RIPARIAN ZONES INCREASE REGIONAL RICHNESS BY SUPPORTING DIFFERENT, NOT MORE, SPECIES: REPLY

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We thank Hylander (2006) for clarifying the interpretation of β-diversity in our paper, Riparian zones increase regional richness by supporting different, not more, species (Sabo et al. 2005). "Narrow-sense" turnover (sensu Koleff et al. 2003) between riparian and upland habitats is, indeed, overestimated by Jaccard’s index of similarity, or "broad-sense" turnover. Nevertheless, in dispelling one myth, our original paper does not give rise to a new one. We will present new analyses of our data that clearly substantiate the claim that riparian zones harbor unique fauna and flora globally and increase regional species richness, albeit by an average 38% rather than the 50% we calculated in our previous paper. Further, our broad-sense turnover calculations (1 − βI; Sabo et al. 2005: Fig. 3) for riparian plants are some of the highest values in the published literature, yet occur across extremely small spatial scales (typically 1 km or less). Here we address Hylander’s two central critiques separately.

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Hylander’s first critique: 1 − βI is not a good measure of (narrow-sense) turnover

As Hylander points out, we used Jaccard’s index, βI, to estimate similarity in species composition between riparian and upland habitats. We then estimated dissimilarity as 1 − βI. Dissimilarity is “broad-sense” turnover (Koleff et al. 2003), and can be estimated as the sum of the species unique to either habitat divided by the regional pool (Gaston et al. 2001), or

\[ 1 - \beta_I = \frac{(a + b)}{(a + b + c)}. \]  

(1)

Hylander’s first critique of our paper is that the “dissimilarity” in species pools is not an accurate estimate of [narrow-sense] turnover (sensu Koleff et al. 2003), because the proportion of species not shared by riparian and upland habitats (a and b) includes species from both habitats. We thank Hylander for this clarification and here provide two new, complementary analyses of β-diversity. First, we estimated the proportion of unique riparian species as

\[ \alpha_{R,u} = \frac{a}{(a + b + c)}. \]  

(2)

This is similar to narrow-sense β-diversity measures described by Simpson (1943) and Lennon et al. (2001). Second, we estimate the proportional increase in the regional species pool due to riparian habitats as

\[ \gamma_R = \frac{a}{(b + c)} \]  

(3)

where \( b + c \) is the regional pool excluding riparian species.

The proportion of unique riparian species (i.e., narrow-sense turnover) is high (mean 0.24, range 0–0.6) with a lower confidence bound of 0.18 for the mean of all studies (Fig. 1a). Thus, narrow-sense turnover is nearly half of broad-sense turnover (Sabo et al. 2005). This result is not surprising, given that we found no significant differences in either α- or cumulative richness between riparian and upland habitats (Sabo et al. 2005: Figs. 1 and 2). On average, riparian zones and upland habitats share half of the regional species pool and harbor half (each) of the remaining “unique” species.

The proportional increase in regional species richness due to riparian habitats is similarly high (mean 0.38, range 0–1.5; Fig. 1b). Thus, our claim that riparian zones increase regional richness by 50% (Sabo et al. 2005:56) is inaccurate. A more accurate estimate of this parameter is 38% (99% CI: 0.258–0.499; Fig. 1b). This lower percentage is still surprisingly high, given that estimates of proportional riparian habitat coverage are small, on the order of 5% or less (e.g., for the entire land mass of the United States, NRC 2002). In both cases (Fig. 1a, b), we assess the significance of proportions using parametric confidence intervals, which brings us to Hylander’s second critique.
Hylander contends that the test of a null hypothesis of no turnover (e.g., \( H_0 = 1 - \beta_j = 0 \)) is "meaningless to underscore with statistics" as "the index may only vary from 0 to 1 and every possible data point is larger than zero (except in the very rare case with two identical lists of species resulting in \( \beta_j = 0 \))." We agree with Hylander that the test of the null hypothesis that turnover is zero may be biased toward rejection (where the mean is low and variance high), he provides no alternative null hypotheses that may be more appropriate. Here we follow through with Hylander’s criticism and propose an alternate, more comparative, null hypothesis that substantiates rather than invalidates our claim that turnover across the riparian–upland transition is high.

First, we point out that our goal in constructing confidence intervals around values of \( 1 - \beta_j \) (Sabo et al. 2005: Fig. 3) was not only to test the null hypothesis of zero turnover, but also to qualify our claim that \( 1 - \beta_j \) was high along the riparian–upland transition with the precision of our estimate of \( 1 - \beta_j \). Our confidence intervals were constructed with a \( t \) distribution after noting that our data (which are binomially distributed proportions) conformed to the normal distribution and were symmetrically distributed about the mean. The binomial distribution conforms to a normal distribution when (1) \( npq > 5 \) (Evans et al. 2000), where \( n \) is the sample size, or the number of proportions making up the sample, \( p = 1 - S_j \), and \( q = 1 - p \); and when (2) \( 0.1 < p < 0.9 \). Both criteria were met with our data set (e.g., \( npq \sim (0.5)(0.5)(54) = 13.5 \) for all studies combined; Sabo et al. [2005: Fig. 3]).

Our lower confidence bound for broad-sense turnover (all studies combined; Sabo et al. [2005: Fig. 3]) was 0.4 (mean = 0.5, 99% CI = 0.4–0.58), suggesting that even in the worst case scenario, broad-sense turnover is 40% across the riparian–upland transition. In short, the calculated CI is narrow and this entire range of the interval is high. A narrow CI and relatively high value for the lower 99% confidence limit substantiates rather than invalidates our claim that turnover across the riparian–upland transition is high.

Second, we note that although Hylander correctly points out that our test of \( H_0 = 1 - \beta_j = 0 \) is biased toward rejection (where the mean is low and variance high), he provides no alternative null hypotheses that may be more appropriate. Here we follow through with Hylander’s criticism and propose an alternate, more comparative, null hypothesis that substantiates rather than invalidates our claim that turnover across the riparian–upland transition is high.
than invalidates our claim that (broad-sense) turnover is high along the riparian–upland transition. Specifically, we ask whether $\beta$-diversity across the riparian–upland ecotone is equivalent to $\beta$-diversity in regions known to have high values for this parameter. In Fig. 2 we compare broad-sense turnover values (i.e., $1 - \beta_2$) from riparian zones worldwide ($n = 53$) to 10 values of the same parameter from other ecosystem types. This group of non-riparian studies includes habitats or species groups known for high $\alpha$-diversity or endemism, such as tropical rain forest trees (Condit et al. 2002) and herbaceous plants in serpentine soils (Harrison et al. 2006). Three results are pertinent to Hylander’s critique of our statistical analysis. First, broad-sense turnover values for riparian plant species are some of the highest values recorded worldwide, rivaling similar values for plants (trees) in tropical rain forests (Condit et al. 2002). Second, the 99% confidence interval (consistent with the confidence interval used in Sabo et al. 2005) for broad-sense turnover values of riparian plants ($\sim 0.55-0.83$) suggests that turnover in riparian plants is either significantly greater than (three records) or equivalent to (six records) turnover in nine out of 10 of our records from other ecosystem types. Finally, it is not so much the magnitude of broad-sense turnover in riparian systems that stands out in our analysis, but rather the comparatively short distance over which large turnover values occur. The average distance between riparian and upland sites in our data set was on the order of 1 km and many records provided examples of extremely high broad-sense turnover (>$0.9$) across distances of much less than 1 km. For comparison, $1 - \beta_1$ of tree species in the neotropics ($\sim 0.84$) occurs over a spatial scale of 1000 km. In other words, some $\beta$-diversity values for riparian plants (single records in upper left-hand corner of Fig. 2) are equivalent to tropical tree $\beta$-diversity, but occur across 1000- to 10 000-fold smaller spatial scales. In this way, riparian habitats provide a compelling example of how micro-geographic turnover in species composition can rival changes observed across much larger, macro-geographic scales. These results have strong implications for the design of conservation portfolios and biogeographic analyses conducted at large and coarse spatial scales.

Revised conclusions about $\beta$-diversity in riparian zones

Riparian habitats can, in some places, be more diverse than uplands (McIntyre 2000, Woinarski et al. 2000, Catterall et al. 2001, Brown and Peet 2003); however, this is not a general pattern across the globe (Sabo et al. 2005: Figs. 1 and 2). Similarly, the percentage of unique riparian fauna ($\alpha_{R,A}$) can be as high as 60% and the percentage increase in regional species richness due to riparian habitats ($\gamma_R$) as high as 150%. These are general patterns across the globe. On average the percentage of unique riparian species is 24% and riparian zones increase regional richness (over upland habitats) by 38%. In conclusion, we agree with Hylander that accurately quantifying “the contribution of different habitats (in [this] case riparian and upland habitats) to the overall species pool” is “an important question which deserves further attention in . . . meta-analyses.” The analyses presented in this reply address this question and suggest that further case studies in riparian systems should focus on quantifying scale dependencies of $\beta$-diversity and the mechanisms that drive species turnover (e.g., gradients in soil moisture, access to surface water, and the like).

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Literature cited


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In the recent paper by Stephanie M. Juice et al. (2006), “Response of sugar maple to calcium addition to northern hardwood forest,” Ecology 87(5):1267–1280, there is an error in Fig. 1 (p. 1271). In the histogram, the scale numbers along the y-axis need to be multiplied by 10 for calcium (they are correct for magnesium).