

Does productivity drive diversity or vice versa? A test of the multivariate productivity–diversity hypothesis in streams

BRADLEY J. CARDINALE,^{1,3} DANUTA M. BENNETT,¹ CRAIG E. NELSON,¹ AND KEVIN GROSS²

¹*Department of Ecology, Evolution, and Marine Biology, University of California–Santa Barbara, Santa Barbara, California 93106 USA*

²*Biomathematics Graduate Program, North Carolina State University, Raleigh, North Carolina 27695 USA*

Abstract. The idea that productivity regulates species diversity is deeply ingrained in the field of ecology. Yet, over the past few decades, an increasing number of experiments have shown that species diversity controls, rather than simply responds to, biomass production. These contrasting perspectives have led to a seeming paradox: Is diversity the cause or the consequence of biological production? Here we present empirical evidence for the multivariate productivity–diversity (MPD) hypothesis, which argues that differing perspectives on productivity–diversity relationships can be resolved by recognizing that historical research has focused on how resource supply regulates both the productivity and richness of local competitors, whereas more recent studies have focused on how the richness of a colonist pool regulates the efficiency by which resources are captured and converted into new tissue. The MPD hypothesis predicts that three pathways operate concurrently to generate productivity–diversity relationships in nature: (1) resource supply directly limits the standing biomass and/or rate of new production by primary producers, (2) producer biomass is directly influenced by the richness of species that locally compete for resources, and (3) resource supply rate indirectly affects producer biomass by influencing the fraction of species from a colonist pool that locally coexist. To examine whether this set of pathways explains covariation between productivity and diversity in natural streams, we used nutrient-diffusing agar “patches” to manipulate resource supply rates in 20 streams throughout the Sierra Nevada mountain range, California, USA. We then measured the fraction of periphyton species from the stream colonist pool co-occurring on each nutrient patch, as well as the standing biomass and rates of primary production. Natural patterns of covariation agreed with predictions of the MPD hypothesis. Algal biomass was an increasing function of nutrient supply, and an increasing function of local richness. The fraction of species from the colonist pool found co-occurring on a patch was a concave-down function of nutrient supply, causing nutrients to indirectly affect biomass via control over local richness. These results suggest that the MPD hypothesis is a viable explanation of patterns of diversity and productivity in natural stream ecosystems, and that it has potential to merge the historical view that productivity drives diversity with a parallel view that diversity drives productivity.

Key words: biodiversity; ecosystem production and function; freshwater algae; species richness.

INTRODUCTION

One of the oldest and richest questions in biology is that of how species diversity relates to the productivity of ecosystems. Historically, species diversity has been viewed as the dependent variable in this relationship. From this perspective, variation in the number of species among communities or ecoregions is presumed to be limited by the productivity of ecosystems (Currie 1991, Rosenzweig and Abramsky 1993, Abrams 1995, Waide et al. 1999, Mittelbach et al. 2001). Researchers who have taken this perspective have documented a variety of relationships, with two of the more common being a

monotonically increasing relationship where diversity increases across all levels of productivity, and a “hump-shaped” (i.e., unimodal) relationship where diversity is highest at intermediate levels of productivity (Currie 1991, Rosenzweig and Abramsky 1993, Tilman and Pacala 1993, Huston 1994, Rosenzweig 1995, Roy et al. 1998, Grace 1999, Leibold 1999, Dodson et al. 2000, Hawkins et al. 2003). The prevalence of these relationships has tended to differ among taxonomic groups, between local vs. regional scales of observation, and between experimental vs. observational studies (Waide et al. 1999, Gough et al. 2000, Gross et al. 2000, Grime 2001, Mittelbach et al. 2001, Chase and Leibold 2002, Chase and Ryberg 2004, Steiner and Leibold 2004). Numerous hypotheses have been proposed to explain why these variable relationships occur (see Rosenzweig and Abramsky 1993, Tilman and Pacala 1993, Abrams 1995 for reviews).

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³ E-mail: cardinale@lifesci.ucsb.edu

Over the past several decades, ecologists have increasingly viewed the relationship between diversity and productivity from a different angle, asking how diversity controls, rather than responds to, the production of biomass (Chapin et al. 2000, Naeem 2002, Hooper et al. 2005). The idea that species diversity directly influences biological productivity has roots that date back to Darwin (1859), and it has a long history in the agricultural literature on intercropping (Vandermeer 1989). However, it wasn't until the 1980s and 1990s that a large body of theoretical and empirical literature began to formalize the hypothesis that the variety of species that comprise natural communities can control the "functioning" of ecosystems, including fundamental ecological processes like primary production (Ehrlich and Ehrlich 1981, Ehrlich and Mooney 1983, Schulze and Mooney 1993). By the mid-1990s, a number of seminal experiments had begun to test this hypothesis, primarily in grasslands, with most showing that reductions in the number of herbaceous plant species leads to less efficient use of soil nutrients and reduced plant biomass compared to more diverse communities (Naeem et al. 1994, Tilman et al. 1996, Hector et al. 1999). Since those seminal studies, 150+ experiments have manipulated the richness of bacteria, fungi, plants, and animals in a wide variety of ecosystems and shown that communities that are severely depleted in species can be up to 50% less efficient at capturing resources and converting those into new biomass (see meta-analyses by Balvanera et al. 2006, Cardinale et al. 2006a, and Stachowicz et al. 2007).

The contrast between the historical view that productivity drives diversity and the more recent view that diversity drives production has led to debate about whether diversity is the cause or the consequence of biological productivity (Huston 1997, Grime 1998, Loreau et al. 2001, Fridley 2002, Schmid 2002, Worm and Duffy 2003). One idea to emerge from this debate is that the historical perspective that productivity drives diversity might be integrated with the more recent perspective that diversity drives productivity by carefully distinguishing between the proximate causal and response variables that have been the focus of past research. Many researchers have pointed to the confusion that has resulted from the multitude of surrogate variables that have been used to represent "diversity" and "productivity" in past studies. For example, those who have focused on the productivity drives diversity perspective have analyzed species diversity as a function of (1) the standing stocks of a wide variety of resources (e.g., water, light, or nutrients per area or volume), (2) the rates of supply of those resources (amounts per area or volume per time), (3) the standing biomass of the focal group of organisms, (4) the rates of new biomass production, and (5) environmental correlates of productivity such as latitude or altitude (see Waide et al. 1999 or Mittelbach et al. 2001 for summaries). Mathematical models have frequently shown that these variables are

not mechanistically interchangeable, and theory has emphasized that species diversity should be driven by the supply rate of one or more resources that constrain the number of competing species that can locally coexist (Tilman 1982, Abrams 1995, Chesson 2000, Gross and Cardinale 2007).

In contrast, researchers who have focused on the alternative perspective that diversity drives productivity have focused on a very different set of causal and response variables. Experiments that have manipulated species richness directly have seldom been run for more than one generation of the focal organisms (Cardinale et al. 2007). As such, it would be hard to argue that they have manipulated or even measured the richness of locally coexisting species. Instead, these studies tend to manipulate the initial number of species added to some experimental unit (e.g., a field plot or greenhouse pot), which is akin to manipulating the richness of an initial colonist pool (Loreau et al. 2001, Cardinale et al. 2004, 2006b). Researchers then ask how the number of initial colonist species impacts the standing biomass (mass per area or volume) of a community after some period of growth. Only rarely have researchers measured the impacts of initial richness on the rate at which new biomass is produced (mass per area or volume per time), and several papers have discussed why standing stocks and rates of production might not respond to diversity in a similar manner (Stocker et al. 1999, Petchey 2003, Balvanera et al. 2006). Thus, confusion about productivity-diversity relationships has been caused, at least in part, by failure to distinguish between (1) the number of species in a colonist pool vs. the richness of a local community, (2) the supply rate of resources that limit production vs. the actual amounts of resources that are captured and converted into new production, and (3) the standing stock biomass vs. the rate at which new biomass is produced by a local community.

Recently, there have been a number of attempts to fuse the perspective that productivity drives diversity with the perspective that diversity drives production. For example, both Loreau et al. (2001) and Schmid (2002) used graphical arguments to emphasize that past research on productivity-diversity relationships has revolved around at least two mechanistically distinct relationships: (1) the impact of inorganic resource supply on the richness of species competing for resources within an ecosystem and (2) the effect of species richness on the amount of biomass produced by species utilizing the same set of resources. Both authors argued that spatial variation in the supply of limiting resources should constrain the diversity of species that can coexist in an ecosystem, but the number of species should influence how efficiently resources are captured and converted into new biomass. Gross and Cardinale (2007) formalized these ideas mathematically by taking one of the most widely used models of competition that describes how resource supply can limit the number of locally coexisting species (resource-ratio theory; Tilman

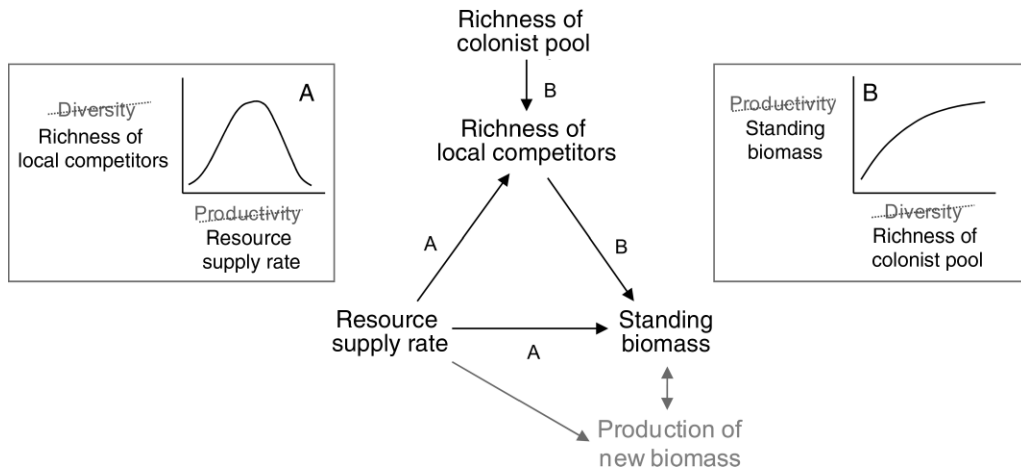


FIG. 1. The multivariate productivity-diversity (MPD) hypothesis merges the historical perspective that productivity drives diversity (panel A) with the more recent perspective that diversity drives productivity (panel B). We argue that the historical perspective has focused not on productivity per se, but rather on how the supply rate of resources that limit biomass also constrain the local richness of competing species. In contrast, the more recent perspective has focused on how the number of species seeded as initial colonists in some experimental unit impacts the standing biomass of a community after a period of growth and interaction. Thus, panels A and B show the incorrect or vague causal/response variables crossed out (gray dashed lines) and replaced with the more accurate variables. Gross and Cardinale (2007) showed mathematically that these perspectives can be unified (middle panel) when we consider how three pathways operate concurrently to influence community biomass: (1) a direct effect of resource supply on standing biomass, (2) a direct effect of local species richness on biomass, and (3) an indirect effect of resource supply on biomass that occurs as it mediates the fraction of species from the colonist pool that locally co-occur. We argue that this conceptual framework can be extended to consider the effects of resource supply and standing biomass on the rate at which new tissue is produced.

1982) and embedding it within a meta-community model (Holyoak et al. 2005) that distinguishes between the richness of species in a “regional” colonist pool and the richness of species that compete for resources within local communities. The predictions of the resulting model, which are summarized conceptually in Fig. 1, argue that three causal pathways operate concurrently to influence community biomass: (1) resource supply rates directly limit the standing stock biomass of producers, (2) local species richness also directly affects producer biomass, and (3) resource supply indirectly affects producer biomass by influencing the fraction of species from a colonist pool that can locally coexist. When resource supply rates are so low as to be stressful or so high that they encourage competitive exclusion, local communities become dominated by superior competitors. In this case, having high diversity of species in a colonist pool simply increases the chance that a highly productive species will colonize and dominate the biomass of species in a local patch. This has been referred to as the “selection effect,” “sampling effect,” or “selection-probability effect” of diversity (Huston 1997, Loreau and Hector 2001). In contrast, when supply rates are sufficient to allow coexistence, a high diversity of species in the colonist pool ensures that local communities are colonized by taxa that are most able to use resources in complementary ways (Tilman et al. 1997). Thus, Gross and Cardinale’s (2007) model argues that resource supply rates place an upper bound on the fraction of species from a colonist pool that can coexist

in a local community, but the richness of the local community ultimately determines how efficiently limiting resources are utilized and converted into new tissue.

Throughout this paper we refer to the model of Gross and Cardinale (2007) as the “multivariate productivity-diversity hypothesis” (hereafter, MPD) because it emphasizes how several distinct variables that have been the focus of past productivity-diversity research might be linked to one another. We argue that the MPD hypothesis can be extended to include not just standing biomass, but the rates at which new biomass is produced. When resources are limiting, increasing the supply rate can either stimulate per capita or mass-specific rates of production, and/or increase standing stock biomass (which may, in turn, feedback to influence rates of production). In “closed” systems where decomposition and remineralization are substantial, one might expect biomass and production to also feedback and influence the rate at which limiting resources are supplied. However, throughout this paper we assume a simpler case where resources are supplied at a constant rate, and recycling within a local community of interacting species is minimal. This simplification might be reasonable for systems like tide-pools, estuaries, rivers/streams (the focus of our work), or other “donor-controlled” habitats where a large fraction of the inorganic resources are subsidized from upstream or external inputs to the system (Polis et al. 1997). In such systems, the MPD posits a hypothetical set of relationships among five mechanistically distinct variables:

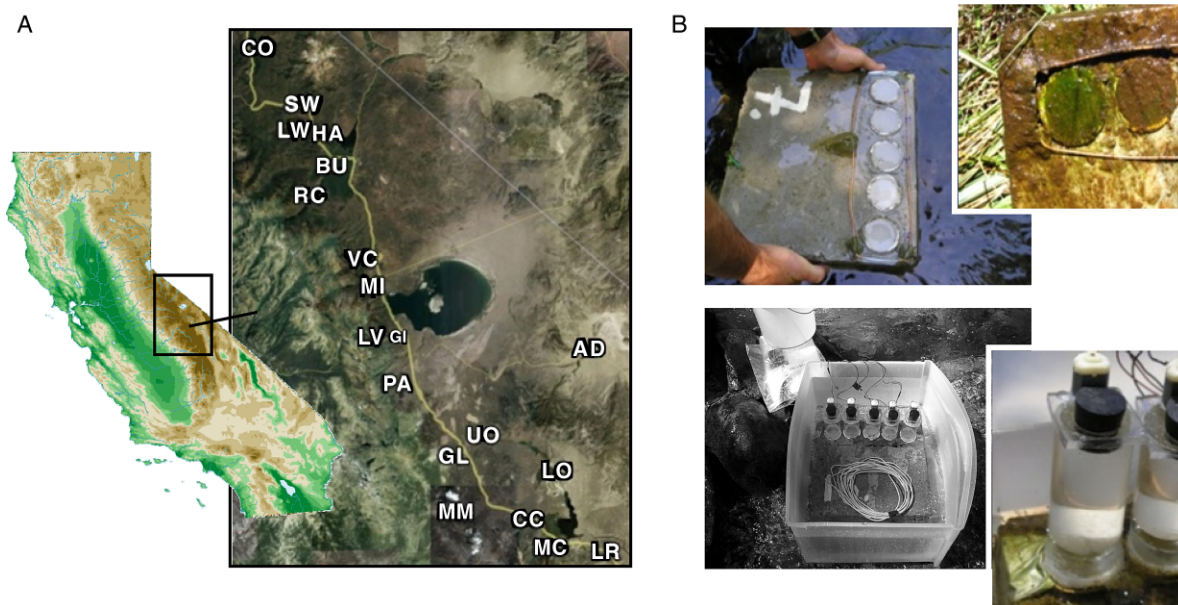


FIG. 2. (A) Location of the stream study sites in the Owens River and Mono Lake basin of the eastern Sierra Nevada mountain range of California, USA. Abbreviations correspond to the complete data set provided in the Supplement. (B) The nutrient-diffusing substrates used to manipulate the supply of nitrate and phosphate in each stream. The top photo shows a concrete block with five agar substrates (the inset shows dense algal biomass at the end of the experiment). The bottom photo shows substrates after being placed in a streamside water bath with each agar well sealed in an air-tight metabolism chamber. (C) Rates of nutrient release from the agar substrates were measured at the end of the 42-day experiment. Final release rates of both N and P were proportional to the initial nutrient concentrations in the agar, indicating that a gradient in nutrient supply was maintained over the duration of the study.

resource supply rate, richness of species in a colonist pool, richness of species in a local community, the standing biomass of a community, and the per capita or mass-specific rate of new biomass production (Fig. 1).

The goal of this paper is to report on the results of a set of experiments in which we asked whether the MPD hypothesis has any potential to explain relationships between the aforementioned measures of diversity and productivity in natural stream ecosystems. We placed nutrient-diffusing agar substrates in 20 streams in the eastern Sierra Nevada Mountains to vary the rates of resource supply (both N and P) in local nutrient “patches.” Streams were chosen to span a large gradient in the number of resident species of algae. Thus, all patches within a stream were exposed to an identical pool of colonists, but the colonist pools themselves differed greatly among streams. After allowing 42 days for colonization, growth, and interactions (roughly 10–15 generations of most algae), we measured the fraction of species from the stream colonist pool that co-occurred on each nutrient patch, as well as the standing biomass and rates of gross primary production of algae on those patches. Because the richness and composition of primary producers was not directly controlled in these experiments (which is not possible in situ), our goal was more modest than that of an experiment where all variables might be fully controlled. We simply asked: Is the set of hypothesized causal pathways in Fig. 1 a

feasible explanation of patterns of covariance among the relevant variables in natural stream ecosystems? If so, we expected that algal biomass and productivity would be influenced by both the direct effects of nutrient supply and local species richness, as well as an indirect effect that occurs as nutrients mediate the fraction of species from the stream colonist pools that locally co-occur on a nutrient patch.

MATERIALS AND METHODS

Study streams

Our experiments were performed concurrently in 20 streams in the Mono Lake and Owens River basins in the eastern Sierra Nevada mountain range of California, USA (Fig. 2A). We selected sites for our experiments based on two criteria. First, we attempted to maximize variation in periphyton assemblages (benthic algae) found in the streams so that there would be large differences in the composition and richness of species able to colonize the experimental units. We did this because our goal was to assess whether regional patterns of covariation were consistent with the MPD hypothesis. Second, we chose sites with secure and/or remote locations so that our experiments would run undisturbed by anglers or hikers during the two-month duration of the project. These two goals, along with land ownership and accessibility limitations, prevented any type of random selection of study sites. Instead, we

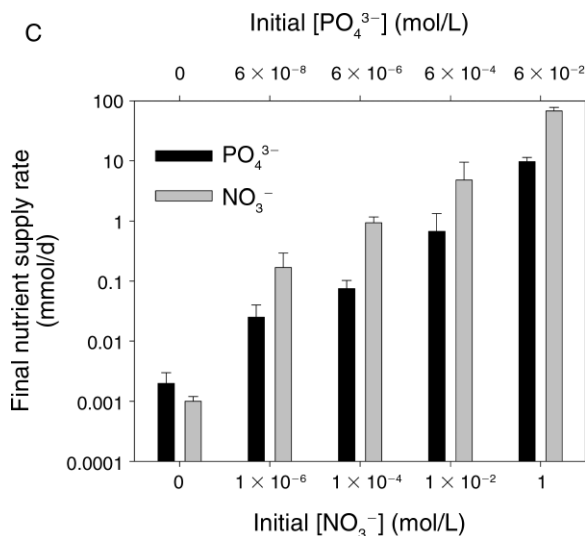


FIG. 2. Continued.

used prior surveys of algal communities in streams through the Sierra Nevada (Herbst and Blinn 2003, 2007) to identify remote or secure streams that spanned a large gradient in algal composition and richness (the number of periphyton species ranged from 37 to 139 species with a mean of 72 and SD 25). We had no a priori knowledge of why these streams varied in richness and composition. We did, however, measure a set of covariates that might influence algal diversity and productivity and statistically controlled for these in our analyses (described in *Potential covariates*).

Nutrient augmentation

Within each of the 20 streams, we placed at least one nutrient-diffusing substrate flush within the streambed sediments. In seven of the streams, we placed a second substrate in the streambed so that we could assess the degree of repeatability in periphyton response to nutrient augmentation. Each nutrient-diffusing substrate was composed of five 500-mL polyvinyl-chloride (PVC) elbows embedded in a 42 cm wide × 42 cm long × 8 cm deep concrete block that was sufficiently heavy to keep the substrate on the bottom of the stream in moderate to high flow (Fig. 2B). The PVC elbows were filled with 2% agar until the agar was flush with the surface of the concrete block to form five agar “patches” on which periphyton grew (see Fig. 2B upper inset). Though the patches were small by standards applied to many types of organisms (12.56 cm²), they were sufficiently large that algal densities on an agar patch averaged more than 14 million individuals (cells, colonies, or filaments) at the end of the experiment. One of the agar patches on each substrate was randomly assigned to serve as a “control” patch, which had no nutrient amendment. This patch allowed us to assess the fraction of species from the stream colonist pool that colonized agar alone. The other four agar patches were

randomly assigned to one of four increasing levels of nutrient amendment ($1.0 \times 10^{-6}/6.25 \times 10^{-8}$, $1.0 \times 10^{-4}/6.25 \times 10^{-6}$, $1.0 \times 10^{-2}/6.25 \times 10^{-4}$, $1.0/6.25 \times 10^{-2}$ mol/L NaNO₃/K₂HPO₄ added to the 2% agar). These levels were chosen to mimic the ambient 16:1 N:P ratio in water of Sierra Nevada streams (see Supplement), and to span the range of ambient concentrations in the control patches to one order of magnitude higher than ambient concentrations that have been observed in the water sources for these streams (Lewis et al. 1999, Sickman et al. 2002).

We chose to vary both nitrogen and phosphorous in concert in this experiment for three reasons. First, although prior studies have suggested that algae in streams in the Sierra Nevada are often nutrient limited (Roll et al. 2005, Taulbee et al. 2005, Green and Fritsen 2006), we are not aware of any studies that have manipulated nutrients in factorial combination across a large number of streams. Thus, we had no a priori information that would help us decide which nutrient was most likely to be limiting in individual streams. Second, even if we had this information, several recent summaries of nutrient addition experiments performed in aquatic ecosystems around the world suggest that algae most often exhibit joint responses to N and P (Francoeur 2001, Elser et al. 2007). This can occur either because different species in a community are limited by different nutrients, or because of synergies that stem from co-limitation. Third, and most important, our goal in this experiment was to mimic the process of cultural eutrophication, which is the primary means by which the supply rate of limited resources are being increased in aquatic ecosystems worldwide (Vitousek et al. 1997, Dodds 2006). Eutrophication does not consistently stem from changes in the availability of a single nutrient. Rather, human activities variably increase the availability of both N and P in most ecosystems (Ryther and Dunstan 1971, Howarth et al. 1996, Carpenter et al. 1998). Thus, in the absence of having detailed information on nutrient limitation across a wide range of streams, manipulating N and P in combination was a practical choice that best mimicked the process of eutrophication.

All nutrient-diffusing substrates were placed in streams during the week of 24–28 July 2006, and they remained in the streams for an average of 42 days (SD = 1 day, range = 39–43 days) during a period of relatively constant baseflow. For most of the periphyton species quantified on the substrates at the end of the experiment, the experimental period represents between 10 and 15 generations of growth.

Measured variables

At the end of the experimental period, we returned to each stream to measure (1) the composition and richness of periphyton species comprising the colonist pool, (2) the composition and richness of periphyton on each nutrient patch, (3) the standing biomass of periphyton,

and (4) the rate of net primary production and respiration on each patch. To characterize the composition and richness of the colonist pool, we selected 10 median-sized rocks (median particle size, $d_{50} \sim 50$ mm) from a minimum of two riffles upstream of our experimental location. We removed periphyton from a 12.56-cm² surface area on each rock using a knife and/or toothbrush, and then pooled samples into a composite that was preserved in 2% formalin. Algal species were later identified and enumerated at 1000 \times magnification using oil immersion on an Olympus BX50 microscope (Olympus America, Center Valley, Pennsylvania, USA) under bright field illumination. Species diversity in each sample was estimated by scanning slides systematically until no new taxon was found in 10 subsequent transects. Species abundances were calculated by enumerating all live cells from a known volume (minimum 300 cells/slide) and then back calculating to areal estimates of density.

After samples of algae were collected from the stream, the nutrient-diffusing substrates were removed from the stream so that metabolism chambers could be placed over each agar patch to measure primary production (Fig. 2B, lower pictures). Metabolism chambers were made of 4.0 cm diameter \times 12.5 cm deep acrylic tubes fitted with a DC motor and propeller that gently stirred water throughout the chamber. Each chamber was sharpened at the based so that it could be pressed 2.5 cm into the agar patch, sealed on the outside with vacuum grease to form an airtight chamber, and then filled with stream water that had been filtered through 40- μ m mesh. The entire substrate with metabolism chambers covering nutrient patches was placed in a water bath in an open canopy area on the stream bank that would experience full sunlight. Water inside the bath was constantly replaced with stream water using hand pumps so that incubations could be performed at ambient stream temperature (mean deviation from initial stream temperature averaged $0.5^\circ\text{C} \pm 1^\circ\text{C}$ [mean \pm SD]).

To measure metabolic rates of periphyton, we first covered the water baths with a black tarp to prevent exposure to light. Community respiration (autotrophs + heterotrophs) on the nutrient patch, R , was measured as the amount of O₂ consumed during a 1-h incubation (using YSI model 556 probes [Yellow Springs, Ohio, USA]). Net primary production, NPP, was then measured as the change in O₂ during a second 1-h incubation in ambient sunlight. Gross primary production was calculated as $\text{GPP} = R + \text{NPP}$. After measuring GPP and removing the metabolism chambers from each nutrient patch, the top 1-mm layer of agar was carefully cut from the nutrient patch and divided into two 6.28-cm² subsamples. The first subsample was preserved in a 10-mL Falcon tube with 90% EtOH, which was transported to the lab on ice, frozen to lyse cells, and analyzed spectrophotometrically to quantify the amount of chlorophyll *a* as a measure of standing algal biomass

(Steinman and Lamberti 1996). The second half was preserved in 2% formalin, which was used to later identify and enumerate the periphyton species in the same manner as already described above.

Potential covariates

Because we did not directly control the richness or composition of algae in the species pool of each stream, we measured and statistically controlled for several factors that might differ systematically among streams and covary with the richness and productivity of algae. A light meter was used to measure photon flux at the surface of each nutrient agar patch at the time of sampling. We also used a densimeter to measure percent canopy cover above each nutrient-diffusing substrate, which is more likely to represent long-term differences in light penetration to the stream benthos. Water samples filtered through Whatman GF-F filters were taken at the end of the experiment to measure ambient concentrations of NH₄⁺, NO₃⁻ and PO₄³⁻ on a flow-injection auto-analyzer (Quickchem 8000; Lachat Instruments, Loveland, Colorado, USA). Flow velocity was measured 5 mm above each agar patch on the final day of experiments using a Sontek Acoustic Doppler Velocimeter. Finally, the biomass of herbivores was measured by removing all invertebrates on each substrate prior to measurements of metabolism. Invertebrates were preserved in 90% EtOH and later identified, enumerated, and biomass determined from ash-free dry mass after combustion at 500°C for 24 hours.

Data analyses

We used mixed-model ANOVAs to examine the bivariate relationships between each of the proposed causal and response variables in the MDP hypothesis (Fig. 1). Each model had the general form $y_{ij} = \mu + \beta_1 x_{ij} + \beta_2 x_{ij}^2 + b_i + \varepsilon_{ij}$, where y_{ij} is the response variable for data point j from stream i , x_{ij} is the associated (centered) independent variable, β_1 and β_2 are the linear and quadratic regression coefficients associated with the independent variable, b_i is the random effect associated with different stream sites i (iid $N[0, \sigma_b^2]$), and ε_{ij} is the residual error. Nutrient supply rates and algal biomass were log₁₀-transformed to reduce heteroscedasticity. These mixed model ANOVAs treat data much like a "meta-analysis," where the goal is to summarize the general trends that occur among 20 independent experiments after accounting for the random variation among streams. To complement our interpretation of these mixed models, we also used linear and quadratic regressions to examine the relationships between nutrient supply, species richness, and biomass production within each individual stream. We did not test for significance of any individual regression since there were many. Rather, we analyzed the distribution of the coefficients from these regressions to assess how many streams exhibited positive or negative relationships, and

to examine the amount of variation explained by the regressions within the average stream.

Though useful for illustrating general relationships, the bivariate analyses described above cannot be used to test the MPD hypothesis directly, since they do not account for the covariances that are explicitly hypothesized between causal and response variables. To test the MPD as a multivariate hypothesis, one must solve all of the proposed relationships simultaneously to obtain the partial regression coefficients for each path. To accomplish this, we used structural equations modeling (SEM; Amos v. 7, SPSS, Chicago, Illinois, USA). SEM is an extension of general linear models in which a set of linear regressions is solved simultaneously to ask whether an entire covariance matrix is consistent with a hypothesized set of causal pathways (Shipley 2000, Grace 2006). Using SEM, we asked whether the covariance matrix describing relationships between all variables could, in theory, have been produced by the proposed set of paths in Fig. 1.

Last, we compared the community composition of periphyton assemblages among streams and among nutrient treatments using distance-based multivariate analyses. We calculated distance matrices from species densities on nutrient-diffusing substrata using the Sørensen dissimilarity index (also known as Bray-Curtis or percent dissimilarity, calculated as $1 - 2W/(A + B)$ where W is the sum of shared densities and A and B are the sums of densities in individual sample units [Sørensen 1948]). To test for significant differences in periphyton community structure and species densities among sample groupings, we used the multi-response permutation procedure (MRPP) and indicator species analyses using the software package PC-ORD (McCune and Mefford 2006). Separate distance-based analyses were conducted using species densities or biovolumes, or with densities/biovolumes aggregated by genera, classes, and groups defined by common morphological forms (species that grow as cells, colonies, filaments). These analyses all led to similar conclusions; therefore, here we focus on comparisons that are based on species densities since species richness is the focus of the MPD hypothesis.

RESULTS

Nutrient treatments

At the end of the experiment, and after all response variables were measured, we verified the success of the nutrient treatments by taking small cores from a subset of agar patches, placing those cores individually in distilled water for 24 hours and then measuring changes in the concentrations of NO_3^- and PO_4^{3-} . Rates of nutrient release at the end of the 42-day experimental period were directly proportional to the initial concentrations in the agar patches (Fig. 2C). Final rates of PO_4^{3-} release spanned four orders of magnitude, and rates of NO_3^- release spanned nearly five. Thus, we were able to maintain a large gradient in the supply of N and

P from the agar patches throughout the duration of the experiment.

Community responses to nutrient enrichment

A total of 294 species of periphyton were identified among the 20 streams, of which 62% were diatoms (Bacillariophyta), 17% were “green algae” (Chlorophyta and Charophyta), and 14% were Cyanobacteria (Cyanophyta). Increasing the supply rate of nutrients from an agar patch significantly altered the species composition of algal assemblages (Fig. 3A). As nutrient supply increased, algal assemblages on the patches grew increasingly dissimilar in species composition compared to those on “control” patches that had no nutrient amendment (ANOVA, $F_{3,97} = 4.16$, $P < 0.01$). Communities also exhibited increasing dissimilarity on nutrient treatments that were farther apart compared to one another (ANOVA, $F_{3,239} = 3.83$, $P = 0.01$). Parameter estimates from a mixed model ANOVA accounting for the random effect of stream and the fixed effect of nutrient supply indicated that communities declined in similarity by an average 3% with each log increase in nutrient supply ($P < 0.01$). Nutrient induced shifts in algal composition appeared to be highly repeatable as species composition on replicate substrata placed in the same stream could not be distinguished from one another for five of the six streams in which we recovered replicate nutrient-diffusing substrates (MRPP $P > 0.1$ except stream CO where $P = 0.03$, note that one of seven replicate substrates was overturned by flow).

For those species found on three or more nutrient patches in a stream, we calculated the Spearman rank correlation relating cell density to nutrient supply and found that roughly equal numbers of species displayed positive or negative density responses to nutrient enrichment (Fig. 3B, note: a detailed summary of species-specific responses to nutrients is given in the Appendix). The dominant source of community variability within the data set was among streams. Indeed, variability among nutrient enrichment treatments within a stream (mean Sørensen distance = 0.67) was much smaller than the dissimilarity of algal communities among streams (mean Sørensen distance = 0.90). Because of this, and because most species were common to only a few streams (the median taxon was found in just two streams, with 47% of all species unique to one stream), we found no taxonomic groups that were consistently associated with a particular nutrient treatment across all 20 streams. Indicator species analysis revealed that the majority of species (157 of 294) and majority of genera (55 of 99) exhibited significant fidelity to a single stream (indicator value > 40 , $P < 0.01$), but none exhibited fidelity to a specific level of nutrient enrichment. Thus, nutrient enrichment consistently altered the composition of communities within a stream in spite of the fact that each stream had a unique community of algae.

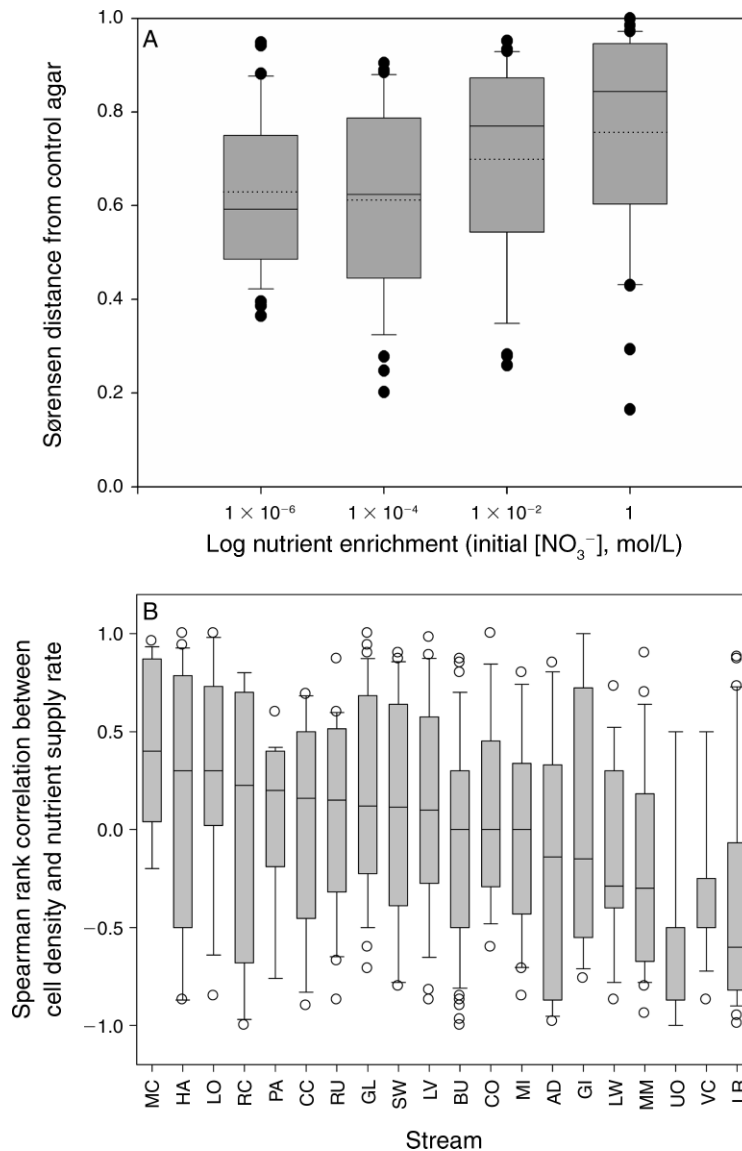


FIG. 3. (A) Community similarity of algal assemblages on nutrient-diffusing agars (y-axis) relative to control agars that had no nutrient amendment (x-axis). Note that as nutrient supply rate increased, algal community composition became increasingly dissimilar relative to control agars (ANOVA, $F_{3,97} = 4.16$, $P < 0.01$). (B) Response of individual algal taxa to nutrient amendment in each of the study streams (x-axis). The y-axis gives the distribution of Spearman rank correlations relating the cell density of each species (no./cm²) and nutrient supply on an agar, with streams ordered along the x-axis from highest to lowest mean correlation. Bar plots give the median (line), 25th and 75th percentiles (bars), 10th and 90th percentiles (whiskers), and outliers (solid circles in panel A, open circles in panel B). The response of all individual species is given in the Appendix.

Bivariate relationships

Although streams were characterized by distinctly different periphyton assemblages, community-level metrics such as algal biomass production and species richness tended to respond to nutrient supply in a consistent manner across streams. Linear regressions of log(chlorophyll *a*) vs. log(N) for individual streams produced an average slope of 0.09 (95% confidence interval = 0.05–0.13) with 14 of 20 streams having a positive regression coefficient (see individual gray lines

and inset for slope b_1 in Fig. 4A). The average R^2 value was 0.48 (95% confidence interval = 0.13 to 0.84), indicating that roughly half of the variation in algal biomass among nutrient patches within any single stream was explained by the nutrient augmentation itself. There was considerable variation in the absolute magnitude of algal biomass among streams, and in the response of algal biomass to nutrient augmentation (for example, note the small number of negative slopes in Fig. 4A). A mixed-model ANOVA fit to all data while accounting for variation among streams estimated that

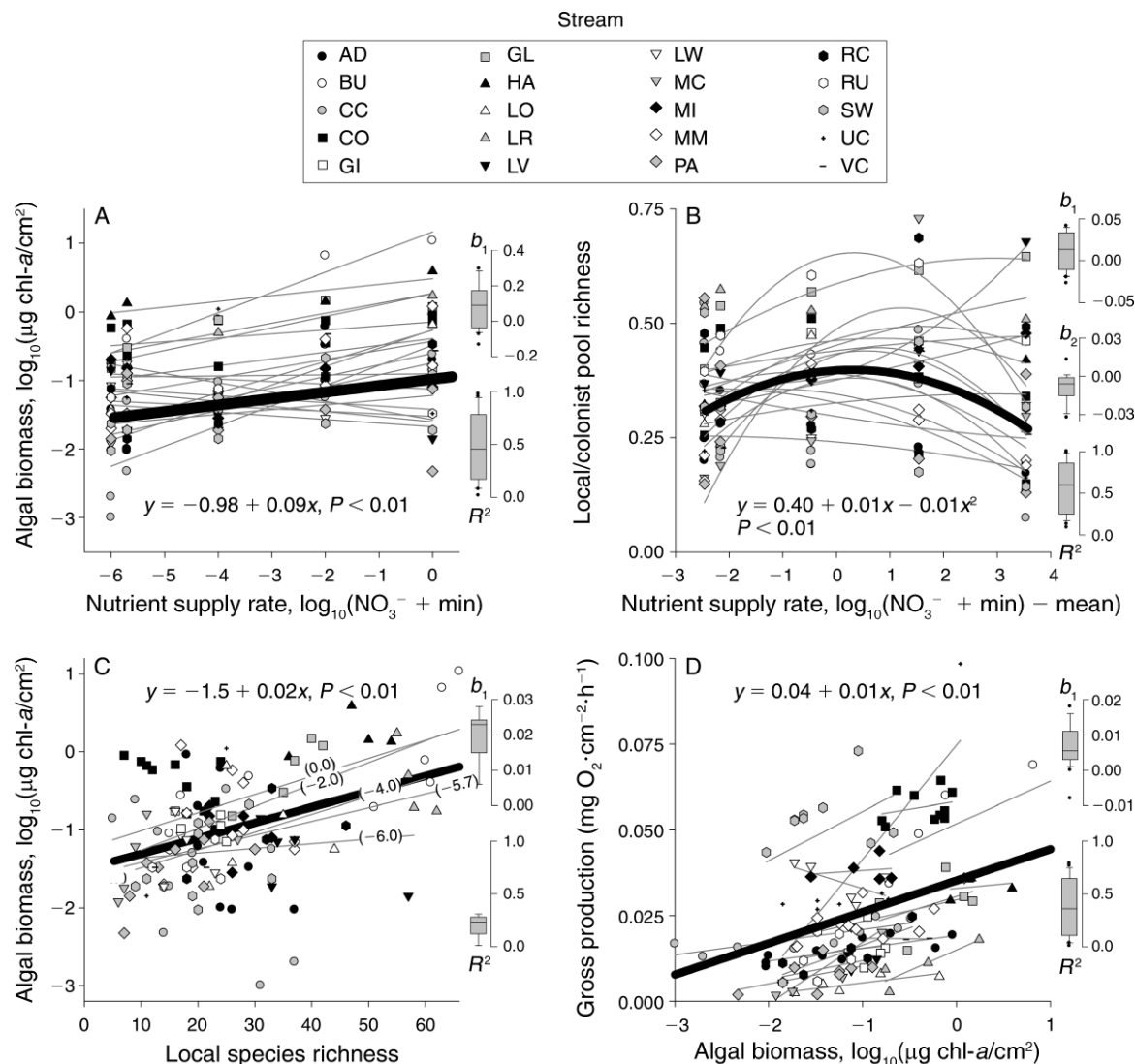


FIG. 4. Bivariate relationships between variables of the multivariate productivity-diversity hypothesis (see Fig. 1). (A) Algal biomass as a function of nutrient supply on diffusing agars. Gray lines give the regressions for each of the 20 streams (symbol key at top), with the distribution of linear slopes (b_1) and variation explained (R^2) shown in box plots inset at right (see Fig. 3 for a description of box plots). The heavy black line and equation in each plot give the best fit from a mixed-model ANOVA that uses maximum likelihood to estimate parameter values after accounting for the random variation among streams. Note that because the supply rate of PO_4^{3-} is directly proportional to that of NO_3^- in this study (see Fig. 2C), only one axis is presented here. (B) The fraction of algal species from the stream colonist pool (i.e. algae sampled and identified from natural substrates) found on an agar patch at the end of the experiment as a function of nutrient supply. The description is the same as in panel A, except that box plots now give the linear (b_1) and quadratic terms (b_2) for the regressions. Note that a constant was added to nutrient supply (the minimum value) to allow log transformation, and nutrient levels were centered to obtain the second-order polynomial, which is why the mean is subtracted. (C) Algal biomass as a function of the number of algal species on an agar patch at the end of the experiment. Data show relationships for each of the five levels of nutrient supply independently, with log-transformed values noted in parentheses. (D) Gross primary production as a function of algal biomass on a patch at the end of the experiment.

chlorophyll *a* increased by an average $10^{0.09}$ (23%) for each order of magnitude increase in nutrient supply rate. Our methods do not allow us to distinguish whether N or P were limiting (see *Materials and methods*); however, these results suggest that one or both of these nutrients stimulated algal biomass, to varying degrees, in the majority of streams that were studied.

Surveys of algae on natural substrates upstream of our nutrient-diffusing agars revealed between 37 and 139 species of periphyton in the colonist pools of the streams (mean \pm SD = 72 ± 25). The fraction of species from the colonist pool that were found locally on an agar patch was a concave down function of nutrient supply rate (Fig. 4B). The quadratic coefficients for polynomial

regressions relating the fraction of species on a nutrient patch to nutrient supply rate were negative for 16 out of 20 streams (mean = -0.009 , 95% confidence interval = -0.014 to -0.003 , see gray lines in Fig. 4B and insets), with the regressions explaining a mean 57% of the variation in local species richness among nutrient patches within a stream (95% confidence interval for $R^2 = 0.42$ – 0.72). However, once again there was a considerable amount of variation in the response of local species diversity to nutrient augmentation among the 20 streams. A mixed-model ANOVA accounting for variation among streams suggested that roughly 30% of species from the colonist pool were found co-occurring on patches with the lowest and highest rates of nutrient supply, whereas a mean 40% were observed at intermediate nutrient supply. While this represents a fairly modest increase in diversity (an additional 4–14 species depending on the stream), the concave-down relationship was a significantly improved fit to the data compared to a model without the quadratic term (AIC with quadratic term = -158 vs. without = -151).

The amount of algal biomass on a nutrient patch at the end of the experiment generally increased with the number of species found on that patch (Fig. 4C). The coefficients relating \log_{10} (chlorophyll *a*) to local species richness were positive for each of the five levels of nutrient supply, and tended to increase as nutrient supply increased (see gray lines in Fig. 4C and inset for b_1). After accounting for random variation among streams, a mixed-model ANOVA indicated that biomass increased by a mean $10^{0.02}$ (roughly 5%) per additional species found in a patch. Gross primary production was positively related to algal biomass in all but two streams (note inset for b_1 in Fig. 4D). A mixed-model ANOVA indicated that GPP increased by a mean 0.01 mg $\text{O}_2\cdot\text{cm}^{-2}\cdot\text{h}^{-1}$ for each \log_{10} increase in chlorophyll *a* (Fig. 4D). We found no evidence that nutrient supply influenced rates of gross primary production independently of its influence on algal biomass. When GPP was modeled as a function of nutrient supply and algal biomass while accounting for random variation among streams, biomass was a significant predictor ($P < 0.01$) but nutrient supply was not ($P = 0.69$) ($\text{GPP} = 0.04 - 0.00014 \times \log_{10}[\text{nutrient supply}] + 0.01 \times \log_{10}[\text{chlorophyll } a]$). In addition, the partial correlation coefficient relating nutrient supply and GPP was nonsignificant ($P = 0.62$) after accounting for the relationship between chlorophyll *a* and GPP. This suggests that nutrient supply influenced GPP, but only through covariation with total biomass of algae on a patch rather than any changes in mass-specific rates of production.

Multivariate model

To assess whether patterns of covariation among all of the relevant variables were consistent with predictions of the MPD hypothesis, we used a structural equations model to estimate all of the partial regression coefficients for the predicted pathways simultaneously (Fig. 5).

Overall, this model proved to be a highly significant fit to the covariance matrix ($\chi^2 = 5.9$, $\text{df} = 7$, $P = 0.56$, $N = 127$). Note that SEM tests the hypothesis that a proposed set of causal pathways cannot reproduce the observed covariance matrix. Thus, high P values indicate that a model cannot be rejected as an explanation of the observations. Parameter estimates for all of the individual pathways led to conclusions that were consistent with those from the bivariate relationships in Fig. 4. No linear effect of nutrient supply rate on the local richness of algae was detected. However, richness on the nutrient patches was a concave-down function of nutrient supply and increased linearly with richness in the colonist pool (Fig. 5). Together, these explained almost half of all variation in algal richness among nutrient patches in the 20 streams.

The standing biomass of algae on a nutrient patch was an increasing function of both nutrient supply rate and the number of locally co-occurring species. The model suggests that chlorophyll *a* increased by $10^{0.10} \sim 26\%$ for each \log_{10} increase in nutrient supply, and by a mean $10^{0.02} \sim 5\%$ for each additional species in a patch. Together, these explained one-fourth of all variation in algal biomass. Removing the path linking local richness to standing biomass caused AIC values to increase from 34 to 56, and χ^2 values to increase from 5.9 to 29.5, indicating that a link between richness and biomass was required for satisfactory model fit.

After accounting for all the partial correlations between nutrient supply, algal biomass, and gross primary production, the direct path linking nutrient supply to rates of GPP was non significant ($P = 0.63$). However, GPP was linearly related to the amount of chlorophyll *a*, which explained almost one-fifth of all variation in new tissue production across all nutrient patches in the 20 streams. Note that, in theory, GPP should “feedback” to increase standing biomass (see Fig. 1). However, in this study, we measured GPP in short 2-h incubations at a single point in time at the end of the experiment. As such, it is not possible to detect a feedback loop, and thus, the arrow linking GPP to algal biomass is shown in Fig. 5 as a unidirectional effect. Regardless, these results are consistent with the bivariate relationships shown in Fig. 4 where nutrients did not influence mass-specific rates of GPP, but rather, only influenced production through covariation with total biomass of algae on a patch.

Covariates and alternative models

We used several covariates measured during the study to construct alternative multivariate hypotheses and explore whether we could find better explanations of covariance in the data set. For example, light is well known to influence the biomass and productivity of algae, and the degree of shading could certainly differ among streams due to variation in channel width and/or the extent of canopy cover. To account for the potential influence of shading, we altered the structural equations

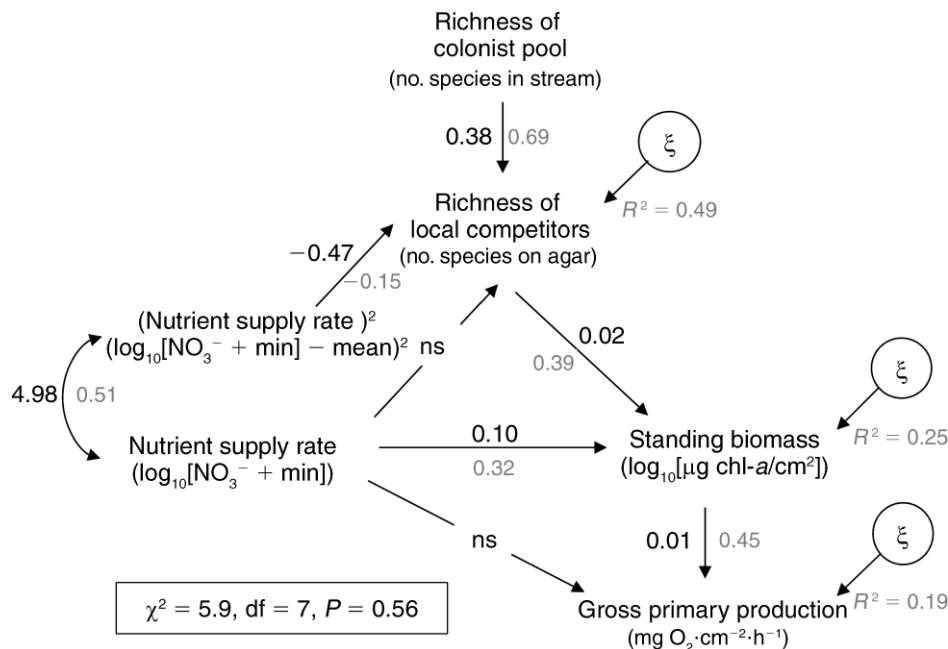


FIG. 5. Results of a structural-equations model used to test whether covariance among variables measured in the stream experiment conform to predictions of the multivariate productivity–diversity hypothesis in Fig. 1. Two values are reported for each path. Unstandardized regression coefficients are shown as the larger-font black numbers presented at the left or top of each arrow. These coefficients give the amount of change in a downstream variable Y per unit change in upstream variable X . The standardized regression coefficients are shown as the smaller-font gray numbers presented at the right or bottom of each arrow. These give the standard deviation change in Y given a standard deviation change in X . Epsilons represent the error term for each “downstream” variable, with the amount of variation explained by the model given by R^2 values at right. Metrics of overall model fit are given in the box at the lower left. These metrics indicate that the model cannot be rejected as a potential explanation of covariance in the data set.

model in Fig. 5 to include two additional paths linking standing biomass and GPP to the percent canopy cover above a stream. This model provided an inferior fit to the data (note the large increase in AIC values, and corresponding decrease in the log-likelihood and Akaike weight in Table 1). We similarly asked whether the impacts of nutrient supply on algal species richness and biomass during the experiments might be related to ambient levels of nutrients in the streams (NH_4^+ , NO_3^- , and PO_4^{3-}), flow velocity on each patch, and herbivore biomass on the nutrient-diffusing substrates. In each case, SEMs modified to account for these additional variables proved to be inferior fits to the data. Among the seven alternative structural equations models that we compared, Akaike weights suggest that the base model presented in Fig. 5 was the most likely explanation of the data set (Table 1).

DISCUSSION

The idea that productivity is a primary determinant of species diversity is deeply entrenched as an ecological paradigm (Connell and Orias 1964, Currie 1991, Rosenzweig and Abramsky 1993, Waide et al. 1999, Mittelbach et al. 2001). Yet, over the last two decades, 150+ studies have experimentally manipulated the number of species in various communities and shown that species richness can exert direct control over the production of

biomass. These contrasting perspectives have led researchers to speculate that species diversity and biological productivity must somehow feedback to influence one another (Worm and Duffy 2003). For example, Grace et al. (2007) recently performed a meta-analysis of productivity–diversity experiments run in terrestrial ecosystems and developed a statistical model that assumed species richness and biomass production exhibit temporal feedbacks, each responding to changes in the other through time.

In contrast to those who have proposed feedbacks, Loreau et al. (2001) and Schmid (2002) both noted that when researchers focus on the productivity drives diversity relationship, the key issue is how differences in resource availability or other components of the abiotic environment (“soil and climate effects” on x -axis of Fig. 4A in Loreau et al. [2001] or “site fertility” axis in Fig. 2 of Schmid [2002]) influence local species richness via competition. In contrast, the diversity drives productivity relationship instead examines how changes in the number of extant species influence the production of biomass when site conditions are held constant. Gross and Cardinale (2007) mathematically formalized some of these arguments by taking a common model of competition (Tilman’s [1982] resource ratio theory) and embedding it within a patch dynamics framework (Holoak et al. 2005). The unique features of their

TABLE 1. A comparison of different structural equations models (SEMs) used to explain patterns of covariance among variables measured in this set of stream experiments.

Model, m_i	Additional effect	Description	df	χ^2	P	AIC	Δ_i	$L(m_i y)$	w_i
1		Base model in Fig. 5	7	5.85	0.56	33.85	0.00	1.000	0.988
Base model with the following additional paths:									
2	herbivores	richness of local competitors = $f(\text{mg herbivores}/\text{cm}^2)$, standing biomass of algae = $f(\text{mg herbivores}/\text{cm}^2)$	11	9.89	0.54	43.89	10.04	0.007	0.007
3	light/shading	standing biomass of algae = $f(\% \text{ canopy cover})$, gross primary production = $f(\% \text{ canopy cover})$	11	10.47	0.49	44.47	10.62	0.005	0.005
4	stream flow	richness of local competitors = $f(\text{velocity, cm/s})$, standing biomass = $f(\text{velocity, cm/s})$	11	15.16	0.18	49.16	15.31	0.000	0.000
5	ambient PO_4^{3-}	richness of local competitors = $f(\text{mmol PO}_4^{3-})$, standing biomass of algae = $f(\text{mmol PO}_4^{3-})$	11	15.39	0.17	49.39	15.54	0.000	0.000
6	ambient NH_4^+	richness of local competitors = $f(\text{mmol NH}_4^+)$, standing biomass of algae = $f(\text{mmol NH}_4^+)$	11	22.26	0.02	56.26	22.41	0.000	0.000
7	ambient NO_3^-	richness of local competitors = $f(\text{mmol NO}_3^-)$, standing biomass of algae = $f(\text{mmol NO}_3^-)$	11	32.81	<0.01	66.81	32.96	0.000	0.000

Notes: Beginning with the “base” model presented in Fig. 5, we added paths to represent additional covariates that might influence the richness, biomass, and productivity of algae, or the response of these variables to our manipulation of nutrient supply. For each model, we report the degrees of freedom, chi-square, and P value. Using the Akaike information criterion (AIC), we calculated the likelihood that each model m_i was the best fit to the data, $L(m_i|y)$, among the candidate models. The likelihood was then expressed as an Akaike weight, w_i , which gives a relative weight of evidence for a model (higher values are more probable explanations of the data).

model were (1) it differentiated the local richness of species competing for common resources from the richness of species in a regional colonist pool, which allowed them to (2) look at how resources, local richness, and richness of a colonist pool directly and indirectly influence the production of biomass across multiple sites. That model, which we have called the multivariate productivity–diversity hypothesis (MPD), predicts that three pathways operate concurrently to control community biomass: (1) resource supply rates directly limit the standing stock biomass of producers, (2) local species richness also directly affects producer biomass, and (3) resource supply indirectly affects producer biomass by influencing the fraction of species from a colonist pool that can locally coexist. Importantly, the MPD hypothesis suggests it is not necessary to invoke feedbacks or changes in the direction of causality among variables in order to merge perspectives on productivity–diversity relationships. Rather, it argues that the historical view that productivity drives diversity has focused on a different set of causal and response variables than the contemporary view that diversity drives productivity. These two perspectives are, nevertheless, part of a broader set of causal pathways that link resource supply, biological productivity, and the richness of species at local and regional scales.

The results of the experiments reported here are consistent with predictions of the MPD hypothesis. We found that nutrient supply had a direct effect on the standing biomass of primary producers and, simultaneously, influenced the fraction of species from a colonist pool that locally co-occurred. Patches with more species tended to attain greater biomass, which translated into higher rates of gross primary production.

As a result, nutrient supply had a second, indirect effect on algal biomass and production by influencing local species richness. Our statistical model of the MPD hypothesis (Fig. 5) explained roughly half of all variation in local producer richness, one-fourth of the variation in standing biomass, and one-fifth of all variation in GPP across the nutrient patches in 20 streams. Although this explained variation is modest, much of the unexplained variation is attributable to differences among streams’ species pools (the median taxon was found in just two streams, and 47% of species were unique to a single stream), and yet, qualitative patterns held consistently across streams despite these differences. These results suggest that the MPD hypothesis may be helpful in explaining patterns of covariation between nutrient supply, species diversity at two different spatial scales, and the production of biomass, at least in communities structured by competition for abiotic resources.

Limitations

There are at least two limitations of our work that should be kept in mind. First, although the observed patterns of covariation in this set of experiments match those predicted by the MPD hypothesis, our findings are phenomenological in the sense that we cannot say whether the mechanisms operating in our experiments are the same as those presumed to operate in models of the MPD. Concave-down relationships between species richness and resource supply rates are usually explained by trade-offs in species abilities to compete for qualitatively different types of resources (Tilman 1980). For example, it is often assumed that at low rates of nutrient supply, communities will be dominated by

species that are superior competitors for nutrients. At high rates of nutrient supply, other resources (e.g., light) limit producers, and a community becomes dominated by species most able to exploit the alternative resource. Diversity is presumed to be greatest at intermediate rates of nutrient supply because trade-offs in species abilities to compete for different resources ensure that some taxa will decline with increasing nutrient supply while others increase. We did, in fact, find that roughly half of all species declined with increasing nutrient supply while the other half increased. However, we cannot say whether these differential responses stemmed from trade-offs in species abilities to compete for qualitatively different types of resources. It is difficult to imagine how these trade-offs could be characterized for periphyton under field conditions, and the obvious next step is to test the assumptions and presumed mechanisms of the MPD hypothesis under controlled laboratory conditions.

We also cannot verify the mechanism(s) by which the diversity of a colonist pool is expected to influence the production of biomass. A greater diversity of species able to colonize a local community can increase biomass via (1) selection effects, whereby diversity maximizes the chance that a highly productive species will colonize, and come to dominate the biomass of a local community, and/or (2) complementarity, whereby diversity ensures colonization by species that have niche differences and are able exploit resources in ways that are unique in space or time. In most studies that have experimentally manipulated diversity, both of these mechanisms operate in concert to increase standing biomass (Cardinale et al. 2007). Unfortunately, distinguishing the two mechanisms in natural communities requires separating the contributions of individual species when together in polyculture (Loreau and Hector 2001, Fox 2006), which is not easily done for estimates of community biomass or metabolism of periphyton.

A second limitation of our work is that many of the variables that might influence periphyton diversity and productivity in streams were not directly controlled in our experiments. We statistically accounted for several of the most likely covariates (light, ambient nutrients, and herbivores) that might have influenced the richness and biomass of algae. Our comparison of different structural equations models did not reveal any confounding variables that, once accounted for, could improve the overall fit to the data. However, we certainly did not account for all possible covariates, and some of our measures were admittedly crude. For example, herbivore biomass may or may not be a good indicator of rates of herbivory.

Given the limitations described above, the results of our experiments are perhaps best interpreted as evidence that is consistent with, but by no means verification of, the MPD hypothesis in natural stream ecosystems. Although this conservative interpretation is prudent, we are encouraged that the MPD hypothesis provides an

empirically supported explanation of relationships observed across a variety of natural stream ecosystems with distinctly different communities of primary producers. Thus, the hypothesis seems to have some promise in resolving historically divergent perspectives on productivity–diversity relationships and warrants testing and refinement under more controlled experimental conditions.

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APPENDIX

Responses of individual periphyton species to nutrient enrichment (*Ecological Archives* E090-079-A1).

SUPPLEMENT

Original data used for all analyses and figures in the main article (*Ecological Archives* E090-079-S1).