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Editor, Nicholas J Gotelli
Manuscript received 26 November 2007
Manuscript accepted 29 November 2007

doi: 10.1111/j.1461-0248.2007.01147.x

REJOINDER TO HARRISON (2008): THE MYTH OF PLANT SPECIES SATURATION

We find ourselves in general agreement with many of Harrison's remarks especially since we both find our data present a '… strong case… that at county to state scales, exotic plant invasions have led to few native plant extinctions' (emphasis added, Harrison 2007: 000). Where we differ appears related to the breadth of scales to which our conclusions may apply. In addition to the 'Myth of Plant Species Saturation' (henceforth, the 'Myth paper') in question, we have published several complementary papers which may alleviate some of Harrison's concerns.

Space-for-time substitutions must be made cautiously

In the Myth paper, our plot data (referenced by Harrison as a space-for-time substitution) are used to complement, not replace, time sequence data presented there and elsewhere. We begin the Myth paper by presenting time series data on immigration and extinction specifically to hold space constant and vary time.

Harrison further cites our failure to adequately consider conceptual models of saturation as reflected in species–area relationships (SAR) and local–regional richness relationship (LRR). We are familiar with the model laid out by Shurin and Srivastava (2005: Fig. 17.2) as it relates to the prediction that saturated communities are characterized by increasing SAR slopes with an increasing ratio of local : regional area. However, it is not obvious to us, that our data as presented in Fig. 6a are easily interpreted in light of that conceptual model. We are also familiar with LRR tests for saturation and all the pitfalls associated with such tests (Hillebrand and Blenckner 2002). In the Myth paper, we focused attention on the ever-increasing nature of both local and regional species pools (Table 1, Figs 1 and 3) as compelling evidence for unsaturation. When our data are presented in a manner consistent with the LRR concept (Fig. 1a), we again find little evidence that we are dealing with saturated species assemblages (Fig. 1b). But, again we also note that the interpretation of LRRs with respect to the notion of saturation is difficult (Shurin and Srivastava 2005). Because the results from LRR analyses are equivocal, we agree with Harrison that much more work is needed on the theoretical and empirical underpinnings of these patterns as they relate to the question of community closure.

Finally, Harrison goes on to ask us all to reconsider whether plant communities below the county scale are

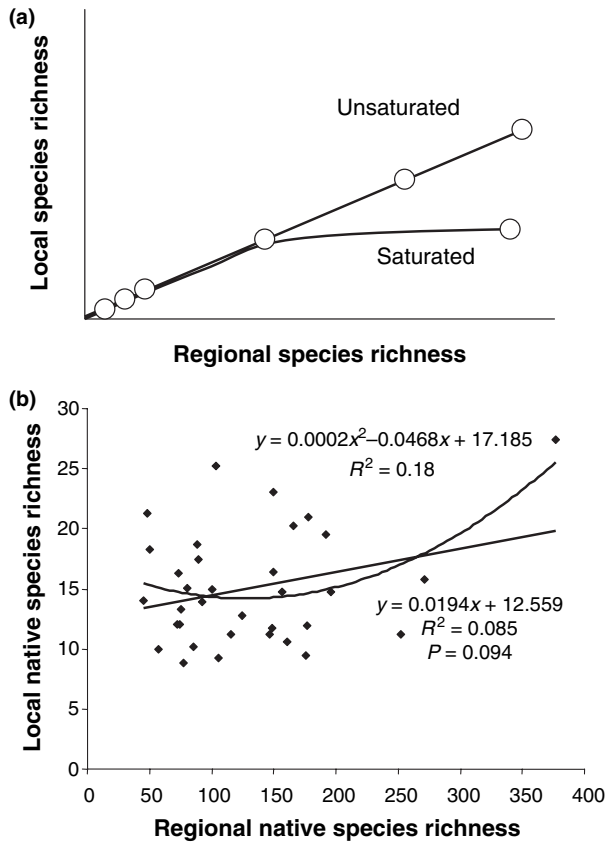

Figure 1 (a) Conceptual local–regional species richness models of saturated and unsaturated assemblages (after Cornell 1985, 1993; Cornell and Lawton 1992) and (b) actual data from 100-m^2 subplots and regional native species richness (estimated from five dispersed 0.1-ha plots in each type). Same data used in the Myth paper: Fig. 5a and b).

saturated. Where do these immigrants settle if not in the plant communities within counties? The answer may be in all of them! In another paper (Stohlgren *et al.* 2006b), we evaluated plot-scale patterns of invasion for 37 vegetation types in the central US. Based on these surveys, we sadly report that none of the vegetation types were free of exotic species, despite the absence of exotic plants at some plot locations. Using this same data set, we also showed that in 1, 10, 100 and 1000-m^2, the slopes of relationships between native and exotic species increased in a predictable, non-linear way, consistent with the 'lack of saturation' model (Fig. 2 in Stohlgren *et al.* 2006b: 411). Native species accumulated more quickly than exotic species, but exotic species richness continued to increase not only despite accumulations of native species, but significantly greater in species-rich vegetation types compared with species poor-types (Figs 3 and 4 in Stohlgren *et al.* 2006b: 412). For these reasons, we contend that plant invaders continue to spread (Myth paper Fig. 2), that it is unlikely they spread from one saturated community to another, and that evidence for saturation below the county level is weak.

Tests of saturation need to separate environmental from competitive influences

We could not agree more. We and many others explored various aspects of native and exotic plant diversity at multiple spatial scales far beyond the native and exotic richness correlation. Interestingly, complex models of species richness often transcend spatial scales. At county scales (Stohlgren *et al.* 2005b), landscape scales (Kumar *et al.* 2006), and local scales (Stohlgren *et al.* 1998), native and exotic species track 'the good life' – high light, warm temperatures, high precipitation and high soil nutrients. Where tree canopies reduces light, we find fewer native and exotic understory species (Stohlgren *et al.* 2000). Where fires reduce competitive influences, of course we find more weeds (Freeman *et al.* 2007), but exotic plants invade many undisturbed sites as well, for example, in grazed and ungrazed sites (Stohlgren *et al.* 1999).

We also agree with Harrison that it might be possible to find a 'residual negative effect of native richness on exotic species richness' (Stohlgren *et al.* 2005), but this may be at local scales, and it may be a weak force (Stohlgren *et al.* 2006b). Such an affect may show 'competitive influences' without demonstrating 'competitive exclusion' to the point of species extirpation from entire plant communities.

Saturation is a scale-dependent phenomena

We strongly agree. We do not ignore 1-m^2 plots, we and many others are just uncertain what they tell us about the saturation of entire plant communities (Stohlgren *et al.* 2006b, Stohlgren 2007). Harrison is correct that 'spatial heterogeneity ensures that invaders can have a strong effect at small scales without having a large influence at regional scales'. This is the primary point already made by Fridley *et al.* (2007).

Most telling is that Harrison fails to offer any examples of closed/saturated plant communities. Meanwhile, consistent with open, unsaturated communities, we find: (i) far greater rates of invasion than extirpation (Table 1); continued invasions over time (Figs 1 and 3); (ii) rapid spread if invaders from county to county (Fig. 2); and (iii) the greatest invasions in species-rich communities (Fig. 5b). We agree with Harrison that improvements are needed in all areas from data to theory. In the meantime, we ask our fellow ecologists to begin assuming that most vegetation types (or communities) should be considered open and unsaturated until proven otherwise.

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Editor, Nicholas J Gotelli
Manuscript received 26 November 2007
Manuscript accepted 29 November 2007

doi: 10.1111/j.1461-0248.2008.01161.x