Molecular Ecology (2009) **18**, 1137–1144 doi: 10.1111/j.1365-294X.2009.04102.x

Parallel changes in genetic diversity and species diversity following a natural disturbance

GUILLAUME EVANNO,*†‡ EMMANUEL CASTELLA,§ CÉLINE ANTOINE,§ GABRIELLE PAILLAT§ and JÉRÔME GOUDET*

**Department of Ecology and Evolution, Biophore, University of Lausanne, 1015 Lausanne, Switzerland, †INRA, UMR 985 ESE, Ecology and Health of Ecosystems, 35000 Rennes, France, ‡Agrocampus Ouest, UMR 985, 35000 Rennes, France, §Laboratory of Ecology and Aquatic Biology, University of Geneva, 18 chemin des Clochettes, 1206 Genève, Switzerland*

Abstract

We examined the spatial and temporal variation of species diversity and genetic diversity in a metacommunity comprising 16 species of freshwater gastropods. We monitored species abundance at five localities of the Ain river floodplain in southeastern France, over a period of four years. Using 190 AFLP loci, we monitored the genetic diversity of *Radix balthica*, one of the most abundant gastropod species of the metacommunity, twice during that period. An exceptionally intense drought occurred during the last two years and differentially affected the study sites. This allowed us to test the effect of natural disturbances on changes in both genetic and species diversity. Overall, local (alpha) diversity declined as reflected by lower values of gene diversity H_S and evenness. In parallel, the among-sites (beta) diversity increased at both the genetic (F_{ST}) and species (F_{STC}) levels. These results suggest that disturbances can lead to similar changes in genetic and community structure through the combined effects of selective and neutral processes.

Keywords: beta diversity, biodiversity, disturbance, floodplain, gastropods, genetic structure

Received 21 July 2008; revision revised 5 December 2008; accepted 17 December 2008

Introduction

Understanding how variation is generated and maintained is a central question in both ecology and evolutionary biology. Genetic and species diversities are two fundamental measures of biodiversity. These measures have been mainly studied separately, and it is only recently that comparisons between these two levels of biodiversity have been developed (review in Vellend & Geber 2005). Antonovics (1976) already recognized that the patterns of species and genetic diversity share a similar determinism (see also Hu *et al*. 2006). Random drift, migration and selection/competition influence the evolution of allele frequencies in populations as well as the identity and the abundance of species in communities (Aarssen 1983; Hubbell 2001; Vellend 2005). Mutation influences genetic diversity, and speciation influences species diversity, but both factors affect populations and communities at a larger timescale than the three other forces. If migration, drift and selection act in parallel on genetic and species diversities, a positive relationship between these two levels is expected, henceforth called the species-genetic diversity correlation (SGDC, Vellend 2004). Reviewing studies documenting a SGDC, Vellend & Geber (2005) found that a positive correlation was the most frequent pattern, although the sign of the SGDC could also be negative (Karlin *et al*. 1984), and one study did not find any significant SGDC (Odat *et al*. 2004).

Results from two recent studies suggested that a positive SGDC is likely to arise in habitats undergoing a disturbance, affecting species diversity and genetic diversity (Vellend 2004; Cleary *et al*. 2006). At a local scale, disturbances (e.g. fire, drought, floods etc.) may decrease population size and thus genetic diversity due to random genetic drift (e.g. Otto & Whitlock 1997). Similarly, a decrease of the total number of individuals in a local community (i.e. community size) could produce a diminution of species diversity via community drift (Orrock & Fletcher 2005; Vellend 2005). Alternatively, selective pressures imposed by the disturbance may also lead to the diminution of genetic diversity and species diversity through the differential survival of certain genotypes or species, respectively (Vellend 2005). As a

Correspondence: Guillaume Evanno, Fax: +33 2 23 48 54 40; E-mail: guillaume.evanno@rennes.inra.fr

result, local (also called 'alpha') species and genetic diversities can be expected to decrease following a disturbance (Vellend 2004; Cleary *et al*. 2006). The among-sites component of diversity (i.e., 'beta' diversity) can also be influenced by a disturbance. Environmental filtering (i.e. counter-selection) of species vulnerable to the disturbance in every site might lead to an increased similarity across sites, hence to a decreased beta diversity (Chase 2007). Such an effect may also influence genetic diversity at selected loci. In contrast, genetic and community drift will tend to lower the similarity among populations and communities, potentially leading to a higher beta diversity following the disturbance (Vellend 2004).

These theoretical predictions suggest that drift and selection may have different effects on beta diversity. Studies based on experimental communities found a lower species beta diversity among disturbed communities consistent with an environmental filtering of species vulnerable to the disturbance (Chase 2007; Jiang & Patel 2008). In contrast, for both genetic and species diversity, Vellend (2004) found a higher structure in secondary forests than in primary forests of central New York State (USA). This latter result is consistent with a major role for community drift. As a result, it seems that a pattern of increased beta diversity is more likely to be revealed under natural conditions than under experimental settings. An additional explanation to Vellend's finding may be that in natural communities, the intensity of a disturbance can vary among sites. Drift and selection may alter species and genetic diversities in heavily disturbed sites, while the patterns of diversity could be more stable in localities undergoing a lower degree of disturbance. Such a spatial heterogeneity in the intensity of disturbances could then contribute to the overall dissimilarity among sites. So far, this hypothesis has not been investigated in studies measuring a SGDC. In addition, no study has yet undertaken a temporal approach to measure genetic and species beta diversities both before and after a disturbance.

Here, we investigate the outcome of a natural disturbance on species and genetic diversities in a metacommunity of freshwater gastropods living in a floodplain habitat located in southeastern France. We used species abundance data collected in 1999, 2002 and 2003 to describe the changes in species diversity in five water bodies. Genetic data collected in 2001 and 2003 on *Radix balthica*, an ubiquitous species of the metacommunity, were used to document the recent changes in genetic diversity. An extended period of drought occurred from 2002 to 2003 (Luterbacher *et al*. 2004; Mouthon & Daufresne 2006) and differentially affected the five study sites. We took advantage of this drought to test whether genetic diversity and species diversity respond similarly to an exceptional natural disturbance. Based on previous empirical and theoretical studies of the effects of disturbances on genetic and species diversity (Vellend 2004; Orrock & Fletcher 2005; Cleary *et al*. 2006; Chase 2007), we made three predictions: (i) both genetic and species alpha diversity should be lower after the disturbance; (ii) genetic beta diversity inferred from neutral markers should increase following the diminution of local population size-enhancing random genetic drift; and (iii) species beta diversity should increase due to community drift and/or heterogeneous effects of the disturbance among sites.

Materials and methods

Study sites and community surveys

The five study sites are floodplain pools located in cut-off meanders of the Ain river, southeastern France (see Figure S1, Supporting information). PL is located in the former meander called 'Le Planet', while BX1 and BX2 and PN1 and PN2 are situated in the meanders called 'Les Brotteaux' and 'Puits-Novet', respectively (Figure S1 and Table S1, Supporting information). In order to quantify the intensity of the disturbance, we estimated the number of days during which each site dried out (see Appendix S1, Supporting information, for a description of the methods used). Drought-frequency data revealed that between 1998 and 2003 BX1, PL and PN2 almost never completely dried out whereas BX2 and PN1 dried out for 30% of that period (Table S2, Supporting information). However, drought frequency was not equal across the years, and from April 2002 to March 2003, BX2 and PN1 dried out 72% longer than during the period October 2000–September 2001. These results clearly show that from 2002 to 2003, an exceptional drought period affected our study area (see also Mouthon & Daufresne 2006). This exceptional drought period was observed all over Western Europe (see for instance Chuine *et al*. 2004 or Luterbacher *et al*. 2004).

Four dates were kept, at which the species diversity of (almost) all five sites was surveyed: September 1999, September 2002, and April and September 2003. Three to 10 quadrats (50×50 cm) were taken in each pool (Antoine 2002), and the aquatic vegetation and the upper sediment were thoroughly sampled with a hand net (500 μm mesh). The material collected was kept in 70° alcohol and sorted under binocular in the laboratory. Gastropods were identified and counted, empty shells were not included. We used the nomenclature of Falkner *et al*. (2001).

Molecular analyses

For the genetic analyses, we used *Radix balthica* (L. 1758), a lymnaeid gastropod that was the only species present in all five water bodies over the study period. Snails were collected in September 2001 and April 2003. Between 17 and 30 individuals were sampled in each site at each time, and a foot sample was used for DNA extraction (Evanno *et al*. 2006). Genetic diversity analyses were performed using

the amplified fragment length polymorphism (AFLP) method. The AFLP procedure was carried out on a total of 247 individuals using two selective primer combinations: E-ACT × M-CTG and E-AGG × M-CAT, which produced 109 and 81 polymorphic bands, respectively (see Evanno *et al*. 2006 for a detailed description of the protocol). Electrophoreses were run on an automated sequencer ABI 377, fragments being visualized using GENESCAN 3.1.2. (Applied Biosystems) and scored with BINTHERE (Garnhart and Kocher, University of New Hampshire) according to Evanno *et al*. (2006). The AFLP data set is available online (Appendix S2, Supporting information).

Data analyses

To estimate genetic alpha diversity, we computed the gene diversity H_S (Nei 1987) for each population and sampling date using the software HICKORY 1.0 (option 'full model', Holsinger *et al*. 2002). Species alpha diversity was estimated by the evenness (E, similar to H_S), and by the species richness (SR, equivalent to allelic richness for codominant markers). H_S is the probability that two randomly chosen alleles at a locus in a population are different (Nei 1987). Likewise, the evenness [equal to $1 - \lambda$, λ being the Simpson (1949) concentration] here refers to the probability that two randomly chosen individuals in a locality are from different species. By considering the community as a single locus and species as alleles at this locus, evenness was calculated using FSTAT 2.9.3 (Goudet 1995). FSTAT is primarily designed to analyze diploid data but is also suitable for haploid data (as explained in the help file) and, thus, species-abundance data. To compare species diversity across the years, we estimated rarefied species richness by re-sampling 10 000 times 10 individuals (the lowest sample size) in each site using ECOSIM (Gotelli & Entsminger 2004). Importantly, the estimators we used (E, H_S and rarefied SR) are all robust to sampling artefact and thus to the unequal number of samples collected across sites and years.

Genetic structure across sites (or genetic beta diversity) was estimated by F_{ST}, the fraction of total genetic variance attributable to differences among populations. It is usually computed in an analysis-of-variance framework following Weir & Cockerham (1984) as:

$$F_{ST} \frac{\sigma_a^2}{\sigma_a^2 + \sigma_b^2 + \sigma_w^2}$$

where σ_a^2, σ_b^2 and σ_w^2 are the components of variance of allele frequencies among populations, between individualsand within individuals, respectively. To account for the dominant nature of the markers we used, F_{ST} was estimated by θ_B, a Bayesian equivalent of F_{ST} implemented in HICKORY (option 'full model': simultaneous estimation of f and θ_B) and by Φ_{ST} using ARLEQUIN 2.0 (Schneider *et al*. 2000). Credible intervals of 95% were computed for Bayesian estimates (Holsinger *et al*. 2002), and Φ_{ST} values were tested by 10 000 permutations in an analysis-of-molecular-variance (AMOVA) framework (Stewart & Excoffier 1996). Spatial pairwise Φ_{ST} were also computed between sites for the two sampling dates.

Similarly, we estimated the community structure (or species beta diversity) by computing F_{STC}, the exact equivalent of F_{ST}. F_{STC} refers to the proportion of total species diversity due to differences among communities and is computed as:

$$F_{STC} = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_b^2}$$

where σ_a^2 and σ_b^2 are the components of variance of species frequencies among localities and among individuals within localities, respectively ($\sigma_w^2 = 0$ since the community is considered as a haploid locus). Compared to genetic data, species data are often characterized by large differences in samples size across localities. For instance in 2003, although using the same sampling scheme, we found 41 individuals in BX2 and 1902 in PL (Table S3, Supporting information). For the genetic data, sample sizes were much more homogeneous since their range varied between 17 and 30 individuals. F_{ST} is based on a ratio of variance components estimated from a hierarchical analysis of variance of allele frequencies, and thus it weights samples according to their size (Weir & Cockerham 1984). For species data, the ratio of the largest to the smallest sample is 79. Variance components estimated from such unbalanced samples would give an enormous weight to the largest compared to the smallest sample. In order to give a similar weight to the different samples we used a rarefaction procedure: F_{STC} was repeatedly estimated from data sets consisting of 24 individuals (the lowest sample size from September 1999 and April 2003) sampled without replacement from each sample. The procedure was repeated 1000 times. For this rarefaction analysis, F_{STC} estimates were calculated using the HIERFSTAT package (Goudet 2005) for R (R Development Core Team 2006). We did not apply the rarefaction procedure to genetic data since F_{ST} is unlikely to be biased by small differences in sample size (Weir & Cockerham 1984).

Overall and pairwise F_{STC} were only computed for September 1999 and April 2003 in order to compare the results with those obtained from genetic data (collected in September 2001 and April 2003). Importantly, we used the statistic F_{STC} instead of standard measures of species beta diversity like Sorensen's or Jaccard's indices because we needed identical statistics for genetic and species data. To test whether genetic (respectively species) alpha diversity decreased after the disturbance we used pairwise t-tests to compare site-specific H_S (respectively E) computed in September 2001 (or September 1999) and April 2003. To test for an increase in beta diversity, we compared: (i) 95% credible intervals computed in HICKORY for pre- and post-disturbance global F_{ST}; and (ii) 95% confidence intervals calculated for

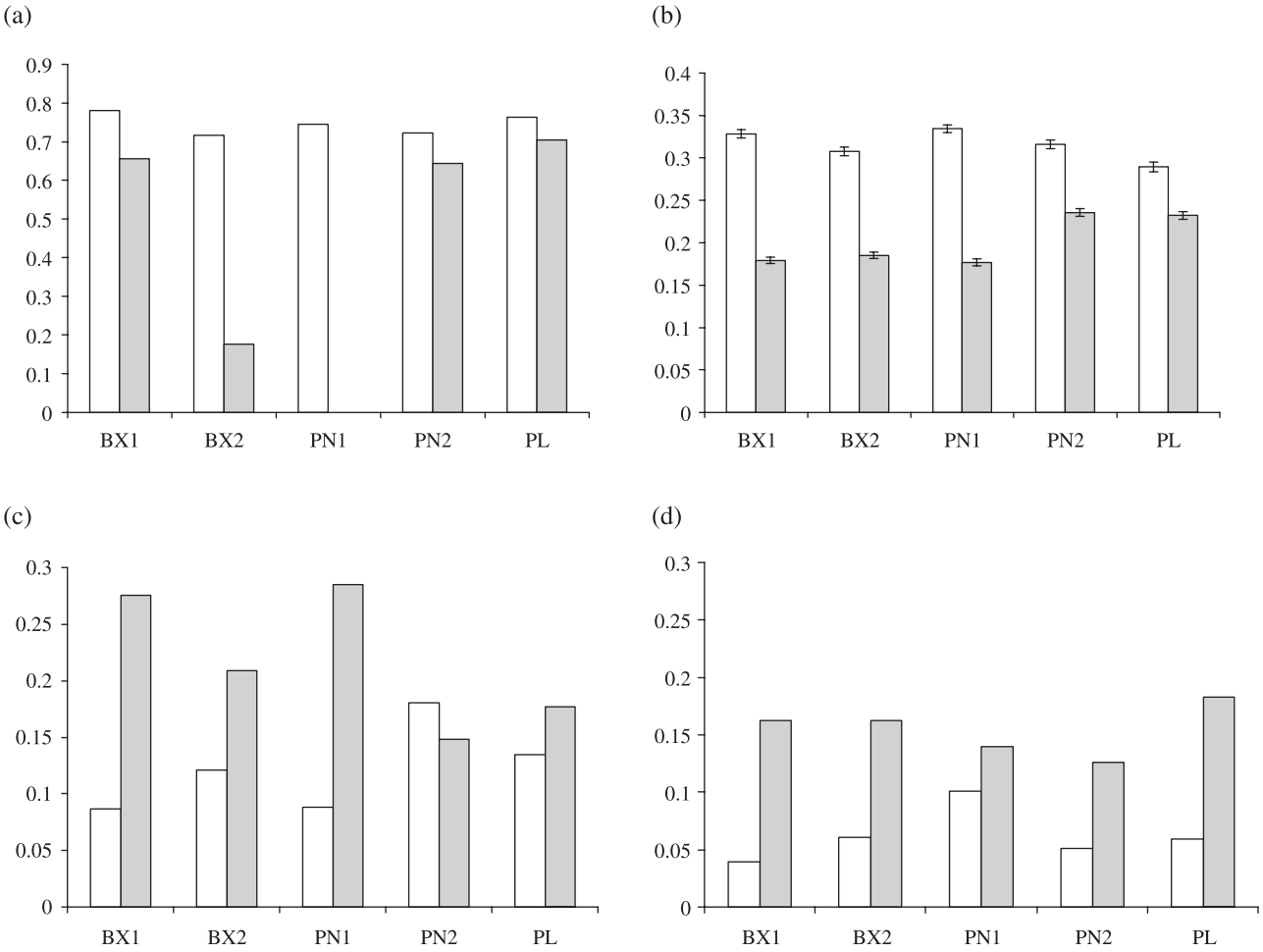

Fig. 1 Evenness (a) and gene diversity ±95% Bayesian CI (b) calculated for each site before (white) and after the disturbance (grey). F_{STC} calculated as the mean of pairwise F_{STC} for the focal site vs. all other localities (c), F_{ST} calculated similarly for each site (d).

the pre- and post-disturbance global F_{STC} from the rarefaction analysis. To test specifically for an increase in species beta diversity, we used the distributions of F_{STC} generated by randomizations above. We generated the distribution of the differences in F_{STC} after and before the disturbance and reasoned that under the null hypothesis of no difference in F_{STC}, this difference should not differ from zero. Under the alternative hypothesis of an increased beta diversity after the disturbance (one-sided test), this difference in F_{STC} should be positive, and very few values from the distribution should be negative. We thus estimated the probability that the two F_{STC} are equal as the proportion of differences less than or equal to zero.

Results

Species and genetic alpha diversity

We identified a total of 5228 individuals from 16 species, among which three were only present in 1999 and three others only in 2003 (see Table S3, Supporting information). Species richness over all sites was 13 in 1999 and 2003 (Table S3, Supporting information). Evenness averaged over all sites was 0.75 in 1999 and 0.44 in 2003. This decline is significant ($t = 2.2$, d.f. = 4, $P < 0.05$) and stronger in BX2 and PN1 than in BX1, PL and PN2 (Fig. 1a). Rarefied SR decreased from 1999 to 2003 in BX1, BX2 and PN1, whereas it remained stable in PN2 and PL (Fig. 2).

A similar decline was observed in gene diversity: computed over 190 polymorphic AFLP loci, H_S averaged over populations was 0.315 (Bayesian CI: 0.309–0.321) in 2001 and 0.202 (Bayesian CI: 0.198–0.206) in 2003. This significant reduction of gene diversity ($t = 5.8$, d.f. = 4, $P < 0.01$) was stronger in BX1, BX2 and PN1 than in PN2 and PL (Fig. 1b).

Species and genetic beta diversity

The decrease in species alpha-diversity was accompanied by a parallel increase in species beta diversity. Overall F_{STC} was 0.13 (95% CI: 0.07–0.18) in September 1999 and 0.23

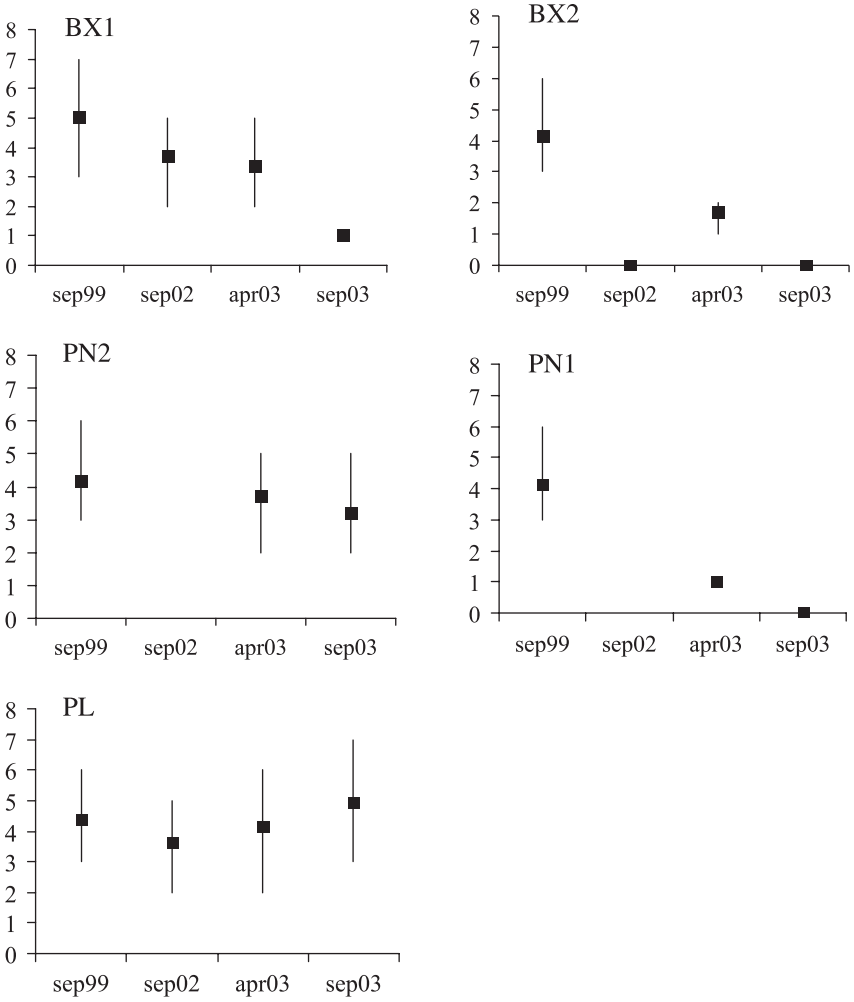

Fig. 2 Changes in rarefied species richness (±95% CI) in each site for four sampling dates from September 1999 to September 2003. Data for September 2002 are missing in PN1 and PN2. Data points without 95% CI represent samples with 10 individuals (the lowest sample size).

in April 2003 (95% CI: 0.17–0.30), the increase being significant between the two years ($P = 0.007$, one sided test based on 1000 randomizations). F_{STC} for each site (calculated as the mean of all pairwise F_{STC} for the focal population) are given in Fig. 1(c) and show the increase of global community structure from 1999 to 2003 with F_{STC} only decreasing slightly in PN2.

Similarly, genetic beta diversity significantly increased after the disturbance with overall θ_B and Φ_{ST} being 0.065 (Bayesian CI: 0.055–0.076) and 0.069 ($P < 10^{-5}$) in September 2001, and 0.169 (Bayesian CI: 0.148–0.192) and 0.160 ($P < 10^{-5}$) in April 2003, respectively (see also Table S4, Supporting information). F_{ST} for each site (calculated as the mean of pairwise Φ_{ST} of the focal population) revealed a strong increase in population structure from 2001 to 2003 (Fig. 1d).

Discussion

The striking result of this study is the parallel change in species and genetic alpha and beta diversities over a short time period during which a natural disturbance occurred. In 1999, species alpha diversity was high and evenly distributed across sites, hence beta diversity was low. In 2001, genetic alpha diversity was also relatively high and evenly distributed among *Radix balthica* populations. In 2003, the situation had drastically changed: following an extended period of drought that started in 2002, we observed a global loss of alpha diversity and an increase of beta diversity. Our initial predictions were validated: species- and genetic alpha diversity declined and species- and genetic beta diversity increased.

The main driver of loss in alpha diversity was probably the decrease of average water levels, which did not affect all sites similarly. From 1999 to 2003, genetic diversity and species diversity decreased in three sites — BX1, BX2 and PN1 — and remained relatively stable in two others: PN2 and PL. Importantly, the levels of species alpha diversity we observed in 1999 were similar to those found by Castella *et al*. (1991) in 1983, which suggests that the effect of the disturbance was not confounded by any long-term decline of species diversity in our study sites. In BX2 and PN1,

the effect of the disturbance was obvious since these sites dried out totally (Table S2, Supporting information). However, BX1 always kept surface water during the study period. Thus, the decline of species diversity observed was not due to the drying out of this locality; an alternative explanation is an increase of the predation pressure imposed by fishes when the volume of the pool was drastically reduced. From September 1999 to September 2003, fishes (*Tinca tinca*) known to feed on molluscs (Keith & Allardi 2001) were always observed in this pool. During this period, the density of *R. balthica* was low (like that of other species, see Table S3, Supporting information), and no individual snail was found in July and September 2003 in the reduced pool. As a result, predation by *T. tinca* is the most likely hypothesis to explain the reduction of species diversity in this site and the low *R. balthica* density. The increased predation level in drying out pools and the negative impact of fish on gastropod communities in confined habitats have been documented in previous studies (Dillon 2000; Lake 2003).

The temporal variation observed in populations of *R. balthica* suggests a strong effect of genetic drift due to a reduction in population size in PN1, BX2 and BX1 (see also Charbonnel *et al*. 2002; Trouvé *et al*. 2005). Gene diversity also slightly decreased in PN2 and PL (despite the fact that these ponds never completely dried out), which suggests that these populations underwent strong fluctuations. In addition to the strong reduction of their water volumes during the drought period, these sites were repeatedly flooded during the winter of 2002–2003, leading to potential fluctuations in population size and/or emigration events, which may have contributed to the observed changes in allele frequencies between 2001 and 2003.

In parallel to the global decline of alpha diversity, beta diversity increased as reflected by the rise of F_{ST} and F_{STC}. Importantly, F_{ST} and F_{STC} were unaffected by variations in sample sizes among populations and communities, as: (i) they are based on the ratio of variance components estimated from hierarchical analysis of variance of allele or species frequencies; and (ii) we applied a rarefaction procedure to account for the extremely large heterogeneity in samples sizes of species data. As Gotelli & Colwell (2001) pointed out, when comparing measures of diversity, it is essential that the statistics used are not affected by unequal samples sizes.

The increase in genetic beta diversity (F_{ST}) measured with AFLPs markers that are mostly neutral could be explained by: (i) amplified effects of drift due to a decline in population size in most sites; and possibly (ii) a reduction of the number of migrants, since F_{ST} depends on the number of migrants rather than on the proportion of migration. The higher post-disturbance species beta diversity could be explained by community drift (Vellend 2004). The intensity of the disturbance was probably strong enough to provoke a decrease in population size for all species in sites BX1, BX2 and PN1, providing the necessary conditions for community drift to occur. At the same time, drought imposed a strong selection pressure on gastropods living in these sites. It seems that *R. balthica* performed well in these harsh conditions since, among the five species present in all sites before the drought period, it was the only one still present in each of them after the disturbance (Table S3, Supporting information). In addition, the fact that the drought did not affect all sites equally may also partly explain the divergence in species' relative abundances among sites. In PN2 and PL, the two sites that were less influenced by the disturbance, we observed lower average F_{STC} than in the three other water bodies that were strongly affected by the drought. Consequently, this combination of strongly and weakly disturbed sites might have further enhanced the divergence among communities. Overall, these results based on a temporal approach are consistent with those of Vellend (2004) who suggested that genetic and community drift can influence natural populations and communities in a parallel manner. However, we suggest that the spatial variation in the intensity of the disturbance may also influence the divergence among communities.

Our results support the hypothesis that the changes observed in species and genetic diversity are best explained by a wide impact of drought via random drift and selection at several levels of biodiversity. Our results demonstrate the importance of studies combining population genetics and community ecology to address questions related to the spatial and temporal dynamics of biodiversity.

Acknowledgements

We thank C. Delucci and D. Savova-Bianchi for their help with molecular analyses, G. Falkner for his help with gastropod identification and D. McCrae for his help with sorting samples. We also thank J. Chave, P. Jarne, J. Jokela and N. Perrin for helpful discussions. We are grateful to R. Petit and three anonymous referees for helpful comments on the manuscript. This work was supported by grants from the Swiss National Science Foundation to E.C. and J.G. (no: 31-59326.99 and no: 3100A0-108194 to J.G.) and from the Société Académique Vaudoise to G.E.

References

Aarssen LW (1983) Ecological combining ability and competition combining ability in plants: toward a general evolutionary of coexistence in systems of competition. *American Naturalist*, **122**, 707–731.

Antoine C (2002) *Déterminismes Des Assemblages de Gastéropodes Aquatiques En Zones Alluviales (Rive Sud Du Lac de Neuchâtel-CH et Basse Plaine de l'Ain-F)*. PhD Thesis. University of Geneva.

Antonovics J (1976) The input from population genetics: 'the new ecological genetics'. *Systematic Botany*, **1**, 233–245.

Castella E, Richardot-Coulet M, Roux C, Richoux P (1991) Aquatic macroinvertebrate assemblages of two contrasting floodplains: The Rhône and Ain rivers, France. *Regulated Rivers*, **6**, 289–300.

Charbonnel N, Quesnoit M, Razatavonjizay R, Bremond P, Jarne P (2002) A spatial and temporal approach to microevolutionary forces affecting population biology in the freshwater snail *Biomphalaria pfeifferi*. *American Naturalist*, **160**, 741–755.

Chase JM (2007) Drought mediates the importance of stochastic community assemblage. *Proceedings of the National Academy of Sciences, USA*, **104**, 17430–17434.

Chuine I, Yiou P, Viovy N *et al*. (2004) Grape ripening as a past climate indicator. *Nature*, **432**, 289–290.

Cleary DFR, Fauvelot C, Genner MJ, Menken SBJ, Mooers AO (2006) Parallel responses of species and genetic diversity to El Nino Southern Oscillation-induced environmental destruction. *Ecology Letters*, **9**, 304–310.

Dillon RT (2000) *The Ecology of Freshwater Molluscs*. Cambridge University Press, Cambridge.

Evanno G, Castella E, Goudet J (2006) Evolutionary aspects of population structure for molecular and quantitative traits in the freshwater snail *Radix balthica*. *Journal of Evolutionary Biology*, **19**, 1071–1082.

Falkner G, Bank RA, Von Proschwitz T (2001) CLECOM-Project. Check-list of the non-marine Molluscan Species-group taxa of the States of northern, Atlantic and Central Europe (CLECOM I). *Heldia*, **4**, 1–76.

Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.

Gotelli NJ, Entsminger GL (2004) *Ecosim: Null Models Software for Ecology*, Version 7. Acquired Intelligence Inc. and Kesey-Bear. Jericho, VT. 05465. http://garyentsminger.com/ecosim/index.htm.

Goudet J (1995) FSTAT Version 1.2.: a computer program to calculate F-statistics. *Journal of Heredity*, **86**, 485–486.

Goudet J (2005) Hierfstat, a package for R to compute and test hierarchical *F*-statistics. *Molecular Ecology Notes*, **5**, 184–186.

Holsinger KE, Lewis PO, Dey DK (2002) A Bayesian approach to inferring population structure from dominant markers. *Molecular Ecology*, **11**, 1157–1164.

Hu XS, He F, Hubbell SP (2006) Neutral theory in macroecology and population genetics. *Oikos*, **113**, 548–556.

Hubbell SP (2001) *The Unified Neutral Theory of Biogeography and Biodiversity*. Princeton University Press, Princeton, NJ.

Jiang L, Patel SN (2008) Community Assembly in the presence of disturbance: a microcosm experiment. *Ecology*, **89**, 1931–1940.

Karlin AA, Guttman SI, Rathbun SL (1984) Spatial auto-correlation analysis of heterozygosity and geographic-distribution in populations of *Desmognathus-Fuscus* (Amphibia, Plethodontidae). *Copeia*, **2**, 343–356.

Keith P, Allardi J (2001) *Atlas des Poissons D'eau Douce de France*. Publications Scientifiques du M.N.H.N., Paris.

Lake PS (2003) Ecological effects of perturbation by drought in flowing waters. *Freshwater Biology*, **48**, 1161–1172.

Luterbacher J, Dietrich D, Xoplaki E, Grosjean M, Wanner H (2004) European seasonal and annual temperature variability, trends, and extremes since 1500. *Science*, **303**, 1499–1503.

Mouthon J, Daufresne M (2006) Effects of the 2003 heatwave and climatic warming on mollusc communities of the Saône: a large lowland river and of its two main tributaries (France). *Global Change Biology*, **12**, 441–449.

Nei M (1987) *Molecular Evolutionary Genetics*. Columbia University Press, New York.

Odat N, Jetschke G, Hellwig FH (2004) Genetic diversity of *Ranunculus acris* L. (Ranunculaceae) populations in relation to species diversity and habitat type in grassland communities. *Molecular Ecology*, **13**, 1251–1257.

Orrock JL, Fletcher RJ (2005) Changes in community size affect the outcome of competition. *American Naturalist*, **166**, 107–111.

Otto SP, Whitlock MC (1997) The probability of fixation in populations of changing size. *Genetics*, **146**, 723–733.

R Development Core Team (2006) R: A language and environment for statistical computing. *R Foundation for Statistical Computing*. Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Schneider S, Roessli D, Excoffier L (2000) *ARLEQUIN, Version 2.00: A software for population genetics data analysis*. Genetics and Biometry Laboratory, Department of Anthropology. University of Geneva, Switzerland.

Simpson EH (1949) Measurement of diversity. *Nature*, **163**, 688.

Stewart Jr CN, Excoffier L (1996) Assessing population genetic structure and variability with RAPD data: application to *Vaccinium macrocarpon* (American Cranberry). *Journal of Evolutionary Biology*, **9**, 153–171.

Trouvé S, Degen L, Goudet J (2005) Ecological components and evolution of selfing in the freshwater snail *Galba truncatula*. *Journal of Evolutionary Biology*, **18**, 358–370.

Vellend M (2004) Parallel effects of land-use history on species diversity and genetic diversity of forest herbs. *Ecology*, **85**, 3043–3055.

Vellend M (2005) Species diversity and genetic diversity: Parallel processes and correlated patterns. *American Naturalist*, **166**, 199–215.

Vellend M, Geber MA (2005) Connections between species diversity and genetic diversity. *Ecology Letters*, **8**, 767–781.

Weir BS, Cockerham CC (1984) Estimating F-statistics for the analysis of population structure. *Evolution*, **38**, 1358–1370.

This study was part of GE's PhD thesis supervised by EC and JG. GE now works on various aspects of evolutionary and conservation biology in fish. EC has a long-term interest in the ecology of wetland aquatic invertebrates and the restoration ecology of riverine floodplains. Under his supervision, CA and GP worked on the determinants of gastropod diversity in the Ain floodplain as part of their PhD and Master theses, respectively. JG is a population geneticist interested in the consequences of population structure and dynamics for neutral and adaptive traits.

Supporting Information

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

Appendix S1 Description of the methods used to quantify the number of days during which each site dried out.

Appendix S2 AFLP data set.

Fig. S1 Map of the study sites located along the Ain river floodplain (southeastern France).

Table S1 Pairwise geographic distances between the study sites

Table S2 Drought frequency in each site for three periods (see also Appendix S1)

Table S3 Species abundances data from September 1999 and April 2003

Table S4 Pairwise genetic distances between *Radix balthica* populations in 2001 and 2003

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.