LETTER

Communities contain closely related species during ecosystem disturbance

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Abstract

Predicting community and species responses to disturbance is complicated by incomplete knowledge about species traits. A phylogenetic framework should partially solve this problem, as trait similarity is generally correlated with species relatedness, closely related species should have similar sensitivities to disturbance. Disturbance should thus result in community assemblages of closely related species. We tested this hypothesis with 18 disturbed and 16 reference whole-lake, long-term zooplankton data sets. Regardless of disturbance type, communities generally contained more closely related species when disturbed. This effect was independent of species richness, evenness, and abundance. Communities already under stress (i.e., those in acidic lakes) changed most when disturbed. Species sensitivities to specific disturbances were phylogenetically conserved, were independent of body size, and could be predicted by the sensitivities of close relatives within the same community. Phylogenetic relatedness can effectively act as a proxy for missing trait information when predicting community and species responses to disturbance.

INTRODUCTION

Ecological communities subject to severe or repeated disturbance are typically low in diversity and contain only stress-tolerant species (Connell 1978; Chase 2007). Disturbance can be thought of as an environmental filter that selects for community members with key traits such as small body size, high dispersal ability, or broad niche breadth (Purvis *et al.* 2000b; Fisher & Owens 2004; Kotiaho *et al.* 2005). However, these key traits are not always indicative of stress-tolerant species. For example, the invasive *Bythotrephes*

longimanus, the spiny water flea, preys upon small-bodied zooplankton, shifting lake zooplankton communities to comprise only large-bodied species (Yan *et al.* 2001). Furthermore, trait synergies and interactions between traits and disturbance magnitude modify species' sensitivities to disturbance in complex ways (Freville *et al.* 2007; Olden *et al.* 2008). Species and community responses to disturbance are thus often difficult to predict in nature.

Closely related species may have similar sensitivity, or resistance, to a given disturbance because they are more likely to share similar traits (i.e., show phylogenetic signal,

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Blomberg *et al.* 2003). For example, closely related angio-sperms have similar sensitivity to climate change due to phylogenetically conserved flowering-time response traits (Willis *et al.* 2008). Of course, phylogenetic similarity may not correlate to the key trait similarity that determines species responses to disturbance because processes such as stabilizing selection and convergent evolution could reduce phylogenetic signal (Blomberg *et al.* 2003; Losos 2008). Nonetheless, phylogenies give objective, *a priori* hypotheses about species' disturbance-response similarities and provide a clear, and little explored, research avenue to understand how disturbance affects ecological communities. When there is phylogenetic signal, a species' response to distur-bance should be adequately predicted with the known response of a close relative even when knowledge about key traits and their interactions is missing. Phylogenetic signal should also translate into phylogenetic patterns of commu-nity composition with communities undergoing disturbance comprising more closely related species than communities not experiencing such disturbance.

The few studies that looked at disturbance and phyloge-netic community composition support this hypothesis (Warwick & Clarke 1998; Terlizzi *et al.* 2005; Verdu & Pausas 2007; Knapp *et al.* 2008; but see Abellán *et al.* 2006). These existing studies are of spatial comparisons of undisturbed and disturbed sites. Because spatial compari-sons may be confounded by community differences not related to disturbance (Warwick & Clarke 1998; Verdu & Pausas 2007), a stronger approach is to compare the same community before and during a disturbance event. Similarly, phylogenetic composition is unlikely to change when a community that already contains stress-tolerant species is impacted by a disturbance similar to the stresses already experienced by the community. For example, Verdu & Pausas (2007) found that as mean annual temperature increased across frequently burned plant communities, the selective effects of fire on closely related species with heat-tolerance traits was reduced. Species in high-temperature communities were already heat tolerant, thus burning did not greatly affect these communities. On the other hand, large changes in community composition could ensue if an already stressed community is disturbed by a different stressor, because the species of that community may be less adaptable to new stress (Paine *et al.* 1998).

Here, we use data on pelagic freshwater crustacean zooplankton community dynamics in several long-term studies of reference and disturbed lakes to assess how phylogenetic community composition changes in response to disturbance. We had two overall objectives. The first was to test if disturbance results in community assemblages of more closely related species. The second was to understand the mechanisms that underlie disturbance-phylogenetic effects. For this objective, we addressed four specific questions. We first asked, if environmental context influ-enced the magnitude of disturbance-phylogenetic effects and if there was evidence that communities already under stress responded differently than unstressed communities to disturbance. Second, because harsh disturbance typically causes reductions in species richness, we asked if the observed overall disturbance-phylogenetic effect was only caused by species that decreased during disturbance. Third, we used time-series models to ask if the overall disturbance-phylogenetic effect was caused by phylogenetic conserva-tism in the sensitivities of species to disturbance. Finally, we asked if the overall effect was caused by related sets of highly sensitive species that were intolerant to all types of disturbance. We addressed this fourth question by devel-oping methods to make predictions of species sensitivities based on the sensitivities of close relatives.

Our study lakes were ideal to accomplish these objectives for three reasons. First, these lakes have experienced a wide variety of disturbances, allowing us to generalize our observations on disturbance-phylogenetic effects across disturbance types (Table 1). Second, undis-turbed lakes were simultaneously monitored permitting temporal comparisons of phylogenetic community com-position in disturbed vs. reference communities. This before-after, control-impact design allowed for a strong test of our hypothesis that disturbance causes community assemblages of more closely related species (Hurlbert 1984; Stewart-Oaten *et al.* 1986). Finally, all lakes sup-ported crustacean zooplankton communities with well-characterized responses to the different disturbances (see references in Table S1). The disturbances were clearly severe enough to affect zooplankton composition, but the question remained: did the various disturbances affect phylogenetic community composition?

METHODS

Data sets

We analysed crustacean zooplankton data from 18 lakes that were either intentionally or unintentionally disturbed (Tables 1 and S1). The lakes were in the north-central United States and southern Canada. Their crustacean zooplankton communities (i.e., Cladocera and Copepoda) on average comprised 15 species and were typical of those in northern temperate lakes (Carter *et al.* 1980; Patalas 1990). The lakes were divided into three groups based on disturbance type: biological (e.g., species introductions), chemical (e.g., acidification), and physical (e.g., water level manipulations). Sixteen disturbed lakes were matched with undisturbed reference lakes that were either the reference lakes used in the original studies or similar lakes sampled in the same region over the same time period. Due to the

Table 1 Lake descriptions

Region	Lake name	Type	Specific disturbance
UNDERC	East	Physical	Lake divider installed, affected water chemistry and circulation
UNDERC	Paul	Reference	East reference
UNDERC	Tuesday	Biological	Decreased planktivory via minnow removal and bass addition
UNDERC	Paul	Reference	Tuesday reference
UNDERC	Peter	Biological	Increased planktivory via bass removal and minnow/trout addition
UNDERC	Paul	Reference	Peter reference
UNDERC	West	Chemical	Nitrogen and phosphorus addition
UNDERC	Paul	Reference	West reference
Dorset/Sudbury	Clearwater	Chemical	Smelter shutdown, changes in pH and decreased deposition of heavy metals
Dorset/Sudbury	Harp	Biological	Invasion, spiny water flea
Dorset/Sudbury	Red Chalk	Reference	Harp reference
Dorset/Sudbury	Mouse	Biological	Decreased planktivory via bass addition
Dorset/Sudbury	Heney	Reference	Mouse reference
Dorset/Sudbury	Ranger	Biological	Increased planktivory via bass removal
Dorset/Sudbury	Chub	Reference	Ranger reference
ELA	L191	Biological	Macrophyte removal
ELA	L373	Reference	L191 reference
ELA	L221	Biological	Decreased planktivory via addition of northern pike
ELA	L382	Reference	L221 reference
ELA	L223	Chemical	Acidification
ELA	L224	Reference	L223 reference
ELA	L226N	Chemical	Nitrogen, phosphorus and carbon addition
ELA	L239	Reference	L226N reference
ELA	L226S	Physical	Water level decrease
ELA	L239	Reference	L226S reference
ELA	L302S	Chemical	Acidification
ELA	L239	Reference	L302S reference
ELA	L375	Biological	Aquaculture, rainbow trout in cages
ELA	L373	Reference	L375 reference
ELA	L979	Physical	Water level increase
ELA	L442	Reference	L979 reference
NTL-LTER	Crystal	Biological	Invasion, rainbow smelt
NTL-LTER	Little Rock Trt.	Chemical	Acidification
NTL-LTER	Little Rock Ref.	Reference	LRT reference

The lakes were in located in three regions: UNDERC-University of Notre Dame Environmental Research Centre, Michigan, USA; Dorset/Sudbury-Dorset Environmental Science Centre and the Laurentian University Cooperative Freshwater Ecology Unit, Ontario, Canada; ELA-Experimental Lakes Area, Ontario, Canada; NTL-LTER North Temperate Lakes Long Term Ecological Research, Wisconsin, USA 'type' is the general type of disturbance that occurred to each lake. See Table S1 for full metadata.

designs of some whole-lake experiments, L239, L373 and Paul served as references for multiple disturbed lakes.

Zooplankton samples were collected through the entire water column of the pelagic zone using a variety of techniques (see references in Table S1), but resulted in comparable data sets (Rusak *et al.* 2002 and references therein). The lakes were sampled both before and during disturbance. We demarcated the initiation and end of disturbance for each lake using both published and unpublished disturbance descriptions. In Crystal and Harp Lakes, disturbances associated with species invasions did not end in the records we analysed. For these lakes, we used data from the first 3 years after the documented invasion because the species richness and zooplankton composition of Harp Lake stabilized within 3 years after invasion (Yan *et al.* 2002). With the exception of L226S, we analysed data only from the first time each lake was disturbed. L226S was manipulated twice: between 1973 and 1978 nitrogen and carbon were added and in 1995 & 1996 the water level was lowered. We analysed the second disturbance as the

zooplankton community had recovered from the first disturbance before the second disturbance began and there were no pre-disturbance or reference data from the first disturbance. We retained all crustacean zooplankton species in the data set except the invasive spiny water flea, which was removed because its invasion was the disturbance event whose effect we quantified in Harp Lake and it was only found in Harp Lake (Yan *et al.* 2002).

We constructed molecular phylogenies of the crustacean zooplankton species found in all lakes (see Appendix S1 for detailed methods). We used the PhyloTA browser to obtain 16 phylogenetically informative sequence clusters from Genbank (i.e., groups of alignable homologous sequences, Sanderson *et al.* 2008; Table S2). These clusters were aligned and combined into a supermatrix (McMahon & Sanderson 2006). The supermatrix contained over 17 000 characters and 56 of our 67 taxa. We performed a parsimony analysis of the supermatrix in PAUP* (Swofford 2002) that resulted in three most-parsimonious trees that differed only slightly (Appendix S1). The root node of each tree was dated to 562 MYA according to Pisani (2009), and nonparametric rate smoothing was used to estimate divergence times for the remaining nodes (Sanderson 1997). The taxa without sequence data were grafted onto the trees (see Appendix S1 for details on placement) and the added branches and nodes were evenly spaced among the tree nodes with the 'bladj' function of PHYLOCOM (Webb *et al.* 2008). To account for tree uncertainty, all analyses we describe below were performed separately on each of the three trees and the results were averaged. We also compared these molecular-based results to those obtained from an informal supertree that we constructed by hand with published molecular/morphological phylogenies and Linnaean taxonomy. The conclusions from the molecular-based and informal supertree analyses were the same (Appendix S2).

Estimating the effect of disturbance on phylogenetic community composition

We calculated the phylogenetic species variability (PSV) of each zooplankton sample (Helmus *et al.* 2007a). Phylogenetic species variability is based on species presence/absence and their phylogenetic relationships. For a sample of n species,

$$\mathrm{PSV} = \frac{n\mathrm{tr}\mathbf{C} - \Sigma\mathbf{C}}{n(n-1)} \qquad (1)$$

where $\mathbf{C}$ is the $n \times n$ sample phylogenetic covariance matrix, $\mathrm{tr}\mathbf{C}$ is the sum of diagonal elements of $\mathbf{C}$, and $\Sigma\mathbf{C}$ is the sum of all elements of $\mathbf{C}$. As species in a sample become more closely related, PSV decreases towards zero; as species

become less closely related, PSV increases towards one. The extreme PSV = 1 occurs if all species in the community are completely unrelated to each other (i.e., the community phylogeny is a 'star'). The statistical expectation of PSV is independent of species richness, thus any change in PSV due to disturbance is not a statistical artefact of varying species richness (Helmus *et al.* 2007a). We also calculated phylogenetic species evenness, PSE, a formulation of the PSV metric that accounts for species abundances, but the conclusions were the same as for Shannon evenness (see below) and we do not present the results here.

For each of the 18 disturbed lakes, we calculated the mean PSV across all samples taken before the disturbance and the mean PSV across all samples taken during the disturbance. Similarly, pre-disturbance and disturbance PSV means were calculated for the 16 reference lakes based on the sampling dates of each corresponding disturbed lake. For each lake, we subtracted the pre-disturbance mean PSV from the disturbance mean PSV to derive the change in PSV during disturbance, $\Delta\overline{\mathrm{PSV}}$. We then calculated the difference between the mean of the disturbed lake $\Delta\overline{\mathrm{PSV}}$ values, $\Delta\overline{\mathrm{PSV}}_{\mathrm{disturbed}}$, and the mean of the reference lake $\Delta\overline{\mathrm{PSV}}$ values, $\Delta\overline{\mathrm{PSV}}_{\mathrm{reference}}$; and tested if this difference was significantly less than zero ($\alpha = 0.05$) with a permutation test that randomized the observed $\Delta\overline{\mathrm{PSV}}$ values across disturbed and reference lakes 1000 times. We performed paired analyses of the 16 disturbed-reference lake pairs and unpaired analyses of the 18 disturbed lakes and 16 reference lakes; both supported identical conclusions (see Results). We similarly assessed non-phylogenetic compositional change with species richness ($\Delta\overline{\mathrm{SR}}$), Shannon evenness ($\Delta\overline{\mathrm{EVE}}$), and natural log total abundance ($\Delta\overline{\mathrm{TA}}$). Appendix S3 contains time-series plots of the metrics for all 34 lake data sets.

We compared our observed data to distributions created under two null models to further test the significance of the observed overall disturbance-phylogenetic effect. The first (null 1) randomized each lake data set by maintaining the observed species richness of each zooplankton sample, while shuffling species prevalence across the samples (i.e., species prevalence is the number of samples that contained each species). This model tested if disturbance induced decreases (or increases) in species richness explained the observed disturbance-phylogenetic effect. The second (null 2) did the opposite. It randomized presence/absence across the pre-disturbance-disturbance boundary by maintaining the observed species prevalence, but allowing species richness to vary. This tested, if the observed disturbance-phylogenetic effect was an artefact of phylogenetic signal in overall species prevalence, not disturbance. For clarity, given a data matrix that contains all the samples of a lake with samples as rows and species as columns, null 1 randomized the presence/absence of species within rows and null 2

randomized within columns. Each lake was randomized with each model 2000 times to create null distributions of mean difference (i.e., $\overline{\Delta PSV}_{disturbed} - \overline{\Delta PSV}_{reference}$), $\overline{\Delta PSV}_{disturbed}$, and $\overline{\Delta PSV}_{reference}$. The observed values were compared to these distributions at $\alpha = 0.05$ with a Bonferroni correction for multiple tests.

All analyses were performed in R with modified functions from the package PICANTE (Kembel *et al.* 2009)

Did environmental context influence the disturbance-phylogenetic effects?

We tested if the pre-disturbance environmental conditions of a lake (i.e., a zooplankton community's environmental context) affected the magnitude of the disturbance-phylogenetic effects. We regressed the 18 disturbed lake $\overline{\Delta PSV}$ values on six pre-disturbance covariates: mean pH, mean total phosphorus ($\mu g\ L^{-1}$), mean total nitrogen ($\mu g\ L^{-1}$), area (ha), maximum depth (m) and mean pre-disturbance species richness; and selected the best fitting models based on AIC. We did this also for the $\overline{\Delta SR}$, $\overline{\Delta EVE}$, and $\overline{\Delta TA}$ values. Variance inflation factors were used to test for multicollinearity in the fitted models (Fox & Monette 1992). The abiotic covariates were selected because they commonly affect lake zooplankton community composition (e.g., Tessier & Welser 1991; Arnott & Vanni 1993; Hoffmann & Dodson 2005), and pre-disturbance species richness may affect community resistance to disturbance (Ives & Carpenter 2007). Furthermore, low pH and phosphorus act as stressors to zooplankton communities, and communities in acidic or phosphorus-limited lakes might already contain stress-tolerant species (Elser *et al.* 2001; Keller *et al.* 2002). Communities in these lakes may respond differently to disturbance than communities in other lakes.

Were the species that decreased with disturbance responsible for the overall disturbance-phylogenetic effect?

We compared our observed $\overline{\Delta PSV}_{disturbed}$ and $\overline{\Delta PSV}_{reference}$ values to null data distributions created under three simple, but specific, hypotheses on potential causes. The first (null 3) maintained the pre-disturbance and disturbance species prevalence by separately randomizing samples within, instead of across as in null 2, the two time periods. This tested if the changes (both increases and decreases) in species prevalence from the pre-disturbance to the disturbance time period explain the observed effect. This model was our most conservative and was only rejected if there was a general propensity for closely related species to be found within the same sample more than expected based on their pre-disturbance and disturbance prevalence. The

second (null 4) tested if it was only the species that increased and the third (null 5) tested if it was only the species that decreased during disturbance that caused the observed effect. These models either maintained the observed data of species that increased with the disturbance (null 4) or the observed data of species that decreased with disturbance (null 5) while randomizing other species across the pre-disturbance and disturbance time periods maintaining their overall observed prevalence.

Were species sensitivities to disturbance phylogenetically conserved?

For the six lakes with the largest disturbance-phylogenetic effects (East, Tuesday, Clearwater, West, Lake 979 and Crystal), we fit the time-series of individual species abundances to disturbed covariate data using univariate first-order autoregressive models (AR1). These six lakes predominantly caused the overall disturbance-phylogenetic effect (see Results). For each species in each lake we fit

$$\mathbf{X}_t = a + b\mathbf{X}_{t-1} + c\mathbf{U}_t \tag{2}$$

where $\mathbf{X}_t$ is a vector of the natural log abundances of the species at time t, a is the intrinsic rate of population increase of the species in the lake, b governs the strength of density dependence (i.e., the first-order autocorrelation coefficient), $\mathbf{U}_t$ is a vector of the disturbed covariate values in the lake at time t, and c is the disturbed covariate coefficient that gives the response of the species to the disturbance (Ives *et al.* 2003; Helmus *et al.* 2007b). For each lake, we removed species with prevalence < 5% and matched the abundance sampling dates to the disturbed covariate sampling dates using linear interpolation on the latter. Disturbed covariate data were not available for Tuesday Lake, so we instead used a binomial covariate that designated samples as pre-disturbance or during disturbance. This covariate described the manipulation well — a constant period of very low planktivory artificially maintained with planktivore removals and piscivore additions (Tables 1 and S1). To address if the species sensitivities to disturbance were phylogenetically conserved, we used a phylogenetic regression based on the Ornstein-Uhlenbeck (OU) model of trait evolution to look for phylogenetic signal in the species response data (i.e., the disturbed covariate coefficients).

The OU process can be implemented as a phylogenetic branch-length transformation to reflect the amount of phylogenetic signal seen in a set of species trait data (Blomberg *et al.* 2003). The transformation is governed by the parameter d that gives phylogenetic signal strength. Low d values indicate low phylogenetic signal in the data and result in phylogenies with long tips and short basal branches — with $d = 0$ producing a complete star phylogeny. A $d = 1$ corresponds to the Brownian motion model of trait

evolution and no branch-length transformation occurs, and $d > 1$ indicates the trait data are more structured than expected given the phylogeny. In this case, the branch lengths at the base of the tree are elongated relative to the tips. Ives & Godfray (2006) use this OU implementation to derive a phylogenetic regression model to test for phylogenetic signal in species bipartite interaction data (e.g., parasite–host interactions).

We simplified the Ives & Godfray (2006) implementation to fit the observed species response data of each lake as

$$\mathbf{R} = b_0 + \varepsilon \tag{3}$$

where $\mathbf{R}$ is the vector of the n species responses to disturbance in a particular lake, b_0 is the phylogenetically corrected mean of the responses, and ε is a $n \times 1$ vector of zero-mean random variables with covariance matrix $\mathrm{E}[\varepsilon\varepsilon'] = \mathbf{W}(d)$. Phylogeny is incorporated as a phylogenetic covariance matrix into the matrix $\mathbf{W}$ with the d value estimated by generalized least squares (see appendix A in Ives & Godfray 2006). To ask if species sensitivities to disturbance were phylogenetically conserved, we fit this model to the species response data and compared its fit to the fit of the same model with $d = 0$.

We also asked, if the variation among species sensitivities could be explained better by body size than phylogeny. Body size is a key trait known to affect zooplankton sensitivities to disturbance (e.g., Brooks & Dodson 1965). The body size data were an average of length measurements made on individuals across lakes (Table S5). We added body size to the model as

$$\mathbf{R} = b_0 + \mathbf{S}b_1 + \varepsilon \tag{4}$$

where $\mathbf{S}$ is a $n \times 1$ vector of species body sizes, and b_1 is the body size regression coefficient. For each lake data set of species responses, we compared eqn 3 fit to eqn 4 fit to address, if phylogeny and/or body size better explained species responses. All model fits were assessed with AIC_c.

Were there clades of highly sensitive species?

Lastly, we tested if the overall disturbance-phylogenetic effect was caused by clades of highly sensitive (or insensitive) species by asking how well the species responses in one lake predict the species responses in another lake. For example, if species of the Copepoda clade are much more sensitive to all types of disturbance than species of the Cladocera clade, then even if no species are shared between two lakes undergoing different disturbances, the sensitivities of species in one lake can be well predicted with the known sensitivities of species in the other lake. For each of the six lakes, we calculated the predicted species sensitivity values from the other five

lakes and correlated these to the observed sensitivities. We then compared these correlations to correlations between the observed and predicted sensitivities estimated only with data from each lake.

Following appendix B in Ives & Godfray (2006), let $\mathbf{W}(\hat{d}) = \sigma^2\mathbf{V}$, where σ^2 is a scalar that gives the rate of species evolutionary divergence and $\mathbf{V}$ is a $n \times n$ phylogenetic covariance matrix that summarizes the correlation structure of a lake community phylogeny. Also let $\sigma^2\mathbf{V}_p$ be an $m \times n$ matrix giving the phylogenetic covariance among the m species in a lake whose sensitivities are to be predicted by the n observed sensitivities in the first lake. The m predicted values, $\hat{\mathbf{Y}}_p$, are then

$$\hat{\mathbf{Y}}_p = \hat{b}_0 - \mathbf{V}_p\mathbf{V}^{-1}(\mathbf{Y} - \hat{b}_0). \tag{5}$$

To predict the sensitivities of the n species of a lake using only the data of that lake, we removed each species in turn, recalculated $\hat{d}$ and $\hat{b}_0$, and then with these estimates and the observed sensitivities of the remaining $n{-}1$ species, used eqn 5 to make a prediction for the removed species.

RESULTS

Lakes contained more closely related crustacean zooplankton species during, than before, disturbance (Fig. 1). The unpaired mean difference between the 18 disturbed and 16 reference lake data sets (i.e., $\overline{\Delta\mathrm{PSV}}_{\mathrm{disturbed}} - \overline{\Delta\mathrm{PSV}}_{\mathrm{reference}}$) was significantly less than zero (-0.0267, $P < 0.01$); as was the paired difference between the 16 disturbed-reference pairs (-0.0225, $P < 0.05$). Phylogenetic species variability decreased in all three types of disturbed lakes, but there were no mean differences among disturbance types (biological: mean $-0.0180 \pm$ SE 0.0123; chemical: -0.0328 ± 0.0167; physical: -0.0467 ± 0.0351). Neither the null model that maintained the observed species richness of samples (null 1), nor the null model that maintained the overall observed prevalence of species across samples (null 2), were able to explain the decrease in PSV in the disturbed lakes (Table 2). The observed $\overline{\Delta\mathrm{PSV}}_{\mathrm{reference}}$ value (-0.0010) did not significantly differ from the null distributions produced by either model. Based on the estimated divergence dates of our phylogenies, the lake with the largest decrease in PSV, East Lake, experienced a 64 MYA per species loss of evolutionary history (i.e., $\overline{\Delta\mathrm{PSV}}_{\mathrm{East}}$: -0.1138 and 0.1138×562 MYA = 64 MYA). The mean decrease in PSV across all the disturbed lakes ($\overline{\Delta\mathrm{PSV}}_{\mathrm{disturbed}}$: -0.0277) corresponded to an average decrease of 16 MYA per species per lake (i.e., 0.0277×562 MYA = 16 MYA). Given that lake communities on average had 15 species, lakes on average lost around 240 MYA of evolutionary history when they were disturbed (i.e., 15×16 MYA = 240 MYA).
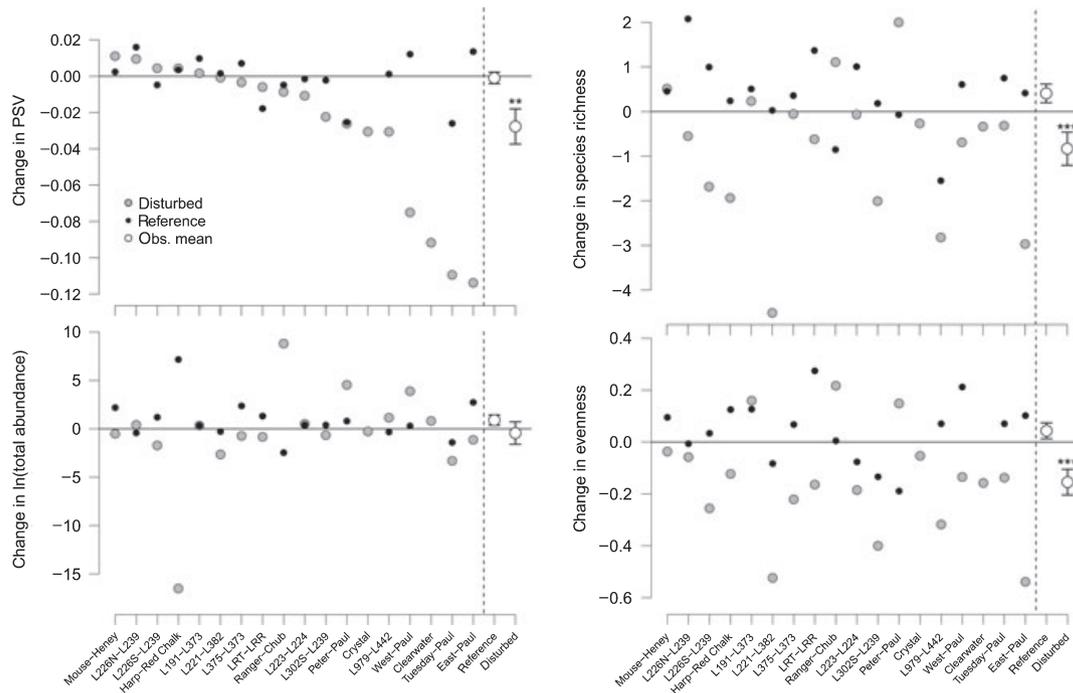
Figure 1 Lakes on average contained zooplankton communities with more closely related zooplankton species, fewer species and decreased evenness during disturbance events. Lower phylogenetic species variability (PSV) indicates communities composed of more closely related species. Lake pairs are identified along the *x*-axis as disturbed-reference and are arranged in descending order based on disturbed lake change in PSV values. This ordering highlights how change in PSV does not correlate with change in the other three metrics. Disturbed and reference lake means are given with standard errors. Asterisks (*) indicate if a disturbed lake mean is significantly different from a reference lake mean via a permutation test. Double symbols indicate $P < 0.01$ and triple symbols, $P < 0.001$.

The PSV metric, species richness and evenness all decreased with disturbance, but $\Delta\overline{\text{PSV}}$ was not correlated with the other metrics ($\Delta\overline{\text{SR}}$: $r = 0.1012$, $P = 0.690$; $\Delta\overline{\text{EVE}}$: $r = 0.2745$, $P = 0.270$; $\Delta\overline{\text{TA}}$: $r = -0.1095$, $P = 0.665$; Fig. 1). Species richness and evenness were strongly correlated with each other ($r = 0.8760$, $P < 0.001$); and mean total abundance did not change with disturbance across lakes and was not correlated with the other metrics ($\Delta\overline{\text{SR}}$: 0.4473, $P = 0.063$; $\Delta\overline{\text{EVE}}$: $r = 0.3315$, $P = 0.179$). These results indicate that PSV summarized community change quite differently than the other metrics.

Environmental context influenced how strongly disturbance affected zooplankton phylogenetic community composition (Table 3). Disturbance affected phylogenetic community composition most in lakes that were prior to disturbance acidic, small and deep. For the 18 disturbed lakes, the best fit linear model explained 64% of the variation in $\Delta\overline{\text{PSV}}$; and the best fit models explained 24, 13 and 34% of the variation in $\Delta\overline{\text{SR}}$, $\Delta\overline{\text{EVE}}$, and $\Delta\overline{\text{TA}}$ respectively (Table 3). Variance inflation factors for covariates in all models were all < 1.4, and thus < 5, a cutoff value that suggests multicollinearity.

Null model analyses indicated that both species increases and decreases during disturbance caused the overall

disturbance-phylogenetic effect (Table 2). Neither the null model that only randomized the presence/absence of species that decreased with disturbance (null 4), nor the model that only randomized species that increased with disturbance (null 5) could explain the overall disturbance-phylogenetic effect. However, the null model that maintained the observed pre-disturbance and during disturbance prevalence of each species (null 3) explained our data well (Table 2).

Species sensitivity to disturbance within communities was phylogenetically conserved (Table 4; Fig. 2). All species response data (i.e., AR1 disturbed covariate coefficients) were best fit with models containing OU parameters greater than zero; and three of the six lakes showed higher phylogenetic signal than expected from Brownian motion evolution (i.e., $d > 1$). Species sizes significantly explained variation only in Tuesday Lake. When the responses of species in this lake were regressed on body size, phylogenetic signal increased from $d = 0.33$ to $d = 2.30$.

There were no clades of species that were generally sensitive (or insensitive) to all types of disturbance (Fig. 2). Thus, correlations between observed and predicted species responses made among lakes were very low (mean correlation: $-0.03 \pm$ SE 0.05) in comparison to the

Table 2 Null model tests on the causes of the observed disturbance-phylogenetic effect

				Difference between disturbed and reference lakes			Disturbed lakes			Reference lakes		
				Mean difference	0.05 Quantile	0.004 Quantile	Mean	0.05 Quantile	0.004 Quantile	Mean	0.05 Quantile	0.004 Quantile
Observed data				−0.0267			−0.0277			−0.0010		
Null data name	randomized	maintained	maintained									
Null 1	across		richness	**−0.0001**	−0.0101	−0.0162	**0.0000**	−0.0076	−0.0114	0.0001	−0.0073	−0.0114
Hypothesis: disturbance induced changes in richness caused the observed disturbance-phylogenetic effect. REJECTED												
Null 2	across		prevalence	**−0.0019**	−0.0086	−0.0124	**−0.0021**	−0.0082	−0.0111	−0.0002	−0.0031	−0.0047
Hypothesis: phylogenetic signal in species overall prevalence, not disturbance, caused the observed disturbance-phylogenetic effect. REJECTED												
Null 3	within		prevalence				−0.0252	−0.0280	−0.0297	−0.0029	−0.0046	−0.0063
Hypothesis: changes in species prevalence during disturbance (increases and decreases) caused the observed disturbance-phylogenetic effect. FAILED TO REJECT												
Null 4	across/decreases		prevalence increases				**−0.0157**	−0.0226	−0.0258	0.0040	−0.0001	−0.0027
Hypothesis: only species that increased with disturbance caused the observed disturbance-phylogenetic effect. REJECTED												
Null 5	across/increases		prevalence decreases				**−0.0136**	−0.0191	−0.0220	0.0047	−0.0009	−0.0047
Hypothesis: only species that decreased with disturbance caused the observed disturbance-phylogenetic effect. REJECTED												

Bolded null mean values highlight null hypotheses rejected at $\alpha = 0.004$ (Bonferroni corrected at $\alpha = 0.05$). 'across' indicates null models that randomized species presence/absence across disturbed-reference time periods. 'within' indicates the null model that randomized within disturbed-reference time periods. 'richness' and 'prevalence' indicate how null models randomized, either by maintaining the observed richness of samples or the observed prevalence of species. The tested hypotheses and our conclusions are written below the data of each null model. A permutation test was rejected if the associated observed mean value (given in the first line of the data table) was less than the 0.004 quantile of its null distribution.

Table 3 Best fit linear regressions of change due to disturbance in zooplankton community phylogenetic species variability (PSV), species richness (SR), Shannon evenness (EVE), and natural log total abundance (TA) on pre-disturbance variables

	PSV	R^2_{adj} = 0.64		SR	R^2_{adj} = 0.24		EVE	R^2_{adj} = 0.13		TA	R^2_{adj} = 0.34	
	Coef.	SE	*P*	Coef.	SE	*P*	Coef.	SE	*P*	Coef.	SE	*P*
Intercept	−0.2949	0.0574	0.0002***	−3.327	3.146	0.307	−0.6276	0.4491	0.183	10.7289	3.816	0.013*
pH	0.0393	0.0087	0.0005***	0.8573	0.5633	0.149	0.1247	0.0804	0.142			
ln(area)	0.0198	0.0055	0.0029**									
Depth	−0.0017	0.0008	0.0431*							−0.3624	0.1194	0.008**
SR before				−0.3737	0.1373	0.016*	−0.0402	0.0196	0.058	−0.7278	0.3539	0.058

Total phosphorus and nitrogen were not selected in any best fit model. 'SR before' is the mean number of species found in all samples of a lake before disturbance, 'Coef.' is the estimated coefficient, 'SE' is the estimated standard error, '*P*' is the probability significance value, *P < 0.05, **P < 0.01, ***P < 0.001.

Table 4 Phylogenetic regression estimates of phylogenetic signal (*d*) in species sensitivities to particular disturbances

Lake	Model description	*d*	Size coef.	SE	AIC$_c$ *star*	AIC$_c$ *phylo*	Within lake *r*	Among lakes mean *r*
East	Surface irradiance	**0.37**			−3.04	**−3.08**	0.39	−0.04
	Surface irradiance on size	0.27	−0.03	0.07	−2.77	−2.79		
Tuesday	Reduced planktivory	0.33			0.87	0.86		
	Reduced planktivory on size	**2.30**	1.10	0.37	1.02	**0.73**	0.58	−0.09
Clearwater	pH	**1.16**			1.72	**1.66**	0.23	0.01
	pH on size	3.75	0.60	0.46	2.42	2.21		
West	TDN	**0.28**			−12.73	**−12.75**	0.19	0.05
	TDN on size	0.23	0.00	0.00	−12.51	−12.54		
	TDP	**0**				**−8.93**		
	TDP on size	0	0.00	0.00	−8.76			
Lake 979	Water level	**0.39**			−3.645	**−3.71**	0.11	−0.22
	Water level on size	0.07	0.05	0.04	−3.63	−3.65		
Crystal	Invasive fish abundance	**1.87**			−0.45	**−0.94**	0.44	0.13
	Invasive fish abundance on size	1.84	−0.23	0.22	−0.45	−0.81		
Overall mean		0.91					0.32	−0.03

Bolded values highlight the lowest AIC$_c$ value and the best fitting linear model. '*star*' models were fit with *d* = 0. '*phylo*' models allowed *d* to vary. Larger *d* values indicate more phylogenetic signal. 'size' is the natural log of body length. TDN and TDP are total dissolved nitrogen and phosphorus. See Tables 1 and S1 for more details on lake disturbances. Correlations (*r*) are between the observed sensitivities of species and either predictions of species sensitivities based on the sensitivities of species within the same lake (within lake *r*) or predictions of species sensitivities based on the sensitivities of species in other lakes (among lakes mean *r*). The overall mean *d* is of the bolded values.

correlations between observed sensitivities and predicted sensitivities that were based on species responses within lakes (mean correlation: 0.32 ± 0.07; Table 4). Thus, phylogenetic signal in species sensitivities to disturbance allowed for adequate predictions to be made for species within lake communities, but not among lake communities.

DISCUSSION

Our results support the hypothesis that disturbance selects for assemblages of more closely related species. Across all disturbance types (biological, chemical, physical), the lake zooplankton communities we studied on average contained more closely related species during, than before, disturbance. These results were independent of species richness, evenness and total community abundance. Thus, a phylogenetic perspective on disturbance and community composition enriched our understanding beyond what we learned from standard, taxonomic metrics of community composition. The overall disturbance-phylogenetic effect was both caused by closely related species that increased and closely related species that decreased with disturbance. The net result was a large loss of evolutionary history in disturbed communities (i.e., ca. 240 MYA on average per community).
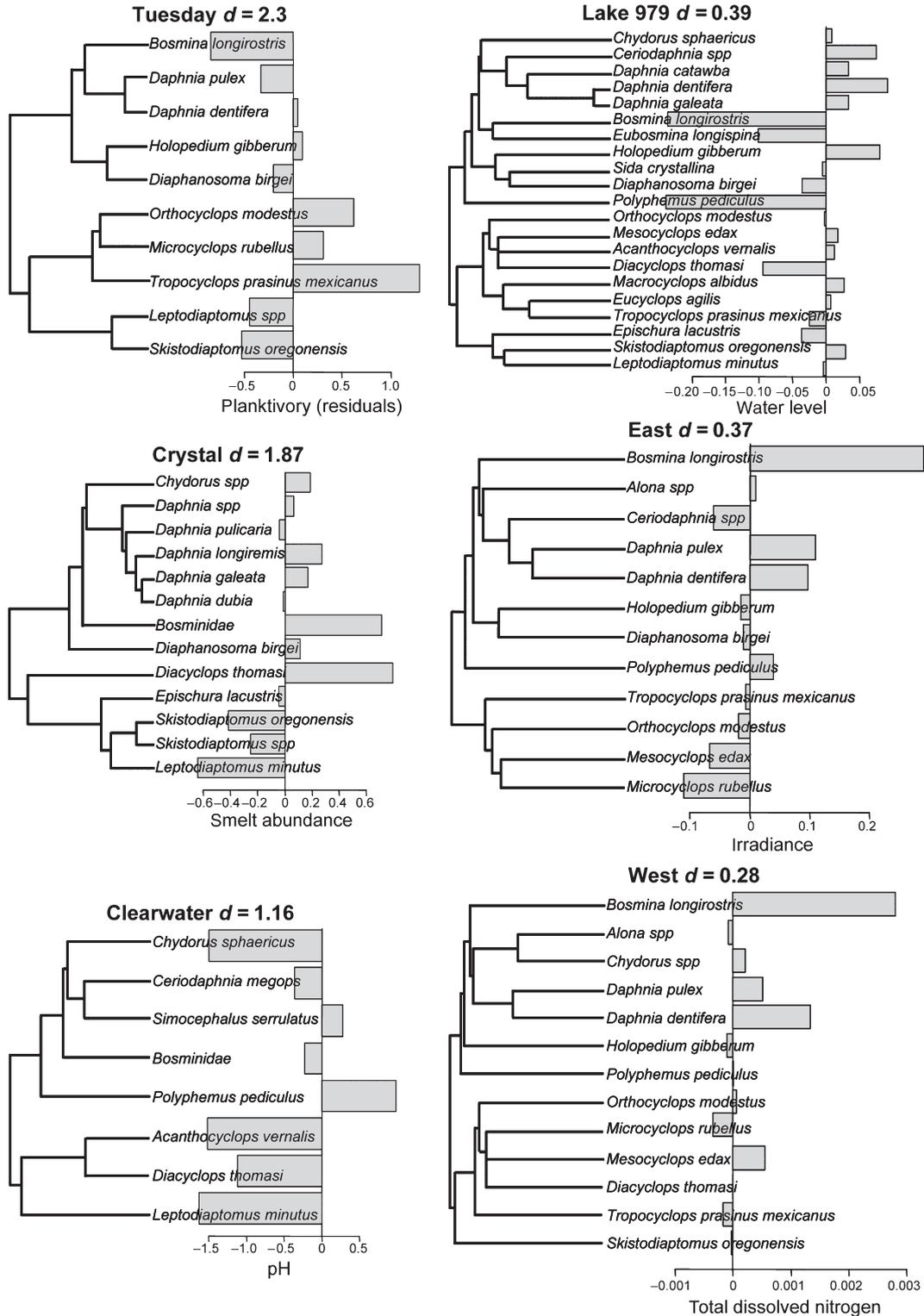
Figure 2 Species sensitivities to particular disturbances are phylogenetically conserved. Grey bars are estimated time-series coefficients of species abundance regressed on the disturbed covariate data for the six lakes with the lowest $\Delta\overline{PSV}$ (Fig. 1). The branch lengths of each community phylogeny are transformed by d, the Ornstein-Uhlenbeck measure of phylogenetic signal estimated in the best fitting phylogenetic regression model (see Table 4 and text for details). A $d > 1$ indicates strong phylogenetic signal and a $d < 1$ indicates weaker signal. The Tuesday Lake values are the residuals from a regression of the coefficients on body size.

However, the interpretation of a loss of evolutionary history due to disturbance must be made with respect to the resilience of the studied group of organisms. Zooplankton are prolific dispersers with fast generation times and dormant eggs that are abundant in lake sediments. These traits make zooplankton communities relatively resilient to disturbance (Allan 1976). For other communities of less-resilient species, the loss of evolutionary history due to disturbance may be long lasting or permanent if the disturbance is broad-scale enough to cause regional or global species extinctions (Purvis *et al.* 2000a).

Disturbed lakes whose zooplankton phylogenetic community composition changed most were acidic. Low pH is a stress to zooplankton and species tolerance to low pH may come at a cost of being less tolerant to other stressors (Vinebrooke *et al.* 2004). This may have resulted in larger disturbance-phylogenetic effects in lakes with low pH. Furthermore, three of our lakes underwent acidifications as their disturbance events (Little Rock, Lake 233, Lake 302S). Of these three lakes, Little Rock changed the least and had the lowest pre-disturbance pH (Fig. 1). Thus, our data suggest that stressed communities exhibit the greatest change in phylogenetic diversity when disturbed by a stressor dissimilar to the stress already experienced by the community.

Lakes that were small and deep also experienced large disturbance-phylogenetic effects. As pre-disturbance richness had no explanatory value, the effects of lake area and depth, both indicators of ecosystem size, do not appear to be related to species richness. We are uncertain as to the lake area effect, but zooplankton in deep lakes may have been impacted directly by disturbance and indirectly by altered planktivory rates. The lowest thermal layer of stratified lakes provides a deep-water predation refuge. Deep lakes have this refuge and shallow lakes usually do not. Any disturbance that impacts the refuge alters planktivory rates and possibly zooplankton phylogenetic community composition (Tessier & Welser 1991). Changes in predation pressure occurred in many of our lakes including those where predators were not directly manipulated (Frost *et al.* 1999; Carpenter *et al.* 2001; Vinebrooke *et al.* 2001).

Based on analyses of the six lakes with the largest disturbance-phylogenetic effects, species sensitivities to a particular disturbance within a particular lake community were phylogenetically conserved. This was not due to phylogenetic signal in a key trait, species body sizes. Body size only explained variation in the sensitivities of species to the disturbance of Tuesday Lake (Table 4, Fig. 2). This Tuesday Lake result supports the well-documented fact that fish predation affects zooplankton body size distributions (Brooks & Dodson 1965). Tuesday and Crystal Lakes both underwent disturbances that greatly modified fish plankti-

vory rates (see references in Table S1). The sensitivities of species in these lakes could be explained by body size (although the body size effect was not statistically significant in Crystal, Table 4). Yet, once the body size effect was accounted for, phylogeny still explained a significant amount of variation in the species sensitivity data (Table 4). Phylogeny explained more variation when body size was included in the Tuesday Lake phylogenetic regression model. Thus, while body size is a trait commonly associated with disturbance sensitivity and generally shows phylogenetic signal (Fisher & Owens 2004), species phylogenetic relationships may better explain species sensitivities to disturbance.

There were no generally resistant or sensitive clades (Fig. 2). Because of this lack of phylogenetic signal in the responses of species across disturbance types, we were not able to accurately predict species responses in one lake with the responses of close relatives in another lake. However, our measure of species sensitivity did not account for the indirect effects of species interactions (e.g., compensatory dynamics, Klug *et al.* 2000). In competitive communities the responses of species to disturbance depend both on disturbance sensitivities and the amplification of the disturbance by interactions among species (Ives *et al.* 1999). Therefore, better statistical tools such as multivariate time-series models that incorporate phylogeny and estimate species interactions must be developed to fully test how well phylogeny predicts species sensitivities across different communities and types of disturbance (Ives *et al.* 2003).

Our data suggest that the phylogenetic relationships among species can be used to assess anthropogenic impacts (Warwick & Clarke 1998; Abellán *et al.* 2006). Monitoring programs should be designed to look for shifts in the phylogenetic composition of communities as indication of ecosystem disturbance. However, monitoring programs should be careful when interpreting static temporal patterns of phylogenetic community composition as the ecosystem being monitored may not be conducive to phylogenetic responses. Incorporating phylogenetics into most monitoring programs should be relatively easy as phylogenies are increasingly available for little-studied species, and many tools are available to construct large phylogenies (e.g., Sanderson *et al.* 2008). Furthermore, our analyses with an informal supertree constructed by hand suggest that more complicated molecular-based phylogenetic reconstructions are not always necessary to detect phylogenetic responses to disturbance (Appendix S2).

Our work is only a preliminary step towards understanding how disturbance affects phylogenetic community composition. We advocate cross-system and cross-taxonomic group comparisons of both natural and anthropogenic disturbances. We suggest more community specific

studies to investigate the mechanisms of how a particular disturbance impacts species and how that translates into the overall pattern of community composition. Existing data sets, such as those from experimental mesocosm studies (e.g., Klug *et al.* 2000), should be reassessed in a phylogenetic context. We argue that incorporating phylogenetics into disturbance studies will lead to enhanced insight into community structure, more accurate predictions on how species may respond to future disturbance events, and a better understanding of how human-impacted ecosystems can be restored.

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SUPPORTING INFORMATION

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

Table S1 Full table of metadata for the lakes used in this study including references that describe the disturbances and zooplankton sampling protocols.

Table S2 The GenBank numbers of the sequences in our 16 phylogenetically informative clusters that we used to construct the crustacean zooplankton molecular phylogeny.

Table S3 Description and citations for our rational of the constrained nodes in our supermatrix parsimony analyses.

Table S4 Description and citations for our rational of the placement of species and nodes on our crustacean zooplankton informal supertree.

Table S5 Body size estimates of the species in the 6 lakes with the largest disturbance-phylogenetic effects.

Appendix S1 Phylogenetic reconstruction.

Appendix S2 Disturbance-phylogenetic effect analyses with an informal supertree.

Appendix S3 Time-series plots.

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