 21.61 °N to 47.18 °N). Each
338 plot is divided into subplots (20 m × 20 m = 0.04 ha). Within each plot, all woody plants
339 with diameter at 1.3 m height \geq 1 cm were measured, mapped, identified, and tagged⁵⁰.
340 All the plots are resurveyed every five years. Our dataset included three inventories for
341 each plot over a period of ten years, yielding a total of more than 1.9 million
342 measurements with 1,013 species.

343

344 **Data compilation at the large spatial grain**

345 To explore the variance in the latitudinal pattern of stability and its stabilizing
346 mechanisms among different spatial grains, we compiled a new dataset at the same
347 spatial grain for all study sites (200 m × 200 m = 4.0 ha) including species richness,
348 species asynchrony, species stability and stability, to minimize scale-dependent biases.
349 To this end, we randomly selected 100 subplots with replacement to create an
350 aggregated community. We then calculated species richness, species asynchrony,
351 species stability, and temporal stability (see next section for details). We repeated this
352 process 100 times to obtain a new dataset for each study site (Fig. S1). We also
353 calculated species richness, species asynchrony, species stability and stability using
354 data from all subplots for each plot. From hereon, we refer to results and analyses at the
355 subplot level as the small spatial grain (0.04 ha) and those at the plot level as the large
356 spatial grain (4.0 ha).

357

358 **Biotic factors and stability**

359 For each spatial grain at all study sites, we calculated species richness (SR), as the

360 number of living tree species per plot. We then averaged species richness across
361 inventories. Stem density of living trees was also counted and averaged at small spatial
362 grain.

363 To test the mass ratio hypothesis, we calculated the community-weighted means
364 (CWMs) of functional traits at the small spatial grain using the relative abundance of
365 each species. SLA (specific leaf area, cm²/g) was selected to reflect the “fast-slow”
366 strategy of trees⁵¹, which we calculated with the following formula:

367

$$368 \quad CWM = \sum_{i=1}^n p_i t_i,$$

369

370 where p_i is the relative abundance of species i in a subplot with n species, t_i is the mean
371 of SLA at species level for species i . SLA of each species was measured by the ratio of
372 leaf area by leaf dry mass.

373

374 Species asynchrony at both spatial grains was calculated following ref⁶:

$$375 \quad \text{Species asynchrony} = 1 - \frac{\sigma^2}{(\sum_{i=1}^N \sigma_i)^2}$$

376 where σ is the standard deviation of aboveground biomass (AGB) across three
377 inventories, and σ_i is the standard deviation of AGB of species i in each grain with N
378 species across the three inventories. A community is perfectly synchronous when the
379 value is equal to 0, and is perfectly asynchronous when the value is equal to 1 (ref⁶).

380 Then, species stability at both spatial grains, i.e., the species level stability weighted by
381 species' relative abundances, was calculated following ref⁵:

$$382 \quad \text{Species stability} = 1 / \sum_{i=1}^N \frac{\mu_i \sigma_i}{\mu \mu_i},$$

383 where μ and μ_i are the mean of AGB of grain and species i within this grain across the
384 three inventories, respectively.

385

386 Temporal stability of aboveground biomass (AGB) at both spatial grains was defined
387 as the ratio of mean (μ) AGB across three surveys to the standard deviation (σ) of
388 AGB⁵². To estimate the aboveground biomass of each individual, we used site- and
389 species-specific allometric equations (see references in Table S2). We then summed
390 aboveground biomass for each inventory.

391

392 **Climate and soil nutrients**

393 We obtained monthly temperature, precipitation, and potential evapotranspiration data
394 for each study site from the National Earth System Science Data Center
395 (www.geodata.cn) with a spatial resolution of 1000 m × 1000 m. Given the lag effect
396 of trees' response to climate, we used climate data for 13 years, including three years
397 before the first inventory at each study site. For all study sites, we calculated mean
398 annual temperature (MAT, °C), mean annual precipitation (MAP, mm⁻¹ y⁻¹), and mean
399 annual potential evapotranspiration (PET, mm⁻¹ y). We also calculated the standard
400 deviation (SD) of MAT, MAP, and PET (Table S3). In addition, we also collected soil
401 nutrient data including soil organic carbon (SOC, g/kg), total nitrogen (TN, mg/g),
402 available phosphorus (AP, mg/kg) and pH within each subplot (Table S3).

403

404 We performed principal component analysis (PCA) to reduce the potential collinearity
405 of the climate variables. The first two axes (ClimatePCA1, ClimatePCA2) explained
406 94% (80% + 14%) of total variation in climatic variables (Table S4; Fig. S2).
407 ClimatePCA1 was positively associated with MAP, MAP, PET and SD of MAP and
408 PET, and negatively associated with SD of MAT. ClimatePCA2 was negatively related
409 to SD of MAP, and positively related to SD of PET. Similarly, we used PCA to reduce
410 the dimensionality of soil nutrient data. The first two PCA axes (SoilPCA1 and
411 SoilPCA2) explained 87% (70% + 17%) of total variation in soil nutrients. SoilPCA1
412 was negatively associated with SOC, TN, pH and AP, whereas SoilPCA2 was
413 positively and negatively associated with pH and SOC, respectively (Table S4, Fig. S2).
414 As the first principal component for both climate and soil nutrients explained a
415 considerable amount of variation, we used the first principal component axis of both
416 soil nutrients and climate in the following statistical analyses.

417

418 **Statistical analyses**

419 Stability and species stability were log₁₀-transformed and species asynchrony was
420 angular transformed (arcsine(square-root(asynchrony))) to meet normality assumptions
421 prior to analysis. First, to test for variation in stability and stabilizing mechanism
422 (species stability and asynchrony) across a latitudinal gradient at both spatial grains, we
423 used linear mixed-effect models with study site as a random intercept at both small and
424 large grains, respectively. Second, to test if there was a variation at spatial grains in
425 bivariate relationships between species richness, species stability, species asynchrony,
426 and stability, we used mixed-effect models with study site as the random effect.

427 Confidence intervals (95%) of mixed effect models were computed using the
428 “ggeffects” package⁵³. Diagnostic plots were used to confirm model assumptions,
429 including the homogeneity and normality of model residuals.

430 To explore the mechanisms shaping stability patterns across the latitudinal gradient at
431 the small spatial grain, we fitted piecewise structural equation models (SEM) across
432 and within study sites⁵⁴. We constructed a hypothetical model based on current theory
433 that we subsequently tested (Fig. S3, Table S5, ref.^{14,15,36,38}). This model contains direct
434 paths from functional trait composition (CWM_{SLA}), species stability, species richness,
435 species asynchrony, and stem density to stability to assess biotic stabilizing
436 mechanisms, and we included direct paths from soil nutrients (SoilPCA1) and latitude
437 to stability to evaluate abiotic stabilizing mechanisms. We also included paths between
438 biotic mechanisms and between biotic and abiotic mechanisms to represent their
439 indirect effects on stability (Fig. S3, Table S5). We used climate (ClimatePCA1) instead
440 of latitude in an alternative model to test the specific effects of climate on stability (Fig.
441 S4). For the across-plot SEM, we used mixed-effect models with study site as the
442 random effect, and for within study site SEMs, we used generalized least square models.
443 Due to spatial autocorrelation in the response variable (i.e., stability) within study sites
444 (Moran’s I test⁵⁵, P -value < 0.05 , Table S6), we constructed several variogram models
445 (Exponential, Gaussian spherical, Linear, Rational, Quadratics) to determine the most
446 parsimonious spatial correlation structure. Models with a Gaussian spherical spatial
447 correlation structure had the lowest AIC, and were subsequently used in both across-
448 and within- study site SEMs. For those study sites without strong spatial autocorrelation
449 (LS and CBS), we used generalized least square models without spatial correlation
450 structures in SEM models (Table S6). Directed separation tests were used to examine
451 whether missing paths should be added; we added non-hypothesized, statistically
452 significant path coefficients ($P < 0.05$) to improve model fit. We also removed paths
453 that were not statistically significant to improve model fit. Akaike information criterion
454 (AICc) and Fisher’s C statistic ($P > 0.05$) were used to estimate the goodness-of-fit of
455 model⁵⁶.

456 To compare the relative importance of the effects of species stability and asynchrony
457 on stability across the latitudinal gradient, we extracted path coefficients from both
458 species stability and asynchrony to stability for each within-plot SEM. We then used a

459 linear model to test whether there is a trade-off in the relative importance of stabilizing
460 mechanisms. Moreover, we also used linear model with path coefficients of species
461 asynchrony and species stability to stability, and their ratio (i.e. asynchrony/species
462 stability) as response variables, and latitude as predictor to test whether this trade-off
463 follow a latitudinal pattern.

464 All statistical analyses were performed using R v.4.0.3⁵⁷. Moran's I test and SEM
465 analysis were performed using the “spdpe”⁵⁵ and “piecewiseSEM” packages⁵⁴
466 respectively, and mixed effects and generalized least squares models were used in the
467 “nlme” package⁵⁸.

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622

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624 X.J.Q. and M.X.J. designed the research; T.Y.Z., N.R.G.-R., D.C. and X.J.Q. conceived
625 ideas; T.Y.Z., compiled and analyzed the data with the help of N.R.G.-R., D.C., H.K.
626 and X.J.Q.; T.Y.Z., N.R.G.-R., D.C., H.K. and X.J.Q. led the writing of the manuscript.
627 All authors revised the drafts and gave final approval for publication.

628

629 **Competing interests**

630 The authors declare no competing interests.