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LETTER

Positive diversity–stability relationships in forest herb populations during four decades of community assembly

Martin Dovčiak[1,2]* **and Charles B. Halpern**[1]
[1]*School of Forest Resources, University of Washington, Box 352100, Seattle, WA 98195-2100, USA*
[2]*College of Environmental Science and Forestry, State University of New York, 459 Illick Hall, 1 Forestry Drive, Syracuse, NY 13210, USA*
**Correspondence: E-mail: mdovciak@esf.edu*

Abstract

It is suggested that diversity destabilizes individual populations within communities; however, generalizations are problematic because effects of diversity can be confounded by variation attributable to community type, life history or successional stage. We examined these complexities using a 40-year record of reassembly in forest herb communities in two clearcut watersheds in the Andrews Long-term Ecological Research Site (Oregon, USA). Population stability was higher among forest than colonizing species and increased with successional stage. Thus, life history and successional stage may explain some of the variability in diversity–stability relationships found previously. However, population stability was positively related to diversity and this relationship held for different forest communities, for species with contrasting life histories, and for different successional stages. Positive relationships between diversity and population stability can arise if diversity has facilitative effects, or if stability is a precursor, rather than a response, to diversity.

Keywords

Disturbance, diversity, forest communities, long-term community dynamics, population stability, succession.

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INTRODUCTION

Human-driven loss of biodiversity may reduce ecosystem stability (Griffin *et al.* 2009), but generalizations remain problematic. Diversity can positively affect stability of community biomass (McNaughton 1977); however, it can decrease the population stability of individual species (Tilman *et al.* 2006). Many ecosystem processes (e.g., soil nutrient cycling) are sensitive to diversity, but also to changes in plant species abundance or community composition (Hooper & Vitousek 1998; Reich *et al.* 2005). As a consequence, ecosystem stability could be negatively affected if diversity destabilizes the abundance of individual species or community composition. Considerably more attention has been devoted to effects of diversity on stability of community biomass than on population stability (Cottingham *et al.* 2001). As a result, the general perception of a positive effect of diversity on ecosystem stability may overlook the potential for diversity to decrease population stability, and thus stability of community composition.

Negative effects of diversity on mean population stability seem to be predominant in experimental grassland communities (Tilman *et al.* 2006; van Ruijven & Berendse 2007), although population stability of individual species can have negative, neutral or positive relationships to diversity (van Ruijven & Berendse 2007). In contrast, positive or neutral relationships have been observed in naturally assembling communities (Valone & Hoffman 2003; Romanuk *et al.* 2009). This variability may be explained by several factors. Observational and some experimental studies tend to include 'third factors' or 'hidden treatments' that covary with diversity, such as species composition, resource availability or successional age (Huston 1997). Some experimental studies have resolved the 'third factor' problem by directly controlling species composition and resource levels; however, they are inherently limited to subjectively chosen sets of species maintained by removing unwanted colonists (Tilman *et al.* 2006). Thus, overall stability and relationships between diversity and stability in experimental communities are likely to differ from those in naturally assembling communities.

In naturally assembling communities, temporary increases in resource availability (e.g., soil moisture or nutrients) caused by climatic variation (Frank & McNaughton 1991;

Tilman 1996) or disturbance (Halpern 1989; Schoennagel *et al.* 2005) can lead to the establishment of colonizing species rather than to simple repartitioning of resources among resident species (Davis *et al.* 2000; Dovčiak *et al.* 2005; Belote *et al.* 2008). Although colonists can take advantage of temporary increases in resources via rapid growth and reproduction, they tend to be poorer competitors with shorter life spans and potentially lower population stability compared to resident species (c.f. Grime 1977; Lepš *et al.* 1982). Over time, colonists tend to be replaced by better competitors. As a result, rates of compositional change tend to decrease with successional time (Anderson 2007). Although compositional changes (species turnover) in natural communities are directly related to population stability, it is not known if local diversity decreases population stability during community assembly or if diversity effects vary with life-history strategy (e.g., colonizing vs. resident species) or successional time.

Declining rates of compositional change during succession can also reflect decreases in resource availability and environmental stress over time. In contrast to grasslands, forest herbaceous communities are affected by taller woody species (shrubs and trees) that reduce available resources (e.g., light) and extremes in microclimate (e.g., heat stress) (Chen *et al.* 1999). As a result, diversity–stability relationships in forest ecosystems may differ substantially between early successional stages dominated by herbs and more advanced stages dominated by woody species. Yet, most diversity–stability studies have been limited to grassland and aquatic systems and to relatively short time spans (*c.* 10 years) (Cottingham *et al.* 2001). Little is known about effects of diversity on population stability in ecosystems dominated by woody species (e.g., forests), or how and why diversity–stability relationships may vary over successional time. Furthermore, within any broad ecosystem type (e.g., forest or grassland), diversity–stability relationships may vary among local communities characterized by different species' compositions driven by local variation in physical environment (topography) or resource availability (soil moisture or nutrients). It has been suggested that relationships between diversity and productivity or invasibility may differ at local (community) and larger (regional) scales (Loreau 2000; Shea & Chesson 2002); however, this scale dependence has not been tested in studies of population stability.

Intense debates in the literature (e.g., Bai *et al.* 2004 vs. Guo 2005; Tilman *et al.* 2006 vs. Bezemer & van der Putten 2007) suggest lack of a unified framework for comparing diversity–stability relationships among community types, species life-history strategies or successional stages. Ives & Carpenter (2007) suggest that diversity–stability relationships may reflect multiple mechanisms and that additional factors should be considered that potentially mediate these relationships. In this article, we use four decades of data from permanent plots at the H. J. Andrews Experimental Forest Long-term Ecological Research (LTER) Site (Oregon, USA) to test how population stability of forest herbs relates to diversity, and how diversity–stability relationships and population stability vary with community type, species life-history and successional stage during community reassembly after stand-replacing disturbance (timber harvest and broadcast burning). We test the following hypotheses:

H1. *Diversity hypothesis*. Mean stability of forest herb populations declines with diversity consistent with a mechanism of increasing competition for resources (Tilman 1999).

H2. *Community-type hypothesis*. Population stability decreases with diversity equally in all communities, but overall stability changes with position along community gradients.

H3. *Life-history hypothesis*. Population stability of colonizing and forest herbs decreases with diversity equally, but overall stability is lower among colonists than forest species.

H4. *Successional-stage hypothesis*. Population stability declines with diversity in both earlier (herbaceous) and later (woody) successional stages, but overall stability increases over time.

METHODS

Study sites

The study was conducted within two *c.* 100-ha experimental watersheds (WS1, WS3) in the H. J. Andrews Experimental Forest-LTER site in the western Cascade Range of Oregon, USA (44°12′ N, 122°12′ W). Elevations range from *c.* 450 to 1000 m and hillslopes are steep (average slope > 50%) and deeply dissected. Soils are shallow to moderately deep, primarily derived from volcanic parent materials (Rothacher *et al.* 1967). Climate is maritime with mild, wet winters and warm, dry summers. Average minimum temperatures are −5.5 °C in January and 11.9 °C in August; average maxima are 5.5 °C in January and 23.3 °C in July. Annual precipitation is *c.* 2300 mm (falling mostly as rain), but only 6% occurs between June and August resulting in frequent summer drought (Bierlmaier & McKee 1989). Prior to experimental harvest, canopies were dominated by mature (125–300 years old) and old-growth (300–500 years old) *Pseudotsuga menziesii*. Subcanopy layers were dominated by *Tsuga heterophylla* with local occurrence of *Thuja plicata*, *Taxus brevifolia*, *Acer macrophyllum*, *Cornus nuttallii* and *Castanopsis chrysophylla* (Dyrness 1973; Halpern 1989). In this steep mountainous terrain, understory composition reflects a steep topographically controlled gradient in soil moisture availability and productivity increasing from dry ridge tops to mesic lower slopes (Rothacher *et al.* 1967; Zobel *et al.*

1976; Grier & Logan 1977). Six plant communities were defined along this gradient (in order of increasing soil moisture/productivity): *Corylus cornuta–Gaultheria shallon*, *Rhododendron macrophyllum–G. shallon*, *Acer circinatum–G. shallon*, *A. circinatum–Berberis nervosa*, *Coptis laciniata* and *Polystichum munitum* (Rothacher *et al.* 1967; Dyrness 1973; Halpern 1989). Nomenclature follows Hitchcock & Cronquist (1973). For additional details, see Dyrness (1973), Halpern (1989), and Lutz & Halpern (2006).

Disturbance history and study design

Sites were clearcut either entirely (WS1, 1962–1966) or partially (WS3, three 5–11 ha patch cuts totalling 25% of the watershed; 1962–1963). Logging slash was broadcast burned in the fall after completion of harvest. Attempts at reforestation included aerial seeding or planting of *P. menziesii*, but most regeneration occurred through natural processes (seed dispersal from adjacent forests, stump sprouting of hardwoods) (Lutz & Halpern 2006).

Prior to logging (1962), 2 m × 2 m permanent plots were established systematically (with a random start) at slope-corrected intervals of 30.5 m along 16 transects; two plots were lost over time due to disturbance (landslide or burial by an old-growth treefall from the edge), yielding a total of 191 plots (131 in WS1, 60 in WS3). Based on species composition and topographic position, plots were assigned to one of the six understory communities (n = 12–44 plots per community). Nine plots that were not easily classified were excluded from community comparisons (but were included in all other analyses; see Data analysis).

At each sampling date, cover (%) of bare ground (a proxy for soil disturbance) and of each vascular plant species (< 6 m tall) was recorded; the summed cover of species within a plot could thus exceed 100%. Plots were sampled prior to logging, after logging, annually after burning until 1972/1973, and less frequently (every 1–5 years) thereafter, yielding a total of 19 temporal samples in WS1 and 21 in WS3. For analysis, we standardized the sampling interval by retaining the first and every third (or next available) post-burning sample. This resulted in 10 temporal samples with a mean sampling interval of 3.9 years.

To assess effects of life-history strategy, all species in the herbaceous layer (herbs and sub-shrubs) were classified as colonists (early successional, absent from the undisturbed forest) or forest species (characteristic of the undisturbed forest) following Halpern (1989). To assess effects of successional stage, temporal samples were divided into two periods (five samples each) characterized by marked differences in resource availability and community structure. Cover of bare ground (area available for colonization) was initially high in the herbaceous stage (1–20 years), but declined to very low levels in the woody stage (21–40 years; Fig. 1a). Herbaceous species (Fig. 1b) and herbaceous colonists in particular (Fig. 1c) responded positively to disturbance, initially dominating the herbaceous stage. Although richness of herbaceous species varied little over time (Fig. 1d), cover of herbaceous species (and especially colonists) decreased (Fig. 1b,c) as woody species (shrubs and trees) became more abundant (Fig. 1e). Additional details on experimental treatments, field sampling and community dynamics can be found in Dyrness (1973), Halpern (1989), Halpern & Spies (1995), and Lutz & Halpern (2006).

Data analysis

Temporal stability can be calculated from measurements of biomass (Tilman 1999), cover (Sankaran & McNaughton 1999), or plant density (Valone & Hoffman 2003). We used repeated measurements of understory plant cover in permanent plots; this avoided destructive sampling of biomass (which was not possible in these permanent plots) and the need for a space-for-time substitution. However, for comparability with previous studies of temperate grasslands and desert annuals where annual above-ground production and standing biomass are highly correlated (e.g., Valone & Hoffman 2003; Tilman *et al.* 2006), we calculated stability of species in the herb layer only. Taller woody species (shrubs and regenerating trees) were not included because their biomass is largely in woody structures (vertical stems and branches) and their temporal stability is not adequately captured by changes in cover. Thus, our long-term cover data permit analyses of population stability among forest herbs, but not overall community or ecosystem stability, for which we lack a common measure of abundance (i.e., biomass) across all growth forms (i.e., herbs, shrubs and regenerating trees). For each plot, we calculated population stability, S, for each herbaceous species for the entire sampling period (years 1–40; 10 temporal samples), and for each successional stage (years 1–20 and 21–40; each with five temporal samples), following Tilman (1999):

$$S = \mu/\sigma,$$

where μ and σ are the mean and standard deviation of species cover in a plot for the time interval of interest. For each time interval, we then computed mean richness (Tilman 1996; Valone & Hoffman 2003) and mean population stability in each plot (Tilman *et al.* 2006) for all species pooled and for the two life-history strategies (colonizing vs. forest species).

We used a series of regression models to test our hypotheses. First, we tested if mean population stability during the entire sampling period declined with mean richness (*H1*). We then tested whether this relationship varied (1) among plant communities (*H2*), (2) between

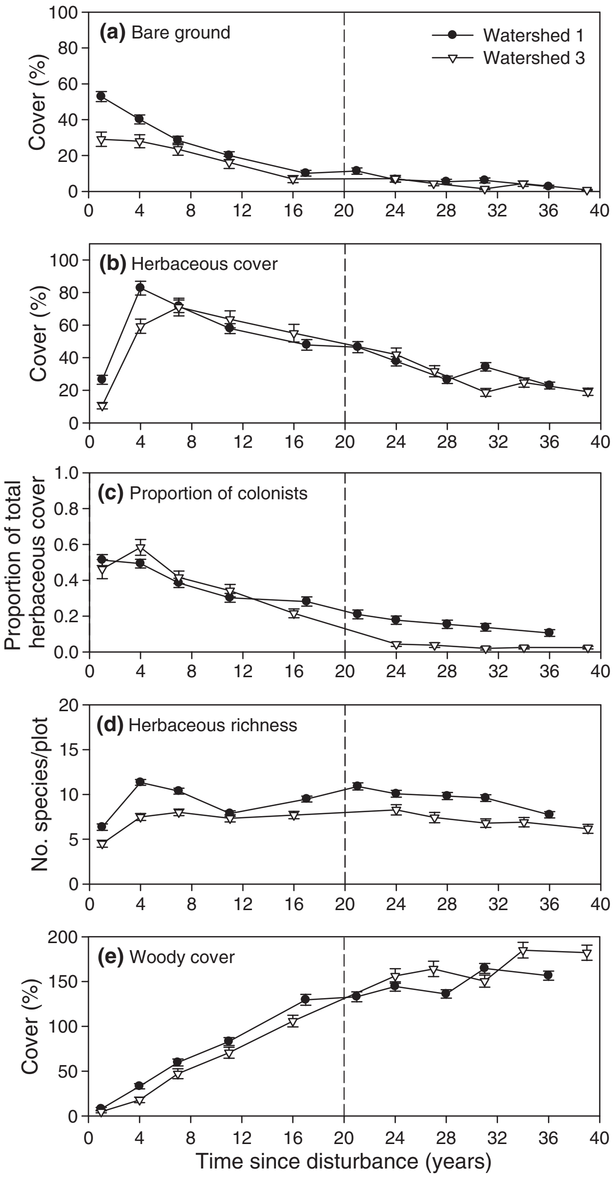

Figure 1 Trends in plant community development in 191 permanent plots during four decades of succession in two experimental watersheds at H. J. Andrews-LTER, Oregon. (a) Cover of bare ground, (b) summed cover of herbaceous species (including subshrubs), (c) relative abundance of colonists (summed cover of colonists/summed cover of herbaceous species), (d) richness of herbaceous species and (e) summed cover of woody species (trees and shrubs). Values are means ± 1 SE. The vertical dashed line divides the sampling period into two successional stages of equal length (20 years) with equal numbers of samples (five): (1) an herbaceous stage with high cover of herbaceous species (and colonists), considerable bare ground, and relatively low cover of woody species; and (2) a woody stage with high cover of woody species and low cover of herbaceous species, colonists, and bare ground. Not all temporal samples are shown; only those selected for the 'standardized' temporal sample used in the analyses (see Disturbance history and study design).

life-history strategies (*H3*) or (3) between successional stages (*H4*). These latter tests were carried out by fitting an appropriate full (distinct) model for each hypothesis that related population stability to richness with separate slopes and intercepts for each community type (*H2*), life-history strategy (*H3*) or successional stage (*H4*). We tested whether the full model for each hypothesis could be simplified, yielding either hypothesized parallel models, or alternative divergent or coincident (identical) regression models. Each simpler model was then tested against the appropriate full model using an *F*-statistic (Weisberg 2005). Simpler models that differed significantly from the full model ($P < 0.05$) were rejected and those indistinguishable from the full model ($P > 0.05$) were accepted (only acceptable models are reported for brevity). The full model was retained if all simpler models were rejected. For each hypothesis (model), we also tested the relationship between cover and richness because a positive correlation between the two can lead to the appearance of a positive relationship between population stability and diversity (due to variance-mean scaling of abundance; Valone & Hoffman 2003).

Finally, we used a more complex model to test whether population stability varied with diversity when all available additional factors were considered. Specifically, this model related population stability to a full set of predictors that included mean richness, proportion of colonists (ratio of colonist to total herbaceous cover), absolute cover of colonists, cover of bare ground (area available for colonization), cover and richness of woody species (measures of resource preemption by woody plants), successional stage, and all two-way interactions. The final model was selected using stepwise regression (mixed direction, *P* to enter/leave ≤ 0.05) (Weisberg 2005). Statistical analyses were performed with JMP for Windows version 5.0 (SAS Institute Inc. 2002).

RESULTS

Our results do not support the hypothesis that population stability is negatively related to diversity (*H1*). Mean stability of all species pooled was positively correlated to diversity over the four decades of study ($R = 0.33$, $P < 0.0001$; Fig. 2a). Moreover, this positive diversity–stability relationship and the overall stability of populations did not vary among communities regardless of composition or position along the soil moisture/productivity gradient (coincident model, $F_{10,170} = 1.2$, $P > 0.1$; Fig. 2b). Consequently, our results do not support the hypothesis that stability decreases with diversity across all community types, nor that overall population stability varies along community gradients (*H2*).

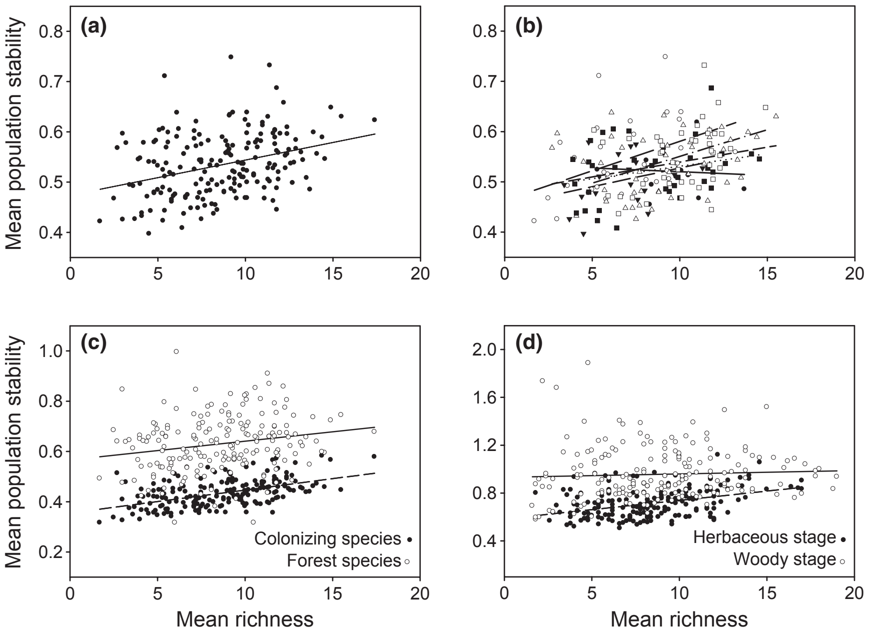

Figure 2 Diversity–stability relationships of forest herb populations in 191 permanent plots during four decades of succession in two experimental watersheds at H. J. Andrews-LTER, Oregon. (a) Overall relationship (*H1. Diversity hypothesis*; all years and species), (b) relationships by community type (*H2. Community-type hypothesis*), (c) relationship by life-history strategy (*H3. Life-history hypothesis*) and (d) relationships by successional stage (*H4. Successional-stage hypothesis*). Mean population stability was calculated for each plot from the stability of individual species, $S = \mu/\sigma$ (Tilman *et al.* 2006), where μ and σ are the mean and standard deviation of species cover on a plot. Community types in (b) in order of increasing soil moisture availability/productivity are: *Corylus–Gaultheria* (●), *Rhododendron–Gaultheria* (○), *Acer–Gaultheria* (▼), *Acer–Berberis* (△), *Coptis* (■) and *Polystichum* (□). Nine plots could not be assigned to communities and were excluded from community analyses (see Study sites). Note that the weak negative relationship in the dry, ridge-top community (*Corylus-Gaultheria*; $n = 12$) is not significant and does not differ statistically from the overall positive relationship. Life-history strategies in (c) were assigned to species based on their absence (colonizing species) or presence (forest species) in the pre-disturbance forest (from Halpern 1989). Successional stages in (d) were defined by dividing the sampling period in half with equal numbers ($n = 5$) of uniformly spaced samples (mean interval of 3.9 years) (see Disturbance history and study design).

Stability increased with diversity for both life-history strategies (colonizing and forest species), counter to expectation (*H3*). However, colonists were less stable at all levels of diversity consistent with our hypothesis (parallel model, $F_{1,378} = 0.3$, $P > 0.1$; Fig. 2c). Diversity was correlated better with the stability of colonists ($R = 0.51$, $P < 0.0001$) than of forest species ($R = 0.21$, $P < 0.005$; Fig. 2c).

Population stability did not decline with diversity in either successional stage (herbaceous vs. woody stages), counter to expectation (*H4*). Stability was higher in the woody stage (as predicted) and unrelated to diversity, and lower in the herbaceous stage but positively related to diversity ($R = 0.39$, $P < 0.0001$) (full distinct model retained, Fig. 2d). Thus, population stability increased over time (between herbaceous and woody stages) but more in low diversity than in high diversity plots (Fig. 2d).

Because positive relationships between diversity and population stability could be an artefact of a positive relationship between species abundance (cover) and diversity, we tested the nature of abundance–diversity relationships (for all species pooled, both life histories, both successional stages and all community types; see Data analysis). Although total (community) cover was positively related to richness ($R = 0.41–0.61$; all $P < 0.001$), cover of individual species was not (regardless of life history, successional stage or community type; all $P > 0.4$). Consequently, positive relationships between diversity and stability in the current study cannot be attributed to a positive relationship between cover and diversity.

Our final, more complex model considered how population stability may be affected by diversity together with concurrent changes in abundance of life-history strategies (proportion and absolute cover of colonists), surrogate measures of resource availability (cover of bare ground, cover and richness of woody species), and effects of successional stage. The model with the best fit corroborated previously described relationships of population stability with diversity (positive), life history (negative effect of colonists), and successional time (higher stability in the woody stage), but did not include either measure of resource availability or any interaction terms (Table 1).

Because diversity and proportion of colonists have opposite effects on population stability (Table 1), the relationship between diversity and proportion of colonists can determine if population stability will increase or decrease with diversity in these naturally assembling communities. In the herbaceous stage, proportion of colonists did not vary with diversity ($R = 0.12$, $P > 0.05$; Fig. 3a); consequently, colonists reduced population stability evenly across diversity levels. In the woody stage, however, proportion of colonists was positively correlated with diversity ($R = 0.34$, $P < 0.0001$; Fig. 3b); consequently, the positive effect of diversity was offset by the negative effect of colonists in higher diversity plots. Thus, diversity and population stability appeared unrelated in the woody stage when proportion of colonists was not considered (Fig. 2d).

DISCUSSION

Counter to our hypotheses and to the results of experimental studies in grasslands (Tilman *et al.* 2006), population stability in forest herbaceous communities was positively correlated to richness. This positive relationship held for individual plant communities distributed over a broad resource gradient; for species with contrasting life-history strategies (colonists vs. forest species); and, after adjusting for proportion of colonists, for different successional stages (herbaceous vs. woody). We tested a number of factors ('third factors' or 'hidden treatments') that could potentially mask the theoretical expectation of a negative relationship between diversity and population stability, but found that population stability remained positively related to diversity – a pattern consistent with other observational studies of naturally assembling communities (e.g., De Grandpré & Bergeron 1997; Kolasa & Li 2003; Valone & Hoffman 2003).

A positive relationship between population stability and diversity can arise, if positive interactions such as facilitation (Callaway & Walker 1997; Cardinale *et al.* 2002) become more important than negative interactions (competitive or destabilizing interactions; Tilman 1999) at higher levels of diversity. However, an alternative to the competition-facilitation argument exists. Diversity may play a very different role from that which is assumed in much of the current diversity–stability literature where diversity tends to be viewed *a priori* as a predictor of stability (Ives & Carpenter 2007). The positive relationships between diversity and population stability in this and other studies of naturally assembling communities (Kolasa & Li 2003; Valone & Hoffman 2003) may imply that stability is a precursor of, rather than a response to, diversity (Carnaval *et al.* 2009). This relationship seems intuitive when considering the assembly of natural plant communities: how could a more diverse community arise locally, unless its component species were more stable than those of surrounding, less diverse communities? This alternative view has major implications for both diversity–stability theory and experimental design: if stability begets diversity (rather than the reverse), current experiments designed to explicitly manipulate diversity (but not stability) cannot fully resolve the mechanisms that control natural community assembly.

Community variation along resource gradients

Broad-scale variation in community composition across topographic and resource gradients could mask local effects of diversity on ecosystem processes such as productivity or invasibility (Loreau 2000; Shea & Chesson 2002), and by extension, effects on population stability. In our study, however, communities spanning a broad resource gradient (warm, dry ridge tops to cool, mesic lower slopes) conformed to the same positive relationship between diversity and population stability; moreover, population

Table 1 Significant terms in the final regression model for population stability of forest herbs during four decades of succession in two experimental watersheds at H. J. Andrews-LTER, Oregon

Predictor	Coefficient estimate	Coefficient SE	*F*-value	*P*-value
Species richness*	0.0122	0.0022	30.4	< 0.0001
Proportion of colonists†	−0.2026	0.0340	35.6	< 0.0001
Successional stage‡	0.1650	0.0181	83.3	< 0.0001

Model terms were selected using a mixed stepwise procedure ($P_{\text{enter/leave}} \leq 0.05$) (Weisberg 2005). Model $R^2_{\text{adj}} = 0.43$; $P < 0.0001$; intercept = 0.6952. An initial full model included species richness, proportion of colonists, absolute cover of colonists, cover of bare ground, cover and richness of woody species, successional stage, and all two-way interactions. *F*-values are based on type III sum of squares and provide a significance test for each variable in the model given the other variables in the model (regardless of their order).

*Mean number of herbaceous species per plot.

†Mean proportion of colonists (i.e., summed cover of colonists/summed cover of herbaceous species).

‡Categorical variable for the herbaceous (0) or woody (1) successional stage.

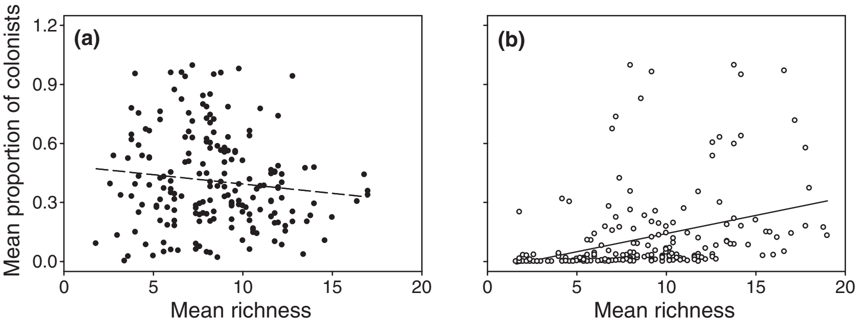

Figure 3 Relationship between mean species richness and the mean proportion of colonists in 191 permanent plots during two successional stages in two experimental watersheds at H. J. Andrews-LTER, Oregon. (a) herbaceous stage (years 1–20) and (b) woody stage (years 21–40). The proportion of colonists was calculated as the mean summed cover of colonists divided by summed cover of herbaceous species in each plot for each successional stage.

stability did not vary along this gradient (in variance with our *H2*). Valone & Hoffman (2003) observed a positive relationship between diversity and population stability, and between diversity and species abundance, for both summer and winter assemblages of desert annuals, and thus concluded that the relationship was driven by microtopography and associated fine-scale variation in moisture and productivity (abundance). Because species abundance (cover) in our study was not positively correlated to diversity, fine-scale variation in resources or productivity appears to be an unlikely explanation for the positive relationship between diversity and population stability. Furthermore, for this relationship to be driven by spatial variation in resources, local variation in soil moisture or productivity would have to be greater than that associated with the broader topographic gradient that structures forest understory communities (Rothacher *et al.* 1967; Zobel *et al.* 1976; Grier & Logan 1977). Soil resources in general, and moisture in particular, are unlikely to vary more at smaller than at larger spatial scales in this steep, mountainous terrain.

Life history

Studies of diversity effects on population stability have included species with life histories that are typical in grasslands (e.g., perennial grasses and forbs; Tilman *et al.* 2006; van Ruijven & Berendse 2007) or in communities of desert annuals (Valone & Hoffman 2003). We have evaluated diversity–stability relationships in populations of herbaceous species (mostly forbs) belonging to two contrasting life histories – those typical of closed-canopy forests and those that colonize after disturbance. As predicted, forest species were more stable than colonists, but population stability increased rather than declined with diversity and equally so for both life-history strategies (c.f. *H3*). The consistency of these positive relationships implies that plant species are more stable in diverse than in species-poor communities regardless of life history. Many observational studies of natural communities have documented positive relationships between diversity of native and invading non-native species (reviewed in Fridley *et al.* 2007). Thus, locally diverse communities appear to arise because they are more likely to be colonized by additional species and because species within them are more stable than in surrounding relatively species-poor communities ('rich get richer'; Stohlgren *et al.* 2003).

The positive relationships between diversity and population stability or invasibility in natural communities contrast sharply with relationships in experimental communities in which both mean population stability and invasibility are negatively related to diversity (Kennedy *et al.* 2002; Tilman *et al.* 2006). These differences may be explained, in part, by differences in community assembly and species life history. While the stability and diversity–stability relationships of individual species may vary (van Ruijven & Berendse 2007), experimental communities are typically constrained to predetermined combinations of species and are maintained by removing colonists that tend to invade lower diversity treatments where resources are not fully utilized (Kennedy *et al.* 2002). As a consequence, target species in experimental communities are likely to exhibit higher population stability on average – especially at lower levels of diversity – whereas there is greater potential to detect competition at higher diversity. In contrast, in naturally assembling communities, temporary increases in resources can lead to the establishment of colonists (Davis *et al.* 2000; Meiners *et al.* 2004) rather than to the partitioning of these resources among resident species. As a consequence, natural communities are likely to exhibit lower mean population stability and higher turnover, especially at lower levels of diversity where resource availability should be greater. Thus, diversity and population stability are more likely to be positively correlated in natural communities and negatively correlated in artificial ones – akin to the dichotomy of diversity–invasibility relationships in natural and experimental communities (Fridley *et al.* 2007).

Successional stage

Although population stability was higher later in succession (woody vs. herbaceous stage), as expected, stability increased with diversity in both stages, even after accounting for the decline in colonists (Table 1), counter to expectation (*H4*). Thus, the positive relationship between population stability and diversity in this system seems robust despite significant changes in structure and composition over the four decades of observation. In contrast, previous studies of much shorter duration (< 10 years) lack the ability to detect long-term trends or temporal invariance in diversity–stability relationships (e.g., Cottingham *et al.* 2001; Valone & Hoffman 2003; Tilman *et al.* 2006; Bezemer & van der Putten 2007). Long-term persistence of a positive relationship between diversity and population stability in our system is especially interesting given that herbaceous and woody stages differ in their overall stability.

Greater stability in the woody stage in our system is consistent with the general observation that stability tends to increase over successional time (Anderson 2007). In our system, this increase is likely to reflect subtle changes within our broadly defined life-history groups (particularly among forest species; Halpern 1989) – towards species with traits that promote stability (c.f. Lepš *et al.* 1982). Increases in stability may also reflect the facilitative effects of taller woody species. Shrubs and trees can increase moisture availability on the forest floor by reducing solar radiation and enhance nutrient availability by increasing leaf-litter inputs (Finegan 1984). Our final model did not indicate a direct positive effect of woody plant cover on mean population stability. However, increased stability in the woody stage could reflect an overall improvement of environmental conditions at a larger spatial scale than could be detected in our plot-level measurements. Regardless of the mechanism for increased population stability over successional time, our data from these forest ecosystems suggest that positive diversity–stability relationships in naturally self-assembling communities may be insensitive to major successional shifts in vegetation structure (i.e., from herb- to woody-dominated).

CONCLUSIONS

Plant communities are rarely stable over time. Instead, they experience complex dynamics or directional changes as they respond to natural or anthropogenic disturbances such as drought (Frank & McNaughton 1991), fire (Schoennagel *et al.* 2005), wind (Canham *et al.* 2001) or logging (Halpern 1989). Previous studies have explored relationships between diversity and population stability over relatively short time frames and thus, cannot fully address effects of longer-term successional changes. Our analysis of four decades of community reassembly suggests that successional stage coupled with inherent differences in the stability of species with different life histories can explain some of the variation in diversity–stability relationships previously observed in natural plant communities (e.g., Tilman *et al.* 2006 vs. Bezemer & van der Putten 2007). However, our results run counter to the negative relationship suggested by theory and demonstrated in experimental communities (Tilman 1999; Tilman *et al.* 2006). We conclude that a positive relationship between diversity and population stability is to be expected in naturally assembling communities. Diverse communities can arise because they maintain more species than surrounding, species-poor communities – either through the facilitative effects of diversity (Cardinale *et al.* 2002) or because population stability is a precursor to diversity (Carnaval *et al.* 2009).

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