

Biodiversity in microbial communities: system scale patterns and mechanisms

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Abstract

The relationship between anthropogenic impact and the maintenance of biodiversity is a fundamental question in ecology. The emphasis on the organizational level of biodiversity responsible for ecosystem processes is shifting from a species-centred focus to include genotypic diversity. The relationship between biodiversity measures at these two scales remains largely unknown. By stratifying anthropogenic effects between scales of biodiversity of bacterial communities, we show a statistically significant difference in diversity based on taxonomic scale. Communities with intermediate species richness show high genotypic diversity while speciose and species-poor communities do not. We propose that in species-poor communities, generally comprising stable yet harsh conditions, physiological tolerance and competitive trade-offs limit both the number of species that occur and the loss of genotypes due to decreases in already constrained fitness. In species-rich communities, natural environmental conditions result in well-defined community structure and resource partitioning. Disturbance of these communities disrupts niche space, resulting in lower genotypic diversity despite the maintenance of species diversity. Our work provides a model to inform future research about relationships between species and genotypic biodiversity based on determining the biodiversity consequences of changing environmental context.

Keywords: biodiversity, disturbance, microbial diversity, richness maintenance

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Introduction

Global climate change and anthropogenic environmental changes are causing the Earth's biodiversity to rapidly decline, and as a result, many species are currently threatened with extinction (Schlapfer & Schmid 1999; McCann 2000). A major concern stems from numerous studies that focus on the ecological consequences of the loss of biodiversity and demonstrate a relationship between species diversity and ecosystem productivity, stability, and sustainability (McCann 2000; Naeem & Li 1997; Tilman *et al.* 2001; Kennedy *et al.* 2002; Hughes & Stachowicz 2004; Crutsinger *et al.* 2006; Ives & Carpenter 2007; Reusch *et al.*

2005). While the majority of biodiversity studies spotlight species diversity, recent studies turn to finer scales of resolution including diversity at the genotypic scale (Treseder & Vitousek 2001; Madritch & Hunter 2002; Bailey *et al.* 2006; Crutsinger *et al.* 2006). In contrast to the traditional view that high species diversity is related to stability (Naeem & Li 1997), these studies suggest that ecosystems of low species diversity also maintain stability through high genotypic diversity within key species (Treseder & Vitousek 2001; Kennedy *et al.* 2002; Madritch & Hunter 2002; Schweitzer *et al.* 2004; Bailey *et al.* 2006; Crutsinger *et al.* 2006). Although these studies establish the importance of genotypic diversity to ecosystem stability, there has been no attempt to relate species diversity with genotypic diversity in the context of disturbance outside of laboratory conditions (Vellend & Geber 2005).

Two parallel yet seemingly unconnected ideas exist regarding the interaction between disturbance and ecological diversity. Below the species level, research revolves around the maintenance of genotypes or polymorphisms (Hedrick 2006). Modelling scenarios suggest that spatial

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and temporal heterogeneity as well as resource partitioning are the principal mechanisms that maintain polymorphisms (Rainey *et al.* 2000). In an experimental context, microcosms of *Pseudomonas* with highly disturbed and homogeneous environments support a single genotype, while undisturbed microcosms with high, fine-scale spatial heterogeneity maintain three ecologically and phenotypically, diverse morphs (Rainey & Trivisano 1998). Similarly, intermediate frequencies of disturbance increase diversity (Buckling *et al.* 2000) and allelic diversity is maintained in temporally varying environments by providing conditions for genotypes that are not favoured by average environmental gradients (Turelli 1981).

At the species level, ecologists focus on the maintenance and stabilization of species diversity and its effect on ecosystem stability (Chesson 2000). The emergent patterns suggest that species diversity is often maintained through stabilizing processes that alter the strength of intraspecific (genotypic) and interspecific competitive interactions involved in species coexistence. The mechanisms that maintain diversity include resource partitioning (Chesson 1991) and other fluctuation-independent mechanisms (Chesson 1994) as well as fluctuation-dependent effects of temporally and spatially varying environments (Chesson 2000). Both models of genotypic and species diversity maintenance rely on environmental variation and the competitive abilities of the genotypes or species (Chesson 2000; Rainey *et al.* 2000), but have thus far been left unexamined simultaneously. Our work is aimed at testing whether the level of phylogenetic resolution examined changes potential conclusions about biodiversity.

We used a meta-analysis approach to examine the relationship between species and genetic diversity focusing on the maintenance of microbial diversity at multiple taxonomic levels. We first classified microbial communities based on disturbance (anthropogenic influence); we then investigated the relationship of diversity between 'species' and 'genotype'. We ask specifically whether the taxonomic scale of investigation biases conclusions regarding the role of disturbance on diversity measures. Our results demonstrate that scale does matter, and that a change in environmental context has a greater effect on genotypic diversity than species diversity.

Materials and methods

Microbial communities

Because of the method of bacterial classification, multiple levels of taxonomic resolution can be simultaneously analysed. Using three different levels of genetic identity, 93% 16S rRNA gene sequence identity cut-off, (Devereux *et al.* 1990), 97% sequence identity cut-off (Devereux *et al.* 1990; Hughes *et al.* 2001; Hagström *et al.* 2002; Schloss &

Handelsman 2005), and > 99% sequence identity cut-off, we compared measures for diversity of 81 different microbial communities (each containing between 100 and 684 16S rRNA gene sequences) amounting to over 16 000 sequences (see Table S1, Supporting Information) collected from a globally distributed, wide range of environmental settings. Each data set was downloaded from the ribosomal database project (<http://rdp.cme.msu.edu>) in a DNA distance matrix format with Jukes Cantor correction (Cole *et al.* 2007). Community sequences downloaded using the hierarchy browser were controlled for coverage and quality by selecting only nearly full-length 16S sequences (> 1200 bp) and only high quality sequences.

After collecting microbial community data sets, we divided the data sets into two categories based on the environmental characteristics of each community. Data sets were categorized as 'anthropogenically influenced' ($n = 31$), comprising environments with high external impact (human or otherwise), and 'undisturbed' ($n = 50$), environments with minimal recent external impacts (Table 1). Because these are naturally occurring extant – and generally unrelated – communities, it is not practical to directly compare diversity values. The design of this study allows us to use within-community diversity along the two taxonomic levels as a gauge to compare diversity of unrelated ecological backgrounds. In order to overcome pitfalls with sample size in comparing class:subclass ratios (Gotelli & Colwell 2001), we compared the average sample size and standard deviation between the disturbed and undisturbed groups. We also compared the rarefaction slopes of both species and genotype for each community for both disturbed and undisturbed groups.

Estimates of biodiversity

Each microbial community was analysed with DOTUR (Schloss & Handelsman 2005) for biodiversity using the Simpson index (Chazdon *et al.* 1998; Hughes *et al.* 2001; Magurran 2004), the Shannon evenness index (Magurran 2004), and the abundance-based coverage estimate (ACE) (Chazdon *et al.* 1998; Hughes *et al.* 2001; Magurran 2004) for richness for all three levels of taxonomic resolution.

Table 1 Brief description of microbial communities divided into undisturbed and anthropogenically influenced environments

<i>n</i>	Undisturbed	<i>n</i>	Anthropogenically influenced
6	Fresh water	10	Contaminated soils
11	Marine water	4	Agricultural soils
11	Sediments	7	Agricultural waste
8	Forest soils	7	Wastewater treatment
12	Grassland soils	3	River water (contaminated)
2	Limestone cave		
50		31	$N = 81$

The Simpson diversity index is a composite that captures both evenness and richness characteristics of community assemblages (Magurran 2004) and is a robust measure for statistical analyses. In addition, the Simpson diversity index is relatively insensitive to undersampling (Chao & Shen 2003). In order to determine the effect of disturbance on each individual characteristic of genotypic diversity, we analysed evenness (Shannon index) as well as richness (ACE). Evenness of microbial communities across all levels of taxonomic resolution was determined using the Shannon evenness measure as described by Magurran (2004). ACE (Chazdon *et al.* 1998) was calculated by DOTUR (Schloss & Handelsman 2005) using the formula following Hughes *et al.* (2001) and Magurran (2004). In addition to approximating richness using the ACE, richness patterns were verified using the Chao1 estimate of richness as described by Magurran (2004).

Data analysis

Data on microbial biodiversity, including evenness and richness components were examined for a disturbance effect by using regression models across phylogenetic levels (that is, we compared 97% sequence identity cut-off diversity values with 93% sequence identity cut-off diversity of the same community and > 99% sequence identity cut-off diversity with 97% sequence identity cut-off diversity). In order to normalize residuals, Simpson index data were transformed using the negative natural log (Rosenzweig 1995). Likewise, in order to compensate for heteroskedasticity and to normalize residuals (Fig. S1, Supporting Information), we used natural log-transformed ACE values (for both 97% and > 99% sequence identity). We used 93% cut-off and 97% cut-off diversity as a covariate in an analysis of covariance (ANCOVA) to determine differences in the relationship of 93% and 97% cut-off diversity to 97% and > 99% cut-off diversity, respectively. For optimum model fit of the relationship between 97% sequence identity and > 99% sequence identity richness estimates, we used Akaike's information criterion (AIC) (Akaike 1974; Burnham & Anderson 2002).

Results

While sample size is often an issue in dealing with diversity indices, this effect is minimized by requiring a large number of taxa (> 99 samples per community) for analyses. We used a phylogenetic approach to stratify communities based on scales of genetic differentiation to compare levels of resolution within each community (Martin 2002). The ratio between the slope of rarefaction curves for each community at the genotype and species level is similar between disturbed and undisturbed groups (see Fig. S2, Supporting Information), indicating

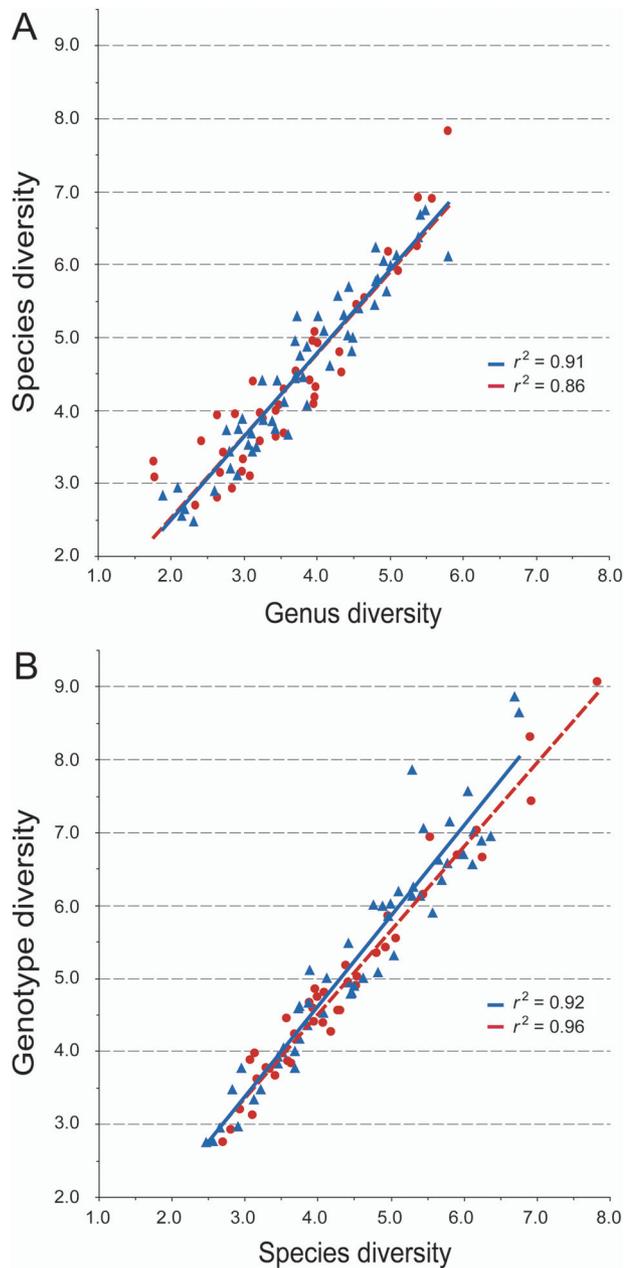


Fig. 1 Effect of anthropogenic influence on biodiversity. Simpson diversity index ($-\ln$) of anthropogenically influenced (●) and undisturbed (▲) microbial communities with linear regression (line) plotted at the 97% identity cut-off level vs. 93% identity cut-off level (A), and > 99% identity cut-off level vs. 97% identity cut-off level (B). Both x- and y-axes are log-scaled.

that any bias introduced by sample size is equal across both groups.

Biodiversity based on Simpson diversity index (SDI) values shows a linear relationship among different levels of taxonomic resolution (Fig. 1). We used an analysis of

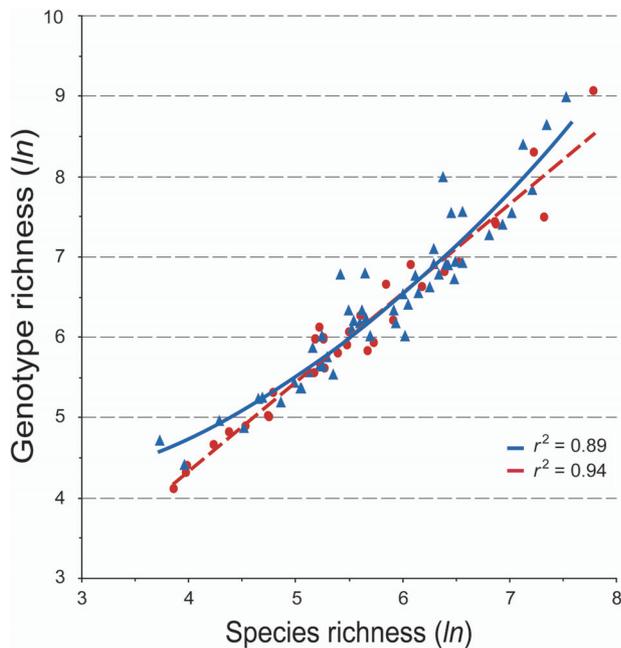


Fig. 2 Effect of anthropogenic influence on genetic richness. Natural log-transformed ACE values of >99% identity richness plotted against 97% identity richness for anthropogenically influenced (●) and undisturbed (▲) communities. Best-fit regression models (AIC) for anthropogenically influenced (red) is linear and for undisturbed (blue) is non-linear.

covariance (ANCOVA), with 93% identity as the covariate, to examine the relationship between 97% and 93% identity cut-off in anthropogenically influenced and undisturbed microbial communities (see methods for details on classification of communities). There was no significant difference in linear regression slopes ($F_{1,78} = 0.57$, $P = 0.453$) between anthropogenically influenced and undisturbed communities (Fig. 1A), indicating no observable difference in diversity between these groups of communities when using 97% identity as the finest level of resolution (see Fig. S3, Supporting Information). Conversely, the relationship of SDI values for >99% identity relative to 97% identity (covariate) is significantly different between anthropogenically influenced and undisturbed communities ($F_{1,78} = 4.33$, $P = 0.041$) (Fig. 1B). The difference in >99% identity diversity between anthropogenically influenced and undisturbed communities is positively correlated with 97% identity diversity.

By analysing the individual components of diversity using the Shannon index of evenness and ACE for determining richness, we can further partition the differences in diversity and hypothesize mechanisms responsible for the observed differences. Analysis of the microbial communities using Shannon evenness index demonstrated that disturbance has no effect on evenness at either the 97% or >99% identity levels (Fig. S3). However, richness above

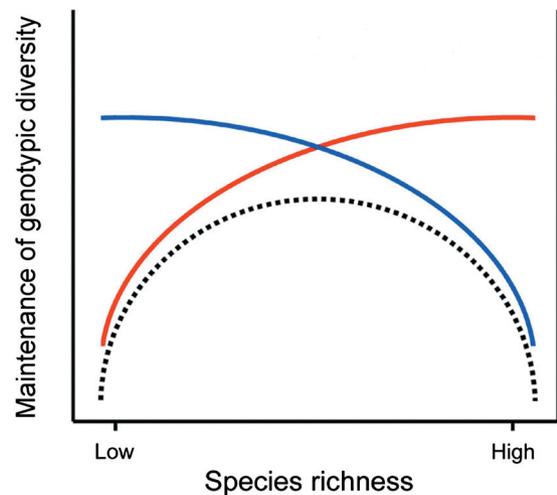


Fig. 3 The effect of anthropogenic disturbance on the maintenance of genotypic richness. The dotted curve is maintenance of genotypic diversity. Low maintenance is due to (i) lowered fitness of specialists due to environmental perturbation (red) in extreme environments where species richness is low, and (ii) disruption of resource partitioning (blue) in complex speciose communities. The highest maintenance of genotypic diversity occurs in communities with intermediate species richness.

99% identity (ACE) was significantly different between these sets of communities (Fig. 2). As with SDI, the difference in richness is not apparent using 97% identity as the finest level of resolution (Fig. S4, Supporting Information). We compared a series of models (as a function of 97% identity richness; quadratic, log-based, linear and the square root of richness) for the purpose of determining if the relationships are the same among the anthropogenically influenced and undisturbed communities. For the anthropogenically influenced communities, the best model based on Akaike's (1974) information criterion (AIC) values is the simple linear model relating >99% identity richness to 97% identity richness. For the undisturbed communities, the best fitting model (based on AIC) was a non-linear (quadratic) model. The best-fit model used to explain the relationship between 97% and >99% identity richness for each community group (anthropogenically influenced = linear; undisturbed = non-linear) describes approximately 90% of the variation (Fig. 3) [similar patterns emerge using the Chao richness estimator (Fig. S5, Supporting Information)].

Discussion

Genetic variation in bacterial communities is characterized from hundreds of environments, and the DNA sequence data from these communities are now readily available (Cole *et al.* 2007). Bacterial systems provide a unique opportunity to examine the relationships between hierarchical

levels of taxonomic diversity via characterization of 16S rRNA gene sequences. Although there is considerable disagreement (see Schloss & Handelsman 2005), microbial ecologists typically assign sequences with greater than 97% sequence identity to the same species (Devereux *et al.* 1990; Hughes *et al.* 2001; Hagström *et al.* 2002; Schloss & Handelsman 2005), and sequences with greater than 93% sequence identity are designated the same genus (Devereux *et al.* 1990). Genotype diversity comprises sequences that are greater than 99% identical. Although taxonomic classification using 16S rRNA gene is somewhat controversial and there are undoubtedly superior methods for taxonomic classification (see Konstantinidis & Tiedje 2007), it provides an objective criterion to partition communities into defined groups of related sequences. By directly comparing biodiversity across multiple taxonomic levels, we demonstrate that the relationship between 'genotypic' diversity and 'species' diversity differs between undisturbed and anthropogenically affected sites. Our analyses illustrate that (i) biodiversity assessment is dependent on phylogenetic scale, and (ii) a low-level resolution (species-centric) assessment of biodiversity may obscure changes in diversity at a higher (genotypic) level.

The difference in genotypic diversity between these sets of communities is greatest at the highest levels of species diversity. Because this study is comparative and not based on a replicated experimental manipulation, or a longitudinal study, it is impossible to directly equate this pattern to the loss of biodiversity in these environments (i.e. anthropogenic influence is not controlled or quantified). The slope of both graphs (e.g. Figs 1 and 2) is consistently greater than unity as an inevitable consequence of the hierarchical nature of phylogenies and classifications (there can never be more species than genotypes of those species). However, we can determine that genotypic diversity in disturbed communities is lower than expected from the trends (comparison of slopes) in undisturbed communities. Differences in biodiversity at the species level across groups is not apparent in these data; accordingly, the traditional focus on species level diversity may overlook a significant component of biodiversity that is changing at the genotypic level well in advance of population and species level changes.

Genotypic diversity is often described as the most fundamental basis of biodiversity (Reusch *et al.* 2005); consequently, the maintenance of genotypic diversity in fluctuating environments potentially contributes to ecosystem maintenance, function, and stability (Hughes & Stachowicz 2004; Schweitzer *et al.* 2004; Reusch *et al.* 2005; Bailey *et al.* 2006; Crutsinger *et al.* 2006). Comparison of genotypic richness and species richness in anthropogenically influenced and undisturbed microbial communities highlights different patterns in the relationship between genotypes and species along a species richness gradient

(Fig. 2). The best-fit model for the relationship between genotypic richness and species richness in anthropogenically influenced communities is linear while the relationship in undisturbed communities is non-linear. The greatest difference between the two sets of communities is manifest at the tails of the species richness distribution. In the lowest and highest species-rich, undisturbed communities, genotypic richness is much higher than in human-influenced communities of similar species richness (Fig. 2). Independent mechanisms may be acting at either end of the species richness continuum. Rainey *et al.* (2000) proposed that the maintenance of genotypic diversity is the result of a combination of competitive trade-offs and ecological opportunity. While these mechanisms are independent, they often overlap to maintain polymorphisms or genotypes.

For both genotypic and species diversity maintenance, the covariance between environmental variation, fitness and the competitive abilities of the genotypes or species are essential for overall diversity maintenance (Rainey *et al.* 2000). Given sufficient niche space and selective pressure, organisms will surrender generalist-like fitness in becoming specialists, thus promoting the occurrence of polymorphisms. This dynamic is consistent with the competition-colonization trade-off and specialization for open space models from niche theory (Chase & Leibold 2003). Niche separation is critical for the maintenance of polymorphisms in *Pseudomonas fluorescens* (Rainey & Travisano 1998) and *Escherichia coli* (Chao & Levin 1981) cultures. Similarly, Boles *et al.* (2004) suggests that increases in diversity within microbial biofilms are a result of random variation and strong selection. Conversely, closely related clades are propagated through purifying selection sweeps and persist where competitive mechanisms are too weak to purge diversity from within them (Acinas *et al.* 2004). One of the principal drivers of microbial diversity is niche separation (McArthur *et al.* 1988; Ramette & Tiedje 2007). In his recent review of the maintenance of diversity in ecological communities, Chesson (2000) referred to analogous situations of equalizing effects, in which changes in fitness result in the loss of genetic diversity. Communities with low species diversity in this data set largely represent extreme or isolated environments (e.g. sand dunes, limestone caves, etc.). As suggested by this research, environments with naturally low species diversity have surprisingly high genetic and functional diversity (Whittaker *et al.* 2003), where genetic or functional diversity may compensate for lack of species diversity (Hughes & Stachowicz 2004; Schweitzer *et al.* 2004; Reusch *et al.* 2005; Bailey *et al.* 2006; Crutsinger *et al.* 2006; Dinsdale *et al.* 2008). When disturbances occur, prevailing environmental conditions shift and many of the bacterial genotypes that have lost generalist characteristic in favour of specialization disappear, leaving only those capable of withstanding the new selective conditions (Boles *et al.* 2004).

The ecological opportunity provided by one genotype, or species, is often required for the maintenance of a competing genotype (Lankau & Strauss 2007). Previous models suggest increasing neutrality with increasing species richness with the assumption that the mechanism generating this relationship is increasing niche overlap with increasing species richness (Gravel *et al.* 2006). Such competitive dominance among species is explained in terms of the resource-ratio hypothesis (Pacala & Tilman 1993) and is defined with regard to community structure (Tilman 2004). The communities in this data set that are high in species richness generally represent complex environments (i.e. wide variety of carbon sources) such as anoxic marine sediments and dairy wastewater where resource partitioning and community structure are expected. Consequently, slight disturbances can disrupt resource availability or physical structure breaking these interactions (Tilman 1982). For example, disruption of resource partitioning destabilizes polymorphism diversity in *E. coli* (Rosenzweig *et al.* 1994; Turner *et al.* 1996; Elena & Lenski 1997; Rozen & Lenski 2000). This destabilization was recently shown to extend beyond polymorphism diversity to include species diversity (Lankau & Strauss 2007).

Our results suggest a continuum between Rainey's *et al.* (2000) mechanisms of ecological opportunity and competitive trade-offs in maintaining polymorphism diversity relative to species richness. Communities with high species diversity are more likely to consist of genotypes whose ecological function complement or facilitate one another, resulting in more efficiency in their use of resources (Huston 1997; Loreau & Hector 2001; Loreau *et al.* 2001; Tilman *et al.* 2001). Accordingly, the effect of competitive trade-offs and specialization in such environments is negligible. On the other end of the species richness continuum, extreme conditions preclude extensive resource partitioning while specialization drives the maintenance of genotypic diversity. Communities of intermediate species richness are influenced by both mechanisms maintaining genotypic diversity (Fig. 3). Because these two mechanisms of polymorphism maintenance are independent, they are disrupted by different mechanisms. Hence, a larger difference in the genotypic diversity is manifest at the extremes of species richness where one mechanism is dominant, while intermediate species richness maintains genetic diversity.

In addition to the expanding investigation of the relationship between disturbance and diversity (Treseder & Vitousek 2001; Kennedy *et al.* 2002; Madritch & Hunter 2002; Schweitzer *et al.* 2004; Bailey *et al.* 2006; Crutsinger *et al.* 2006), our study indicates that further focus on genetic diversity is warranted, particularly as information on microbial communities extends to functional diversity (Dinsdale *et al.* 2008; Lozupone & Knight 2007). Due to the meta-analytical nature of this study, microbial communities

are not controlled for disturbance; however, the trends found within these communities justify future studies with regard to disturbance and genetic biodiversity. In anthropogenically influenced environments, the lower genotypic variation occurs without any observable effect of species diversity. Highly impacted communities may lose important functional components of biodiversity required for the maintenance of ecosystem stability at the genetic level long before they are recognized as impaired at higher taxonomic levels (Dinsdale *et al.* 2008). In fact, lower genotypic diversity in species-rich communities indicates that the greatest differences in genetic and species diversity may occur in communities that are considered intact. The impact of lower diversity may be particularly relevant when considering multifunctional ecosystems (Lozupone & Knight 2007). While our investigation is based on microbial communities, we suggest that our conclusions may extend well beyond the dynamics of these communities. Future investigations are needed that identify the functional significance of the observed patterns of diversity to assess impact of loss at the genotype level in microbial communities as well as more comprehensive ecosystem models (Dinsdale *et al.* 2008). Additionally, examination of the shifts in diversity on a phylogenetic level (i.e. comparing different groups of bacteria) to determine stability of different specific groups to disturbance is warranted. Such investigations will provide valuable information on the effects of specialization and ecological niches at a higher phylogenetic resolution in ecosystem modelling.

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J. Parnell's research includes microbial diversity and functional ecology in environmental systems. Crowl utilizes genetic and phenotypic modelling in aquatic ecosystems. Weimer's research involves microbial genomics, metabolism, and adaptation. Pfrender's research uses molecular genetic and functional genomic approaches to study ecological speciation, evolutionary responses to changing environments, and the relationship between biodiversity and ecosystem function.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1 Effect of anthropogenic influence on biodiversity: species and genus.

Fig. S2 Potential bias of biodiversity estimates based on class:sub-class ratio as a function of sample size.

Fig. S3 Effect of anthropogenic influence on Shannon evenness.

Fig. S4 Effect of anthropogenic influence on species richness (ACE).

Fig. S5 Effect of anthropogenic influence on richness (Chao 1).

Table S1 Reference and description of 84 microbial communities

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