**Table 2.** Cover of different grass parts (means ± SEM, $n = 3$ experimental blocks) in plots cattle accessed exclusively (C) or shared with wild herbivores excluding (WC) or including (MWC) megaherbivores. Column means listed in bold fonts and bearing different superscripts are statistically different ($P < 0.05$, Tukey's post hoc test).

| | Live leaves (hits/100 pins) | Dead leaves (hits/100 pins) | Live stems (hits/100 pins) | Dead leaves (hits/100 pins) |
|---|---|---|---|---|
| | | *Dry season* | | |
| C | 88.7 ± 9.1 | 147.6 ± 7.0 | 15.4 ± 2.9 | 76.6 ± 8.7 |
| WC | 75.9 ± 3.3 | 131.5 ± 6.1 | 18.2 ± 2.2 | 76.1 ± 5.6 |
| MWC | 80.7 ± 16.1 | 139.4 ± 31.8 | 10.9 ± 1.8 | 62.4 ± 12.2 |
| F | 0.5 | 0.2 | 1.8 | 1.4 |
| P | 0.7 | 0.8 | 0.3 | 0.3 |
| | | *Wet season* | | |
| C | 181.1 ± 12.3 | 64.8 ± 6.1 | 33 ± 5.5 | **42.1[a] ± 2.8** |
| WC | 175.6 ± 4.6 | 58.2 ± 1.3 | 27.9 ± 4.6 | **33.7[b] ± 2.7** |
| MWC | 160.8 ± 6.6 | 61.8 ± 8.9 | 21.5 ± 4.2 | **31.6[b] ± 2.2** |
| F | 1.4 | 0.3 | 1.2 | **18.1** |
| P | 0.3 | 0.8 | 0.4 | **0.01** |

in catalyzing a "grazing succession" that culminates into enhanced access to high-quality forage by native ruminants in the Serengeti ecosystem (*18*, *20*, *21*).

We suggest that the net effects of species interactions in all ecological systems are a result of both competitive and facilitative effects, with the net effect being the one that is quantitatively greater. One paradigm of interspecific facilitation is that it tends to be greater in more stressful environments (*22*). This paradigm arose from plant facilitation research in which the main mechanism of facilitation was lessening of environmental stress (*24*). Our results suggest that other types of facilitation will produce different patterns, depending on the underlying mechanism. Here, the net facilitation was during superficially less "stressful" conditions. Similarly, in another examination of trophic interactions in this study system, it has been suggested that competition is greater in sites characterized by lower productivity (*25*). We extend this pattern to demonstrate that a decrease in competition occurs with temporal as well as spatial increases in productivity and that this trend can be so great that it results in not simply less competition but actual facilitation between two key herbivore guilds. The net effect of these competitive and facilitative forces will be driven by the relative proportions of "dry" and "wet" times throughout the year and probably by additional factors, such as herbivore densities and ecosystem productivity.

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# Disentangling the Drivers of β Diversity Along Latitudinal and Elevational Gradients

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Understanding spatial variation in biodiversity along environmental gradients is a central theme in ecology. Differences in species compositional turnover among sites (β diversity) occurring along gradients are often used to infer variation in the processes structuring communities. Here, we show that sampling alone predicts changes in β diversity caused simply by changes in the sizes of species pools. For example, forest inventories sampled along latitudinal and elevational gradients show the well-documented pattern that β diversity is higher in the tropics and at low elevations. However, after correcting for variation in pooled species richness (γ diversity), these differences in β diversity disappear. Therefore, there is no need to invoke differences in the mechanisms of community assembly in temperate versus tropical systems to explain these global-scale patterns of β diversity.

Some of the most striking and frequently documented patterns in ecology are that species richness in local communities generally declines with increasing latitude and elevation, such that the diversity of many clades peaks in lowland, tropical areas (*1*, *2*). The mech- anisms underlying these gradients are often difficult to distinguish because multiple processes operating at multiple scales may govern geographic variation in diversity (*3*). For example, declines in diversity with elevation and latitude could result from deterministic community
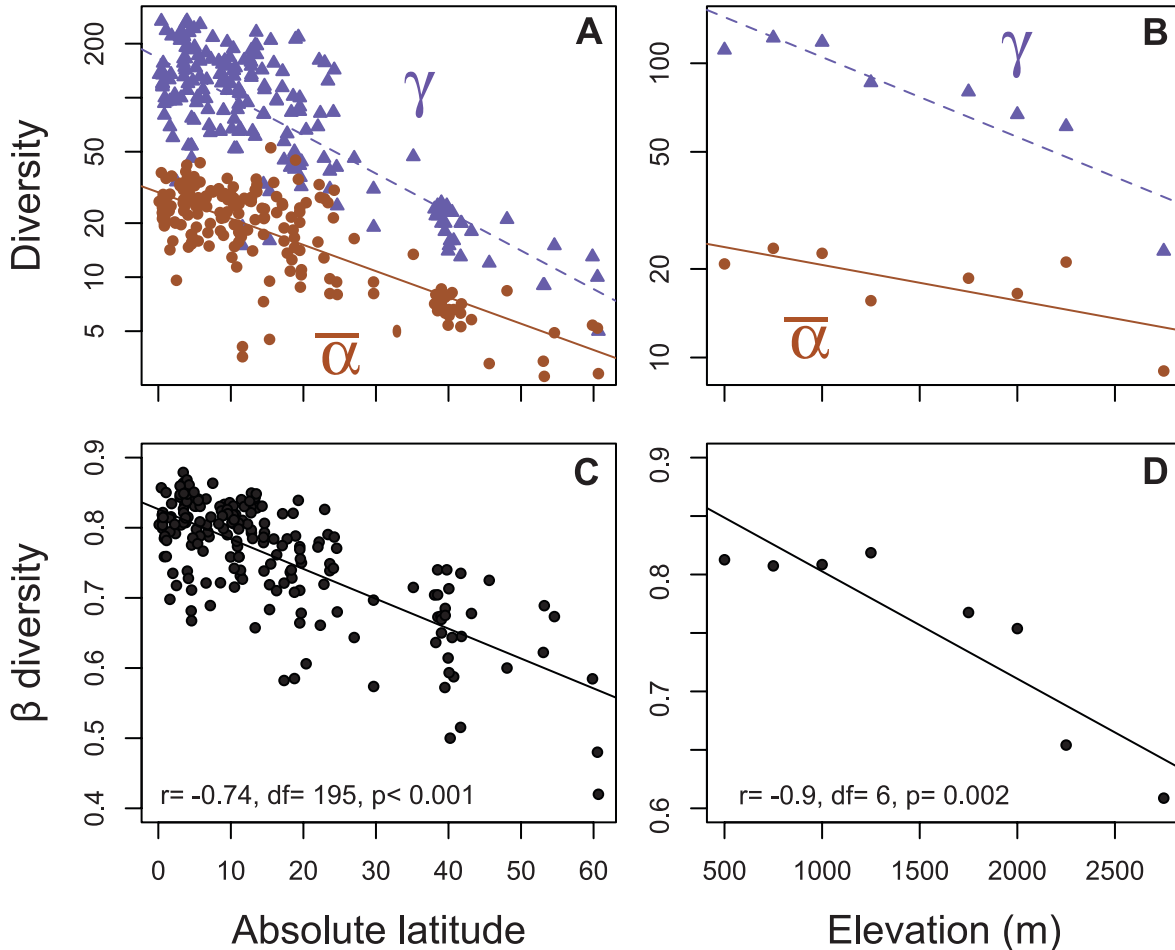
**Fig. 1.** Latitudinal and elevational trends in mean $\alpha$ and $\gamma$ diversity for woody plants (**A** and **B**) drive a significant correlation between latitude and $\beta$ diversity (**C**) and elevation and $\beta$ diversity (**D**). $\beta$ diversity is measured as the $\beta$ partition ($\beta = 1 - \overline{\alpha}/\gamma$).

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assembly processes at local scales (*4*, *5*). Alternatively, spatial variation in local diversity could depend on processes that operate at larger scales (e.g., speciation, extinction, and biogeographic dispersal), which trickle down to affect diversity in the embedded localities (*6*, *7*). One way to disentangle such multiscale effects is to examine patterns of diversity across scales, with a particular focus on $\beta$ diversity (a measure of compositional differences among samples), which links local ($\alpha$) to larger-scale ($\gamma$) diversity (*8*–*11*). Differences in $\beta$ diversity along biogeographic gradients have been interpreted as reflecting differences in the ecological processes acting along these gradients, including variation in the range size (*11*) and dispersal ability (*9*) of species and in the strength of local processes, such as habitat filtering (*8*).

As an example of how $\beta$ diversity decreases with latitude and elevation, and the corresponding changes in $\alpha$ and $\gamma$ diversity, we use two data sets of woody plants. The first is from 197 locations along a latitudinal gradient spanning more than 100° (*12*, *13*), and the second is a similar set of eight locations spanning a 2250-m elevational gradient in Carchi, Ecuador (*14*, *15*). We define $\alpha$ diversity as the species richness of a single 0.01-ha subplot, $\gamma$ diversity as the total richness of the

10 subplots (totaling 0.1 ha) at a location, and $\beta$ diversity as the heterogeneity in species composition (*16*) among the 10 subplots of 0.01 ha each established at each location, measured as the multiplicative $\beta$ partition ($\beta = 1 - \overline{\alpha}/\gamma$) (*17*, *18*). This spatial scale is smaller than has been used in many other studies of $\beta$ diversity, but it is appropriate to capture responses to fine-grained environmental heterogeneity (*19*), as well as the local neighborhood interactions that are known to strongly influence community assembly in temperate (*20*) and tropical (*21*) forests, although it does not capture coarser-grained environmental effects.

In these data sets, sampled woody plant diversity at both smaller ($\alpha$ diversity) and larger ($\gamma$ diversity) spatial scales declines with increasing latitude (Fig. 1A) (*12*, *22*) and elevation (Fig. 1B) (*14*). Because $\gamma$ diversity declines more rapidly along both gradients than does $\alpha$ diversity, $\beta$ diversity therefore declines with increasing latitude (Fig. 1C) and elevation (Fig. 1D). Thus, these data sets, although collected at small spatial scales, show the same patterns typically seen in larger-scale analyses (*8*).

Although a common explanation for these declines in $\beta$ diversity would help explain latitudinal and elevational diversity gradients, caution is needed

**Fig. 2.** The relation between β and γ diversity (**A**) expected algebraically, based on the mean probability that a species occurs in a subplot when sampled from a larger species pool where abundances follow a lognormal distribution. Curves represent β-diversity values, measured as the β partition $(1 - \overline{\alpha}/\gamma)$, for 10 subplots each composed of *n* individuals, as indicated. Similar relations are observed in empirical data from woody plants along a latitudinal (**B**) and elevational (**C**) gradient. See supporting online material for simulations showing similar relations for other common measures of β diversity and for samples generated from uniform abundance distributions.
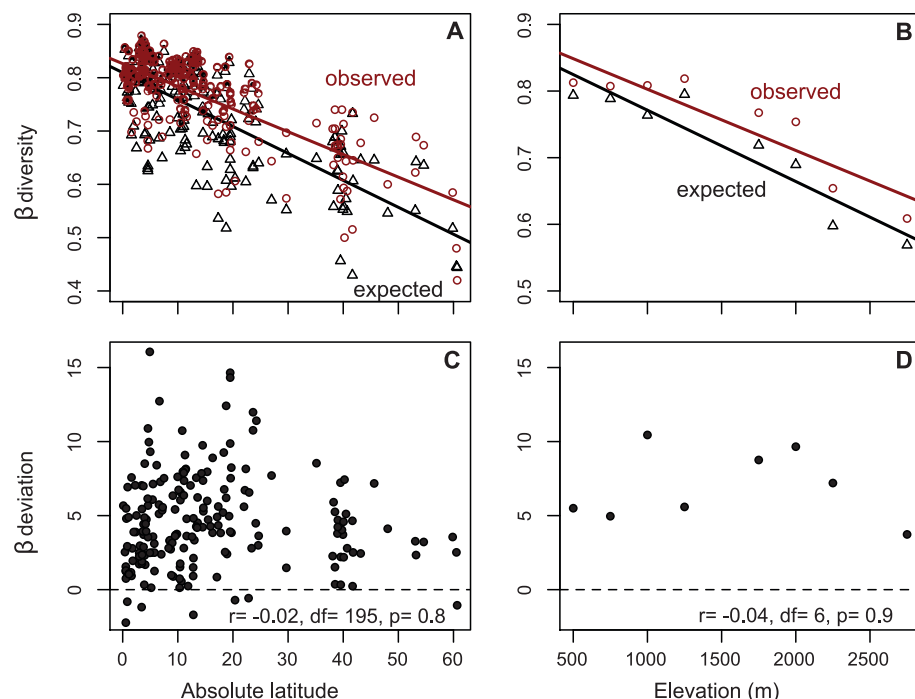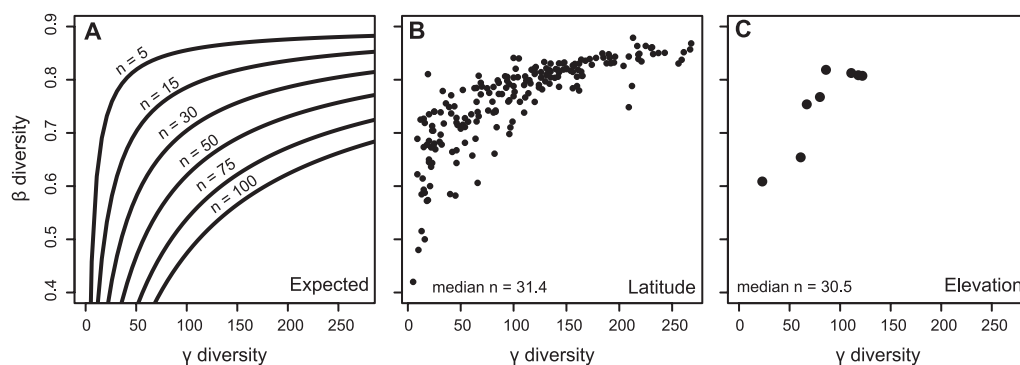


**Fig. 3.** Patterns in observed (red) and expected (black) β diversity of woody plants along a latitudinal (**A**) and an elevational (**B**) gradient and patterns in the β deviation, a standard effect size of β-diversity deviations from a null model that corrects for γ dependence, with either latitude (**C**) or elevation (**D**).

before ascribing any possible ecological mechanisms to these declines in β diversity. It is widely recognized that β diversity is a simple function of α and γ diversity regardless of how it is calculated (e.g., multiplicative, $\beta = \gamma/\overline{\alpha}$; additive, $\beta = \gamma - \overline{\alpha}$; or β partition, $\beta = 1 - \overline{\alpha}/\gamma$), and, therefore, is not independent of variation in either α or γ diversity (*16, 23, 24*). Even supposed "true" measures of β diversity (*25*) can vary simply because of changes in γ diversity (*26*). Because γ diversity varies along both latitudinal and elevational gradients, its influence on α and β diversity must be accounted for before any ecological explanations are offered.

To account for effects of variation in γ diversity, we first explored the relation between γ diversity and β diversity in the absence of any process other than random sampling. We found that expected β diversity increased with γ diversity, which can be shown algebraically for the

multiplicative β partition (Fig. 2A) (*27*), or with a simple simulation model using a wide variety of other traditional β diversity metrics (fig. S2). This expected relation between β diversity and γ diversity holds regardless of the specific scales used to measure α and γ diversity (e.g., Fig. 2A).

Furthermore, in the woody plant data sets presented here, the correlation between γ diversity and observed β diversity along either the latitudinal (Fig. 2B) or elevational (Fig. 2C) gradient was consistent with the pattern expected, solely on the basis of random sampling of individuals from the species pool. Because of this consistency, it is not yet parsimonious to infer that ecological mechanisms (e.g., niche-based processes or habitat associations) drive the observed differences in community structure along these biogeographic gradients. Instead, a null modeling approach is first needed to determine if β diversity deviates from the

expectations of a random (stochastic) assembly process and whether the magnitude of the deviation varies along latitudinal and elevational gradients.

Using the woody plant data sets, we compared observed patterns of β diversity to patterns generated by a null model. The null model randomly shuffles individuals among subplots while preserving γ diversity, the relative abundance of species at the location, and the number of individuals per subplot (*28*). This explicitly corrects for γ dependency (fig. S4) and provides expected values of β diversity for each site based solely on random sampling from the species pool.

It was surprising that the null model analysis revealed that β diversity is generally greater than expected at nearly all locations along both latitudinal and elevational gradients (Fig. 3). This suggests that species tend to be more aggregated within local subplots than expected by chance (*29*). Aggregation across the range of species pools, climates, and forest types in our study could be explained by habitat filtering (*30*), dispersal limitation (*31*), and/or priority effects (*32*). However, the magnitude of the deviation did not vary systematically along latitudinal or elevational gradients (Fig. 3, C and D). In other words, after correcting for differences in species pool size, β diversity was the same both at tropical and temperate sites and at high- and low-elevation sites. This means that the net outcome of local community assembly processes is consistent (in terms of their effect on β diversity) across these gradients (*33*) at the scale of our study.

Taken together, our results indicate that variation in β diversity across broad biogeographic gradients is more likely to be driven by γ diversity than by differences in the mechanisms of community assembly (e.g., niche versus neutral) (*32, 34*); range size and dispersal; or density-dependent interactions (*21, 35*). Therefore, there may be no need to invoke different local assembly processes when trying to explain latitudinal or elevational differences in β diversity. Instead, a more plausible explanation is that variation in biogeographic or regional processes sets the size of the species pool (*3*), and the combined influence of local processes acts in a consistent way across large-scale diversity gradients (*33*) to produce the patterns of species turnover that are ubiquitous in the natural world.

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# A Role for Snf2-Related Nucleosome-Spacing Enzymes in Genome-Wide Nucleosome Organization

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The positioning of nucleosomes within the coding regions of eukaryotic genes is aligned with respect to transcriptional start sites. This organization is likely to influence many genetic processes, requiring access to the underlying DNA. Here, we show that the combined action of Isw1 and Chd1 nucleosome-spacing enzymes is required to maintain this organization. In the absence of these enzymes, regular positioning of the majority of nucleosomes is lost. Exceptions include the region upstream of the promoter, the +1 nucleosome, and a subset of locations distributed throughout coding regions where other factors are likely to be involved. These observations indicate that adenosine triphosphate–dependent remodeling enzymes are responsible for directing the positioning of the majority of nucleosomes within the *Saccharomyces cerevisiae* genome.

Chromatin has the potential to influence all genetic processes that act on the underlying DNA. The application of genomic technologies to study chromatin organization has revealed a striking alignment with respect to transcribed genes, consisting of a nucleosome-depleted region upstream of the transcriptional start site (TSS) followed typically by an array of nucleosomes whose positioning decays with progression into the coding region (*1–3*). This organization appears to be a conserved feature of the organization of eukaryotic genomes, and an assortment of factors have been proposed to contribute to its establishment (*2, 3*).

Prime candidates are remodeling enzymes related to the yeast Snf2 protein that have been shown to be capable of repositioning nucleosomes (*4*). Of these enzymes, ISWI- and Chd1-containing remodeling enzymes have been shown to be particularly effective in repositioning nucleosomes in vitro (*5–7*). These enzymes share structural motifs that may adapt them for the purpose of nucleosome spacing (*8*), exhibit sensitivity to an epitope in the N-terminal tail of histone H4 (*9, 10*), and have been shown to alter chromatin at specific loci in vivo (*11–15*). This prompted us to investigate the extent to which deletion of any one of these proteins contributes to the overall organization of nucleosomes in vivo. To do this, we took advantage of recently published data for *ISW1* (*14*) and *ISW2* (*15*) and our own data for a strain in which the *CHD1* gene had been deleted. Numerous alterations to chromatin structure are apparent in each strain. However, when the average chromatin structure with respect to TSSs is aligned for all yeast genes, the individual deletions were observed to have relatively minor effects (Fig. 1, A to C).

The phenotypes associated with deleting individual *ISW1*, *ISW2*, or *CHD1* genes are relatively minor, whereas deletion of all three genes results in synthetic phenotypes (*6*). This led us to investigate chromatin organization in strains deleted for all combinations of these enzymes. Micrococcal nuclease digestion of chromatin isolated from these strains indicated the presence of spaced nucleosomes, except in the case of the *isw1Δ, chd1Δ* and *isw1Δ, isw2Δ, chd1Δ* strains (fig. S1). To characterize chromatin organization in these strains in more detail, nucleosomal DNA fragments were isolated and subject to paired-end sequencing.

The locations of nucleosome dyads were estimated as the midpoint of each paired-end read. A plot illustrating how the dyads map to a representative chromosomal locus (chromosome I coordinates 100,000 to 120,000) is illustrated in fig. S2. In the wild-type strain, a clear periodic enrichment of nucleosomal dyads is observed with a mean spacing of ~15 base pairs (bp). In the *isw1Δ, chd1Δ* and *isw1Δ, isw2Δ, chd1Δ* strains, many nucleosomes were observed to be less organized than in the wild-type strain. However, it is also notable that while many nucleosomes lose positioning relative to the TSS in the triple mutant, a subset of nucleosomes are retained. Alignment of nucleosomal dyads with the TSS reveals that nucleosome organization is grossly perturbed in these strains (Fig. 1, D and E). Especially prominent is a loss of nucleosome positioning through the coding regions while depletion of nucleosomes within the vicinity of the -1 nucleosome is unaffected. The

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