Evol Ecol (2011) 25:1107–1125
DOI 10.1007/s10682-010-9457-3

ORIGINAL PAPER

Species and genotype diversity drive community and ecosystem properties in experimental microcosms

Leigh C. Latta IV · Michelle Baker · Todd Crowl · J. Jacob Parnell · Bart Weimer · Daryll B. DeWald · Michael E. Pfrender

Received: 13 May 2010 / Accepted: 12 December 2010 / Published online: 28 December 2010
© Springer Science+Business Media B.V. 2010

Abstract Species diversity is important to ecosystems because of the increased probability of including species that are strong interactors and/or because multiple-species communities are more efficient at using resources due to synergisms and resource partitioning. Genetic diversity also contributes to ecosystem function through effects on primary productivity, community structure and resilience, and modulating energy and nutrient fluxes. Lacking are studies investigating the relationship between ecosystem function and diversity where hierarchical levels of biological diversity are systematically varied during experimentation. In this experiment, we manipulated both species and genotypic diversity of two *Daphnia* species in microcosms initially seeded with *Chlamydomonas* and measured community- and ecosystem-level properties to determine which level of diversity was most important for explaining variation in the property. Our results show that species diversity alters bacterial community composition while high genotypic diversity reduces bacterial richness and primary productivity. In addition, the highest levels of genotypic and species richness appear to increase community and ecosystem stability. These findings reveal that species and genotypic diversity are significant drivers of community and ecosystem properties and stability.

Keywords Species diversity · Genotype diversity · Microcosm · Community composition · Ecosystem productivity · *Daphnia*

Introduction

Understanding the interaction between organisms and their environment and the relationship between these interactions and ecosystem functions such as productivity and stability is the central goal of ecosystems ecology. The concept that species diversity is

L. C. Latta IV (✉) · M. Baker · T. Crowl · J. Jacob Parnell · B. Weimer ·
D. B. DeWald · M. E. Pfrender
Department of Molecular and Cellular Biology, Harvard University, 16 Divinity Ave.,
Cambridge, MA 02138, USA
e-mail: latta@fas.harvard.edu

functionally important to ecosystem performance is widely accepted. Two mechanisms have been identified; increased probability of including species that are strong interactors (Hooper and Vitousek 1997; Huston 1997; Tilman et al. 1997), and/or increased efficiency of resource use via complementary functional traits (Tilman et al. 2001) and resource partitioning (Chapin et al. 1997). Although not as well documented as the relationships between species diversity and ecosystem function, population genetic variation also affects community and ecosystem-level processes (Hughes et al. 2008) such as the biodiversity of communities (Wimp et al. 2004), nutrient flux (Schweitzer et al. 2005; Madritch et al. 2006), and ecosystem resilience (Hughes and Stachowicz 2004).

Changes in the composition or number of species alter ecosystem processes through species-specific traits that govern the rates, efficiencies and pathways that process nutrients and energy. This premise has led ecologists to identify suites of traits that are likely to be important in modulating energy and nutrient flows (Vitousek 1990; Vitousek et al. 1987). Species with traits that alter biogeochemical cycles in similar ways, or species that extract energy from the same trophic levels are often combined into functional groups to determine how alterations in this higher level of biodiversity might affect ecosystem responses (Naeem et al. 1995). Changes in genotypic diversity can also alter functional diversity through changes in genetically based phenotypic variation (Johnson et al. 2006) or changes in community susceptibility to invasion (Crutsinger et al. 2008).

Genetic diversity can further influence ecosystem-level properties via impacts on interacting species. For instance, high above-ground net primary productivity associated with genetically variable populations of *Solidago* determines arthropod abundance (Crutsinger et al. 2006) and genetic variation in leaf litter determines the decomposer community and hence the rates of decomposition and nutrient release (Schweitzer et al. 2005; Madritch et al. 2006). Genotypic diversity also enhances the ability of ecosystems to resist global disturbance (Hughes and Stachowicz 2004).

One shortcoming of the current literature on the relationship between ecosystem function and diversity is that often only one level of biological diversity, either species or genetic, is experimentally varied despite the recent call to focus on the connections between genetic and species diversity (Vellend and Geber 2005). Such designs preclude the ability to assess how different types of diversity influence ecosystem properties and the degree of correlation between types of diversity. As a first step in addressing the correlation between genetic and species diversity, our goal with this study was to determine the relative contribution of genotypic and species diversity in a novel experimental design to vary both variables and subsequently measure community and ecosystem properties in aquatic microcosms. First, we tested which level of biological diversity, genetic or species, was the best predictor of community and ecosystem properties. Second, we tested which level of diversity was important for community and ecosystem stability. We defined properties as mean trait values and stability as the coefficient of variation for those traits.

Here, we used two model systems, *Daphnia* and *Chlamydomonas*, which were previously used in microcosm experiments to assess fundamental ecological hypotheses (McCauley et al. 1999; Nelson et al. 2005). The phytoplankton *Chlamydomonas reinhardtii* was utilized as a model system for understanding the effects of genetic diversity on productivity (Bell 1991) and for studies of experimental evolution in microcosms (Collins and Bell 2004). The microcrustacean *Daphnia* has emerged as one of the most tractable and ecologically relevant of genetic model systems (e.g., Eads et al. 2007) that can act as a keystone species in freshwater aquatic assemblages (Sarnelle 2005). In our experiment, we systematically manipulated the species and genotypic diversity of *Daphnia* in microcosms while employing a single genotype of *Chlamydomonas* as a food resource. After 2 weeks

we measured the means and variances of community and ecosystem traits, and then determined which level of *Daphnia* diversity, genotypic or species, was most important for explaining the observed patterns.

Our results show that species diversity is an important predictor of bacterial community composition while genotypic diversity is an important predictor of bacterial community richness and ecosystem productivity (gross primary production and community respiration). The highest level of genotypic and species diversity increased community and ecosystem stability; however, the diversity-stability relationship is not consistent across traits. Our findings strongly suggest that variation in species and genotypic diversity result in significant alterations of community and ecosystem properties and stability.

Materials and methods

Study organisms

Phytoplankton

The alga used in the microcosms was strain CC-1928 of *C. reinhardtii*, acquired from the *Chlamydomonas* Culture Collection (www.chlamy.org). The strain was maintained axenically in semi-continuous cultures in three aerated 5 L carboys containing 4 L of modified Bold's Basal Medium (BBM; Stein 1973). Every 2–3 days 2 L of fluid were removed from the carboy and replaced with fresh BBM. Algal cultures were maintained in a 16L:8D photoperiod at 20°C in order to synchronize our cultures to liberate mitotically produced daughter cells once every 24 h. Because we clonally propagated a single strain of *C. reinhardtii* there was essentially no population genetic variation among our treatments.

Zooplankton

Two clones of *Daphnia pulex* (Px1 and Px2) and two clones of *Daphnia pulicaria* (Pu1 and Pu2) were used in this study. The clones of *D. pulex* were collected from a temporary pond in Michigan while the clones of *D. pulicaria* were collected from a permanent lake in Michigan. Stock cultures of each *Daphnia* clone were maintained by clonal reproduction in 19 L plastic buckets containing 15 L of filtered well-water under constant temperature (18°C) and light (16L:8D). Water levels were maintained by periodic addition of double-distilled water. *Daphnia* cultures were fed a pure culture of *C. reinhardtii* every 3–4 days.

To ensure that clones from each species constituted unique genotypes we used two methods. First, we used a common garden experiment (Lynch et al. 1999; Pfrender and Lynch 2000) to assay quantitative genetic variation. Briefly, five single immature females of each clone were taken from the stock isolates, each representing an experimental line. The lines were maintained as single asexually-produced progeny for two generations. In third generation individuals we measured two traits, number of eggs in the brood pouch and body size, upon reaching maturity (defined as the first instar with the deposition of eggs into the brood pouch). Each experimental line was maintained in a 250 mL beaker containing 150 mL of filtered well-water supplemented with a constant concentration (98.5% light transmittance) of *C. reinhardtii*. All beakers in the life-table assay were maintained in a controlled temperature room with a 16L:8D photoperiod at 18°C and their position in the chamber changed every 2 days to minimize micro-environmental differences. The food/water mixture in all beakers was replaced every other day.

Second, we screened each clone for neutral molecular genetic variation with 16 microsatellite markers (Colbourne et al. 2004). We extracted genomic DNA from ten individuals of each clone with a standard proteinase-K digestion followed by phenol/chloroform/isoamyl alcohol extraction (Sambrook and Russell 2002). DNA was amplified with 1 μL of a 10 μM primer stock (IDT, Coralville IA, USA) in a PCR mix containing 0.2 mM of each dNTP (Fisher Scientific, Pittsburgh PA, USA), 2.5 mM $MgCl_2$, 0.1 μg bovine serine albumin (New England Biolabs, Ipswich MA, USA), and 0.25 U Taq polymerase (Fisher Scientific, Pittsburgh PA, USA) using the following PCR conditions: 95°C for 5 min, and 30 cycles of 94, 54°C 0.5 min, 72°C 0.75 min followed by 5 min at 72°C. PCR products were diluted tenfold and sequenced using a 3730 DNA analyzer (Applied Biosystems, Foster City CA, USA). Microsatellites were typed using ABI prism software (Applied Biosystems). We found a single microsatellite locus (P7 H4) that differentiated three of the four clones using three alleles (169, 189, 194) with Px1 identified as a 189/194 heterozygote, Px2 a 189/189 homozygote, and both *D. pulicaria* clones 169/169 homozygotes. Despite screening the clones with 16 microsatellite loci we were unable to find a molecular marker that differentiated the two *D. pulicaria* clones.

Bacterial community

The bacterial community was assayed in a subset of the microcosms using tRFLP. Specifically, a 300 mL water sample was taken from each of 2–3 replicates of each treatment at the end of the experiment and filtered onto a 0.22 μm cellulose nitrate filter. Community DNA was extracted from each filter using the DNeasy® DNA extraction kit (QIAGEN, Hilden, Germany). The 16S rRNA genes were amplified using 1 μL of a 10 μmol stock of both universal bacterial primers 27f (FAM labeled) and 1392r in a PCR mix containing 0.2 mM of each dNTP (Fisher Scientific, Pittsburgh PA, USA), 2.5 mM $MgCl_2$, 0.1 μg bovine serine albumin (New England Biolabs, Ipswich MA, USA), and 0.25 U Taq polymerase (Fisher Scientific, Pittsburgh PA, USA) with the following PCR conditions, 95°C for 9 min, and 25 cycles of 95, 59°C 1 min, 72°C 1.67 min followed by 10 min at 72°C. PCR products were purified using the Qiaquick® PCR purification kit (QIAGEN). PCR-amplified sequences were digested using HhaI (New England Biolabs, Ipswich MA, USA) and visualized using a 3730 DNA analyzer (Applied Biosystems). We used *E. coli* K12 as a positive control. The restriction fragments were analyzed using FragSort software (http://www.oardc.ohio-state.edu/trflpfragsort/index.php).

Microcosm establishment and maintenance

To ensure homogeneity of the medium in each microcosm 270 L of well-water, 30 L of BBM for algal growth, and 1 L of concentrated *C. reinhardtii* were initially mixed in a clean 500 L tub. The levels of BBM and *C. reinhardtii* used here ensured that nutrients were not a limiting factor for algal growth and reproduction and that algal density was not a limiting factor as a food resource for *Daphnia*. Microcosms were then established in 3.8 L glass jars by aliquotting 3 L of the medium into each microcosm so that each microcosm contained 2.7 L of filtered well-water, 0.3 L of 100% BBM, and a uniform concentration of *C. reinhardtii* cells (98.5% light transmittance). Microcosms were maintained in a controlled temperature room with a 16L:8D photoperiod at 18°C and their position was haphazardly rotated daily to minimize micro-environmental differences. We should note that the 2°C reduction in temperature between our stock *C. reinhardtii* cultures and our experimental conditions does not alter algal performance.

Table 1 Experimental design indicating the specific clonal mixtures used in the experiment (Treatment), the species and genotypic diversity associated with each treatment (Species and Genotypes, respectively), and the initial and final relative abundances (%) of each genotype

Treatment	Species	Genotypes	Initial relative abundance	Final relative abundance
No Daphnia	0	0	0	0
Px1	1	1	1	1
Px2	1	1	1	1
Pu1	1	1	1	1
Pu2	1	1	1	1
Px1/Px2	1	2	50:50	53:47
Pu1/Pu2	1	2	50:50	U:U
Px1/Pu1	2	2	50:50	18:82
Px2/Pu2	2	2	50:50	36:64
Px1/Px2/Pu1	2	3	33:33:33	14:17:69
Px2/Pu1/Pu2	2	3	33:33:33	13:U:U
Px1/Px2/Pu1/Pu2	2	4	25:25:25:25	9:21:U:U

"U" indicates genotypes for which we were unable to determine relative abundance because we did not identify a microsatellite marker that distinguished the two *D. pulicaria* clones

Twelve experimental treatments were established (Table 1). The design was not fully factorial, with four possible treatments not included due to ecosystem property sampling limitations. One treatment contained only *C. reinhardtii* and was replicated six times to establish baseline measurements of community and ecosystem properties but was not included in any analyses conducted to assess the effects of genotype and species diversity. The remaining 11 treatments were replicated six times and each replicate contained 84 mature *Daphnia*. Treatments were established to cover a range of species (0–2) and genotypic (0–4) diversity. Each replicate contained the same initial density of *Daphnia*. Individual *Daphnia* were divided equally among genotypes and/or species to maintain this density in all treatments. Ecosystem properties were sampled over 3 days at the beginning (Days 1–3) and end (Days 14–16) of the experiment. Each 14 day interval (i.e. Days 1 and 14, Days 2 and 15, and Days 3 and 16) was treated in statistical analyses as a block and each of the three blocks contained two replicates from each experimental treatment. For each block a total of 24 microcosms were sampled that represented an even fraction of each of the 12 experimental treatments. At the end of the experiment all individuals in microcosms from one randomly chosen replicate in each block of each treatment, representing a total of three replicates, were filtered through nitex mesh, placed in 95% ethanol and subsequently counted to obtain an estimate of total *Daphnia* abundance in each microcosm. At the end of the experiment we also screened 25–50 adult *Daphnia* from multi-genotype treatments with a single microsatellite marker (P7 H4) that distinguished the clones to estimate relative abundance and ensure that competition among clones did not result in the extinction of a clonal line during the course of the experiment. The variability in the number of individuals screened with microsatellites was due to variability in adult availability in each of the microcosms. Our protocol was to screen up to 50 adult *Daphnia* from each microcosm, but in cases where there were fewer than 50 adults we screened all available adults.

Characterization of ecosystem function

Ecosystem metabolism

We measured net productivity (NEP) and community respiration (CR) in each microcosm by monitoring dissolved CO_2 concentrations during light and dark incubations, respectively. Each microcosm was sealed with a gas-tight lid that was fitted with a rubber septum to allow sampling of the 1.1 L headspace. Incubations were performed at 20°C on a shaker table at 50 RPM to allow for equilibration between the water and headspace within the microcosm (Kling et al. 1992). CO_2 samples were collected from the headspace every 30–40 min over the course of 1–2 h, and stored in evacuated glass vials (Vacutainer, Franklin Lakes NJ, USA) for later analysis by gas chromatography. CO_2 was quantified on a calibrated SRI 8610 gas chromatograph (Torrance, CA) with thermal conductivity detector. NEP was calculated as the slope of the line relating CO_2 concentration and time during light incubations, and CR was similarly calculated using samples collected during dark incubations. Gross primary productivity (GPP) was calculated from these values as NEP-CR.

Water chemistry

At the end of each set of light/dark incubations, we collected 60 mL of water from each microcosm. A known volume (30–60 mL) was filtered onto a precombusted glass fiber filter (Whatman GF/F, nominal pore size 0.7 μm). The filter was preserved by freezing for analysis of chlorophyll *a*. The remaining water was similarly filtered into acid-rinsed HDPE bottles and frozen for analysis of total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP). Total dissolved N was quantified using a potassium persulfate digestion (Nydahl 1978) followed by cadmium reduction for measurement of $NO_3 + NO_2$ (APHA 1998). Measures of TDP were made using a potassium persulfate digestion followed by an ascorbic acid molybdenum reaction for soluble reactive phosphorus (Murphy and Riley 1962). Both colorimetric analyses were done using an automated analytical system with FASPac II data acquisition software (Astoria Pacific International, Portland OR, USA). Chlorophyll *a* on filters was extracted using 90% acetone and quantified fluorometrically (AquaFluor Turner Designs, Sunnyvale CA, USA). Samples were corrected for phaeophytin using 0.1 N HCl (Steinman et al. 2006).

Statistical analyses

Clonal identity

Clone-specific estimates of body size and fecundity from the common-garden experiment were analyzed using one-way analysis of variance (ANOVA) with clone representing the single fixed main effect. We also used two-way ANOVA with clone and block as main effects on a data subset that consisted only of single-genotype microcosms to determine if the clones differed for the community and ecosystem properties.

Characterization of bacterial community

Two metrics were used to characterize the bacterial community in the subset of microcosms for which the bacterial community was sampled. First, the number of unique 16S

rRNA fragments was used as an estimate of bacterial richness. Second, we used non-metric multidimensional scaling (NMDS) as implemented by the vegan package (Oksanen et al. 2008) in Program R (www.R-project.org) to estimate bacterial community composition. Initial input was a presence/absence matrix that characterized bacterial community composition. A community dissimilarity matrix based on the presence/absence matrix was constructed using the Bray-Curtis index. The community dissimilarity matrix was then subjected to NMDS and the scores for each microcosm were used as a quantitative estimate of the bacterial community for use in subsequent analyses. Preliminary results indicated that the bacterial communities associated with the *Chlamydomonas*-only treatments were substantially different from any of the treatments that contained *Daphnia*. Therefore, we restricted our analyses of bacterial community composition to only those microcosms that included *Daphnia*.

Description of hypotheses and datasets

We tested three hypotheses regarding the effects of genotypic and species diversity on community and ecosystem properties. First, we tested the joint contributions of genotypic and species diversity on zooplankton and phytoplankton abundance, ecosystem productivity, and water chemistry using data from the microcosms that contained *Daphnia* (hereafter referred to as the full dataset). To test the joint effect of genotypic and species diversity on bacterial diversity we used the subset of the full dataset for which the bacterial community was sampled. However, one problematic statistical issue that arises with an analysis of the full dataset is that the predictor variables, species richness and genotype richness, are not orthogonal and could result in variance inflation. To overcome the lack of orthogonality among predictor variables we partitioned the full dataset so that one level of diversity was constant while the other was free to vary. We used one data partition to test the specific effects of genotypic diversity on community and ecosystem properties by using a subset of data that included only those microcosms in which the level of species diversity was constant (2 species), but levels of genotype diversity varied (2–4 genotypes; referred to as the genotype dataset). To test the effects of genotype diversity on the bacterial community we used the subset of the genotype dataset for which bacterial communities were sampled. A second data partition was used to assess the specific effects of species diversity on community and ecosystem properties. This subset of the data included only those microcosms in which the level of genotype diversity was constant (2 genotypes), but levels of species diversity varied (1–2 species; referred to as the species dataset). To test the effects of species diversity on the bacterial community we used the subset of the species dataset in which bacterial communities were sampled.

Ecosystem properties during the first sampling interval

Based on the experimental design we were certain that the mean and variance for a majority of the ecosystem properties (zooplankton abundance, chlorophyll and phaeophytin levels, dissolved nitrogen and phosphorous, and nitrogen:phosphorous ratio) were identical across treatments at the beginning of the experiment. However, we could not be certain that measures of ecosystem productivity were equal during the first sampling interval. Therefore, we used species number, genotype number, and block as fixed main effects in two-way (for the genotype and species datasets) and three-way (for the full dataset) ANOVA to test for effects of these factors on community respiration, net productivity, and gross primary productivity.

Analyses for the full dataset

To examine the relative importance of genotypic and species diversity we used stepwise regression procedures to build general linear models to explain variation in our community and ecosystem response variables. *Daphnia* species richness, *Daphnia* genotypic richness, block effects, and all possible interactions were included as candidate predictor variables. The best model for each response variable was selected based on Akaike's information criterion (AIC), where the smallest AIC indicates the best model. Our protocol for determining which variables were significant predictors of a response variable was first to take the best regression model based on AIC values and examine the *P*-value associated with the regression model. If the *P*-value of the best regression model was greater than 0.05 then we concluded that no predictor variables were important for explaining variation in the response variable. If the *P*-value of the best regression model was less than 0.05 we then examined the importance of each predictor variable individually using ANOVA that only included variables included in the best regression model. If the *P*-value associated with the predictor variable in the context of the ANOVA model was greater than 0.05 then we did not consider the variable a significant predictor of variation in the response variable. If the *P*-value of the predictor variable in the context of the ANOVA model was less than 0.05 then we concluded that the predictor variable was a significant contributor to variation in the response variable.

To test the relationship between diversity and stability we estimated coefficients of variation (CV) for each community and ecosystem property measured at each level of genotypic or species diversity. Because the experimental design and set-up resulted in equal means and variances for each of the ecosystem properties across treatments we were certain that the CV's for each level of both species and genotype diversity were zero at the beginning of the experiment and thus only needed to estimate CV's for the second sampling interval to provide an estimate of ecosystem stability. The CV's were calculated by dividing the standard deviation of replicates within a treatment by the mean of the replicates within a treatment. A CV estimated in this manner yields a dimensionless measure that facilitates comparisons across treatments and properties. In this context, stability is inversely correlated with CV such that low estimates of CV suggest high stability. All analyses were conducted in Program R.

Analyses for the genotype and species datasets

To examine the specific importance of genotype or species diversity we used stepwise regression procedures to build models to explain variation in the community and ecosystem response variables. Our approach was identical to that described for the full dataset except our initial candidate predictor variables differed. For the genotype dataset our predictor variables were *Daphnia* genotypic richness, block effects, and their two-way interaction. For the species dataset, our predictor variables were *Daphnia* species richness, block effects, and their two-way interaction. Our criteria for determining significant predictor variables and exploring the diversity-stability relationship were the same as those used for the full dataset.

Results

Clonal uniqueness

Body size and fecundity varied significantly among clones reared in the common garden experiment (Fig. 1a, ANOVA $P < 0.001$, df $= 3$, F $= 38.37$; Fig. 1b, ANOVA $P = 0.018$,

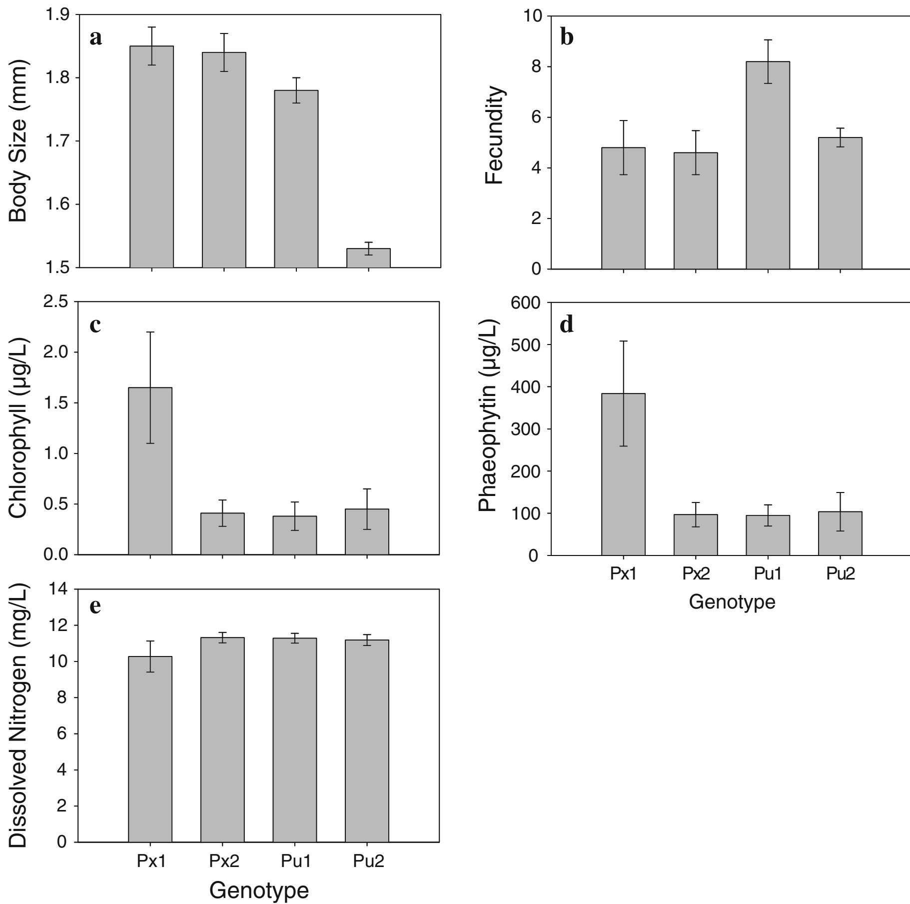

Fig. 1 Life-history traits of each clone used in the microcosms based on a common-garden experiment (**a** and **b**), and clonal differences after the second sampling interval (**c**–**e**). Error bars are ±2 SE

df = 3, F = 4.47). At the species level, *D. pulex* clones are larger (*t*-test $P = 0.001$, df = 13, t = 4.04) and produced fewer offspring (*t*-test $P = 0.046$, df = 18, $t = 2.15$) than *D. pulicaria* clones. At the genotypic level, Pu2 was smaller than the other three genotypes while Pu1 produced more eggs than the other three genotypes. Examination of the single genotype microcosms showed that the Px1 genotype treatment had significantly higher levels of chlorophyll (Fig. 1c; ANOVA df = 3, F = 15.35, $P < 0.001$) and phaeophytin (Fig. 1d; ANOVA df = 3, F = 16.14, $P < 0.001$), and lower levels of total dissolved nitrogen (Fig. 1e; ANOVA df = 3, F = 4.06, $P = 0.021$) relative to the other three clones.

Predictors of community and ecosystem properties

First sampling interval

Neither level of diversity significantly affected ecosystem productivity (CR, NEP, GPP) in any of the data subsets during the first sampling interval. However, there were significant

block effects in the full dataset for GPP (df = 1, F = 4.68, $P = 0.034$) and NEP (df = 1, F = 12.31, $P < 0.001$). There was also a significant block effect in the species dataset for NEP (df = 1, F = 8.71, $P = 0.008$). We interpret these block effects as evidence for our anticipated ecological changes in the microcosms because blocks 1–3 represent sampling during days 1–3 of the experiment, respectively.

Bacterial community richness and composition

For the full dataset, the best predictive model of bacterial community composition included species diversity, genotypic diversity, block and the genotype*block interaction ($R^2 = 0.70$, $P < 0.0001$). However, based on ANOVA results, only species diversity and block were significant predictors of bacterial community composition. In the genotype dataset, the best predictive model was not significant ($R^2 = 0.14$, $P = 0.090$). In the species dataset, the best predictive model included species diversity and block ($R^2 = 0.70$, $P = 0.003$) and both were significant based on ANOVA results (Fig. 2).

For bacterial richness, the best predictive model from the full dataset included species diversity, genotype diversity, block, a species*genotype interaction, and a species*block interaction ($R^2 = 0.28$, $P = 0.022$). However, only species diversity was a significant predictor based on ANOVA. In the genotype dataset, genotype diversity and block were included in the best model ($R^2 = 0.44$, $P = 0.013$), and both were significant predictors based on ANOVA with high levels of genotype diversity resulting in reduced bacterial richness (Fig. 3a). The best predictive model for the species dataset included species diversity and block, but the overall model was not significant ($R^2 = 0.21$, $P = 0.161$).

Zooplankton abundance

The total abundance of *Daphnia* in the microcosms did not vary as a function of species diversity, genotype diversity, or block in any of the data sets.

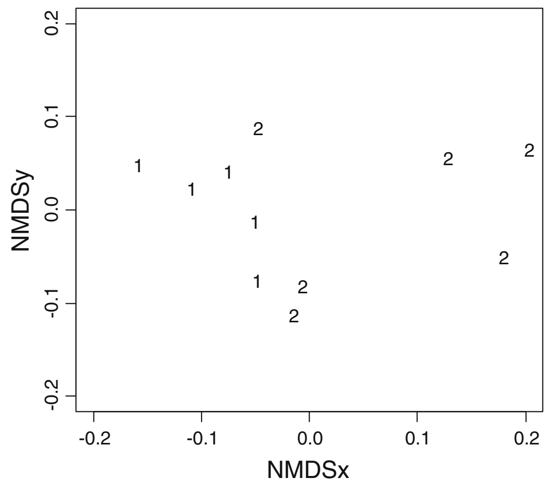

Fig. 2 NMDS plot of bacterial community composition for two levels of species diversity (*1* and *2*)

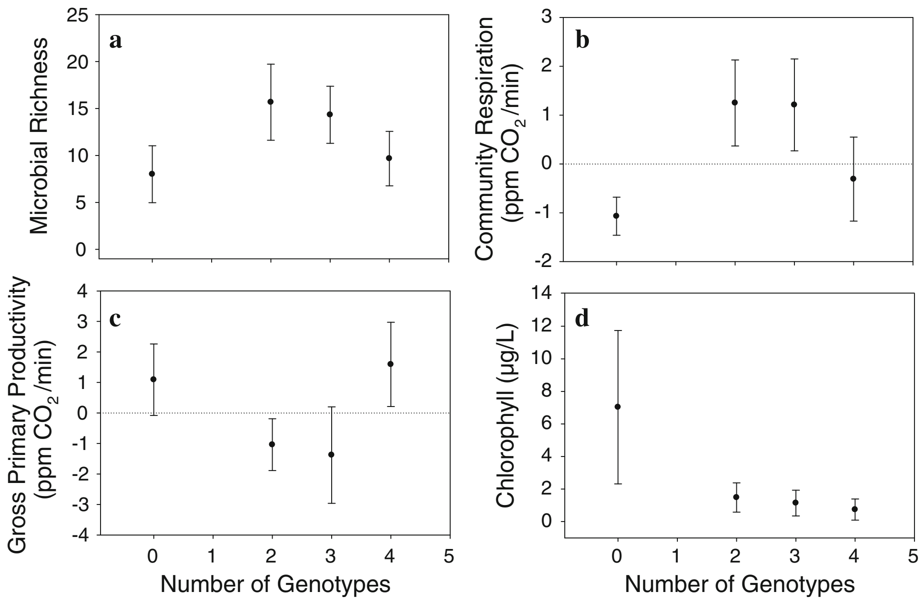

Fig. 3 The effect of genotypic diversity on community (**a**) and ecosystem properties (**b–d**) when species diversity is constant. Note that the y-axis for two ecosystem properties (**b** and **c**) are given in units of ppm CO_2/min so that positive values suggest a net loss of primary productivity while negative values suggest a net gain in primary productivity. The *Chlamydomonas*-only treatment (Number of Genotypes = 0) was not included in the analyses and is provided only as a reference. *Error bars* are ±2 SE

Community respiration

In the full dataset, all single variables, two-way and three-way interactions were included in the best model describing CR ($R^2 = 0.31$, $P = 0.0002$), with only block and the species*genotype interaction explaining a significant amount of variation in respiration (ANOVA). In the genotype dataset, genotype and block were the only terms in the best model ($R^2 = 0.27$, $P = 0.014$), and both were significant predictor variables based on ANOVA with high levels of genotypic diversity resulting in low levels of CR (Fig. 3b). The best model of CR for the species dataset was not significant ($R^2 = 0.23$, $P = 0.111$).

Net productivity

Species and genotype diversity were included in the best model describing NEP in the full dataset but the overall model was not significant ($R^2 = 0.04$, $P = 0.156$). None of the candidate predictor variables were important for describing variation in NEP in both the species and genotype datasets.

Gross primary productivity

All single variables, two-way, and three-way interactions were included in the best model describing variation in GPP in the full dataset ($R^2 = 0.27$, $P = 0.007$). Block and the species*genotype interaction were the only significant predictors based on ANOVA.

Genotype diversity and block were also significant predictors of GPP in the genotype dataset ($R^2 = 0.24$, $P = 0.025$). Genotype diversity was the only significant predictor of gross primary productivity based on ANOVA and showed that high genotypic diversity resulted in low GPP (Fig. 3d). The best model describing GPP for the species dataset was not significant ($R^2 = 0.32$, $P = 0.066$).

Algal pigments

In the full dataset, genotype diversity was the only predictor included in the best models explaining variation in chlorophyll and phaeophytin content ($R^2 = 0.09$, $P = 0.008$; $R^2 = 0.10$, $P = 0.007$, respectively) and was a significant predictor for both pigments based on ANOVA. In the genotype dataset, genotype diversity and block were included in the best fit models ($R^2 = 0.24$, $P = 0.009$; $R^2 = 0.20$, $P = 0.020$), but block was the only significant predictor for both pigments based on ANOVA. In the species dataset the best models for both pigments included only block, but neither model was significant ($R^2 = 0.10$, $P = 0.069$; $R^2 = 0.05$, $P = 0.142$).

Dissolved nutrients

Dissolved nitrogen was predicted by block in the full data set, although genotype and block were included in the best model ($R^2 = 0.10$, $P = 0.013$). In contrast, genotype diversity was included in the best model describing dissolved phosphorous and the N:P ratio in the full dataset ($R^2 = 0.09$, $P = 0.017$; $R^2 = 0.05$, $P = 0.042$, respectively) and in both cases was significant based on ANOVA. In the genotype dataset, block was the only significant predictor in the best model for nitrogen, ($R^2 = 0.19$, $P = 0.010$). Similarly, in the species dataset, block was the only significant predictor of dissolved nitrogen ($R^2 = 0.19$, $P = 0.019$). The best models of dissolved phosphorous were not significant in the genotype dataset ($R^2 = 0.06$, $P = 0.210$) and the species dataset ($R^2 = 0.02$, $P = 0.360$). The best models of N:P ratio were not significant in the genotype dataset ($R^2 = 0.06$, $P = 0.205$) and the species dataset ($R^2 = 0.04$, $P = 0.289$).

Ecosystem stability

Our results concerning the diversity-stability relationship were hindered due to the experimental design. Specifically, we only obtained a single estimate of the CV for each treatment and thus were unable to perform any statistical tests of the diversity-stability relationship. In light of this limitation, our results and conclusions regarding diversity-stability relationships are purely descriptive in nature.

In general, there is a pattern of lower CVs at higher levels of both genotype and species diversity (Table 2). The pattern of low CVs at high diversity is clearest for zooplankton abundance, and to a lesser extent, chlorophyll content, phaeophytin levels, and dissolved nitrogen. Several properties (net productivity, gross primary productivity, dissolved phosphorous, and N:P ratio) show a pattern of the lowest CVs at low (1 genotype) and high (4 genotypes) levels of genotype diversity with high CVs occurring at intermediate levels of genotype diversity. Community respiration shows a pattern of increasing CVs with increasing species and genotype diversity.

Table 2 Coefficients of variation (CV) for each ecosystem property as a function of diversity levels for each of the three datasets

Dataset	Diversity	Richness	Composition	Abundance	CR	NEP	GPP	Chlorophyll	Phaeophytin	N	P	N:P
Full (Genotype diversity)	1	0.31	2.83	0.71	1.33	1.40	6.20	0.89	0.87	0.07	0.13	0.10
	2	0.33	10.24	0.51	1.04	3.26	1.53	0.53	0.51	0.03	0.09	0.08
	3	0.26	2.57	0.33	1.17	2.73	1.71	0.55	0.54	0.04	0.14	0.11
	4	0.26	1.45	0.25	3.46	0.67	1.06	0.44	0.42	0.02	0.11	0.10
Full (Species diversity)	1	0.30	3.89	0.69	1.26	1.82	3.03	0.86	0.84	0.06	0.12	0.09
	2	0.32	3.31	0.32	1.67	6.53	4.47	0.59	0.58	0.03	0.13	0.10
Genotype	2	0.32	14.46	0.35	1.06	2.08	1.15	0.59	0.59	0.03	0.09	0.09
	3	0.26	2.23	0.33	1.17	2.73	1.71	0.55	0.54	0.04	0.14	0.11
	4	0.26	1.45	0.25	3.46	0.67	1.06	0.44	0.43	0.02	0.11	0.10
Species	1	0.30	0.52	0.69	1.04	5.08	1.70	0.46	0.44	0.03	0.09	0.07
	2	0.32	1.48	0.35	1.06	2.08	1.15	0.59	0.59	0.03	0.09	0.09

Discussion

Research that jointly considers ecological and evolutionary principles has enjoyed a surge in the recent literature. This is perhaps most prominently displayed by the contributions of the burgeoning fields of community and ecosystem genetics that integrate the disciplines of evolution, ecology, and population genetics (Whitham et al. 2006). While numerically few, these studies convincingly show that varying levels of genetic diversity can profoundly influence community structure (e.g., Wimp et al. 2005; Johnson and Agrawal 2005; Johnson et al. 2006) and ecosystem function (e.g., Hughes and Stachowicz 2004; Crutsinger et al. 2006). Our goal was to elaborate on the traditional studies of community- and ecosystem-level consequences of species and genetic diversity by examining the importance of variation in one hierarchical level of diversity while simultaneously maintaining a constant level of diversity in the other hierarchical component. Our results suggest that species diversity is important for determining the composition of bacterial communities while genotypic diversity is a significant predictor of bacterial community richness and ecosystem metabolism in experimental microcosms (Table 3).

An important consideration for investigations of the effects of genetic and species diversity on communities and ecosystems is ensuring that there is enough functional variability among genotypes and species. Experiments in which genetic variation among genotypes is low, or different species are functionally redundant, may lead to the potentially false conclusion that genetic and species diversity do not influence communities and ecosystems. In this experiment we obtained four different sets of results that suggest there was sufficient variation among genotypes and species to warrant inclusion in our study.

Table 3 Summary of levels of diversity (Genotype, Species) and their interaction (G*S) that are significant predictors of ecosystem and community properties based on stepwise regression results from the full, genotype and species datasets

Property	Level of diversity		
	Genotype	Species	G*S
Bacterial community			
Composition	–	F, S	–
Richness	G	F	–
Zooplankton abundance	–	–	–
Community respiration	G	–	F
Net productivity	–	–	–
Gross primary productivity	G	–	F
Chlorophyll	F	–	–
Phaeophytin	F	–	–
Dissolved nitrogen	–	–	–
Dissolved phosphorous	F	–	–
N:P ratio	F	–	–

F, S, G refer to the datasets (full, species, genotype, respectively) in which variation in the specific level of diversity is a significant predictor of variation in the ecosystem property based on inclusion in a significant best regression model and significant at $P < 0.05$ based on ANOVA that included only variables in the best regression model

"–" Indicates no relationship between the level of diversity and ecosystem property

First, a common-garden experiment that tested the quantitative genetic differences among genotypes and species showed that *D. pulex* is larger and produces fewer offspring than *D. pulicaria*, and that among *D. pulicaria* clones Pu1 is larger and produces more offspring than Pu2 (Fig. 1a,b). These results show clear quantitative genetic differences between the two species used in this experiment, and also between the genotypes of *D. pulicaria*. Second, screening with microsatellite markers showed that *D. pulex* and *D. pulicaria* differ at the molecular genetic level. Of the 16 microsatellite loci tested, 7 amplified in all four clones, and none of the alleles present in *D. pulex* were present in *D. pulicaria*. Among genotypes, there was no molecular genetic variation between Pu1 and Pu2, but Px1 and Px2 differed for 4 of the seven loci that amplified in all four clones. These results then suggest that there are molecular genetic differences between the species, and also among genotypes of *D. pulex*. Third, results from the single genotype microcosm treatments showed that Px1 treatments had higher levels of chlorophyll and phaeophytin, a degradation product of chlorophyll that lacks the central Mg^{2+} ion, and lower levels of dissolved nitrogen compared to the other three genotypes (Fig. 1c–e). These results imply that Px1 may be an inefficient grazer relative to the other genotypes. Finally, in treatments that contained a single genotype from each species, estimates of relative abundance suggest that *D. pulicaria* may be a superior competitor to *D. pulex* (Table 1). Taken together, these results provide evidence that the species and genotypes used in this experiment differ through some combination of quantitative genetic traits, neutral molecular genetic markers, resource utilization, and competitive ability.

The most significant findings from our microcosm experiment are that *Daphnia* genotype diversity determines the richness of bacterial communities and governs estimates of ecosystem metabolism. Our first result, that genotype diversity drives bacterial richness, parallels numerous other studies that have documented the relationship between genotypic diversity and community structure (e.g., Johnson et al. 2006). We initially hypothesized there would be a positive relationship between *Daphnia* genotype diversity and bacterial richness because we presumed that each genotype harbored a unique community of microbes, and that the successive addition of *Daphnia* genotypes would lead to an increasingly rich bacterial community. However, our results suggested the opposite, where increases in genotype diversity resulted in less rich bacterial communities. We are aware of few studies that documented a reduction in community biodiversity with increasing levels of genetic diversity (Kanaga et al. 2009).

Second, our results show that *Daphnia* genotype diversity determines the rate of ecosystem metabolism. The relationship between two- and three-genotype diversity treatments and gross primary productivity is consistent with the notion of a balance between phytoplankton reproduction and zooplankton grazing. In contrast, the four-genotype treatment suggests grazing pressure from the zooplankton community outpaces the reproductive capabilities of the phytoplankton population, resulting in a net loss of primary productivity. This notion is corroborated by the observed reduction of phytoplankton abundance (as measured by chlorophyll content) in the high genotype diversity treatments, compared to low genotype treatments (Fig. 3d), although phytoplankton reduction was statistically significant only for the full dataset.

One potential explanation for the reduced bacterial richness, ecosystem metabolism, and phytoplankton abundance in genotypically rich microcosms is that each *Daphnia* genotype occupies a unique filter-feeding niche, and that the system-wide rate of filter feeding in the high genotype diversity treatments was higher than low genotype diversity treatments. Two traits measured directly in this experiment and that were shown to vary across genotypes influence *Daphnia* feeding rate. First, large *Daphnia* are able to consume more than small

Daphnia. If body size were important we would expect that the three-genotype treatment that contained the three large-bodied genotypes (Px1, Px2, Pu1) should be as efficient at grazing as the four-genotype treatment. However, despite equal zooplankton abundance between these treatments (*t*-test $P = 0.20$, df = 4, t = 1.55) the three-genotype treatment had substantially lower estimates of gross primary productivity (*t*-test $P < 0.01$, df = 8, t = 3.48). A second trait that may influence feeding rate is fecundity (Elser et al. 2000). If fecundity were important then the single-genotype treatment with the highest fecundity (Pu1) should have higher zooplankton abundance and lower gross primary productivity than the four-genotype treatment, yet we again observe no statistical difference in zooplankton abundance (*t*-test $P = 0.07$, df = 4, t = 2.48) and also no difference in gross primary productivity (*t*-test $P = 0.14$, df = 9, t = 1.62). Although these analyses do not seem to corroborate the hypothesis that feeding rate is the functional trait that varies in our microcosms it is possible that our use of abundance, which serves as a surrogate for biomass which is more strongly correlated with feeding rate than abundance (Lehman and Sandgren 1985), obscures the importance of body size and fecundity in this experiment.

Additionally, relationships between experimentally manipulated eukaryotic diversity and ecosystem parameters can be mediated by prokaryotic organisms that were not manipulated (Zak et al. 2003). Thus, a second potential explanation for the observed effect of genotypic diversity on ecosystem metabolism is that the changes in bacterial richness are driving the changes in ecosystem metabolism due to the positive correlation between bacterial diversity and genotypic diversity. Yet another factor that we cannot rule out is the potential effect of bacterial biomass on ecosystem function. It is highly likely that the genetic composition and abundance of the microbes present jointly influence estimates of ecosystem productivity due to normal growth and metabolism during the experiment. Given our results that suggest surrogate estimates of zooplankton biomass may be insufficient to specifically identify important functional traits, and that bacterial community richness is related to levels of genotypic diversity, future endeavors should seek to quantify zooplankton and bacterial biomass in addition to indices of zooplankton abundance and bacterial diversity.

Our finding that species diversity was only important for predicting bacterial community composition and not other ecosystem properties is not particularly surprising because we only examined two levels of species diversity (one and two). Most studies that have documented significant effects of species diversity on communities and ecosystems have examined levels of species diversity that exceed the levels used in our experiments (reviewed in Hooper et al. 2005). Furthermore, despite evidence for phenotypic and molecular differences between the species utilized in this experiment, and the fact that they have evolved decidedly different life-history strategies to deal with their native environments (*D. pulex* resides in temporary ponds while *D. pulicaria* inhabit permanent lakes), they are sister taxa. Thus, the close phylogenetic relationship between these species likely makes functional differences between these species much more subtle than functional differences between more distantly related crustaceans.

The possible functional redundancy in our chosen taxa may also explain the generally weak patterns of increased ecosystem stability with increasing genotype and species diversity we observed. Zooplankton abundance did display a convincing positive correlation between stability and genotypic diversity, and there was a two-fold reduction in the stability of abundance with increased species diversity suggesting genotypic and species diversity both serve to stabilize zooplankton abundance. High species diversity also appears to stabilize estimates of net primary productivity. However, high species diversity destabilizes bacterial community composition. In the context of our NMDS analysis this

result means that the bacterial species that make up communities at low *Daphnia* species diversity are more similar to one another than the bacterial species that comprise communities at high *Daphnia* species diversity. This result may be explained by species-specific differences in the bacterial communities associated with *Daphnia*. With these few exceptions, the remaining properties showed essentially no change, or a pattern of low stability at intermediate levels of genotypic diversity.

One important goal of investigations that systematically vary both genetic and species diversity is to resolve the relationship between these two types of diversity. A majority of the characters investigated in this experiment were influenced by only one type of diversity, genetic or species. However, two ecosystem properties, community respiration and gross primary productivity, were best explained by models in which a significant genotype*species interaction term was included in the model. While our experimental design (only two species and two genotypes per species) is not conducive to a thorough statistical treatment of this result due to non-overlapping reaction norms, some discussion on the nature of the interaction between genotype diversity and species diversity is warranted. For the two ecosystem properties in question, the nature of the interaction between genotypic diversity and species diversity changes depending on the level of species diversity (Fig. 4). Specifically, at low species diversity (one), increasing genotype diversity does not significantly affect gross primary productivity (*t*-test $P = 0.25$, df = 8, t = 1.25) or community respiration (*t*-test $P = 0.23$, df = 8, t = 1.28). Conversely, at high species diversity (two), increased genotypic diversity is associated with a reduction in gross primary productivity (regression $P = 0.06$, $R^2 = 0.16$) and a significant increase in community respiration (regression $P = 0.05$, $R^2 = 0.17$). Overall, it appears as if the effects of genotypic diversity on ecosystem properties are dependent on the level of species diversity, although due to the limitations imposed by our experiment we cannot be certain that this pattern is robust to higher levels of genotypic and species diversity. If this observed pattern is a common feature of natural systems it suggests, at least, that the design of conservation strategies aimed at preserving local ecosystems may be guided by the relative amounts of genetic and species diversity contained therein. In speciose ecosystems, the manipulation of genetic diversity may have large impacts on ecosystems, whereas in genotypically depauperate ecosystems the manipulation of species diversity will lead to more pronounced ecosystem change.

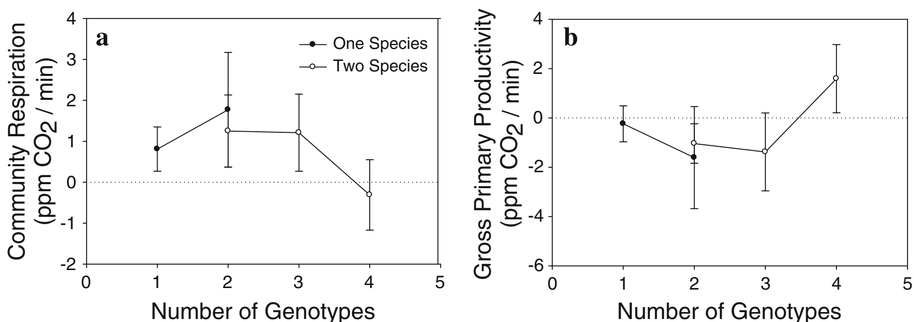

Fig. 4 The interaction between species diversity and genotype diversity for community respiration (**a**) and gross primary productivity (**b**). Note that the y-axis is given in units of ppm CO_2/min so that positive values suggest a net loss of primary productivity while negative values suggest a net gain in primary productivity. *Error bars* are ±2 SE

To conclude, we found that genotype diversity is an important predictor of bacterial community richness and ecosystem metabolism. We also found that species diversity was important in shaping the composition of the bacterial community but not important for other ecosystem properties. Finally, we provide tentative evidence that the impacts of manipulating genetic diversity are dependent on the level of species diversity. Future research that utilizes a phylogenetically rich assemblage of zooplankton and quantifies zooplankton and bacterial biomass will more accurately address the relative importance of species versus genotype diversity in aquatic microcosms and aid in the identification of the relevant functional traits that may drive community and ecosystem change. Overall, these results highlight the importance of examining basic ecosystem properties in systems where genetic and species diversity can be controlled and strongly suggest that declines in species and genetic diversity can substantially alter ecosystem performance.

Acknowledgments The authors wish to thank Kevin Landom, Brian Hines, Laura Curry-Hines, Alison Scoville, Ian Washbourne, Angie Benedetto, Aubrey Holyoak, Stanton Meats, Christina Sparks, and Dave Cole for assistance setting up the experiment and with data collection. We also wish to thank Susan Durham, Adele Cutler, and Brian Gall for assistance with statistical analysis and presentation. Support for this project was provided by the USU Ecology Center and the USU Center of Integrated BioSystems.

References

APHA (American Public Health Association) (1998) Standard methods for the examination of water and wastewater. APHA, Washington DC

Bell G (1991) The ecology and genetics of fitness in *Chlamydomonas*. IV. The properties of mixtures of genotypes of the same species. Evolution 45:1036–1046

Chapin FS III, Walker BH, Hobbs RJ et al (1997) Biotic control over the functioning of ecosystems. Science 277:500–504

Colbourne J, Robison B, Bogart K et al (2004) Five hundred and twenty-eight microsatellite markers for ecological genomic investigations using *Daphnia*. Mol Ecol Notes 4:485–490

Collins S, Bell G (2004) Phenotypic consequences of 1, 000 generations of selection at elevated CO2 in a green alga. Nature 431:566–569

Crutsinger GM, Collins MD, Fordyce JA et al (2006) Plant genotypic diversity predicts community structure and governs an ecosystem process. Science 313:966–968

Crutsinger GM, Souza L, Sanders NJ (2008) Intraspecific diversity and dominant genotypes resist plant invasions. Ecol Lett 11:16–23

Eads BD, Andrews J, Colbourne JK (2007) Ecological genomics in *Daphnia*: stress responses and environmental sex determination. Heredity 100:184–190

Elser J, Sterner R, Gorokhova E et al (2000) Biological stoichiometry from genes to ecosystems. Ecol Lett 3:540–550

Hooper DU, Vitousek PM (1997) The effects of plant composition and diversity on ecosystem processes. Science 277:1302–1305

Hooper DU, Chapin FS III, Ewel JJ et al (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75:3–35

Hughes AR, Stachowicz JJ (2004) Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. P Natl Acad Sci USA 101:8998–9002

Hughes AR, Inouye BD, Johnson MTJ et al (2008) Ecological consequences of genetic diversity. Ecol Lett 11:609–623

Huston MA (1997) Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. Oecologia 110:449–460

Johnson MTJ, Agrawal AA (2005) Plant genotype and environment interact to shape a diverse arthropod community on evening primrose (*Oenothera biennis*). Ecology 86:874–885

Johnson MTJ, Lajeunesse MJ, Agrawal AA (2006) Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. Ecol Lett 9:24–34

Kanaga MK, Latta LC IV, Mock KE et al (2009) Plant genotypic diversity and environmental stress interact to negatively affect arthropod community diversity. Arthropod-Plant Inte 3:249–258

Kling GW, Kipphut GW, Miller MC (1992) The flux of CO_2 and CH_4 from lakes and rivers in arctic Alaska. Hydrobiologia 240:23–36

Lehman JT, Sandgren CD (1985) Species-specific rates of growth and grazing loss among freshwater algae. Limnol Oceanogr 30:34–46

Lynch M, Pfrender ME, Spitze K et al (1999) The quantitative and molecular genetic architecture of a subdivided species. Evolution 53:100–110

Madritch M, Donaldson JR, Lindroth RL (2006) Genetic identity of *Populus tremuloides* litter influences decomposition and nutrient release in a mixed forest stand. Ecosystems 9:528–537

McCauley E, Nisbet RM, Murdoch WW et al (1999) Large-amplitude cycles of *Daphnia* and its algal prey in enriched environments. Nature 402:653–656

Murphy J, Riley JP (1962) A modified single solution method for the determination of phosphate in natural waters. Anal Chim Acta 27:31–36

Naeem S, Thompson LJ, Lawler SP et al (1995) Empirical evidence that declining species diversity may alter the performance of terrestrial ecosystems. Philos T R Soc B 347:249–262

Nelson WA, McCauley E, Wrona FJ (2005) Stage-structured cycles promote genetic diversity in a predator-prey system of *Daphnia* and algae. Nature 433:413–417

Nydahl F (1978) On the peroxodisulfate oxidation of total nitrogen in waters to nitrate. Water Res 12:1123–1130

Oksanen J, Kindt R, Legendre P et al (2008) Vegan: community ecology package. R package version 2.7.1

Pfrender ME, Lynch M (2000) Quantitative genetic variation in *Daphnia*: temporal changes in genetic architecture. Evolution 54:1502–1509

R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0

Sambrook J, Russell DW (2002) Molecular cloning: a laboratory manual. Cold Spring Harbor Laboratory Press, New York

Sarnelle O (2005) *Daphnia* as keystone predators: effects on phytoplankton diversity and grazing resistance. J Plankton Res 27:1229–1238

Schweitzer JA, Bailey JK, Hart SC et al (2005) Nonadditive effects of mixing cottonwood genotypes on litter decomposition and nutrient dynamics. Ecology 86:2834–2840

Stein JR (1973) Handbook of phycological methods: culture methods and growth measurements. Cambridge University Press, London, p 448

Steinman AD, Lamberti GA, Leavitt PR (2006) Biomass and pigments of benthic algae. In: Hauer RF, Lamberti GA (eds) Methods in stream ecology. Academic Press, San Diego, pp 358–380

Tilman D, Knops J, Wedin D et al (1997) The influence of functional diversity and composition on ecosystem processes. Science 277:1300–1302

Tilman D, Reich PB, Knops J et al (2001) Diversity and productivity in a long-term grassland experiment. Science 294:843–845

Vellend M, Geber MA (2005) Connections between species diversity and genetic diversity. Ecol Lett 8:767–781

Vitousek PM (1990) Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos 57:7–13

Vitousek PM, Walker LR, Whiteaker LD et al (1987) Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. Science 238:802–804

Whitham TG, Bailey JK, Schweitzer JA et al (2006) A framework for community and ecosystem genetics: from genes to ecosystems. Nat Rev Genet 7:510–523

Wimp GM, Young WP, Woolbright SA et al (2004) Conserving plant genetic diversity for dependent animal communities. Ecol Lett 7:776–780

Wimp GM, Martinsen GD, Floate KD et al (2005) Plant genetic determinants of arthropod community structure and diversity. Evolution 59:61–69

Zak DR, Holmes WE, White DC et al (2003) Plant diversity, soil microbial communities, and ecosystem function: are there any links? Ecology 84:2042–2050