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The influence of extreme climatic events and human disturbance on macroinvertebrate community patterns of a Mediterranean stream over 15 y

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Abstract. We analyzed long-term changes in macroinvertebrate communities in a Mediterranean temporary stream in southern Portugal over 15 y (1993–2008) at 10 locations with 3 degrees of physicochemical disturbance (reference, high disturbance, and mild disturbance). We related year-to-year variation of macroinvertebrate communities to long-term (59 y) information on precipitation and temperature. Our goals were to: 1) determine the stability of macroinvertebrate communities in the stream, 2) establish the influence of physicochemical disturbance on community stability, 3) assess the influence of climate change on the macroinvertebrate communities, and 4) assess the interactive effects of climate change and disturbance level on macroinvertebrate communities. Community structure varied naturally from year to year, but changes in taxon richness and evenness were much stronger and more unpredictable in disturbed than in other sites. In the long term, the more diverse (reference) and the poorest (disturbed) communities were stable, whereas communities affected by mild disturbance slowly decreased in taxon richness (slope $= -0.07$, $r^2 = 0.38$). This decrease could be a response to the continuous stress or to climate change. The multivariate patterns over time of invertebrate communities at mildly disturbed sites were the only patterns significantly correlated with climatic patterns. In the past 59 y in this Mediterranean area (southeastern Europe), winter temperature has increased 1°C and precipitation has decreased 1.5 mm/d. Marked changes in community composition (70–80% Bray–Curtis dissimilarity) occurred only in years of extremely low precipitation or temperature. In years of climatic extremes and at chemically disturbed sites, Orthocladiinae and Simuliidae became dominant. In this stream, a shift in community equity occurs before species elimination. This shift might be useful as an early warning for biodiversity loss because of disturbance or climate change. We recommend continued sampling of reference sites for monitoring purposes so that effects of climate change can be established and so that contemporary human disturbance can be assessed relative to an adjusted reference condition.

Key words: long term, macroinvertebrates, chemical disturbance, climate changes, precipitation, temperature, extreme events, Mediterranean stream.

Macroinvertebrates are important components of freshwater ecosystems and are good indicators of stream health (De Pauw and Vanhooren 1983, Furse et al. 2006). However, temporal stability of invertebrate communities in streams over long time scales (>10 y) is not well understood (but see review by Jackson and Füreder 2006). Bioassessment based on the reference-condition approach (Reynoldson et al. 1997), where an ideal community is defined by reference sites, might be inaccurate when sites have been sampled over a short time interval (e.g., 1 or 2 y) because communities change naturally in time. The issue of temporal variability is becoming more important under a global-climate-change scenario in which reference conditions are expected to drift as temperature changes and extreme events increase in frequency

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and intensity (Easterling et al. 2000, Palmer and Räisänen 2002, Diffenbaugh et al. 2005, De Toffol et al. 2009).

The possible responses of biota to climate change are being studied (Easterling et al. 2000) in terms of ecosystem functioning (Hauer et al. 1997, Melack et al. 1997, Schindler 1997, 2001) and responses of individual invertebrate and fish species (Daufresne et al. 2004, Burgmer et al. 2007, Acuña et al. 2008, Tixier et al. 2009). However, these studies of streams in wetter climates might have only little relevance to Mediterranean systems, which are naturally subject to stress from high variability of flows and interruption of superficial water flow for several months during the dry period. Moreover, Mediterranean stream communities are composed of taxa adapted to such harsh conditions (Lytle and Poff 2004, Bonada et al. 2007).

Conservation programs like the Biodiversity Support Program of the World Wildlife Fund (http://www.worldwildlife.org/bsp/aboutus.html) are based on the assumption that more diverse communities contribute to healthier ecosystems that function better (because of higher trait diversity) and are more resistant to environmental change (McNaughton 1977, Chapin et al. 2000) than less diverse communities, but this assumption is still being discussed and tested (Johnson et al. 1996, Covich et al. 2004).

We began by assuming that more diverse communities would be better buffered against environmental changes than less diverse communities and tested the hypothesis that communities from unperturbed sites are more resistant to extreme climate events and, therefore, are more stable over time than communities subjected to human perturbation. However, human disturbance might mask or enhance the effects of extreme climatic events (Hauer et al. 1997). Most of Europe has undergone intensive historical land use, so the ability to predict combined effects of climate change and physical and chemical disturbance is important.

We analyzed: 1) the stability of macroinvertebrate communities of a Mediterranean temporary stream system over 15 y, 2) the influence of human disturbance on community stability by comparing changes in communities at reference sites and sites with different degrees of disturbance (mildly disturbed and disturbed sites), 3) the influence of climate changes (extreme events and continuous change of mean winter precipitation and temperature) on the macroinvertebrate communities, and 4) the relative influence of climate changes on invertebrate communities under different levels of disturbance.

Methods

Study area

We analyzed data from 10 study sites distributed along an ~30-km stretch of a temporary Mediterranean stream in southern Portugal. Rainfall in this region is highly seasonal and the landscape is flat. Streams generally flow during 3 mo of the year and are reduced to ponds during summer. The stream substrata are dominated by sedimentary rocks and a mixture of sediment types from bedrock to sand. Biological samples were collected in late winter (February) over a period of 15 y (1993–2008). In February, stream flow is normally uninterrupted, and air temperatures range from 10 to 15°C.

The stream receives industrial effluent, and chemical disturbance is caused by increases in NO_3, SO_4, and Cu concentrations, which lead to high conductivity. Our data were taken from 10 biomonitoring sites, which we classified as reference (3 sites), disturbed (3 sites), and mildly disturbed (4 sites) on the basis of the degree of impairment observed in the physical and chemical data and biological assessments made over time (Coimbra et al. 1996).

Climate data

We used temperature and winter precipitation (January–March) data collected between 1950 and 2009 at the nearest station (~40 km) of the Institute of Meteorology (IM), Portugal, for evidence of climate change because the climate data measured at the study area did not cover the whole study period (1993–2008). Winter precipitation and temperature measured at the nearest IM station were highly correlated (Pearson correlation: $r = 0.708$, $p < 0.05$ for temperature and $r = 0.812$, $p < 0.001$ for precipitation) with the available data from the study area (1995–2008).

Physical and chemical data

We collected water samples for analysis of NO_3 (mg/L; molecular absorption spectrometry, method 624; NP 1972), SO_4 (mg/L; volumetric method, M017; internal laboratory method, certified in 2008), PO_4 (mg/L; molecular absorption spectrometry, methods SMEWW4500P-B, E; APHA 1999), Fe (mg/L; flame atomic absorption spectrometry, method SMEWW3030P-F; APHA 1997), Cu (mg/L; flame atomic absorption spectrometry, method ISO8288; ISO 1986), and alkalinity (mg/L; volumetric method, ISO9963-1; ISO 1994). Conductivity (μS/cm) and temperature (°C) were measured in situ with a field meter (330i/SFT; WTW, Weilheim, Germany). We plotted means

($\pm$1 SD) for the 3 disturbance groups (reference, disturbed, and mildly disturbed) from 1995 to 2008 (no physicochemical data were available from before 1995) and plotted the data for visual inspection.

Biological pattern data

We sampled macroinvertebrates with a kick net and identified them to the highest possible taxonomic resolution (generally species and genus) (described by Coimbra et al. 1996). Mediterranean streams are highly variable over the year because of fluctuations in water level and temperature (Gasith and Resh 1999, Bêche et al. 2006). The community is most diverse and more Plecoptera and Ephemeroptera taxa occur in this stream during flowing conditions (winter–early spring) than at other times of the year (Coimbra et al. 1996). Therefore, we sampled in only 1 season (late winter) to reduce natural variability in the biological data and the consequent noise in data analyses.

We expressed taxon richness in terms of the Margalef index (d) for all sites and sampling occasions as:

$$d=(S-1)/\log(N)$$

where S is the number of taxa and N is the number of individuals in the sample. Margalef's index is a measure of the number of taxa present for a given number of individuals and, therefore, is less dependent on sample size than is the total number of taxa (Clarke and Warwick 2001). We calculated the year-to-year variability in taxon richness as the absolute difference in taxon richness between consecutive years and compared the variance of the differences among disturbance groups.

We analyzed for differences among the communities of the 3 disturbance groups with nonmetric multidimensional scaling analysis (NMDS) of a site $\times$ taxon abundance matrix after double $\sqrt{(x)}$-transformation (which produced the most clear patterns) to reduce the weight of very abundant taxa (Primer, version 6; Primer-E Ltd, Plymouth, UK). NMDS provides a visual representation of the pattern of proximities of n objects so that the interpoint distances correspond to dissimilarities between objects (Kruskal 1964).

We tested for differences in communities among the disturbance groups with analysis of similarity (ANOSIM; 999 permutations; Primer 6). ANOSIM is based on rank similarities between samples in the underlying triangular similarity matrix (Clarke and Warwick 2001). We used similarity percentages (SIMPER; Primer 6) to determine % dissimilarity among disturbance groups and to identify those taxa that most strongly contributed to the differences. SIMPER uses a species Bray–Curtis similarity matrix to compute the average dissimilarity between all pairs of intergroup samples and disaggregates this average into separate contributions from each species (Clarke and Warwick 2001). No transformation was applied to obtain a list of the discriminant taxa ordered by their frequency in the various sites of each group and by their real abundance.

We used a 2nd-stage analysis of multiple Bray–Curtis similarity matrices (double $\sqrt{(x)}$-transformation), each one based on the sites sampled in 1 y (15 matrices) to investigate whether the communities changed over time and whether the patterns of similarity between sites were constant over the years (i.e., highly correlated). The routine calculates the Spearman rank correlation between pairs of matrices, and builds a new similarity matrix based on the correlation coefficients. This matrix is then used for 2nd-stage cluster analysis (hierarchical agglomerative clustering) as described in Clarke and Gorley (2006). We repeated the analysis for the sites in each disturbance group.

We used k-dominance curve plots (Primer 6) to analyze patterns in evenness and taxon richness over time for each disturbance group. In k-dominance curve plots, taxa are ranked in decreasing order of abundance on each date, and their percentage of total abundance in the sample (y-axis) is plotted against increasing rank (x-axis). The y-axis is cumulative relative abundance. Therefore, curves for years with higher evenness begin lower on the y-axis and extend further along the x-axis before reaching 100% abundance. Curves for years with lower evenness and low diversity begin higher on the y-axis and reach 100% abundance quickly.

We ran SIMPER with untransformed abundance data for the years that experienced extreme events to compare community structure between years with extreme and normal climate conditions and to produce a list of the taxa responsible for the differences. We grouped years on the basis of temperature and precipitation. High precipitation/temperature years had the highest peaks during the study period (1993–2008) in Fig. 1. Low precipitation/temperature years had the lowest peaks in Fig. 1. Years with moderate precipitation/temperature had a ratio of precipitation/mean precipitation or temperature/mean temperature for 1950–2009 of $\sim$1.

We tested for interactive effects of climate and disturbance with RELATE (Primer 6.0). This routine uses Spearman rank correlation to test for the absence of a relationship between 2 similarity matrices and

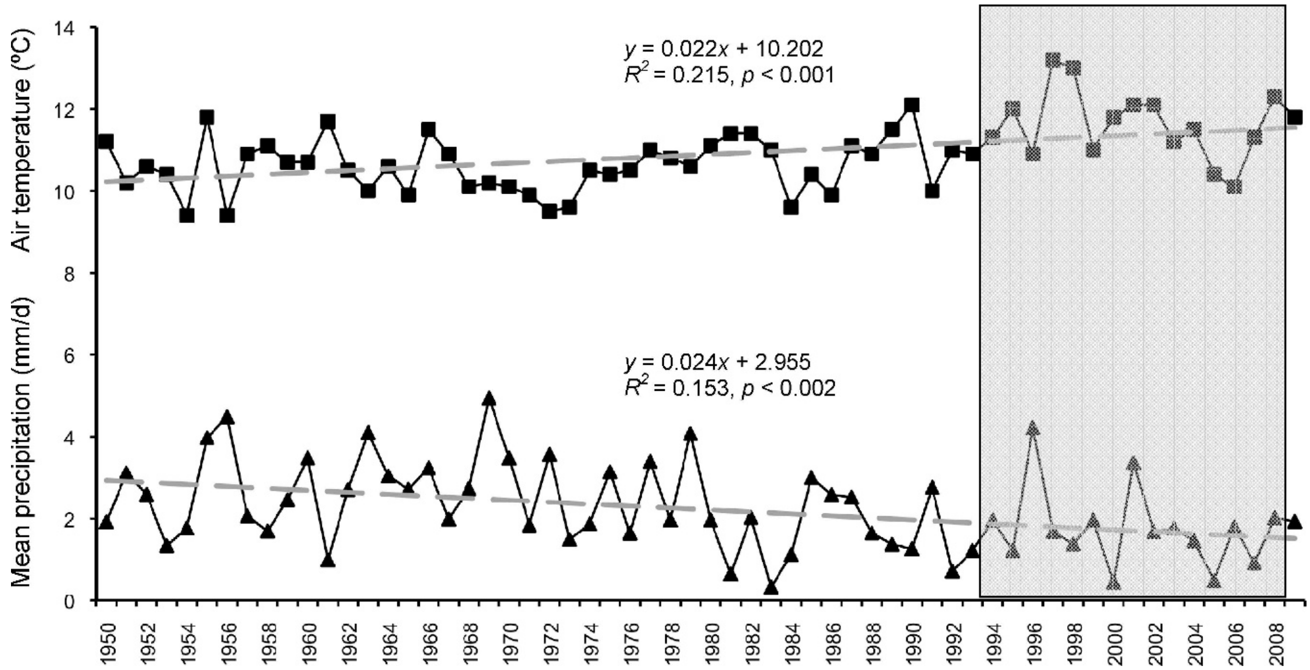

FIG. 1. Plots for mean winter daily precipitation and mean winter air temperature (°C) vs year (1950–2008) and the equations and R^2 values of the linear regression for the period 1950 to 2009. The study period is indicated in gray.

compares the outcome with results from randomly permuted samples. The output is a p statistic and a ρ value that can be used to compare the results of different tests. We used double $\sqrt{(x)}$-transformed abundance data for all taxa sampled between 1993 and 2008 and Bray–Curtis similarity to obtain the biological matrix. We used normalized (to reduce the effect of different measurement scales) winter temperature and precipitation data and Euclidean distance to obtain the abiotic matrix. We analyzed data separately for each disturbance group.

Results

Physicochemical and climatic patterns

From 1950 to 2008, mean winter air temperature increased ~1°C, and mean winter daily precipitation decreased ~1.5 mm/d (Fig. 1). From ~1967 to 1983, winter temperature was similar from year to year. Biological data were available for the period 1993 to 2008. During this period, the years 1996 and 2001 had extremely high precipitation (highest positive deviations from the tendency line), and the years 2000 and 2005 had low precipitation (highest negative deviations from the tendency line). Winter temperatures were highest in 1997 and 1998 and lowest in 2006. However, the deviation from the tendency line was smaller for mean air temperature than for precipitation. During the study period, dry years were much more frequent than wet years. The years 1996 and 2001 were the wettest during the study period, but precipitation in these years was within the normal range for the period before 1993. On the other hand, precipitation during the driest years during the study period (2000 and 2005) was extremely low for the whole 59-y period. A similar situation was evident for the air temperature. Winter temperatures in 1997 and 1998 were the highest during the study period and for the 59-y period, whereas the lowest temperature for the study period (2006) was within the normal range for the period before 1993.

Values of most physical and chemical variables related to human disturbance, especially conductivity, NO_3, and SO_4, were lowest at reference sites and highest at disturbed sites and had intermediate values at mildly disturbed sites (Fig. 2A–H). Water temperature did not vary among the 3 disturbance groups (Fig. 2A). The concentrations of Cu were often higher in disturbed sites and had similar values in reference and mildly disturbed sites (Fig. 2E). Variation was generally higher at disturbed than at reference sites.

Biological variables

We counted >134,000 specimens and identified 135 different taxa in the 160 invertebrate samples. NMDS of all sites based on macroinvertebrate communities

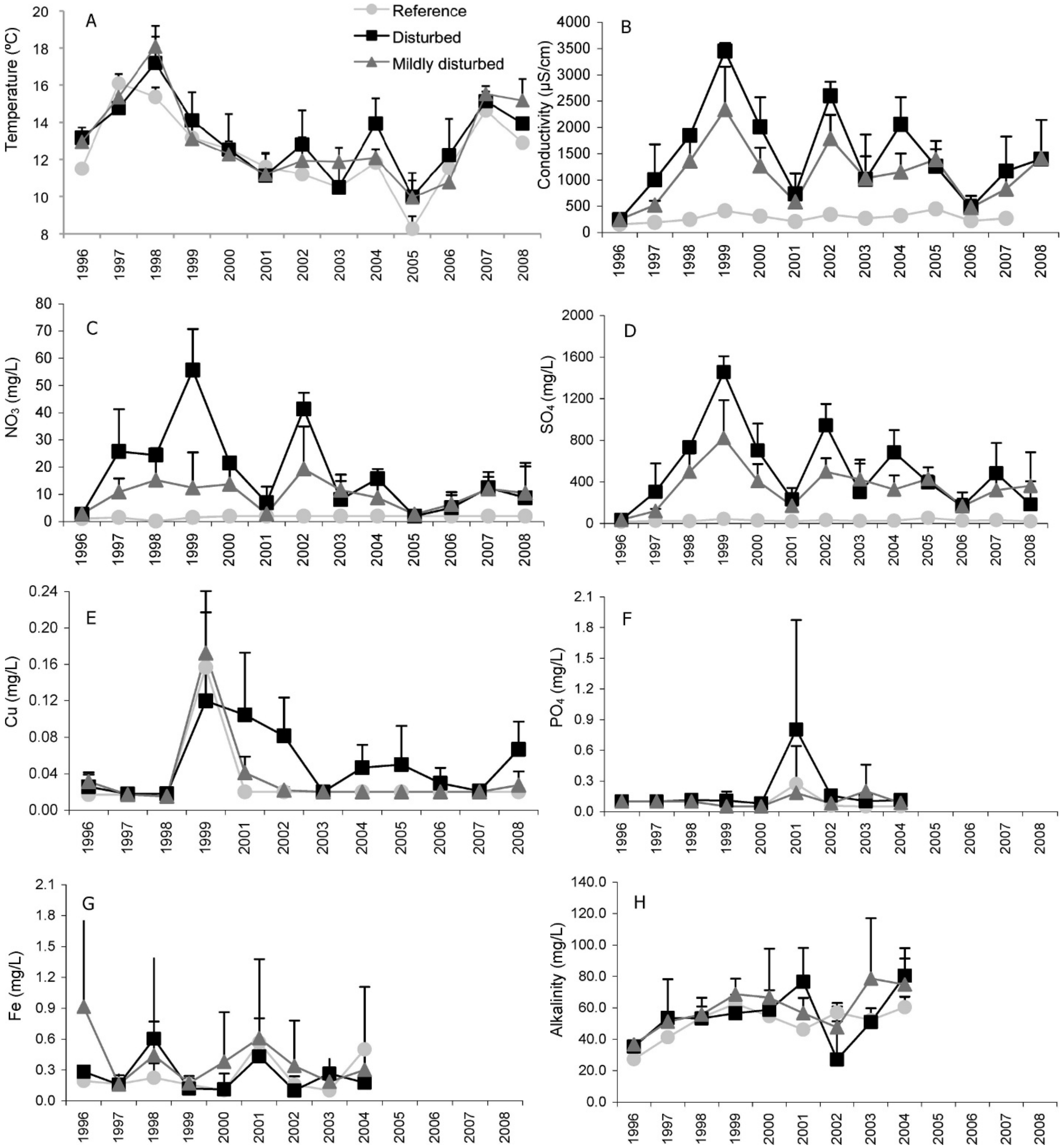

FIG. 2. Mean (±1 SD) winter temperature (A), conductivity (B), NO_3 (C), SO_4 (D), Cu (E), PO_4 (F), Fe (G), and alkalinity (H) of the water between 1996 and 2008.

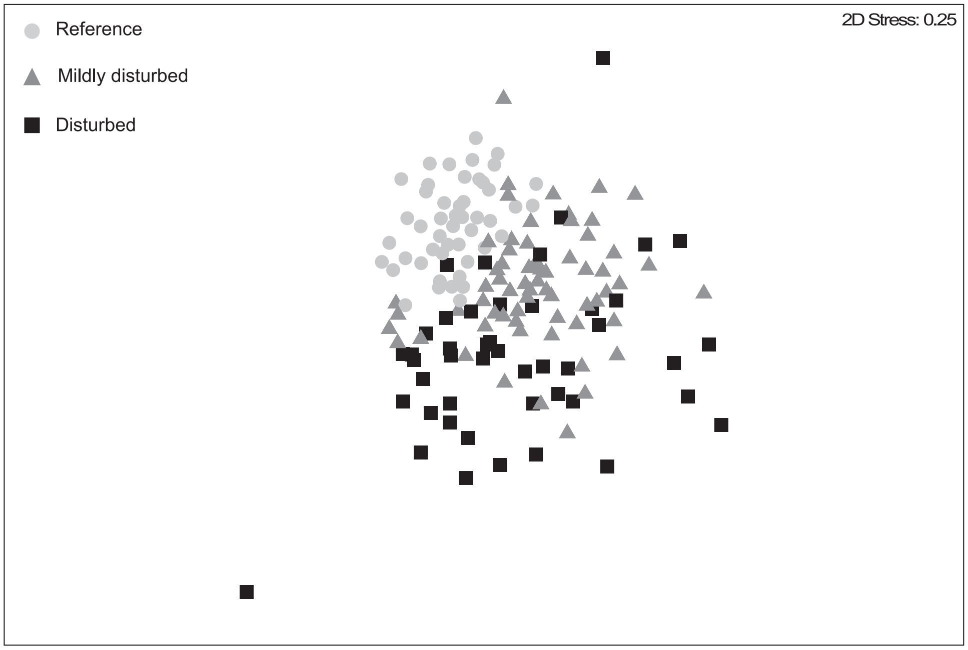

FIG. 3. Nonmetric Multidimensional Scaling (NMDS) plot for sites based on invertebrate composition in winter samples collected annually from 1993 to 2008. Sites are coded by disturbance group (reference, disturbed, and mildly disturbed). 2D = 2 dimensional.

discriminated the 3 a priori defined groups of sites (reference, disturbed, and mildly disturbed) as biologically distinct (Fig. 3). Communities were less variable among reference sites than among disturbed or mildly disturbed sites.

Taxon richness was greatest at reference sites and tended to increase over the 15-y study, whereas taxon richness tended to decrease at the mildly disturbed and disturbed sites over the study period (Fig. 4). Year-to-year differences were greater at disturbed

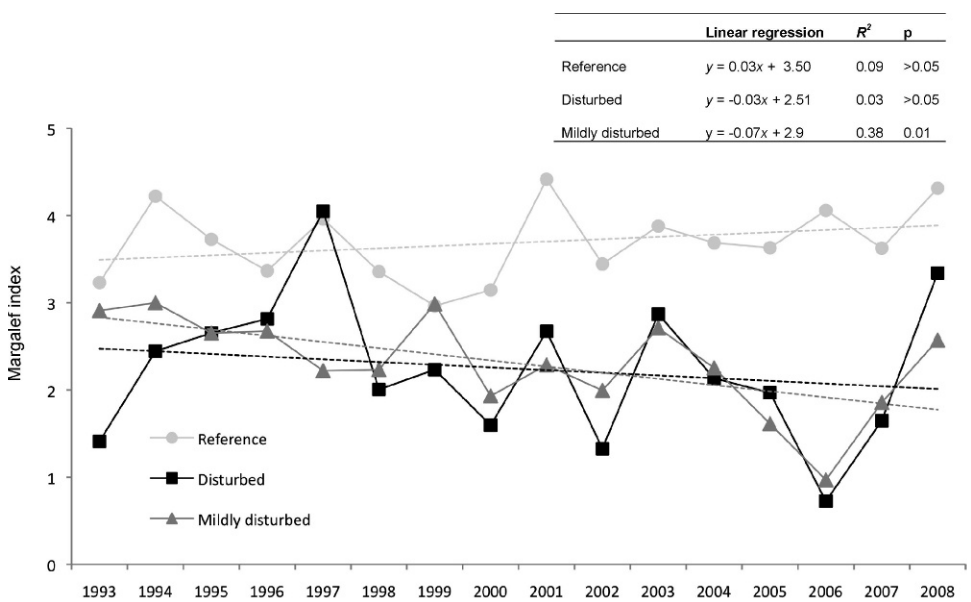

FIG. 4. Mean taxon richness (Margalef index) vs year (1993–2008) for sites grouped by disturbance level (reference, disturbed, mildly disturbed) and respective linear regressions.

TABLE 1. Analysis of Similarity (ANOSIM) results for global and pairwise tests between reference, disturbed, and mildly disturbed sites.

Test	R	p
Global	0.359	0.001
Pairwise tests		
Reference vs disturbed	0.442	0.001
Reference vs mildly disturbed	0.405	0.001
Disturbed vs mildly disturbed	0.26	0.001

(variance = 0.350) than at mildly disturbed (variance = 0.099) and reference sites (variance = 0.108).

Community structure differed significantly among disturbance groups despite high variability within groups (ANOSIM, Global $R = 0.359$, $p < 0.001$). Pairwise tests revealed significant differences between all pairs of groups ($p < 0.001$; Table 1). Reference and disturbed sites were the most dissimilar (SIMPER, 88%), whereas disturbed and mildly disturbed sites were less dissimilar (79%). Taxa that contributed most to the dissimilarities among groups were Chironomidae (especially Orthocladiinae and Tanypodinae), Simuliidae, *Micronecta* sp., Coenagrionidae (more abundant at disturbed sites), Ephemeroptera (*Baetis*, *Cloeon*, *Caenis*), Plecoptera (*Nemoura*, *Tyrrenoleuctra*, *Choroterpes picteti*, *Isoperla*), and Coleoptera (*Oulimnius*; almost absent from disturbed sites and more abundant in reference sites) (Table 2). Two taxa, Tanytarsini and *Atyaephyra desmarestii*, were more abundant in mildly disturbed sites than in reference or disturbed sites.

Macroinvertebrate communities were less variable between years (more predictable) at reference than at disturbed or mildly disturbed sites (Fig. 5A–C), particularly in the years 1995–1997 and 2002–2008, and had maximum correlation coefficients = 1 (2$^{\text{nd}}$-stage clusters; Fig. 5A). Correlations between years were weakest for mildly disturbed sites (Fig. 5C). For these sites, years were clustered into 2 large groups with almost no correlation between groups and correlation coefficients that were <0.5 within groups. The communities at mildly disturbed sites in year 2000, a very dry year, were very different from communities in all other years (Fig. 5C).

Evenness and taxon richness were higher at reference sites than at disturbed or mildly disturbed sites (*k*-dominance curves; Fig. 6A–C). Evenness was low at disturbed sites, and a few taxa numerically dominated most of the samples (Fig. 6B). Evenness and richness were intermediate at mildly disturbed sites (Fig. 6C). Years of maximal and minimal evenness differed across disturbance groups. The curves were not sequential in time and showed no clear trend over the 15 y.

TABLE 2. Mean abundance of the taxa that contributed to up to 90% of Bray–Curtis similarity (similarity percentages analysis) between samples from sites with similar levels of degradation (reference, disturbed, mildly disturbed sites). Boldface indicates taxa with the highest mean abundance among the 3 groups of sites.

Taxon	Reference	Disturbed	Mildly disturbed
Simuliidae	117	**336.57**	285.55
Orthocladiinae	57.77	**247.45**	154.11
Caenis sp.	**130.83**	35.36	109.7
Micronecta sp.	28.65	**53.15**	12.47
Tyrrenoleuctra sp.	**50.94**	1.49	1.11
Cloeon sp.	**42.17**	4.19	9.89
Tanytarsini	36.58	66.62	**68.17**
Tanypodinae	18.1	**64.68**	15.48
Chironomini	27.46	**45.43**	30.13
Baetis sp.	**47.69**	5.51	26.2
Hydracarina	**30.52**	2.83	0.41
Nemoura sp.	**22.6**	0.26	1.33
Choroterpes picteti	**19.15**	0.02	0.89
Oulimnius sp.	**17.52**	0.53	0.56
Tubificidae	**14.54**	1.74	2.66
Isoperla sp.	**12.71**	2.23	6.22
Naididae	**18.92**	2.7	0.08
Ceratopogonidae	**9.98**	4.81	2.05
Atyaephyra desmarestii	8.04	0.02	**21.73**
Coenagrionidae	3.5	**8.62**	0
Hydropsyche sp.	0	0	**9.13**

Communities were 79 to 81% dissimilar among the 3 groups of years with different precipitation, but within-group variability was high (20–24%) (SIMPER; Table 3). The diversity and abundance of taxa were higher in years with moderate and high precipitation (favored taxa: *Isoperla*, *Tyrrenoleuctra*, *Platycnemis*, Coenagrionidae, *Caenis*, *Cloeon*, *Micronecta*, Hydracarina, and *Atyaephyra desmarestii*) than in dry years (favored taxa: Chironomini, Orthocladiinae, Simuliidae, and Tanypodinae) (SIMPER; Table 3).

Communities were 72 to 78% dissimilar between the groups of years with highest and lowest temperature, but within-group similarities were low (17–27%) (SIMPER; Table 4). *Atyaephyra desmarestii*, *Baetis*, Ceratopogonidae, and Hydracarina predominated in years with extreme high temperatures, and Chironomini, Orthocladiinae, and Simuliidae were favored in years with extreme low temperatures.

Climate, defined by temperature and precipitation, and macroinvertebrate community structure were significantly correlated at mildly disturbed sites (RELATE, $\rho = 0.219$, $p < 0.002$) but not at reference and disturbed sites ($\rho = 0.016$, $p < 0.381$; $\rho = 0.047$, p

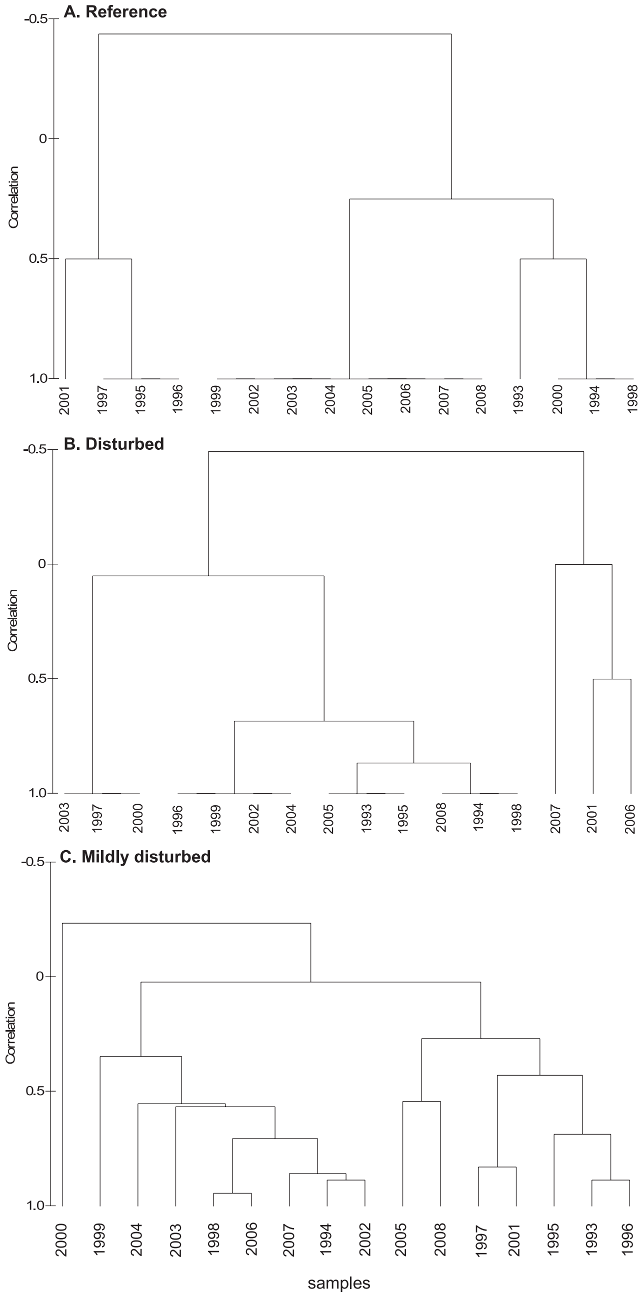

FIG. 5. Second-stage cluster analysis for reference (A), disturbed (B), and mildly disturbed (C) sites sampled from 1993 to 2008. The *y*-axis is Spearman's rank correlation coefficient (see text for details).

= 0.256; respectively). This result indicates that mildly disturbed sites are most likely to be affected by climate change.

Discussion

Mediterranean streams are naturally exposed to high variability in discharge with predictable floods and loss of connectivity (Gasith and Resh 1999, Lytle and Poff 2004, Bonada et al. 2006). Accordingly, we found that macroinvertebrate taxonomic composition and taxon richness fluctuates across years. However, our reference (taxon-rich) sites were more buffered against climate changes (Margalef richness oscillations < 3; Fig. 4) than were mildly disturbed sites (richness oscillations ≈ 5). However, communities at disturbed sites also were more stable than communities at mildly disturbed sites and changed mostly through abundances of Chironomidae and Simuliidae (Table 2).

Increases in temperature and decreases in precipitation in the previous 59 y are suggestive of the effects of climate change. The change in temperature values in our study area agree with the 0.6°C rise in temperature reported in the past 100 y by the IPCC (2001), but precipitation during the study period was almost always below the mean precipitation for the last 59 y (2.2 mm/d), a result that does not agree with the decadal increase of 0.5 to 1% (mostly in autumn and winter) reported by Walther et al. (2002). We did not observe evidence of response to climate changes in invertebrate communities at reference sites over time (Figs 5A–C, 6A–C).

On the other hand, extreme events, which are predicted to become more frequent because of global climate change (Easterling et al. 2000, Palmer and Räisänen 2002, Diffenbaugh et al. 2005, De Toffol et al. 2009), were accompanied by changes in community structure. Species losses and decrease in abundances did occur in years of low precipitation or temperature (Tables 3, 4). When precipitation was <1.8 mm/d below average or temperature was <0.6°C below average, communities shifted toward dominance by Chironomidae and Simuliidae, and most Plecoptera, Odonata, and Crustacea were lost. The effect of lower-than-average precipitation (drought) was stronger than the effect of higher-than-average precipitation (spates), a result that had been observed in other perennial and temporary streams (Canton et al. 1984, Boulton et al. 1992).

Winter precipitation is especially important for Mediterranean stream invertebrates. Therefore, the effects of the apparently continuous decrease in precipitation enhanced by water abstractions probably will cause major changes in stream communities, especially in sites with fewer taxa (but not in extremely low-diversity sites). We suggest that anthropogenic disturbances, such as chemical contamination, negatively affect the ability of stream communities to resist external disturbances without structural changes (Gregorius 2001) and the possibility of recovery (Gregorius 2001). Our *k*-dominance

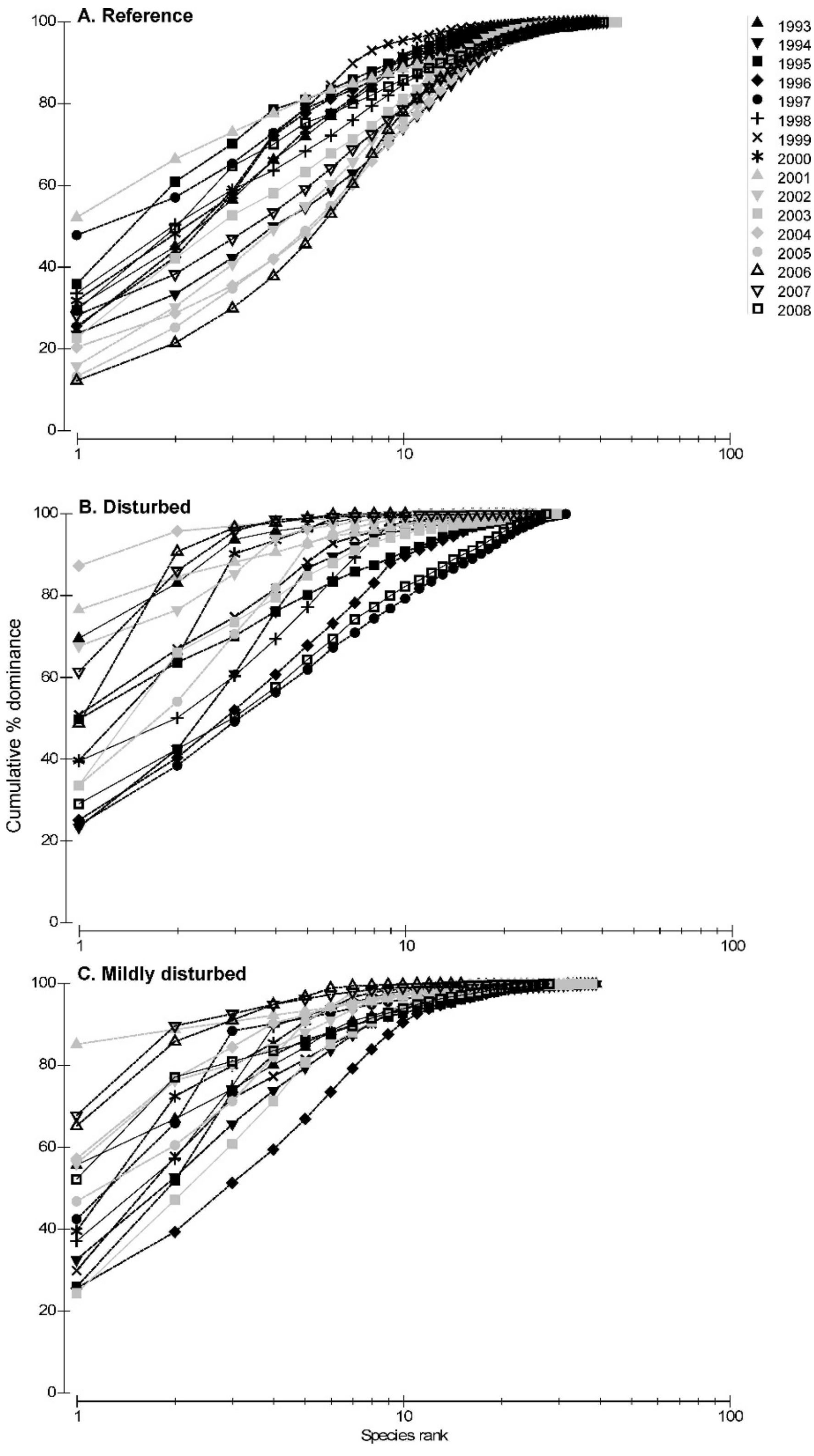

FIG. 6. *k*-dominance curves for mean invertebrate abundance at sites sampled from 1993 to 2008 at reference (A), disturbed (B), and mildly disturbed (C) sites.

Table 3. Mean abundance of the taxa that contributed up to 90% of Bray–Curtis similarity (similarity percentages analysis) between the samples of years with very high precipitation (1996, 2001), years with very low precipitation (2000, 2005), and years with moderate precipitation (1994, 1999, 2008). Boldface indicates taxa with the highest mean abundance among the 3 groups of years.

Taxon	High precipitation	Low precipitation	Moderate precipitation
Atyaephyra desmarestii	0	0	**17.5**
Caenis sp.	38.25	66.2	**123.8**
Ceratopogonidae	4.05	0	**5.4**
Chironomini	5.6	**41.05**	23.97
Cloeon sp.	0	0	**16.73**
Coenagrionidae	5.6	0	**7.27**
Hydracarina	**3.85**	0	0
Isoperla sp.	**4.25**	0	0
Micronecta sp.	42.85	0	**43.8**
Orthocladiinae	109.55	**244**	35.83
Platycnemis sp.	**2.6**	0	0
Simuliidae	24.2	**271.75**	98.9
Tanypodinae	5.2	**24.25**	7.2
Tanytarsini	4.1	29.25	**38.83**
Tyrrenoleuctra sp.	**35.6**	0	18.7

Table 4. Mean abundance of the taxa that contributed to up to 90% of Bray–Curtis similarity (similarity percentages analysis) between communities in years with very high temperature (1997, 1998), years with very low temperature (2006), and years with moderate temperature (1993, 1996, 1999, 2003, 2007). Boldface indicates taxa with the highest mean abundance among the 3 groups of years.

Taxon	High temperature	Low temperature	Moderate temperature
Atyaephyra desmarestii	**9.6**	0	0
Baetis sp.	**63.65**	0	44.72
Caenis sp.	96.55	31.5	**113.44**
Ceratopogonidae	**7.85**	0	4.8
Chironomini	14.35	**29.5**	25.62
Coenagrionidae	0	0	**3.74**
Hydracarina	**10.4**	0	0
Micronecta sp.	0	0	**34.06**
Orthocladiinae	127.95	**169.9**	106.88
Simuliidae	165.95	**326.9**	283.48
Tanypodinae	16.05	0	**35.68**
Tanytarsini	0	0	**29.74**
Tyrrenoleuctra sp.	10.8	0	**24.84**

plots (Fig. 6A–C) indicated that a shift in community evenness occurs before taxon elimination, a pattern that also was observed by Chapin et al. 2000. This shift could be used as an early warning for biodiversity loss. Sustainable management should focus on maintaining ecosystem resilience because doing so might enable stream communities to absorb changes (Scheffer et al. 2001, Folke et al. 2004).

We expect that results similar to ours will be found for other Mediterranean stream assemblages, such as macrophytes (Hughes et al. 2009), algae (Sabater et al. 1992), and riparian trees (Salinas and Casas 2007) that are directly (current velocity, connectivity) or indirectly (nutrient availability) dependent on hydrology. However, this possibility can be tested only with long-term data series. Fish communities of Mediterranean streams apparently recover well from droughts, but the effect of extreme and long-lasting climate changes might lead to the decline or extinction of the most sensitive species (Magalhães et al. 2003, 2007).

If climate change results in increased extreme climatic events, we predict a general decrease in taxon richness in intermittent streams, with the loss of rheophilic taxa, such as Plecoptera and Odonata, and an increase in abundance of Chironomidae and Simuliidae. This prediction is in agreement with results of a recent long-term study in Australian streams (New South Wales; Chessman 2009), where families of invertebrates that live in faster-flowing habitats and cold waters were most likely to have declined during a 13-y period of decreasing rainfall and river flow.

Future research should focus on determining whether taxonomic changes in the invertebrate communities caused by extreme events also have repercussions for ecosystem functioning, or if instead, functional overlap among species could mitigate the effects of taxonomic changes. Such research also could help disentangle the effect of natural climate variability on macroinvertebrate communities (e.g., Margalef richness oscillations; Fig. 4) from changes caused by extreme events because less fluctuation is expected from communities with trait profiles that are less susceptible to rainfall and temporal variability (Bêche et al. 2006, Bêche and Resh 2007). A multiple-traits approach also could be a useful alternative for studying a system affected by multiple stressors (e.g., discharge variation, climate change, and chemical disturbance in the study stream) because individual trait categories can have specific responses to different stressors (Bonada et al. 2007, Statzner and Bêche 2010).

If industrial development in the Mediterranean area results in physicochemical perturbations in streams, then the species erosion and decreased functionality of systems might be amplified under climatic change. Our results are relevant in the light of the application of the European Water Framework Directive (Directive 2000/60/ EC; EUWFD 2000). The directive states that streams should reach a "good ecological status" by 2015. However, if the reference conditions are taken from historical and past biological data, under a global change scenario, we might introduce error caused by changes that are independent of land use and human activities in the catchment. Therefore, for monitoring purposes, regular assessment of reference sites will be needed to adjust classification systems for climate-induced changes because invertebrate communities are expected to change over the medium to long term.

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